Re-introduction of the Eurasian lynx *(Lynx lynx)*to the United Kingdom
A Deer Initiative Briefing Paper

Introduction

1.1 The Deer Initiative wishes to take an informed position on the possible consequences, both positive and negative, of the reintroduction of large carnivore species to England/UK. The need to take such a position is clear. Foxes are already established as opportunistic predators of roe and muntjac fawns (see below) and it is clear that, in addition to any depredations on domestic livestock which might result from reintroduction of wolf or lynx, establishing resident populations of these large predators would also have consequences for British deer populations. Currently the debate is focussed on the Eurasian lynx [1] and this paper similarly focusses on this species.

1.2 Much of the popular argument for such introduction is often based on idea that it will help control/regulate ‘expanding populations of deer in UK’ which human management is deemed unable to control.Such a premise is based on presumptions:

i) that deer populations are expanding rapidly in the landscape and
ii) that human management is not currently capable of controlling deer numbers.

1.3 Neither assumption has been formally tested/proven and there is also some doubt as to whether introduced large carnivores would themselves impose a regulatory effect on deer population numbers or would merely, themselves, “track” changes in deer population size (again, see further below).

1.4 While formal counts of red deer population size are undertaken across large areas of the Highlands of Scotland and there was evidence of an increase in numbers at least between the late 1960s and 2000 (Clutton-Brock et al., 2004), more recent evidence suggests that recent efforts by the Deer Commission for Scotland (and subsequently SNH) to encourage increased culling has resulted in most areas in stability or designed reductions in deer numbers (and that regulation of numbers is not out-with human control at least in these more open landscapes). If this is the case, there is no justification for reintroduction of predators to ‘control’ deer populations which are otherwise uncontrolled and presenting such a justification for reintroduction is inappropriate and misleading. However there is a commitment under the Rio Convention and subsequent international agreements, for each signatory state to restore as much as is possible of the original fauna of the region which has been lost.

1.5 Evidence for changing population size and distribution of deer in southern Scotland and England and Wales is less clear, since no regular and stratified surveys have ever been taken across the country as a whole; the only national surveys undertaken at present report simply presence/ absence, while detailed studies of changing population size are generally restricted to research studies focused on individual populations or restricted study areas.

[1] The **Eurasian lynx** (*Lynx lynx*) is a medium-sized cat native to European and Siberian forests, South Asia and East Asia. It is also known as the European lynx, common lynx, the northern lynx, and the Siberian or Russian lynx. While its conservation status has been classified as "Least Concern", populations of Eurasian lynx have been reduced or extirpated from western Europe, where it is now being reintroduced. http://en.wikipedia.org/wiki/Eurasian_lynx

1.6 Despite this, it does seem probable that there is an increase in England and Wales, for some species of deer, in both numbers within existing areas of distribution (fallow, muntjac, red deer) and range (muntjac, to a lesser extent: red deer); however, many commentators are concerned that roe deer in parts of the country may be showing a decline in population number - and reasons for this are unclear.

1.7 To be reductionist: if the perceived decline is in part due to competition from muntjac deer (Chapman *et al*., 1993; Hemami *et al*., 2005) and if an introduced predator such as lynx were to specialise in muntjac and not roe, this might reverse the balance. But in truth such specialisation on muntjac is unlikely in the extreme. By contrast if declines in roe number are in response to overhunting by humans, or inappropriate age-sex selection within hunting harvests, then (since predation by lynx or wolf has been shown to be additional to and not replace human harvest), this would result in increased pressure on populations already in decline.

1.8 Here again, it is not possible to justify reintroduction of large carnivores on the basis that they may help control deer populations which are otherwise shown to be inadequately regulated by human hunting; the evidence simply does not exist. The justification of re-introduction of species recently extirpated by human activity of course still stands here also, but we should be aware of the possible consequences on native species of deer which may already be in decline.

1.9 To inform the Deer Initiative's view, this paper reviews available evidence on patterns of predation by wolf, lynx and red fox where they occur in sympatry with wild deer (primarily red and roe) to examine prey preferences and impacts on prey populations. We will specifically ask the question whether predators can regulate or limit the numbers of prey populations and whether or not predation by large carnivores is complementary to (thus additional to) or simply replaces hunting by humans (thus that where natural predation levels are high, there are fewer deer 'left' to be killed by hunters, so that hunting harvest declines and overall impact remains constant).

1.10 This review is based on published and unpublished studies from UK and continental Europe and is based primarily on reviews already compiled by Putman (2008) and Jedrejewski et al.(2011). A more detailed summary of findings is offered in the Appendix 1.

1.11 It should be noted the bulk of available published material focuses on the interaction between populations of large carnivores with red deer and roe. While fallow deer are relatively widespread in other European countries, sika occur (within Europe but outside the British Isles) only in Austria, Czech Republic, Denmark, France, Germany, Poland (and in relatively low population number), while outside England, Wales and Ireland, free-ranging muntjac occur only in Belgium and the Netherlands. [A number of individuals of Chinese muntjac have also be introduced to private collections in France (Norma Chapman, *pers. comm*.) but it is not known if escapes have established persistent feral populations]. It is thus not possible to explore specifically, differential selection by different species of predators for roe or muntjac (for example) or for sika vs roe, although we may nonetheless establish more general principles.

