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IS NATURALISATION OF THE BROWN HARE IN IRELAND A THREAT TO THE ENDEMIC IRISH HARE?

Neil Reid and W. Ian Montgomery

ABSTRACT

On islands, one of the greatest risks to native wildlife is the establishment of alien species. In Ireland, the Irish hare (*Lepus timidus hibernicus*), the only native lagomorph, may be at risk from competitive exclusion and hybridisation with naturalised brown hares (*L. europaeus*) that were introduced during the late nineteenth century. Pre- and post-breeding spotlight surveys during 2005 in the north of Ireland determined that brown hare populations are established in mid-Ulster and west Tyrone. In mid-Ulster, brown hares comprised 53%–62% of the hare population, with an estimated abundance of 700–2000 individuals between pre- and post-breeding periods. Comparison of habitat niches suggest that Irish and brown hares have comparable niche breadths that at times completely overlap, suggesting the potential for strong competition between the species. Anecdotal evidence suggests that both species may hybridise. Further research is urgently required to assess the degree of risk that naturalised brown hares pose to the Irish hare population and what action, if any, is needed to ensure the future ecological security and genetic integrity of the native species.

INTRODUCTION

One of the greatest problems facing conservation in Britain and Ireland is the spread and establishment of introduced species (Harris and Yalden 2004; Stokes *et al.* 2006). Integrated and co-ordinated species surveillance and monitoring is imperative to document the arrival, establishment, spread and impact of alien species (DEFRA 2003; Harris and Yalden 2004). Despite its recent decline across Europe (Smith *et al.* 2005), the European brown hare (*Lepus europaeus*, Pallas 1778) has naturalised successfully in many countries beyond its former range. The species is native across mainland Europe except in Scandinavia, Iberia and the Mediterranean region and extends east throughout the central Asian steppes (Flux and Angermann 1990). Its success as an invasive species has resulted in its colonisation of 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, Réunion and the Falklands (Flux and Angermann 1990). It was established in Great Britain during pre-Roman times, where it was introduced for food (Yalden 1999), but remained absent from Ireland until the mid-late nineteenth century, when it was introduced for hare coursing (Barrett-Hamilton 1898). Fourteen recorded introductions took place throughout Ireland from 1848 to the 1890s, including six in Northern Ireland (Barrett-Hamilton 1898). Several populations successfully

established and proliferated, but most died out by the turn of the twentieth century (Barrett-Hamilton 1898). Since then only two confirmed reports of brown hares in Ireland have been made: in Tyrone and east Donegal (Fairley 2001; Sheppard 2004).

The Irish hare (*Lepus timidus hibernicus*, Bell 1837) is Ireland's only native lagomorph and is classified as an endemic subspecies of mountain hare (*L. timidus*, Linnaeus 1758). However, recent genetic evidence suggests it may warrant full species status (Hughes *et al.* 2006). In contrast to mountain hares elsewhere, which inhabit high mountains, tundra, heath and boreal forest (Angerbjörn and Flux 1995), the Irish hare occurs at all altitudes and can be found in most habitats throughout Ireland (Hayden and Harrington 2000). In Sweden, the mountain hare has been completely lost from a lowland area > 11,000 km² in the south of the country following the introduction and naturalisation of the brown hare in the mid- to late 1800s (Nilsson 1820; Lönnberg 1908; Gerell 1977; Thulin 2000). Thulin (2003) suggests that interspecific competition and hybridisation, along with possible disease transmission, may have contributed to the displacement of the native Swedish hare.

Leporid grazing affects the availability of herbaceous vegetation (MacCracken and Hansen 1982), while food shortages may control leporid densities (Gibb 1981). Consequently, strong competition between sympatric leporids is

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Pl. I— Comparison of a) an Irish hare (*Lepus timidus hibernicus*), b) a European rabbit (*Oryctolagus cuniculus*) and c) a European brown hare (*Lepus europaeus*). Note that the European brown hare was photographed in mid-Ulster (54°47'01"N, 06°31'58"W) during 2003.

known (Homolka 1987; Chapuis 1990; Flux 1993). Most species of hare exist in allopatry, with competitive exclusion being the proposed separating mechanism (Flux 1981). Each hare 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, making sympatry a transient phenomenon (Flux 1981). It has been suggested that competitive exclusion rather than habitat preferences related to species-specific food utilisation may explain the restricted distribution of mountain hares in Europe (Wolfe *et al.* 1996). Consequently, as observations in Sweden suggest, following brown hare colonisation, mountain hares in lowland areas may be relegated to less optimal habitats for brown hares, such as higher ground and deep forests.

