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# European hare (*Lepus europaeus*) invasion ecology: implication for the conservation of the endemic Irish hare (*Lepus timidus hibernicus*)

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**Abstract** European hare *Lepus europaeus* populations have undergone recent declines but the species has successfully naturalised in many countries outside its native range. It was introduced to Ireland during the mid-late nineteenth century for field sport and is now well established in Northern Ireland. The native Irish hare *Lepus timidus hibernicus* is an endemic subspecies of mountain hare *L. timidus* and has attracted major conservation concern following a long-term population decline during the twentieth century and is one of the highest priority species for conservation action in Ireland. Little is known about the European hare in Ireland or whether it poses a significant threat to the native mountain hare subspecies by compromising its ecological security or genetic integrity. We review the invasion ecology of the European hare and examine evidence for interspecific competition with the mountain hare for habitat space and food resources, interspecific hybridisation, disease and parasite transmission and possible impacts of climate change. We also examine the impact that introduced hares can have on native non-lagomorph species. We conclude that the European hare is an emerging and significant threat to the conservation status of the native Irish hare. Invasive mammal species have been successfully eradicated from Ireland before and immediate action is often the only opportunity for cost-effective eradication. An urgent call is issued for further research whilst the need for a European hare *invasive Species Action Plan* (iSAP) and *Eradication strategy* are discussed.

**Keywords** Climate change · Eradication · Hybridisation · Interspecific competition · Mountain hare · *Lepus timidus*

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## Introduction

The European hare *L. europaeus* (Pallas 1778), widely known as the brown hare, is native to mainland Europe except most of the Iberian Peninsula, the Mediterranean and Scandinavia, and extends east throughout the central Asian steppes (Flux and Angermann 1990). It is an open grassland specialist and probably underwent a range expansion throughout Europe after Holocene forest clearances and the spread of pastoral agriculture (Tapper 1987; Roberts 1998). Despite recent declines throughout its native range (Smith et al. 2005), the European hare has naturalised successfully in many countries including Great Britain, Sweden, Norway, eastern Canada, north-eastern USA, most of South America below 28° south, Australia, Tasmania and New Zealand, as well as many small islands including Barbados, Reúnion and the Falklands (Flux and Angermann 1990).

The Irish hare *Lepus timidus hibernicus* (Bell 1837) is an endemic subspecies of the mountain hare *L. timidus* (Linnaeus 1758), and is the only lagomorph native to Ireland (Fairley 2001; Hamill 2001). The Irish hare is morphologically, ecologically and behaviourally distinct from other mountain hares (Barrett-Hamilton 1910); Fairley 2001; Thulin and Flux 2003; Reid 2006). Most notably, it possesses a comparatively high number of unique genetic forms (mitochondrial haplotypes) that are not shared by any other mountain hare subspecies (or other hare species) outside Ireland (Hughes et al. 2006). The genetic structure of its population is consistent with the hypothesis that it survived the last ice age in a glacial refuge and is, therefore, one of Ireland's oldest paleoendemic mammal residents. Indeed, Hughes et al. (2006) contend that the Irish hare may warrant full species status under the evolutionary and phylogenetic species concepts arguing that there is greater genetic divergence between Irish hares and other *L. timidus* than between the Arctic hare *Lepus arcticus* (Ross 1819) and Alaskan hare *Lepus othus* (Merriam 1900), both of which are considered separate species. However, drawing taxonomic conclusions from genetic investigations alone, particularly using mtDNA, can be problematic due to the prevalence of paraphyly and introgression within the genus *Lepus*.

In addition to its intrinsic conservation value, the Irish hare has attracted major conservation concern following a long-term population decline during the twentieth century synchronous with changes in land management practices associated with agricultural intensification and landscape homogenisation (Dingerkus and Montgomery 2002; Reid et al. 2007a, 2010a). The subspecies is listed on Appendix III of the Bern Convention (Anonymous 1979) and Annex V(a) of the EU Habitats Directive (EEC 43/92 1992), and was listed as an internationally important subspecies in the first Irish Red Data Book (Whilde 1993). In the Republic of Ireland, it is protected under the Wildlife Act 1976 and Wildlife (Amendment) Act 2000 whilst in Northern Ireland it is protected under the Wildlife Order (NI) 1985 and annual amendments to the Game Preservation (Special Protection for Irish Hares) Order (Northern Ireland) 2003. Furthermore, the Irish hare is subject to a Northern Ireland and an All-Ireland Species Action Plan (Anonymous 2000, 2005) and is one of the highest priority species for conservation action in Ireland (Reid et al. 2007b).

The European hare was introduced to Great Britain in pre-Roman times as a food source (Yalden 1999), but its relatively recent introduction to Ireland during the mid-late nineteenth century was largely for the field sport of hare coursing (Barrett-Hamilton 1898). The European rabbit *Oryctolagus cuniculus* (Lilljeborg 1873) was also introduced to Ireland, but much earlier during the twelfth or thirteenth century (Lever 2009). All three lagomorphs can be easily distinguished (Fig. 1), but discrimination in the field by untrained observers can result in dubious records. A total of thirteen to fifteen discrete introductions of the European hare occurred between 1848 and the 1890s (Table 1); seven or eight in the Republic of Ireland and six or seven in Northern Ireland (Fig. 2a). Barrett-Hamilton (1898) reported that several populations established successfully and proliferated, but most had gone extinct by the end of the nineteenth century.