1.12 From the more detailed material presented in the appendix, the conclusions will be clear. Within a multi-prey species assemblage, wolves appear to show strong selection preference for red deer (e.g. Okarma *et al*., 1995) and select against roe deer as prey (Okarma *et al.,* 1995, as also Gazzola *et al*, 2005). Thus in communities where significant numbers of wolves occur they may cause significant mortality among red deer populations; while there is some evidence to suggest where populations of natural prey are present in high abundance, these are preferred over sheep and other domestic livestock (e.g Okarma, 1995) experience in other countries suggests that losses of domestic stock to wolf predation remains significant.

1.13 By contrast it would appear that lynx are specialist predators on roe (Breitenmoser and Haller, 1993; Linnell *et al*., 1996; Okarma *et al.*, 1997; Molinari-Jobin *et al.* , 2002) [2]. Although more than 30 species are found in the diet of lynx (Jedrzejewska and Jedrzejewski 1998), roe deer constitutes up to 90% of the biomass in lynx diet (Jedrzejewski *et al*., 1993), and each lynx is estimated to kill between 30 – 70 roe deer annually (Jobin *et al.* 2000, R. Andersen, *unpubl. data*). The proportion of animals that died from lynx predation in one long-term study in Norway (1995-2005; Melis *et al.,* 2010) was significantly higher at low density (0.01- 0.25 individuals harvested / km^2), with respect to medium to high density (0.26 - 2.50 individuals harvested / km^2) ($\div^2$ = 15.035, d.f. = 1, $P < 0.001$; Melis *et al*., 2010), so that in practice at low roe deer density, predation by lynx removed annually about 22% of the population, compared to 9% at medium and high density.

1.14 This inverse density-dependence of lynx predation on roe deer has been previously described by Jêdrzejewska and Jêdrzejewski (1998) in the multipredator system of Bialowieza Primeval Forest. The fact that lynx are clearly an efficient roe deer specialist and are not expected to change their kill rate with varying roe deer density implies that predation by lynx will only have a limiting, and not a regulating effect on prey populations (*sensu* Sinclair, 1989)[3].

1.15 It also implies that since individual lynx do not increase their kill rate with increasing numbers of prey, any increase in predation can only result from increases in lynx numbers (a so-called numerical response (*sensu* Holling 1961, 1964) implying that lynx population size tracks and responds to changes in prey population number with some timelag, rather than themselves exercising control over prey numbers. Even such response in lynx population size however may be limited since this species is highly territorial and thus effective density may be limited by territoriality and minimum individual range size. Thus there is likely to exist some stable relation between lynx populations and the equally 'territorial' populations of the preferred prey, roe.
[It is recognised that only roe buck are strictly *territorial* in a technical sense and even then, only seasonally. However both bucks and does are faithful to a relatively restricted and relatively small home range for much of the year].

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[2] although, as noted above, no studies have been carried out where there were significant populations of muntjac so we have no idea as to whether these would be treated equally or preferentially as prey.

[3] Ecologists classically distinguish between factors which may restrict or limit overall population size (keeping it below levels which might be set by environmental carrying capacity/availability of resources), as **limiting factors** and those which may **regulate** population size - contributing significantly to dynamics of the population

1.16 Red fox - the only one of these predators currently resident in the UK - are known to prey actively on neonatal juveniles of roe, muntjac and sika. Although red foxes can kill adult roe deer in winter when snow conditions give them an advantage (Borg, 1962; Cederlund and Lindström, 1993; Melis *et al*., unpublished ms) they usually prey primarily on juveniles in their first summer – or indeed within the first 60 days of life (Linnell *et al*., 1995; Aanes and Andersen, 1996; Kjellander and Norstrom, 2003; Jarnemo *et al*., 2004; Panzacchi, 2007). Janermo *et al*. (2004) report that 85% of fawns are killed before 30 days of age and 98% before 40 days.

1.17 Predation is also patchy between years, with high impacts localised in relation to higher prey availability in some years than others. But because of this ability to adapt predation rate and respond to higher availability of ungulate prey in particular locations or particular years, Melis *et al.* conclude that fox predation may genuinely be expected to have a regulating effect on prey populations" (Panzacchi 2008a,b; Melis *et al.* 2010; Melis *et al.* unpublished manuscript).

1.18 Finally a number of studies have suggested that human culls may be directly additive to (rather than compensatory for) mortality due to natural predation - and that thus due allowance may need to be made in setting (human) cull allocations from a given herbivore population where natural predation may play an increasing role.

1.19 In their studies in multi-predator systems involving foxes, lynx and humans, Melis et al. concluded (as above) that lynx killed a higher proportion of roe deer at lower roe deer density; foxes killed a higher proportion of fawns at higher roe deer density. Hunters however were shown to take the same proportion of roe deer at any density. Further while lynx, foxes and hunters did not select for any of the two sexes, lynx showed no specific selection for any age-class, foxes preferentially selected young fawns and hunters took more adults and yearlings than fawns.

1.20 Melis *et al.* conclude that while the functional response of the different natural predators changed with roe deer density and the impacts of predation by lynx and foxes appeared to be compensatory with respect to each other, mortality through hunting was largely additional to that from natural predation. They also note that since adult survival rates in their study populations were lower by about 35% than those reported in environments without human harvest and with no natural predators, **mortality by hunting and predation combined are also likely to be additive to mortality from other causes.**

Summary of conclusions:

2.1 The available evidence from studies across Europe suggests that while in certain situations foxes may be able to exert a regulatory impact on populations of smaller species (roe; possibly also muntjac and sika), the pattern of predation by lynx and wolf and the way in which predation rates respond to prey density suggest that while there predators may limit the total population size of prey species, they cannot impose any responsive, regulatory effect.[4]

2.2 In such case there is no justification for reintroduction of predators to 'control' deer populations. although the additional mortality imposed by predation may act to limit overall population size and thus result in population numbers lower than those controlled purely by resource availability.