This paper aims to establish the current distribution and abundance of introduced brown hares in the north of Ireland. We consider the potential risk posed by brown hares to Irish hares by assessing the degree of ecological niche overlap and review the evidence for hybridisation. Recommendations are made with respect to future management and monitoring of brown hares and Irish hares in areas of sympatry.

METHODS

FIELD SURVEYS

The abundance of hares in the north of Ireland was assessed by a nocturnal distance sampling spotlight survey. Three 625km² survey squares were centred on the locations of known brown hare introductions at Strabane and Baronscourt, Co. Tyrone (54°49'30"N, 07°26'49"W and 54°41'15"N, 7°24'39"W, respectively), Lurgan Estate, Co.

Armagh (54°27'45"N, 06°18'48"W) and Cleenish Island, Fermanagh (54°17'59"N, 07°36'07"W), while a fourth survey square centred on recent confirmed sightings by one of the authors (N.R.) in mid-Ulster. To test the feasibility of differentiating brown hares from Irish hares at night, a pre-breeding pilot survey was conducted in winter (February and March) 2005 within the mid-Ulster survey square. A full post-breeding survey was completed in all four survey squares during Autumn (November) 2005.

Each 625km² survey square contained roughly parallel line transects running along a north-west to south-east axis, placed approximately 3km apart. Removing areas of urban settlement, each square contained between 100–150km of transect. A 2 × 10⁶ candle-power spot lamp was used from a platform on a modified pick-up truck, elevating the observer's head height >2m above ground level (above most hedgerows). Each transect was driven at 15–25km h⁻¹, with both sides of the road being swept twice with the light beam. Care was taken to cover as much ground behind obstacles as possible. Animals were positively identified using 10 × 40 binoculars. For each cluster of hares observed, the species, cluster size (i.e. number) and approximate perpendicular distance of the cluster from the transect (judged to the nearest 5m by eye) was recorded. Surveys did not begin until one hour after sunset.

HABITAT UTILISATION

The UK Land Cover Map 2000 (Fuller *et al.* 2002) was used to quantify habitat use and availability within the study areas using ArcView GIS 3.3[©] software (ESRI, California, USA). Each hare sighting was buffered to a distance of 174m to create a 30ha area, approximating an average hare home range (Wolfe and Hayden 1996; Smith *et al.*

2004). The proportion of habitats represented within this area was taken as a measure of habitat use. Each transect was buffered to a distance of 280m, representing the maximum distance at which a hare was observed plus the radius of a 30ha buffer, representing the maximum area available to animals observed during the survey. The proportion of habitats represented within this area was taken as a measure of habitat availability within the area surveyed.

STATISTICAL ANALYSES

Where sufficient observations allowed, the density and abundance of hares (both Irish and brown combined) was calculated using Distance v.4 software (Thomas *et al.* 2004). Error in the measured or estimated distance to each detection can substantially bias the calculated animal density (Buckland *et al.* 2004). To preserve the assumption that all distances should be measured accurately, the error associated with estimating distances by eye was accounted for by calibration using a laser rangefinder (which became available after the completion of the survey). A sample of 100 distances estimated by eye and subsequently measured by laser rangefinder were regressed, using a simple linear function, and the equation of the slope was used to correct survey distance estimates. The length of all transects within each survey square were summed and entered as a single transect with a survey effort equal to 1. Six commonly used models were constructed (Buckland *et al.* 2004), including uniform cosine, uniform simple polynomial, half-normal cosine, half-normal hermite polynomial, hazard rate cosine and hazard rate simple polynomial. The parsimony of each model was evaluated using Akaike's Information Criterion (AIC) with the best model selected on the basis of the lowest AIC value. Using the best model, the proportion of sightings of each species was then used to calculate the relative density and abundance of both Irish and brown hares.

Measures of relative habitat utilisation by each species were assessed using Hurlbert's niche breadth (Hurlbert 1978) and Pianka's niche overlap (Pianka 1973) using the formulae:

$$B' = \frac{1}{\sum_i^n (p_i^2/a_i)}$$

$$O_{jk} = \frac{\sum_i^n p_{ij}p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where B' is Hurlbert's niche breadth and O_{jk} is Pianka's niche overlap, both of which vary between 0 and 1. p_{ij} is the proportion of habitat i utilised by

species j (Irish hare) or k (brown hare) and a_i is the proportion that habitat i is of the total habitats available.