Since the early twelfth century, the occurrence and distribution of the European hare in Ireland has remained largely unclear. Ni Lamhna (1979) mapped records throughout the north of the island in counties

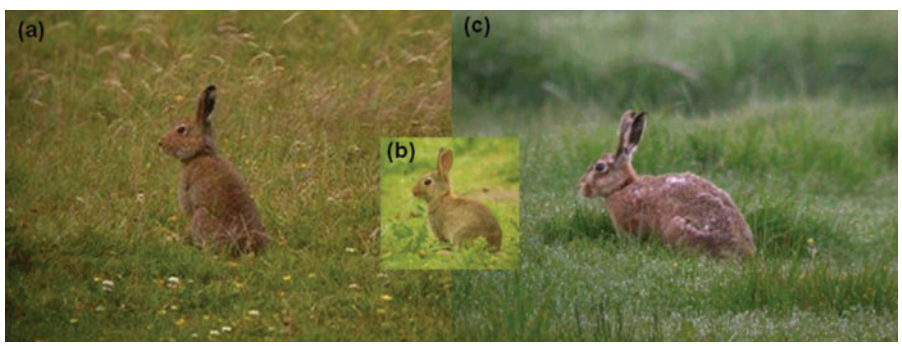


**Fig. 1** Comparison of **a** an Irish hare *Lepus timidus hibernicus*, **b** a European rabbit *Oryctolagus cuniculus* and **c** a European brown hare *Lepus europaeus*. Extracted and reproduced with permission from Reid and Montgomery (2007)

**Table 1** Recorded introductions of European hare *L. europaeus* in Ireland

| # | Date | County | Locality | Introduced by | Comment |
|---|---|---|---|---|---|
| 1 | c 1848 | Cork | Ballyhooley | Listowel family | Established quickly but eventually shot out |
| 2 | c 1852 | Cork | Castlemarty | Earl of Shannon | Survived for a few years |
| 3 | c 1858 | Cork | Cregg North | Mr Hyde | Large numbers introduced and observed years later > 6 km away. No sightings after 1878 |
| 4 | c 1865–1866 | Wicklow | Powerscourt | Viscount Powerscourt | 40 animals introduced |
| 5 | c 1867 | Armagh | Brownlow House | Lord Lurgan | Proliferated for at least 30 years |
| 6 | c 1868 | Down | Big Island, Copelands | David Kerr | Did not establish and expired |
| 7 | c 1876 | Tyrone | Baronscourt Estate | Duke of Abercorn | |
| 8 | 1876–1877 | Tyrone | Strabane | John Herdman | 65 introduced |
| 9 | 1882 | Cork | Trabulgan | Lord Fermoy | Locally extinct by 1888 |
| 10 | ≈1880s | Fermanagh | Cleenish island | Captain Collum | |
| 11 | ≈1880s | Galway | Salrock | General Thompson et al. | |
| 12 | ≈1880s | Kerry | Dingle | ? | |
| 13 | ≈1880s | Londonderry | ? | Mr Stevenson | |
| 14 | c 1892 | Donegal | Ballyconnell | Mr Olpert | Increased in number post-introduction |
| 15 | ? | Fermanagh | Kesh | ? | One individual shot during 1895 |

*Source*: Barrett-Hamilton (1898)

Antrim, Armagh, Fermanagh, Tyrone, Londonderry and Donegal but also cited occurrences throughout the south in counties Carlow, Cork, Galway, Kildare and Waterford, but uncertainty in their georeferencing prevented accurate mapping (Fig. 2a). Further uncertainty was generated when Smiddy (1994) examined 'hundreds or perhaps thousands' of hares in counties Cork and Waterford yet confirmed only the native Irish hare. Ni Lamhna (1979) recognised the difficulty with misidentification and confusion with the Irish hare, whilst Smiddy (1994) hypothesised that interspecific hybridisation may have confused identification yet further. Wolfe (1994) suggested that natural extremes of variation in the pelage of the Irish hare, most particularly tail colouration, was such that any European hare record based on coat colour was highly dubious. Such was the uncertainty that Fairley (2001) concluded that "there has been only one absolutely reliable record of [European] hares in Ireland in the last 100 years and this was almost certainly from Tyrone". The latter being caught by the Dungannon Coursing Club, Co. Tyrone during 1995 (Dingerkus 1997).

The range of naturalised European hare populations in the north of Ireland was not fully described until targeted surveys were conducted by Reid and Montgomery (2007). Pre- and post-breeding spotlight surveys during 2005 confirmed that established populations existed in mid-Ulster and west Tyrone (Fig. 2b). At that time, the total abundance of the mid-Ulster population was estimated at ≤2,000 individuals, whilst up to 62% of the hare population in that area was composed of the European hare rather than the native Irish hare (Reid and Montgomery 2007).

The Hare Survey of Ireland 2006/07 failed to confirm any records of the European hare in the Republic of Ireland (Reid et al. 2007a). However, Sheppard (2004) suggested that the species was present in east Donegal between 1976 and 2000, although this was based on very few isolated records. Thus, whilst populations of European hare have been confirmed as established in Northern Ireland, its status in the Republic of Ireland remains uncertain.

The European hare may pose a significant threat to the native Irish hare in Ireland by compromising its

ecological security or genetic integrity. It is, therefore, timely to review the invasion ecology of the European hare and draw inferences for the likely outcome of its colonisation of Ireland.