2.3 The fact that all available evidence indicates that the effects of natural predation and human hunting are additive, not compensatory, suggests that introduction of large carnivores would thus result in further decrease in overall deer population number…. for those species of deer which are limited by each individual species of predator. [Thus overall numbers of red deer would be affected by introduction of wolves; overall population size of roe - and possibly muntjac- by introduction of lynx]

2.4 But by corollary, where large predators do exert an impact on prey population numbers (limit the size of those prey populations), then predation by large carnivores is likely to reduce the number of ungulates available for harvest by human hunters. There may also be significant consequence in local areas on populations of native species of deer which may already be in decline.

2.5 Further, and not so far discussed in these pages, there may also be additional unintended consequences. Lynx, for example, as the species probably the most likely candidate for reintroduction to the UK, might present a direct competitor to remaining populations of native wildcat (*Felis sylvestris*) where refuge populations remain. While lynx prey preferentially on larger prey items, they will of course take other prey species when these are opportunistically available, or in periods when preferred prey are scarce. This may pose a direct competition to wildcats challenging their persistence in areas where they still remain and inhibiting any range expansion. It is probable also that in areas of range overlap, the larger lynx would themselves prey directly upon or at least kill the smaller wildcat.

2.6 There is also a risk of predation on domestic dogs and cats, as well as on sheep and other domestic livestock. A study of wolf predation on sheep in Sweden did suggest that losses of livestock were reduced in areas with higher abundance of preferred natural prey [L. Johnsson, MSc thesis University of Aberdeen]. High rates of predation of sheep by lynx are reported from both Norway and Sweden (e.g Odden *et al.*, 2002, 2008) but here again Odden *et al.* (2008) report that predation of domestic livestock is lower in areas of high roe deer abundance/habitat suitability. These authors suggest that livestock, rather than being actively selected, are mainly killed by lynx incidentally when encountered during other lynx activities (e.g., searching for natural prey species).

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[4] Here as above [Footnote 3] we should distinguish clearly between an impact which may restrict or limit overall population size (keeping it below levels which might be set by environmental carrying capacity/availability of resources) and those which may regulate population size - contributing significantly to dynamics of the population

Therefore, any management practice that separates lynx and sheep, such as concentrating livestock into small patches or less preferred habitats, may reduce depredation.

Specific questions for discussion

3.1 The Deer Initiative poses some specific questions to help inform further debate on this subject. These are set out below together with our view of the current evidence, or lack of it. We hope these questions will provide a stimulus and focus for further discussion:

- **What is the likely contribution to deer management that could be made by lynx with high density deer populations – including roe, fallow and muntjac (eg Thetford)?**

3.2 While male lynx are capable of killing prey animals as large as yearling red deer, all available evidence suggests that they are by preference roe deer specialists. We have no available evidence relating to predation on sika, fallow deer or muntjac [see for example summary tables in Jedrejewski *et al.* 2011] and thus do not know how these might rank in preference tables for lynx. Domestic livestock appear to be taken opportunistically while lynx are hunting for more preferred species (Odden *et al.* 2002, 2008) which suggests that even if non-preferred, some predation on sika , fallow and muntjac may occur, but that, if preference for roe is maintained, then this is unlikely to be at levels which impose a significant control over population numbers.

3.3 But equally, current evidence suggesting a preference amongst lynx for roe simply reports such preference in relation to preference for red door or domestic stock. We have no knowledge of what might be comparable preference or avoidance of sika, fallow or muntjac. If lynx were to show equal preference for these species, predation pressure would be expected to be more evenly divided between all three.

3.4 However, as already noted, predation rate of individual lynx does not show any clear response to prey density. Thus, given limitations to predator density imposed by territoriality and also limits to individual predation rates [equivalent to between 30-70 roe deer per lynx per year], it seems unlikely that lynx would be able to exert any major effect on roe deer population numbers. If this limited predation rate were to fall equally between roe and muntjac, or roe muntjac and fallow then - given limitations of potential lynx population density imposed by territoriality - impacts on population numbers would probably be even less significant.

- **Is prey selection likely to favour one species over another eg roe over muntjac**

3.5 While it is clear that lynx show high preference for roe deer over red deer, or over domestic livestock, there are no published studies exploring relative preference for sika, fallow or muntjac, since these do not regularly occur within their current distributional range. It is notable that where alpine chamois occur together with roe, lynx seems to show similar preference for both[5].

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[5] and it would be our expectation that lynx would not show any distinction in preference for roe or muntjac, treating the two potential prey equally; however, this is an informed guess because simply there are no actual data.

- **Can we learn anything relevant from fox predation on deer in the UK or elsewhere?**

3.6 Little work has been done on fox predation within the UK, although there is evidence that in some years foxes may take a significant proportion of sika calves, and roe kids (I myself have regularly observed predation of neonatal roe). All available evidence however, from studies in very comparable systems in Norway and Sweden, suggest that foxes are opportunistic predators of ungulate fawns and respond by increasing predation rates in years or locations where ungulate prey is more abundant. Because of this ability to adapt predation rate and respond to higher availability of ungulate prey in particular locations or particular years, we may conclude that fox predation may genuinely be expected to have a regulating effect on prey populations.