Species specific habitat selection was assessed using compositional analysis (Aebischer *et al.* 1993), which allows comparison of used habitat proportions with available habitat proportions by means of MANOVA analysis of transformed log-ratios. Utilised habitats that were zero for >50% of individuals within a data subset were excluded from analysis, while remaining proportions equal to zero were replaced by a value of 0.001 (Aebischer *et al.* 1993). Open water, roads and rural development (houses and farmyards) were excluded from calculations of available and utilised habitat proportions as these areas are likely to be incidental to hare ranges. Departure from random habitat selection was tested using Wilks' Λ and χ^2 values, the significance of which was determined using data randomisation based on 1000 iterations (Manly 1997). Habitats were ranked by relative use and significant differences identified (Aebischer *et al.* 1993). Habitat selection analysis was achieved using the 'Compositional Analysis Add-In Tool' for Excel 2002 (Version 4.1; Peter Smith, Wales, UK). Hurlbert's niche breadth of both species, their relative habitat selection and Pianka's niche overlap between the species were calculated for the mid-Ulster pre-breeding survey and across all survey areas during the post-breeding survey.

RESULTS

During the pre-breeding pilot survey brown hares were easily distinguished from Irish hares at night based on the length of the ears in proportion to the head, pelage colouration, the presence of black tips on the ears and a black top to the tail as well as the absence of white flanks and feet, characteristic of Irish hares during winter (Pl. I).

Of the 100 distance estimates checked by laser rangefinder, 67 were underestimated. The mean distance estimated by eye was 54.3m (SD = 32.8m), and the mean distance measured using the rangefinder was 58.4m (SD = 35.0m), suggesting a 7% underestimation of distances by eye. Estimated distances were calibrated prior to analysis using the regression slope ($y = (0.909 \cdot x) + 1.216$).

During spring, 49 hares were observed in mid-Ulster. The mean perpendicular distance to a hare from the transect was 36.6m (SD = 21.8m). A uniform cosine distance model described the data best when grouped into 22m-wide bins (Fig. 1a), producing an estimated density of 3.11 hares km⁻² (95% CI = 2.11–4.59 hares km⁻²) within the study area. The proportionate composition of the hare community in spring is given in Table 1.

Fig. 1—Uniform cosine detection probability of hares in mid-Ulster during (a) pre-breeding and (b) post-breeding surveys during 2005.

Of the four regions surveyed in autumn, brown hares were detected in two. In the Strabane survey square, 14 (73.7%) were Irish hares and 5 (26.3%) were brown hares and in the mid-Ulster square, 19 (38.0%) were Irish hares and 31 (62.0%) were brown hares. Two Irish hares were detected in the Lurgan survey and 32 Irish hares in the Fermanagh survey square. Fig. 2 shows the distribution of Irish hare and brown hare sightings within the surveyed areas and all hare sightings recorded over the last decade. Only the mid-Ulster survey yielded sufficient detections to enable a successful distance model to estimate the density

and abundance of brown hares during autumn 2005. The mean perpendicular distance to a hare from the transect was 35.0m (SD = 23.3m). As with the pre-breeding data, a uniform cosine distance model described the detection of sightings best when they were grouped into 22m-wide bins (Fig. 1b), producing an estimated density of 3.24 hares km^{-2} (95% CI = 1.98–5.28 hares km^{-2} CI) within the study area. The proportionate composition of the hare community in autumn is given in Table 1. While the 95% confidence intervals overlap substantially between the pre-breeding and post-breeding population estimates, the estimated mean density of Irish hares in mid-Ulster decreased by 18.7%, while the estimated mean density of brown hares increased by 17.9%.

Depending upon the subset of data analysed, the habitat niche breadth of Irish hares varied from 0.80 to 0.87, while that of brown hares varied from 0.65 to 0.89 (Table 2). Pianka's niche overlap between the species varied between 0.94 and 1.00 (Table 2). Significantly, both species selected improved grasslands over any other habitat type (Tables 3 and 4). Niche overlap was greatest in mid-Ulster (Pianka's = 1.00) during the post-breeding period in autumn.

During the spring pilot survey, a pair of hares, one Irish and one brown, were observed chasing one another, sparring and boxing, a typical pre-copula behaviour of hares (Holley and Greenwood 1984). Furthermore, two individuals were observed in autumn (one on the survey and one at another time) that were difficult to positively identify as either species, having features common to both (N.R., pers. obs.). A review of the literature suggests that at least one supposed *L.t. hibernicus* $\times$ *L. europaeus* hybrid has been recorded in the past (Harting 1897).