## Species interactions

### Interspecific competition for habitat space

Demonstrating ecological competition in the wild is notoriously difficult. In the genus *Lepus*, interspecific competition has been inferred using broad-scale biogeographical patterns of species occurrence (Thulin 2003). Most species of hare exist in mutually exclusive allopatry; species ranges rarely overlap with sympatry tending to be a temporally transient phenomenon (Flux 1981). Each species, in the absence of another, can inhabit the potential range of its closest geographical neighbours, but upon contact each usually retreats to its preferred optimum habitat. Consequently, Flux (1981) hypothesised that competitive exclusion was not only the main separating mechanism but a notably powerful force within the genus *Lepus*. Wolfe et al. (1996) supported the suggestion that the restricted distribution of mountain hares in Europe may be explained by competitive exclusion by the European hare rather than habitat preferences related to species-specific food resources. Introduced European and native Irish hares occupy similar habitats within their zone of sympatry, and have nearly identical habitat niche breaths and almost complete habitat niche overlap (Reid and Montgomery 2007). Consequently, they are candidates for strong interspecific competition for habitat space. The date of origin of extant European hare populations in Northern Ireland is unknown but may be recent (Reid and Montgomery 2007). Developing the transient sympatry hypothesis, we might posit that European and Irish hare ranges in Ireland may diverge subsequent to the initial lag phase post-introduction; the length of the latter being unknown.

### Interspecific competition for food resources

Continental *L. timidus* are restricted to high mountains, boreal forest and tundra where they browse predominately on hard plant material such as heather *Calluna vulgaris* (Flux and Angermann 1990; Thulin and Flux 2003). European hares feed predominately on grasses, including agricultural species (Flux and Angermann 1990) and, therefore, generally displace mountain hares in lowland farmland (Thulin 2003). In contrast to mountain hares elsewhere, the Irish subspecies is distributed from the inter-tidal zone (Wolfe et al. 1996) to mountain summits (Walker and Fairley 1968) and, similar to the European hare, is particularly abundant in pastoral landscapes (Reid et al. 2007a). Whilst capable of surviving on a diet dominated by heather and other hard plant species on upland heath and bog (Walker and Fairley 1968), Irish hares prefer to forage predominantly on soft grasses, most notably, agricultural ryegrass *Lolium perenne* (Tangney et al. 1995; Jeffery 1996; Dingerkus and Montgomery 2001; Strevens and Rochford 2004). Thus, European and Irish hares are likely to be closer ecological equivalents, in terms of dietary overlap, than European hares and mountain hares elsewhere, thus increasing the potential for strong competition for food resources and, by extension, habitat space.

### Interspecific hybridisation

Hybridisation between introduced and native species is a common problem (Rhymer and Simberloff 1996). For example, introduced Sika deer *Cervus nippon* freely hybridise with native Red deer *Cervus elaphus* in Scotland and Ireland, producing fertile offspring which are at no competitive disadvantage compared to either parental species (Abernethy 1994; Hayden and Harrington 2000).

Hybridisation between European and mountain hares is well known (Lönnberg 1908; Fraguglione 1959; Gustavsson and Sundt 1965; Gustavsson 1971; Schröder et al. 1987; Thulin and Tegelström 2002), with male European hares capable of mating with female mountain hares to produce fertile offspring (Lönnberg 1905; Gustavsson and Sundt 1965; Gustavsson 1971; Schröder et al. 1987; Thulin and Tegelström 2002). In Ireland, Harting (1897) recorded a supposed *L. europaeus* × *L.t. hibernicus* hybrid whilst contemporary observations of both species sparing and boxing, a typical precopula behaviour of hares (Holley and Greenwood 1984), and the occurrence of phenotypically ambiguous animals lead Reid and Montgomery (2007) to suspect that both species hybridised in the wild.

Hughes et al. (2006) failed to provide any molecular evidence consistent with the presence of European