- **Are there any specific examples where lynx have been reintroduced to control deer numbers – if so did it work?**

3.7 We are not aware of any deliberate introductions; most studies have been undertaken within ranges colonised naturally by lynx. (but would welcome information to the contrary)

- **Are there any examples of unintended consequences eg dog/cat predation?**

3.8 Where lynx or wolf populations occur naturally, there is consequential predation on domestic livestock. Even though wild prey seem to be preferred by both species of large carnivore, some (significant) losses of sheep, cattle and goats still occur even in areas of comparatively high abundance of natural prey {see for example Odden et al. 2002, 2008).

3.9 In addition, lynx are far more tolerant than wolves of human disturbance and are regularly encountered within a few hundred metres of human settlements and towns. Thus predation on domestic pets is also frequently reported. The potential impact of lynx on relict population of native wildcat in Scotland, whether through direct predation or via competition should also be considered.

- **Should we try it?**

3.10 It seems clear that any justification for reintroduction of large carnivores on the basis that established populations will help control ‘expanding’ populations of wild deer is hard to substantiate. As already noted there is little formal evidence to demonstrate that ungulate populations are increasing in numbers or distribution across Scotland or in England and Wales (even though there may be some anecdotal evidence for increases in some local areas. Nor is there adequate evidence to suggest that current and traditional management methods are unable to contain such expanding populations.

3.11 Thus the reintroduction of large carnivores as a device to control expanding deer populations is not justified since there is not sufficient objective evidence of such expansion or that current management methods *if properly applied* are inadequate.

3.12 Further, all available evidence would suggest that while predation by wolf and lynx may reduce overall population numbers of specific species of deer below levels at which these might be limited by environmental carrying-capacity (availability of forage or shelter), they are not able to regulate populations more closely. Predation of both species, on ungulates, is at a fixed rate which is not responsive to prey density. Thus impacts on population size are likely to be evident as the imposition of a certain overall reduction in absolute population size. In the case of lynx, even this reduction is likely to be comparatively small, since it is in itself limited by limits to lynx density imposed by territoriality - although Jedrejewski and Jedrejewska (2005) do report reductions in population number of red and roe deer in the Bialowieza National Park during periods where wolf and lynx populations were present.

3.13 All such arguments imply in effect that decisions about whether or not to introduce particular species of large carnivores to the UK should be justified primarily in terms of restoration of a wider fauna and reintroduction of species recently extirpated, rather than by some rather flimsy arguments about their ecological impacts.

3.14 That said, successful establishment of populations of wolf or lynx would have clear ecological and economic implications. Even though natural prey species are preferred, both wolf and lynx also inflict significant losses on domestic livestock even where these are not preferred. Lynx are know to prey on domestic dogs and cats and if introduced in the north of Scotland may pose a challenge to remaining populations of the native wildcat. Finally, it is clear that predation by wolf and lynx is additive to, not compensatory with human hunting activity. In areas of significant predator density, available harvest which might be taken from wildlife populations by human hunters will be significantly reduced.

3.15 What we think is clear is that the ‘benefits’ are marginal, beyond a simple increase of biodiversity by reintroducing a single species which used to be present. We believe that the risks are not insignificant and any planned reintroduction should have a very clear and robust system in place for monitoring of both the carnivore populations and their impacts……. and that any reintroduction proposed should have a clear, feasible and affordable exit strategy.

APPENDIX 1: MORE DETAILED REVIEW BY SPECIES

Red fox:

4.1 Because predation on ungulates is limited to a very restricted time window, most studies of prey use by red fox would suggest that foxes take a comparatively small number of young ungulates, mainly relying on fruits and rodents (e.g. Jȩdrzejewski and Jȩ drzejewska 1992; Lanszki *et al.,* 2006; Sidorovich *et al*. 2006; Webbon *et al.*, 2006; Dell'Arte *et al* 2007; Rosalino and Santos-Reis, 2009) In part, however, this low representation of ungulates within the overall annual dietary composition may be due to the fact that even where foxes do take ungulate prey, predation is predominantly targeted on juveniles and thus restricted to a short and markedly seasonal time-window.

4.2 Although as we have noted above red foxes can kill adult roe deer in winter when snow conditions give them an advantage (Borg, 1962; Cederlund and Lindström, 1993; Melis *et al*., *in press*) they usually prey primarily on juveniles in their first summer – or indeed within the first 60 days of life (Linnell *et al*., 1995; Aanes and Andersen, 1996; Kjellander and Norstrom, 2003; Jarnemo *et al*., 2004; Panzacchi, 2007; Melis *et al*. unpublished ms).

4.3 In some instances, however, predation by foxes, even during this restricted period, may be highly significant. For example, foxes may take up a significant proportion of sika calves born in UK and the Republic of Ireland (O'Donoghue 1991) and in a number of countries the impact of fox predation on infant roe deer may also have a very significant impact (see for example: Kramer, 1990; Liberg *et al*., 1993; Lindström *et al*., 1994; Linnell *et al*., 1995; Aanes and Andersen, 1996; Kjellander and Norstrom, 2003; Jarnemo *et al*., 2004; Panzacchi, 2007; Hewison and Staines, 2008). In Norway, Aanes and Andersen (1996) reported a 48% mortality of radiocollared fawns to fox predation within 60 days of birth, and similar results are reported by subsequent authors with 30% of 107 radiocollared fawns lost in studies of Melis *et al.* (2010); an average of 34% of 233 marked neonates were taken by foxes in studies of Jarnemo *et al.* (2004) in Sweden; in 3 out of 14 years in this long-term study mortality rates exceeded 85%.