Table 1—Pre- and post-breeding hare density and abundance estimates for mid-Ulster during 2005. 95% confidence intervals are shown in parentheses.

	Pre-breeding 2005		Post-breeding 2005	
	Irish hare	Brown hare	Irish hare	Brown hare
Number of hares recorded	23	26	19	31
Percentage of sightings	46.9	53.1	38.0	62.0
Mean density (hares km^{-2})	1.46 (0.99–2.15)	1.65 (1.12–2.44)	1.23 (0.75–2.01)	2.01 (1.23–3.28)
Estimated abundance	910 (616–1346)	1031 (697–1524)	769 (471–1255)	1254 (768–2047)

Fig. 2— The distribution of Irish hare (○) and brown hare (●) sightings during surveys from 1995 to 2005 (Dingerkus 1997; O'Mahony and Montgomery 2001; Preston *et al.* 2003; Tosh *et al.* 2004; 2005). Grey circles or lines represent survey effort. The current survey focused on four 625km² survey squares centred on (a) Strabane, (b) mid-Ulster, (c) Lurgan and (d) Fermanagh.

DISCUSSION

This is the first paper to establish the distribution and estimate abundance of brown hares in Ireland. Over the last decade Northern Ireland has been intensively surveyed for hares (Dingerkus 1997; O'Mahony and Montgomery 2001; Preston *et al.* 2003; Tosh *et al.* 2004; 2005), but no previous reports of brown hares have been confirmed, suggesting that their distribution may be limited to that demonstrated here (Fig. 2). We identified a substantial population of brown hares west of Lough Neagh (mid-Ulster) in counties Londonderry and Tyrone, while further sightings were recorded near Baronscourt, Co. Tyrone. Both these areas have not been sampled during previous hare surveys, and thus the populations have escaped notice until now. An introduction at Baronscourt during 1876 (Barrett-Hamilton 1898) seems to be the likely origin of the animals in west Tyrone, but the source of the mid-Ulster population remains unknown, although they may have originated from an introduction at an unknown site in Co.

Londonderry (Barrett-Hamilton 1898). In mid-Ulster, during 2005, the population was estimated at between 700 and 2000 individuals, suggesting that brown hares are well established. The size of the Strabane population remains unknown. It is likely that the total abundance of brown hares in Northern Ireland may be in the low thousands, probably <5% of the total hare population (inferred from Tosh *et al.* 2005). Sheppard (2004) suggests that brown hares may also exist in east Donegal not far from the Strabane and Baronscourt introduction sites. However, the failure of the Hare Survey of Ireland 2006/07 to detect brown hares in the Republic of Ireland may suggest that, if present, their distribution is limited (Reid *et al.* 2007).

The pre-breeding estimate of hare density in mid-Ulster (3.11 hares km⁻²) was equal to the total mean estimate of hare density for Northern Ireland during winter 2005 (3.10 hares km⁻², Tosh *et al.* 2005); however, 53% of the hare population in mid-Ulster were brown hares. This may suggest that the presence of the introduced species has not affected the overall carrying capacity of hares but

Table 2—Habitat niche breadth and overlap of Irish and brown hares.

		Niche breadth		Pianka's niche overlap
		Irish hare	Brown hare	
Spring 2005	(mid-Ulster)	0.85	0.65	0.94
Autumn 2005	(mid-Ulster)	0.80	0.81	1.00
Autumn 2005	(all survey areas)	0.80	0.81	0.96

that a proportion of the native population may have been replaced by brown hares. While the post-breeding density of hares in Mid-Ulster was not significantly different from the pre-breeding density, the mean estimates suggest that the density of brown hares may have increased (+18%) by a similar degree to the decrease observed in the mean estimate of Irish hare density (−19%). Stokes *et al.* (2006) suggest that the most prominent negative impact of alien species in Ireland is direct competition with native biota. While sample sizes were small, if the trend in population change is real, one hypothesis may be that competition between the two species in mid-Ulster may favour the growth of the brown hare population more than that of the native Irish hare.