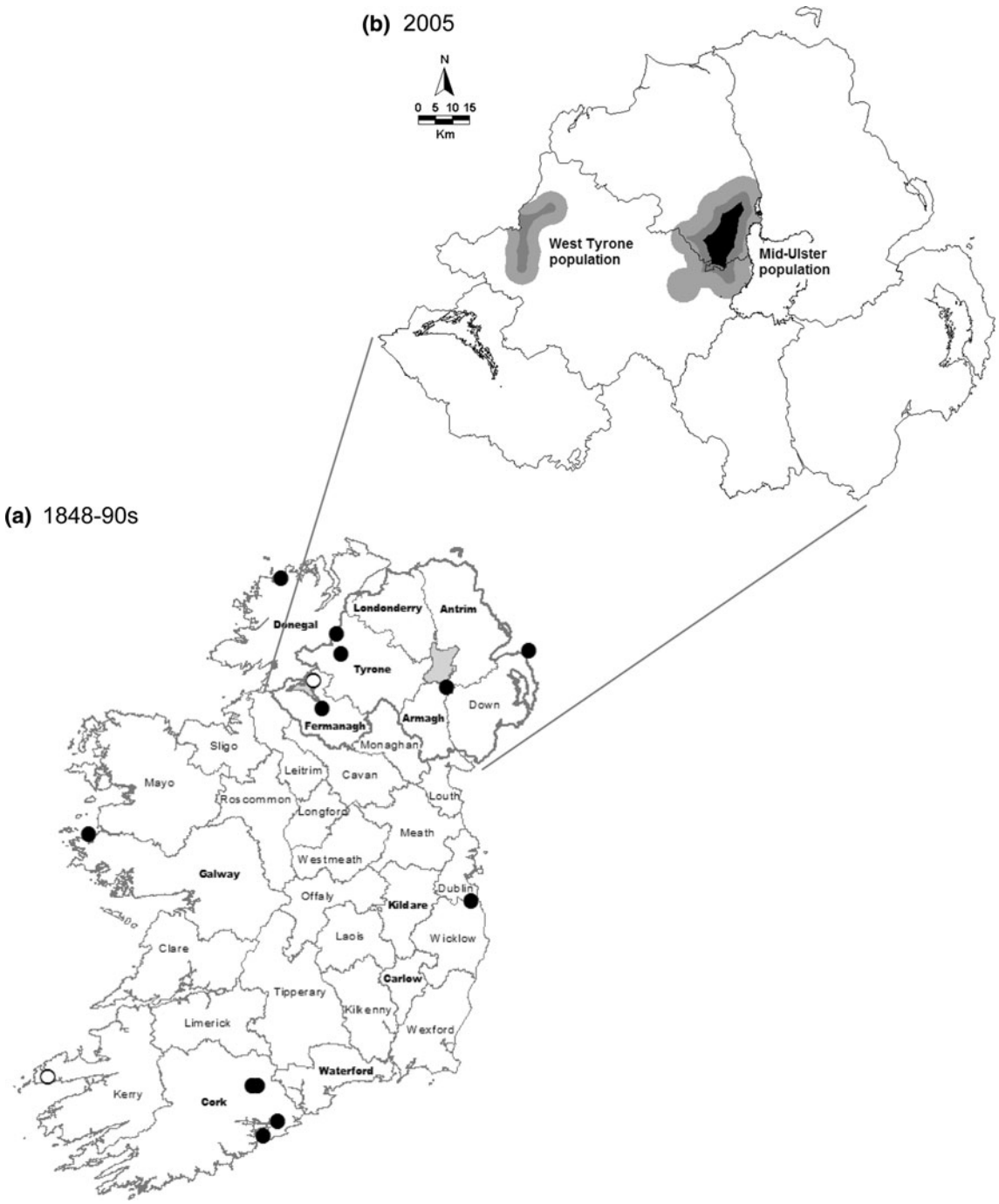


**Fig. 2** **a** Thirteen introductions of the European hare took place for which details are available (*filled circles*) with a further two suspected introductions (*open circles*) throughout Ireland between 1848 and 1890s (Barrett-Hamilton 1898). The *bold grey line* indicates the Northern Ireland border whilst county names are given for orientation. *Bold text* indicates those counties listed by Ni Lamhna (1979) as containing records of the European hare during the early-mid twentieth century. **b** The only extant populations known are now in Mid-Ulster and west Tyrone recorded during 2005 (Reid and Montgomery 2007). *Black shading* indicates the core range of the introduced species, *dark grey* indicates a zone of sympatry with the native Irish hare and *light grey* indicates an area of low European hare density predominated by native Irish hares

hares or interspecific hybridisation anywhere in Ireland. However, more recent molecular examination of 33 hares involved in road traffic accidents within the zone of sympatry in Mid-Ulster (Fig. 2b) assigned 51% as Irish hares, 18% as European hares and 18% as interspecific hybrids (Hughes et al. 2006). Four individuals (12%) could not be reliably identified. Bilateral hybridisation of both species was confirmed: five hybrids were the result of male European hares (♂) mating with female Irish hares (♀), whilst one hybrid appeared to be the result of a reciprocal mating of a female European hare (♀) with a male Irish hare (♂).

Thulin (2003) suggested that in Sweden the loss of species-specific litters, as a result of male competitive dominance and interbreeding, persistently eroded native mountain hare population densities enabling introduced European hares to become dominant. If extant European hare populations in Northern Ireland are descended from individuals introduced during the late 1800s, their geographically restricted range may indicate that hybrids have a reduced reproductive fitness. Thus, despite hybridization, both sympatric species may be able to maintain their own genetic integrity. Conversely, if European hares were introduced recently and interspecific mating is directionally skewed, it follows that hybridization may represent a significant threat to the native mountain hare. Whilst Hughes et al. (2006) demonstrated reciprocal hybridisation their sample size was insufficient to quantify the degree of directionality and, therefore, level of threat.

Moreover, in the scenario of an early introduction (during the late nineteenth century), local adaptation of European hares via natural selection may have reduced the Irish hare's competitive edge allowing recent expansion of the European hare population. A century may seem like a short evolutionary timespan, however, local adaptation of coat colour and winter moulting patterns has been observed among introduced mountain hares on the Faeroe Islands (cf. Bergengren 1969). Conversely, in the scenario of a recent introduction (during the late twelfth century), local adaptation through hybridisation (Arnold 1997) may have influenced European hare establishment. The transfer of genes associated with metabolic differences which sustain the local superiority of the Irish hare may have transferred to hybrid populations further endangering the Irish hare's competitive advantage.

There are no data by which to evaluate these hybridisation hypotheses; consequently, more work is required to fully establish the level of genetic threat posed by the European hare to the native Irish hare.

## Disease and parasite transmission

Invasive species which harbour sub-clinical pathogens can act as vectors of lethal infection to native species which are naïve and therefore susceptible to any foreign disease. For example, invasive North American grey squirrels *Sciurus carolinensis* were once thought to disadvantage sympatric Eurasian red squirrels *Sciurus vulgaris* in Great Britain through ecological competition alone. However, it is now well established that grey squirrels are vectors of squirrel poxvirus (SQPV), formerly called parapox, which is lethal to native red squirrels and is a significant component in their displacement (Sainsbury et al. 2000; Tompkins et al. 2002).