4.4 Despite the highly seasonal and largely opportunistic nature of predation by foxes on neonatal ungulates, a number of authors have however shown that red fox predation on roe fawns may have a significant effect on population density (Kramer, 1990; Liberg *et al*., 1993; Lindström *et al*., 1994; Aanes and Andersen, 1996) and some would argue (e.g. Kjellander and Norstrom, 2003; Panzacchi, 2007) that, since the dynamics of large herbivore populations tend in any case to be characterised by relatively constant adult survival, but marked variation in juvenile recruitment, variable rates of predation on neonates may be of major significance in the dynamics of particular populations.

4.5 Throughout, we must emphasise the opportunistic nature of fox predation. Predation by foxes on roe (and on sika calves) is not only strongly seasonal but also varies markedly from year to year, dependent on the density of fox populations, the density of roe or sika populations and the relative availability of alternative prey. It is clear that predation rates vary with landscape type (Aanes and Andersen, 1996; Panzacchi, 2007; Panzacchi *et al*., 2009: predation is higher in open landscapes) and with the relative availability of both roe deer fawns and alternative prey; high predation rates tend to coincide with reduced availability of alternative prey (such as voles; Kjellander and Nordstrom, 2003; Panzacchi, 2007; Panzacchi *et al.*, 2008a) and relatively higher proportional availability of roe kids.

In consequence, overall mortality, and predation rates amongst roe deer fawns show strong annual variation (Jarnemo *et al.*, 2004 ; Panzacchi, 2007). In the same way, mortality rates reported for sika calves in the Republic of Ireland (O'Donoghue, 1991; Burkitt and Raymond, unpublished) show pronounced year to year variation, which has a profound affect on recruitment rates and population dynamics.

4.6 As we have already noted, predation of roe kids by foxes seems restricted to a very limited time-window, with predation rates lower in the first week of life (while fawns are still 'hiders'; Aanes and Andersen, 1996) and with the bulk of fawns killed before 60 days (Aanes and Andersen, 1996; Jarnemo *et al*., 2004). Indeed Jarnemo *et al*. report that 85% of fawns are killed before 30 days of age and 98% before 40 days). Panzacchi *et al*. (2008a) note that roe deer remains occurred more frequently in scats found at fox dens than in the scats of adult foxes indicating that vixens were using fawns primarily to feed their cubs or at least that, during the period they were available, fawns were a profitable and significant food source for vixens raising cubs. This observation that vixens may be taking fawns primarily to feed cubs, and the restricted period of vulnerability of fawns, this may help to explain the extremely restricted time window in which fawns are taken.

4.7 Timing of predation (and ultimately total amount) may also be affected by relative density of foxes and roe deer. Panzacchi (2007; Panzacchi *et al*., 2008b) notes that in one study area in Norway where roe deer were at comparatively low abundance, foxes responded to this new source of prey purely opportunistically. Foxes were most successful in hunting roe fawns when surveying open areas, and when conducting less prey-specific searches. In consequence roe deer fawns were killed for the most part opportunistically when they were encountered in the peak of their availability (and fawns born at the beginning of the season were comparatively safe).

4.8 In a different study site where roe were present at higher density, the higher abundance of fawns within the predator's home range triggered an early prey-switch on the part of the fox, promoting a higher degree of specialisation on this prey source. Foxes started to search actively for roe fawns early from the very beginning of the birth season and caused a higher predation risk for fawns before or at the beginning of the birth peak. Given the limited time in which fawns are vulnerable to fox predation, the earlier prey switch also resulted in a higher overall impact on neonatal mortality rates in this second area and the proportion of animals killed by foxes was higher at higher density (Melis *et al.,* unpublished).While in the latter case, during periods of high abundance of roe deer fawns, foxes become more specialised in actively seeking such prey, this is more of a matter of degree, and in both cases foxes are primarily responding opportunistically to roe as prey. Melis *et al.* conclude that as typical opportunistic feeders, foxes are likely to specialize in predating fawns only when their occurrence in the environment makes it worthwhile to actively spend time in their search.

4.9 Since roe deer fawns can only represent a seasonal food for red foxes, it is unlikely that availability or density of fawns will have a significant effect on fox density (since the foxes can readily switch to other prey in periods where few roe fawns are available; see also Aanes *et al*., 1998; Panzacchi *et al*., 2008a). Since, in addition, roe fawns (and other juvenile ungulates) are taken only opportunistically, it seems probable that the actual impact on prey population dynamics, as well as the style of fox predation, will be significantly different from that of larger carnivores which are hunting ungulate prey of all ages and throughout the year.

Indeed we may expect that while predation by wolves or lynx (as ungulate specialists) is likely to have a limiting, and not a regulating effect on prey populations (*sensu* Sinclair 1989), fox predation, where it does impose a significant impact, may genuinely be expected to have a regulating effect on prey populations.

Wolf:

4.10 While this report is not advocating reintroduction of wolves to UK, and it seems probable that this is a non-starter within England and Wales for a variety of other reasons in completing this review it is only proper to summarise what information has emerged from other studies in Europe where wolves, by natural expansion or by deliberate reintroduction are expanding their distribution.

4.11 Jêdrzejewski *et al* (2011) emphasise that red deer has been reported in a number of studies as a clearly preferred prey of wolves (eg. Jêdrzejewski *et al.*, 2000; Gazzola *et al*., 2005). Indeed, throughout Europe, comparison of the percentage of red deer in wolf diet in relation to actual red deer abundance was generally bigger than expected from its relative frequency within the ungulate community. Wolves show no dietary response to changes in roe deer relative abundance, and in general select against roe deer as prey (Okarma *et al.,* 1995, as also Gazzola *et al*, 2005).