The hypothesis that interspecific competition exists between Irish and brown hares is further strengthened by examination of their habitat use. Even at its lowest during winter, habitat niche overlap was high (Pianka's = 0.94). The distribution of hares in late winter, the peak of the mating season, may not accurately reflect habitat-specific food or space utilisation, as the distribution of male animals may be skewed towards the home ranges of a few oestrous females. Consequently, niche breadth and overlap in autumn may provide a better means to assess the potential for competition as distribution is more likely to be influenced by the choices made by individuals. Furthermore, at the end of the growing season the best food resources may be in short supply, increasing the likelihood of competition. Both species demonstrate different habitat selection, but in autumn they share similar proportions of the major components of their habitat space, and consequently niche overlap is complete (Pianka's = 1.00). Both species select improved grassland over any other habitat type. Irish hares prefer neutral grasslands over arable areas during autumn, while brown hares prefer arable areas over the remaining

habitat types (Table 4). Compared to mid-Ulster, across all the study areas Irish hares had a greater proportion of their habitat use made up of neutral grasslands, suggesting that this habitat type may be important to Irish hares across the country as a whole. The similarity between the habitat niche breadth of both species and the high degree of niche overlap suggests the potential for competition between the species for space within habitats if resources are limiting. Here, we hypothesise that the strength of competition between both species may be influenced not only by the availability of habitats but the subtle differences between their habitat choices. Throughout Europe, the brown hare is more common in arable areas rather than pastoral landscapes (Tapper and Parsons 1984; Hutchings and Harris 1996; Klansek *et al.* 1998; Vaughan *et al.* 2003). We suggest that in areas with greater prevalence of arable horticulture, brown hares may find it easier to establish and push out the native Irish hare, while in predominately pastoral areas the Irish hare may remain the dominant species. The small number of brown hares introduced to Ireland and the balance of competition between Irish and brown hares may have restricted their spread over the last 100–150 years. Furthermore, hare populations are known to exhibit extreme interannual and multiannual variation (Watson *et al.* 1973; Krebs *et al.* 2001; Reid *et al.* 2007), making them vulnerable to stochastic extinction events even in relatively large populations (Morris 1993). Other explanations for the initial 'lag phase' in the growth and spread of introduced species populations have included biotic and abiotic environmental change and genetic founder effects (Crooks and Soule 1999). Some alien species have demonstrated lag phases lasting decades prior to them becoming invasive (Mack 1981). However, once naturalisation is achieved they can spread rapidly, dominating native counterparts (e.g. *Bromus tectorum* in the USA, see

Table 3—Habitat selection by Irish and brown hares in Northern Ireland: MANOVA analysis of transformed log-ratios of habitat use (within putative home ranges) versus habitat availability (within total study area).

Season (site)	Species	Wilks' Λ	χ^2	df	P
Pre-breeding (mid-Ulster)	Brown hare	0.001	185.38	9	< 0.001
	Irish hare	0.007	114.44	8	< 0.001
Post-breeding (mid-Ulster)	Brown hare	0.027	111.82	6	< 0.001
	Irish hare	0.001	138.63	8	< 0.001
Post-breeding (all study areas combined)	Brown hare	0.027	130.28	6	< 0.001
	Irish hare	0.015	147.95	8	< 0.001

Mack 1981). Anthropogenic factors may further facilitate the spread of some invasive species. For example, climate change prediction models suggest that summers in Ireland will become warmer and drier, which is likely to increase cereal yields (Holden *et al.* 2003), making the country more suitable for arable horticulture. Such changes may favour the further expansion of brown hare populations in some areas of the country. Evidence from the Peak District and the Isle of Man, where both hare species are present, suggests that where suitable conditions exist in sympatry, both species settle into altitudinally distinct ranges, with mountain hares occupying higher elevations than brown hares (Yalden 1971; Fargher 1977).

Hybridisation between introduced and native species is a common problem among plants (Abbott *et al.* 2003), but it also occurs in mammals. ‘Extinction by hybridisation’, a concept explored by Rhymer and Simberloff (1996), may constitute a threat to mountain hare populations that occur in sympatry with brown hares (Thulin 2003). Hybridisation between both species is well known (Lönnberg 1905; Fraguglione 1959; Gustavsson and Sundt 1965; Gustavsson 1971; Schröder *et al.* 1987; Thulin and Tegelström 2002). Thulin (2003) suggests that loss of species-specific litters as a result of interbreeding may persistently erode mountain hare population densities, enabling brown hares to become dominant. Observations

of Irish and brown hares sparring and boxing during the peak mating season may suggest that they view one another as potential mates, while records of phenotypically ambiguous animals arouse suspicions that both species hybridise. There is no published evidence of genetic introgression between the species in Ireland; nonetheless, the potential risk to the Irish hare from genetic pollution should not be ignored.