Similarly, European hares appear less susceptible to a number of infections that may well be lethal to naïve mountain hare populations (Mörner 1994, 1999; Thulin 2003), including tularaemia and European Brown Hare Syndrome (EBHS). Moreover, hares are host to ticks, fleas and other ectoparasites. In Scotland, mountain hares are frequently culled on grouse moors to regulate tick populations (Laurenson et al. 2003). Few studies have focused on the differential susceptibility of European and mountain hares to disease or parasites (Mörner 1994, 1999). Nevertheless, Thulin (2003) placed 'great importance' on the potential roles that parasite and disease susceptibility might play in determining species coexistence. The Irish hare has been isolated in Ireland for 30,000–60,000 years since the last glacial maximum (Hughes et al. 2006) and has only recently been exposed to another congeneric species. It seems likely, therefore, that if the European hare invasion poses a threat to native mountain hare populations through immunological naïvety, the Irish hare is more likely to be susceptible than mountain hare subspecies elsewhere. No data exist on this issue, and further research is urgently required to determine the role interspecific transmission of pathogens and parasites might play in Irish hare population declines.

## Impacts on non-lagomorph species

Throughout its non-native range the European hare has been shown to compete for forage with a wide range of native non-lagomorph herbivores. For

example, in South America European hares share most of their food resources with rodents such as the plains vizcacha *Lagostomus maximus*, mountain vizcacha *Lagidium viscacia* and mara *Dolichotis patagonum* (Puig et al. 2006; Galende and Raffaele 2008) as well as larger ungulates such as the guanaco *Lama guanicoe* and brown brocket deer *Mazama gouazoubira* (Puig et al. 2006; Kufner et al. 2008).

The relationship of European hares and other species are often complex and not always negative. For example, grazing by brent geese *Branta bernicla*, a species of conservation concern throughout Europe, is actively facilitated by the presence of European hares on salt marsh in the Netherlands (van der Wal et al. 2000). Conversely, long-term grazing by large herbivores, for example, domestic stock can facilitate European hare grazing by favourably altering sward structure and potentially influencing hare population dynamics even though both species appear to compete for forage in the short-term (Kuijper et al. 2008).

The complexity of community interactions and trophic cascade effects makes it impossible to predict with any confidence what effect European hare invasion might have on non-lagomorph species in Ireland. However, it is well established that islands, most notably those with an impoverished flora and fauna, are particularly vulnerable to the impact of invasive species (Harris and Yalden 2004; Stokes et al. 2006).

## Climate change

Where snow predominates in winter, for example in northern Sweden, latitude has been suggested as a limiting factor in the northern expansion of invasive European hares and the preservation of native mountain hare populations (Jansson and Pehrson 2007; Jansson et al. 2007). The same could also be said of elevation in Scotland. Consequently, winter warming as a result of global climate change has been identified as a significant threat to mountain hare populations above the snow line with increased temperatures facilitating the spread of European hares (Jansson and Pehrson 2007). Climate change has therefore already been implicated in the invasion ecology of this species.

Neither persistent winter snow nor high elevations exist in Ireland to present a significant barrier to European hare dispersal and spread. However, climate change models predict that summers in Ireland will become warmer and drier, making the country more favourable for arable agriculture (Holden et al. 2003). European hares are generally more abundant in intensively farmed arable landscapes and more scarce in less intensively farmed pastoral landscapes (Tapper and Parsons 1984; Hutchings and Harris 1996; Tapper 1999; Smith et al. 2005). Where grassland predominates European hares benefit from habitat heterogeneity with a mixture of arable fields (Tapper and Barnes 1986; Smith et al. 2004). Hence, small increases in arable activity throughout Ireland will create a more heterogeneous landscape which may increase its favourability for the European hare (Reid and Montgomery 2007). Moreover, landscape scale changes may well be detrimental to the Irish hare which is most prevalent on pastoral agriculture (Reid et al. 2007a, 2010a). Furthermore, we might hypothesise that the Irish hare, being a glacial relict, may suffer physiologically more from increased summer temperatures than European hares of central European and Asian descent.

## Discussion

The dynamics of most hare populations are generally complex and often exhibit significant interannual and multiannual periodicity and defined cyclicity (Elton and Nicholson 1942; Keith 1963, 1990; Krebs et al. 1986, 2001; Ranta et al. 1997; Kauhala et al. 2005). Intraspecific density-dependent processes such as competition for space and food resources and disease and parasite transmission are known to drive population change through variance in fecundity (Krebs et al. 2001). For example, female snowshoe hares *Lepus americanus* suffer reduced fecundity during peaks in their 10-year population cycle which initiate the subsequent decline phase (Krebs et al. 2001). Conversely, fecundity is released from depression during troughs in the population cycle. Recent empirically-informed agent-based models have demonstrated that intraspecific competition may also be a primary regulating factor in European hare population dynamics (Topping et al. 2010). Whilst these processes are generally intraspecific, there is no reason to assume that they cannot operate interspecifically; particularly where two ecologically similar

congeneric species occur in sympatry. Thus, we might hypothesise that where European hares invade the range of another hare species, for example, the mountain hare (including the Irish subspecies), that mechanisms hitherto operating intraspecifically may increasingly exert interspecific pressures. Moreover, if one species, for sake of argument the native, is more susceptible to the reduced fecundity imposed by competition for space or resources or disease and parasite transmission, then its population may decline to a greater degree during peak population years than the invading species driving native population suppression and the expansion of the invader's population. Thulin (2003) also implicated 'extinction by hybridisation' (Rhymer and Simberloff 1996) as a major contributing factor in the decline of mountain hares within the non-native range of European hares and the post-glacial contraction of the mountain hare's range in Europe. Moreover, the emerging threat of climate change may well interfere directly and indirectly with all the processes discussed, most particularly affecting habitat favourability through changes to farming systems.

A cautionary tale can be taken from Sweden where European hares were introduced into the south of the country during the mid-late 1800s and have now advanced north entirely replacing the native mountain hare subspecies over its southerly range (Nilsson 1820; Lönnberg 1908; Gerell 1977; Thulin 2000). The native mountain hare has been completely displaced within the province of Skåne and within 100–150 years the invading European hare has occupied a region of sympatry approximately twice the land area of Ireland (ca. 180,000 $km^2$).