4.12 A few studies have attempted to quantify the kill rates or total predation by wolves based on their metabolic rates or daily food consumption (G³owaciñski and Profus, 1997; Gazzola, 2007). These are, however, underestimates of the true kill rates. In Europe, so far two field studies – in Scandinavia and Eastern Poland – endeavoured to estimate the actual kill rates by wolves. Scandinavian wolves hunted predominantly moose. Polish wolves, which coexisted with a multispecies community of ungulates, killed, on average, 42 large prey (mainly red deer) per year *per capita* and their mean daily consumption under natural conditions was 5.6 kg of food per wolf (Jedrzejewki *et al*., 2002).

4.13 A long-term study of wolf predation in the Bia³owie¿a Forest, Eastern Poland, documented that, the percentage predation on red deer and wild boar (number of deer or boar killed by wolves annually as percent of their respective densities) showed a tendency to be negatively related to densities of those prey. Wolf predation did not vary with changing densities of roe deer (Jêdrzejewski *et al*., 2002). Thus, wolves are not capable of regulating the populations of their prey, but do have the potential to limit their numbers.

4.14 In Bia³owie¿a Primeval Forest (Poland and Belarus), wolves and lynxes were exterminated twice during the last 100 years. During the whole long-term data series, the combined abundance of five species of ungulates (European bison, moose, red and roe deer, and wild boar, expressed as crude biomass of all species per unit area) was strongly positively correlated with annual temperature. Biomass of ungulates increased as the climate warmed up in both situations: when predators were scarce or absent, and when they were numerous. (Jêdrzejewski *et al*., 2011). However, the relative roles of temperatures and predation differed greatly among species of ungulates. Climate was crucial for the bison and wild boar, and had the smallest effect on population dynamics of red and roe deer. The opposite trend was manifest in the role of predation, which was most significant in red and roe deer (Jêdrzejewska and Jêdrzejewski, 2005).

Lynx:

4.15 While wolves appear to select against roe as prey when larger prey ungulates are available, contrast it would appear that lynx are specialist predators on roe (Breitenmoser and Haller, 1993; Linnell *et al.*, 1996; Okarma *et al.*, 1997; Molinari-Jobin *et al.* , 2002).

4.16 In published studies of lynx diet, roe deer constitutes up to 90% of the total biomass (Jedrzejewski *et al*., 1993), and each lynx is estimated to kill between 30 – 70 roe deer annually (Jobin *et al.* 2000, Andersen, *unpubl. data*). Earlier studies in Switzerland (Molinari-Jobin *et al*., 2002) indicated that roe deer does were most often killed, but studies in Poland (Okarma *et al*., 1997) and Norway (Karlsen, 1997; Andersen *et al.,* 2007) have indicated that roe deer fawns and adults are killed more or less in proportion to their occurrence in the population. More recently Mejlgaard *et al*. (2013) have suggested that lynx actively selected adult roe deer of both sexes. In their study, there was a clear selection against yearlings and fawns over the summer, but in winter, lynx selected male yearlings (Mejlgaard *et al*., 2013).

4.17 By contrast with results cited for predation by foxes, the proportion of animals that died from lynx predation in one long-term study in Norway (1995-2005; Melis *et al.,* 2010) was significantly higher at low density (0.01- 0.25 individuals harvested / km^2), with respect to medium to high density (0.26 - 2.50 individuals harvested / km^2) ($\div^2$ = 15.035, d.f. = 1, $P < 0.001$; Melis *et al*., 2010 and unpublished ms), so that in practice at low roe deer density, predation by lynx removed annually about 22% of the population, compared to 9% at medium and high density. The fact that lynx are clearly an efficient roe deer specialist and are not expected to change their kill rate with varying roe deer density implies that predation by lynx will only have a limiting, and not a regulating effect on prey populations (*sensu* Sinclair, 1989).

4.18 Overall impact will also be limited (as above) by the fact that adult lynx are strongly territorial and thus increase in lynx population number in an area in response to high prey availability is limited by constraints of minimum territory size which in turn places an upper limit on potential lynx density.

4.19 It is clear that lynx are also capable of preying upon red deer calves, and adult male lynx are reported to take hinds or yearling males. I know of no formal studies however to suggest the significance of lynx predation on red deer populations.

Natural predation vs hunting

4.20 Both Melis et al. and Jędrzejewski *et al*. (2011) emphasise that the effects of predation by large carnivores and 'predation' by human hunting are additive. In their studies in multi-predator systems involving foxes, lynx and humans, Melis *et al*. concluded that lynx killed a higher proportion of roe deer at lower roe deer density; foxes killed a higher proportion of fawns at higher roe deer density. Hunters, however, were shown to take the same proportion of roe deer at any density. Further while lynx, foxes and hunters did not show biased harvest in relation to sex, lynx showed no specific selection for any age-class (Anderson et al. 2007) or actively selected for adult prey (Mejlgaard *et al*. 2013), foxes preferentially selected young fawns and hunters took more adults and yearlings than fawns.

Melis *et al*. therefore concluded that while the functional response of the different natural predators changed with roe deer density and the impacts of predation by lynx and foxes appeared to be compensatory with respect to each other, mortality through hunting was largely additional to that from natural predation. They also note that since adult survival rates in their study populations were lower by about 35% than those reported in environments without human harvest and with no natural predators, mortality by hunting and predation combined are also likely to be additive to mortality from other causes.

References:

Aanes, R. and Andersen, R. (1996) The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. *Canadian Journal of Zoology*, **74**, 1857-1865.