Given the conservation importance of the Irish hare in Ireland, the UK and Europe, the emerging threat that European hares pose to its future ecological security and genetic integrity cannot be underestimated. Moreover, the UK and Ireland have international obligations under the Convention on Biological Diversity (Anonymous 1992), the Bern Convention (Anonymous 1979) and the EU Habitats Directive (EEC 43/92) to address invasive species issues. Immediate action is often the only opportunity for cost-effective eradication (Stokes et al. 2006). Both muskrats *Ondatra zibethicus* and roe deer *Capreolus capreolus* were successfully eradicated from Ireland during the early twelfth century (Fairley 2001; Failey et al. 2002), setting a precedent for the attainability of total extermination if a population is targeted early in its establishment phase.

## Recommendations

Integrated and co-ordinated species surveillance and monitoring is imperative to document the spread and impact of alien species (DEFRA 2003; Harris and Yalden 2004). Monitoring of European hare populations in Ireland is urgently required to establish an accurate distribution for the species and determine temporal trends in its population trajectory. Utilisation of field sports networks, including the Irish Coursing Club, may provide a cost effective means by which to monitor European hare sightings and local populations (Reid et al. 2010b). Further genetic work involving systematic sampling of hares from within zones of sympatry is required to establish the full extent of interspecific hybridisation with the Irish hare including the prevalence of backcrossing and introgression. Individual and long-term population fitness consequences of bilateral hybridisation are unknown and difficult to quantify in the wild. Any genetic study would benefit from an experimental approach to establish hybridisation under captive conditions. This would greatly increase the utility of data collected from the wild. Finally, a European hare *invasive Species Action Plan* (iSAP) and *Eradication strategy* are required. Such a strategy should include an evaluation of the efficacy of potential population management intervention and the most effective means by which this can be achieved.

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## References


Abernethy K (1994) Establishment of a hybrid zone between red and sika deer (genus *Cervus*). Mol Ecol 3:551–562

Anonymous (1979) Convention on the conservation of European wildlife and natural habitats (aka The Bern Convention). Council of Europe, Strasbourg, France. http://europa.eu/legislation_summaries/environment/nature_and_biodiversity/l28050_en.htm last access 28/05/2010

Anonymous (1992) Convention on Biological Diversity. Rio de Janeiro, Brazil. http://www.cbd.int/ last accessed 28/05/2010

Anonymous (2000) Biodiversity in Northern Ireland: species action plans—Irish Hare, Chough & Curlew. Environment and Heritage Service Northern Ireland, Department of Environment, Belfast, UK, pp 6–9

Anonymous (2005) All Ireland Species Action Plans: Irish Lady's-tresses (*Spiranthes romanzoffiana*), Pollan (*Coregonus autumnalis*), Irish hare (*Lepus timidus hibernicus*), and Corncrake (*Crex crex*) Environment and Heritage Service Northern Ireland, Department of Environment, Belfast, UK and National Parks & Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Republic of Ireland, pp 6–9

Arnold ML (1997) Natural hybridization and evolution. Oxford Series in Ecology and Evolution, Oxford University Press, USA

Barrett-Hamilton GEH (1898) Notes on the introduction of the brown hare into Ireland. Irish Nat J 7:69–76

Barrett-Hamilton GEH (1910) A History of British Mammals, vol 2. London, UK pp 325–348

Bergengren A (1969) On genetics, evolution and history of distribution of the heath-hare, a distinct population of the Arctic Hare, *Lepus timidus* L. Swedish Wildlife 6:381–460

DEFRA (2003) Review of non-native species policy report of the working group. Department for Environment, Food and Rural Affairs (DEFRA), London

Dingerkus SK (1997) The distribution and ecology of the Irish hare *L. t. hibernicus* in Northern Ireland. Unpublished PhD Thesis, The Queen's University of Belfast, Belfast, UK

Dingerkus SK, Montgomery WI (2001) The diet and landclass affinities of the Irish hare *Lepus timidus hibernicus*. J Zool 253:233–240. doi:10.1017/S0952836901000206

Dingerkus SK, Montgomery WI (2002) A review of the status and decline in abundance of the Irish hare (*Lepus timidus hibernicus*) in Northern Ireland. Mammal Rev 32:1–11

EEC 43/92 (1992) Directive on the Conservation of Natural Habitats of Wild Fauna and Flora. Official Journal of the European Union L 206:7

Elton CS, Nicholson M (1942) The ten-year cycle in numbers of the lynx in Canada. J Anim Ecol 11:215–244

Failey J, Gore-Booth J, Shiel C (2002) The Roe deer of Lissadell. Deer 12:243–249

Fairley J (2001) A basket of weasels. Privately published, Belfast

Flux JEC (1981) Field observations of behaviour in the genus Lepus. In: Myers K, MacInnes CD (ed.) Proceedings of the world lagomorph conference. Guelph, University of Guelph, Canada. pp 377–394

Flux JEC, Angermann R (1990) The hares and jackrabbits. In: Chapman JA, Flux JEC (eds) Rabbits, hares and pikas: Status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Oxford

Fraguglione D (1959) Les anomalies du pelage chez les lièvres commun et variable. Diana 4:57–59

Galende I, Raffaele E (2008) Space use of a non-native species, the European hare (*Lepus europaeus*), in habitats of the southern vizcacha (*Lagidium viscacia*) in northwestern Patagonia, Argentina. Eur J Wild Res 54:299–304. doi:10.1007/s10344-007-0148-5