Aanes, R., Linnell, J.D.C., Perzanowski, K, Karlsen, J. and Odden, J (1998) Roe deer as prey. In: R. Andersen, P. Duncan and J.D.C. Linnell (eds.) **The European Roe Deer: the biology of success**, Scandinavian University Press, 139-160.

Andersen, R., Karlsen, J., Austmo, L. B., Odden, J., Linnell, J. D. C. and Gaillard, J. M. (2007) Selectivity of Eurasian lynx and recreational hunters for age, sex and condition in roe deer. *Wildlife Biology* **13**, 467-474.

Borg, K. (1962) Predation on roe deer in Sweden. *Journal of Wildlife Management* **26**, 133-136.

Breitenmoser, U. and Haller, H. (1993) Patterns of predation by reintroduced European lynx in the Swiss Alps. *Journal of Wildlife Management* **57**, 135-144.

Cederlund, G. and Lindström, E. (1993) Effects of severe winters and fox predation on roe deer mortality. *Acta Theriologica* **28**, 129-145.

Chapman NG, Claydon K, Claydon M, Forde PG, Harris S, 1993. Sympatric populations of muntjac and roe deer: a comparative analysis of their ranging behaviour, social organisation and activity. *Journal of Zoology* **229**, 623-640.

Clutton-Brock, T.H., Coulson, T.and Milner, J.M. (2004). Red deer stocks in the Highlands of Scotland. *Nature* **429**, 261-262.

Dell'Arte, G.L., Laaksonen, T., Norrdahl, K.and Korpimäki, E. (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecologica* **31**, 276-281.

Gazzola, A., Bertelli, I., Avanzinelli, E., Tolosano, A., Bertotto, P. and Apollonio, M. (2005) Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *Journal of Zoology, London* **266**, 205-213.

Gazzola, A., Avanzinelli, E., Bertelli, I., Tolosano, A., Bertotto, P., Musso, R. and Apollonio, M. (2007) The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps. *Italian Journal of Zoology* **74**, 297-307.

Gazzola, A., Capitani, C., Mattioli, L. and Apollonio, M. (2008) Livestock damage and wolf presence. *Journal of Zoology, London* **274,** 261-269.

G³owaciñski, Z. and Profus, P. (1997) Potential impact of wolves *Canis lupus* on prey populations in eastern Poland. *Biological Conservation* **80**, 99-106.

Hemami, M.R., Watkinson, A.R. and Dolman, P.M. (2005) Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. *Forest Ecology and Management* **215**, 224-238.

Hewison, A.J.M. and Staines, B.W. (2008) Roe deer. In: S. Harris and D.W. Yalden (eds.) **Mammals of the British Isles: Handbook**, 4th edition. The Mammal Society, London, 605-617.

Holling, C.S. (1961) Principles of insect predation. *Annual Entomological Review* **6**, 163-182.

Holling, C.S. (1964) The analysis of complex population processes. *Canadian Entomologist* **96**, 335-347.

Jarnemo A., Liberg O., Lockowandt S., Olsson A. and Wahlstrom K. (2004) Predation by red fox on European red deer fawns in relation to age, sex, and birth date. *Canadian Journal of Zoology* **82,** 416-422.

Jê drzejewski, W. and Jêdrzejewska, B. (1992) Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Bia³owie¿a National Park, Poland. *Ecography* **15,** 212-220.

Jê drzejewska, B. and Jêdrzejewski, W. (1998) **Predation in vertebrate communities. The Bia³owie¿a Primeval Forest as a case study.** Springer Verlag, Berlin/ New York.

Jê drzejewska, B. and Jêdrzejewski, W. (2005) Large carnivores and ungulates in European temperate forest ecosystems: Bottom-up and top-down control. In: J.C. Ray, K.H. Redford, R.S. Steneck and J. Berger (eds**.) Large Carnivores and the Conservation of Biodiversity.** Island Press, Washington, 230-246.

Jê drzejewski, W., Apollonio, M., Jêdrzejewska, B. and Kojola, I. (2011) Ungulate-large carnivore relationships in Europe. In: **Ungulate Management in Europe: Problems and Practices** (eds. R.J.Putman, M. Apollonio and R. Anderson); Cambridge University Press, pp 284-318.

Jê drzejewski, W., Jêdrzejewska, B., Okarma, H., Schmidt, K., Zub, K. and Musiani, M. (2000) Prey selection and predation by wolves in Bia³owie¿a Primeval Forest, Poland. *Journal of Mammalogy* **81**, 197-212.

Jê drzejewski, W., Niedzia³kowska, M., Mys³ajek, R. W., Nowak, S. and Jêdrzejewska, B. (2005) Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. *Acta Theriologica* **50**, 417-428.

Jê drzejewski, W., Schmidt, K., Mi³kowski, L., Jêdrzejewska, B. and Okarma, H. (1993). Foraging by lynx and its role in ungulate mortality: the local (Bia³owie¿a Forest) and the Palaearctic viewpoints. *Acta Theriologica* **38,** 385-403.

Jê drzejewski, W., Schmidt, K., Theuerkauf, J., Jêdrzejewska, B., Selva, N., Zub, K. and Szymura, L. (2002) Kill rates and predation by wolves on ungulate populations in Bia³owie¿a Primeval Forest (Poland). *Ecology* **83**, 1341-1356.

Karlsen, J. (1997) **The impact of lynx (*Lynx lynx*) predation and hunting on a roe deer (*Capreolus capreolus*) population in southeastern Norway.** Unpublished Candidatus scientiarum thesis, Norges Teknisk-Naturvitenskapelige Universitet, Trondheim,Norway.