Game Preservation (Special Protection for Irish Hares) Order (Northern Ireland) 2003. Statutory Rule No. 114/2003. Government Printer for Northern Ireland. ISBN 0337964181

Gerell R (1977) Skånes däggdjur—Resultat från en intervjuundersökning. Skåne Jakt 2:6–14

Gustavsson I (1971) Mitotic and meiotic chromosomes of the variable hare (*Lepus timidus* L), the common hare (*Lepus europaeus* Pall) and their hybrids. Hereditas 67:27–34

Gustavsson I, Sundt CO (1965) Anwendung von künstlicher Befruchtung bei der Hybridisierung von zwei Hasenarten. Z Jagdwiss 11:155–158

Hamill R (2001) A study of the genetic structure and phylogeography of *Lepus timidus* L subspecies in Europe using microsatellite DNA and mtDNA Unpublished PhD thesis, University College Dublin, Ireland

Harris S, Yalden DW (2004) An integrated monitoring programme for terrestrial mammals in Britain. Mammal Rev 34:157–167

Harting JE (1897) A supposed hybrid between the common and the Irish hare. Zoologist 4:95–96

Hayden T, Harrington R (2000) Exploring Irish mammals. Townhouse and Country house Ltd, Dublin

Holden NM, Brereton AJ, Fealy R, Sweeney J (2003) Possible change in Irish climate and its impact on barley and potato yields. Agr Forest Meterol 116:181–196

Holley AJF, Greenwood PJ (1984) The myth of the mad March hare. Nature 309:549–550

Hughes M, Montgomery WI, Prodöhl P (2006) Population genetic structure and systematics of the Irish Hare. Report prepared by Quercus for the Environment and Heritage Service (DOE, NI), UK

Hutchings MR, Harris S (1996) The current status of the brown hare *Lepus europaeus* in Britain. Joint Nature Conservation Committee, Peterborough

Jansson G, Pehrson Å (2007) Causes of the recent expansion of the brown hare (*Lepus europaeus*) in Sweden and its influence on mountain hare (*L timidus*) populations. Eur J Wild Res 53:125–130

Jansson G, Thulin CG, Pehrson Å (2007) Factors related to the occurrence of hybrids between brown hares *Lepus europaeus* and mountain hares *L. timidus* in Sweden. Ecography 30:709–715

Jeffery RJ (1996) Aspects of the ecology and behaviour of the Irish hare, *Lepus timidus hibernicus* (Bell, 1837) on lowland farmland. Unpublished PhD thesis, Trinity College, University of Dublin, Ireland

Kauhala K, Helle P, Hiltunen M (2005) Population dynamics of mountain hare *Lepus timidus* populations in Finland. Wildlife Biol 4:299–307

Keith LB (1963) Wildlife's ten-year cycle. University of Wisconsin Press, Madison

Keith LB (1990) Dynamics of snowshoe hare populations. Current Mammal 2:119–195

Krebs CJ, Gilbert BS, Boutin S, Sinclair ARE, Smith JNM (1986) Population biology of snowshoe hares: demography of food-supplemented populations in the southern Yukon. J Anim Ecol 55:963–982

Krebs CJ, Boonstra R, Boutin S, Sinclair ARE (2001) What drives the 10-year cycle of snowshoe hares? Bioscience 51:25–35

Kufner MB, Sepulveda L, Gavier G, Modoery L, Giraudo L (2008) Is the native deer *Mazama gouazoubira* threatened by competition for food with the exotic hare *Lepus europaeus* in the degraded Chaco in Córdoba, Argentina? J Arid Environ 72:2159–2167

Kuijper DPJ, Beek P, Van Wieren SE, Bakker JP (2008) Time-scale effects in the interaction between a large and a small herbivore. Basic Appl Ecol 9:126–134

Laurenson MK, Norman RA, Gilbert L, Reid HW, Hudson PJ (2003) Identifying disease reservoirs in complex systems: mountain hares as reservoirs of ticks and louping-ill virus, pathogens of red grouse. J Anim Ecol 72:177–185

Lever C (2009) The naturalized animals of Britain and Ireland. New Holland Publishers Ltd, London, p 63

Lönnberg E (1908) Några villebrådsarters nutida utbredning i Skåne. Svenska Jägareförbundets Tidskrift 46:7–16

Mörner T (1994) Tularemia in Hares in Sweden with Special Reference to Identification of *Francisella tularensis*. PhD Thesis, Swedish University of Agricultural Sciences and National Veterinary Institute, Uppsala. Sweden. p 131

Mörner T (1999) Monitoring diseases in wildlife—a review of diseases in the orders Lagomorpha and Rodentia in Sweden. Proceedings Symposium of Zoo Animals, Vienna, Austria, 39:255–262

Ni Lamhna E (1979) Provisional distribution atlas of amphibians, reptiles and mammals in Ireland, 2nd edn. An Foras Forbartha, Dublin

Nilsson S (1820) Skandinavisk Fauna Del 1: Däggande Djuren Berlingska boktryckeriet, Lund. Sweden

Puig S, Videla F, Cona MI, Monge SA (2006) Diet of the brown hare (*Lepus europaeus*) and food availability in northern Patagonia (Mendoza, Argentina). Mammal Biol 72:240–250

Ranta E, Lindstrom J, Kaitala V, Kokko H, Linden L, Helle E (1997) Solar activity and hare dynamics: a crosscontinential comparison. Am Nat 149:765–775

Reid N (2006) Conservation ecology of the Irish hare (*Lepus timidus hibernicus*). Unpublished PhD thesis, Queen's University Belfast, Belfast, UK

Reid N, Montgomery WI (2007) Is naturalisation of the brown hare in Ireland a threat to the endemic Irish hare? Biol Environ 107:129–138

Reid N, Dingerkus K, Montgomery WI, Marnell F, Jeffrey R, Lynn D, Kingston N, McDonald RA (2007a) Status of hares in Ireland: hare survey of Ireland 2006/07. In: Marnell F, Kingston N (eds) Irish wildlife manuals, No 30. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin

Reid N, McDonald RA, Montgomery WI (2007b) Mammals and agri-environment schemes: hare haven or pest paradise? J App Ecol 44(6):1200–1208

Reid N, McDonald RA, Montgomery WI (2010a) Homogenous habitat can meet the discrete and varied resource requires of hares but may set an ecological trap. Biol Conserv 143:1701–1706

Reid N, Magee C, Montgomery WI (2010b) Integrating field sports, hare population management and conservation. Acta Theriol 55(1):61–71

Rhymer JM, Simberloff D (1996) Extinction by hybridization and introgression. Annu Rev Ecol Syst 27:83–109

Roberts N (1998) The holocene: an environmental history. Oxford Blackwell Ltd, Oxford

Sainsbury AW, Nettleton P, Gilray J, Gurnell J (2000) Grey squirrels have a high seroprevalence to a parapoxvirus associated with deaths in red squirrels. Anim Conserv 3:229–233

Schröder J, Soveri T, Soumalainen HA, Lindberg LA, van der Loo W (1987) Hybrids between *Lepus timidus* and *Lepus europaeus* are rare although fertile. Hereditas 107:185–189

Sheppard R (2004) Brown hares *Lepus europaeus* Pallas in NW Ireland. Irish Nat J 2712:484–485

Smiddy P (1994) Hare species in Co Cork. Irish Nat J 24:417–418

Smith RK, Jennings N, Robinson A, Harris S (2004) Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? J Appl Ecol 41:1092–1102

Smith RK, Jennings N, Harris S (2005) A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. Mammal Rev 35:1–24

Stokes K, O'Neill K, McDonald RA (2006) Invasive species in Ireland. Report to Environment and Heritage Service, Belfast and National Parks and Wildlife Service Dublin by Quercus, Queen's University Belfast, Belfast

Strevens TC, Rochford JM (2004) The diet and impact of the Irish hare *Lepus timidus hibernicus,* Bell 1837 in a young plantation. Biol Environ 104:89–94

Tangney D, Fairley J, O'Donnell G (1995) Food of Irish hares *Lepus timidus hibernicus* in western Connemara, Ireland. Acta Theriol 40:83–111

Tapper S (1987) The Brown hare. Shire Publications Ltd, Aylesbury

Tapper SC (1999) A question of balance: game animals and their role in the British countryside. Game Conservancy Trust, Fordingbridge

Tapper SC, Barnes RFW (1986) Influence of farming practices on the ecology of the brown hare (*Lepus europaeus*). J Appl Ecol 23:39–52

Tapper S, Parsons N (1984) The changing status of the Brown hare (*Lepus capensis* L.) in Britain. Mammal Rev 14: 57–70

Thulin CG (2000) Hybridisation between introduced brown hares and native mountain hares in Sweden. PhD thesis, Uppsala University, Uppsala, Sweden

Thulin CG (2003) The distribution of Mountain Hares (*Lepus timidus*, L 1758) in Europe: a challenge from Brown Hares (*L. europaeus*, Pall 1778)? Mammal Rev 33:29–42

Thulin CG, Flux JEC (2003) *Lepus timidus* (Linnaeus 1758). Schneehase. In: Krapp F (ed) Handbuch der Saugetiere Europas, Band 3/II, Lagomorpha. Aula Verlag, Koblenz, pp 155–185

Thulin GC, Tegelström H (2002) Biased geographical distribution of mitochondrial DNA that passed the species barrier from mountain hares to brown hares genus *Lepus*: an effect of genetic incompatibility and mating behaviour? J Zool 258:299–306

Tompkins DM, Sainsbury AW, Nettleton P, Buxton D, Gurnell J (2002) Parapoxvirus causes a deleterious disease in red squirrels associated with UK population declines. Proc R Soc Lond B Biol Sci 269:529–533

Topping CJ, Hoye TT, Olesen CR (2010) Opening the black box-development, testing and documentation of a mechanistically rich agent-based model. Ecol Model 221: 245–255

van der Wal R, van Wijnen H, van Wieren S, Beucher O, Bos D (2000) On facilitation between herbivores: how brent geese profit from brown hares. Ecol 81:969–980

Walker J, Fairley JS (1968) Winter food of Irish hares in County Antrim, Northern Ireland. J Mammal 49:783–785

Whilde A (1993) Threatened mammals, birds, amphibians and fish in Ireland. Irish Red Data Book II: Vertebrates HMSO, Belfast

Wildlife (Amendment) Act 2000 No 38/2000. Irish Statute Book Office of the Attorney General, Dublin, Republic of Ireland

Wildlife (Northern Ireland) Order 1985, No 171(NI 2), Her Majesty's Stationery Office, Belfast. UK

Wildlife Act (1976) No 39/1976. Irish Statute Book Office of the Attorney General, Dublin, Republic of Ireland

Wolfe A (1994) Coat colour in the Irish hare and the status of the brown hare. Irish Nat J 24:472

Wolfe A, Whelan J, Hayden TJ (1996) Dietary overlap between the Irish mountain hare, *Lepus timidus hibernicus* and the rabbit *Oryctolagus cuniculus* on coastal grassland. Biol Environ 96B:89–95

Yalden DW (1999) The history of British mammals. London Poyser Natural History, London