Kjellander, P. and Nordström, J. (2003) Cyclic voles, prey switching in red fox and roe deer dynamics – a test of the alternative prey hypothesis. *Oikos* **101**: 338-344.

Kramer, A. (1990) Uberden einflussder fuchsdichte auf die zuwachsraten des rehwildes in der Schweiz. *Transactions of the Congress of the International Union of Game Biologists, Trondheim* **19**, 53-58.

Lanszki, J., Heltai, M., Szabó, L. (2006) Feeding habits and trophic niche overlap between sympatric golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) in the Pannonian ecoregion (Hungary). *Canadian Journal of Zoology* **84**, 1647-1656.

Liberg, O., Johansson, A., Lockowandt, S. and Wahlstrom, K. (1993) Red fox predation as a dominant cause of neonatal mortality in roe deer fawns. Abstract; *Swedish Hunters' Association Conference*, Lund, 12-12.

Lindström, E.R., Adren, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jädeberg, L., Lemnell, P.A., Martinsson, B., Sköld, K., and Svenson, J.E. (1994) Disease reveals the predator: sarcoptic mange, red fox predation and prey populations. *Ecology* **75**: 1042-1049.

Linnell, J. D. C., Aanes, R. and Andersen, R. (1995) Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology,* **1**, 209-224.

Mejlgaard, T., Loe, L.E., Odden, J., Linnell, J.D.C. and Nilsen, E.B. (2013) Lynx prey selection for age and sex classes of roe deer varies with season. *Journal of Zoology* **289**, 222-228.

Melis C., Basille, M., Herfindal I., Linnell J.D.C., Odden, J., Gaillard, J.-M., Høgda K.-A. andAndersen R. (2010) Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. *Ecoscience* **17**, 166-174.

Melis, C., Jêdrzejewska, B., Apollonio, M., Bartoñ, K. A., Jêdrzejewski, W., Linnell J. D.C.,Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A., Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovich, V. E., Zawadzka, B. and Zhyla S. (2009) Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Global Ecology and Biogeography* **18,** 724-734.

Melis, C., Linnell, J.D.C., Odden, J. and Andersen, R. [unpublished manuscript] Survival rates and causes of mortality of roe deer *Capreolus capreolus* in a multi-predator system. [copy lodged with the Deer Initiative]

Molinari-Jobin, A., Molinari, P., Breitenmoser-Wursten, C. and Breitenmoser, U. (2002) Significance of lynx *Lynx lynx* predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. *Wildlife Biology* **8**, 109-115.

Odden, J., Herfindal, I., Linnell, J.D.C. and Andersen, R. (2008)Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *Journal of Wildlife Management* **72**, 276-282.

Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T. and Andersen, R. (2002) Lynx depredation on domestic sheep in Norway. *Journal of Wildlife Management* **66**, 98-105.

Odden, J. , Linnell, J.D.C., Andersen, R. (2006) Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: The relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research* **52**, 237-244.

O'Donoghue, A. (1991) **Growth, Reproduction and Survival in a Feral Population of Japanese Sika Deer (*Cervus nippon*)** Unpublished PhD thesis, University College, Dublin, Ireland

Okarma, H., Jêdrzejewska, B., Jêdrzejewski, W., Krasiñski, Z. A. and Mi³kowski, L. (1995) The roles of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Bia³owie¿a Primeval Forest, Poland. *Acta Theriologica* **40**, 197-217.

Okarma, H., Jedrzejewski, W., Schmidt, K., Kowalczyk, R. & Jedrzejewska, B. (1997) Predation of Eurasian lynx on roe deer *Capreolus capreolu*s and red deer *Cervus elaphus* in Bia³owie¿a Primeval Forest, Poland. *Acta Theriologica*, **42**, 203-224.

Panzacchi, M. (2007) **The ecology of red fox predation on roe deer fawns, with respect to population density, habitat and alternative prey.** Unpublished PhD thesis University of Bologna.

Panzacchi, M., Linnell, J.D.C., Serrao, G., Eie, S., Odden, M., Odden, J. and Andersen, R. (2008a) Evaluation of the importance of roe deer fawns in the spring-summer diet of red foxes in southeastern Norway. *Ecological Research* **23**, 889-896

Panzacchi, M., Linnell, J.D.C., Odden, J., Odden, M. and Andersen, R. (2008b) When a generalist becomes a specialist: Patterns of red fox predation on roe deer fawns under contrasting conditions. *Canadian Journal of Zoology* **86**, 116-126.

Panzacchi, M., Linnell, J.D.C., Odden, M., Odden, J. and Andersen, R. (2009) Habitat and roe deer fawn vulnerability to red fox predation. *Journal of Animal Ecology* **78**, 1124-1133.

Putman, R.J. (2008) **A review of available data on natural mortality of red and roe deer populations.** Contract report for the Deer Commission for Scotland, Inverness.

Sidorovich, V. E., Tikhomirova, L. L. and Jêdrzejewska, B. (2003) Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. *Wildlife Biology* **9**, 103-111.

Sidorovich, V.E., Sidorovich, A.A., Izotova, I.V. (2006) Variations in the diet and population density of the red fox *Vulpes vulpes* in the mixed woodlands of northern Belarus. *Mammalian Biology* **71**, 74-89

Sinclair, A.R.E. (1989) Population regulation in animals. In: J.M. Cherret (ed.) **Ecological concepts.** Blackwell Scientific Publications, Oxford, 197-241.

Webbon, C.C., Baker, P.J., Cole, N.C. and Harris, S. (2006) Macroscopic prey remains in the winter diet of foxes *Vulpes vulpes* in rural Britain *Mammal Review* **36**, 85-97.