The naturalisation of brown hares in Ireland, particularly in view of putative changes to climate and Irish farming systems, may pose a significant risk to the ecological security and genetic integrity of the Irish hare. The UK and Ireland have international obligations under the Convention on Biological Diversity (1992), the Bern Convention (1979) and the European Habitats Directive (EEC 43/92) to address invasive species issues. By 1932, muskrats (*Ondatra zibethica*) had successfully established in fourteen counties in Great Britain (Fairley 2001). However, this species was successfully eradicated by 1936 after almost 4,500 individuals had been killed (Warwick 1940). Similar efforts successfully eradicated both muskrats and roe deer (*Capreolus capreolus*) from Ireland during the early twentieth century (Fairley 2001; Fairley *et al.* 2002), demonstrating the attainability of total extermination if a population is targeted early in its establishment phase. Immediate action is often the only opportunity

Table 4—Habitat selection by Irish and brown hares. Habitat types are ranked according to their relative use: the most used are at the top of the lists. Habitat categories that are not significantly different from one another are indicated with the same lower-case letter. The % column indicates the mean percentage of the putative home range constituted by that habitat.

Pre-breeding 2005 (mid-Ulster)				Post-breeding 2005 (mid-Ulster)				Post-breeding 2005 (all areas surveyed)			
Irish hare ^a	%	Brown hare	%	Irish hare	%	Brown hare	%	Irish hare	%	Brown hare	%
Improved grass ^a	64.0	Improved grass	69.0	Improved grass	66.7	Improved grass	76.8	Improved grass	57.2	Improved grass	79.3
Arable ^a	17.3	Acid grass ^a	20.4	Neutral grass ^a	4.7	Arable ^a	18.5	Neutral grass ^a	18.2	Arable ^a	16.5
ODSH ^a	0.8	Calcareous grass ^a	3.4	Arable ^a	18.8	Calcareous grass ^a	0.7	Arable ^a	11.1	Calcareous grass ^a	0.6
DSH ^a	3.7	ODSH ^a	0.3	Woodland ^a	1.5	ODSH ^a	0.4	Woodland ^a	4.3	ODSH ^a	0.3
Neutral grass ^a	9.6	Neutral grass ^a	4.1	ODSH ^a	<0.1	DSH ^a	0.5	ODSH ^a	1.5	DSH ^a	0.6
Calcareous grass ^a	1.5	DSH ^a	0.4	Fen, marsh and swamp ^a	2.5	Neutral grass ^a	2.4	Fen, marsh and swamp ^a	1.3	Neutral grass ^a	2.1
Woodland ^a	0.1	Bracken ^a	1.7	Acid grass ^a	3.6	Acid grass ^a	0.7	Acid grass ^a	4.7	Acid grass ^a	0.6
Acid grass ^a	3.0	Arable ^a	0.7	DSH ^a	2.2			DSH ^a	1.7		

DSH = Dwarf scrub heath.
ODSH = Open dwarf scrub heath.

for cost-effective eradication (Stokes *et al.* 2006). Further research is required urgently to assess the degree of risk that brown hares pose to Irish hare populations prior to the consideration of eradication plans.

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REFERENCES

Abbott, R.J., James, J.K., Milne, R.I. and Gillies, A.C.M. 2003 Plant introductions, hybridization and gene flow. *Philosophical Transactions of the Royal Society of London, Series B—Biological Sciences* **358** (1434), 1123–32.

Aebischer, N.J., Robertson, P.A. and Kenward, R.E. 1993 Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–25.

Angerbjörn, A. and Flux, J.E.C. 1995 *Lepus timidus*. *Mammalian Species* **495**, 1–11.

Barrett-Hamilton, G.E.H. 1898 Notes on the introduction of the brown hare into Ireland. *Irish Naturalists' Journal* **7**, 69–76.

Bern Convention 1979 Convention on the conservation of European wildlife and natural habitats. Bern Convention. Council of Europe, Strasbourg.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2004 *Advanced distance sampling*. Place of Publication. Oxford University Press.

Chapuis, J.L. 1990 Comparison of the diets of two sympatric lagomorphs, *Lepus europaeus* Pallas and *Oryctolagus cuniculus* L. in an agro-ecosystem of the Ile-de-France. *Zeitschrift für Säugetierkunde* **55**, 176–85.

Convention on Biological Diversity 1992 Convention on Biological Diversity. Rio de Janeiro. Brazil. Name of Publisher.

Crooks, J.A. and Soule, M.E. 1999 Lag times in population explosions of invasive species: causes and implications. In O.T. Sandlund, P.J. Schei. and A. Viken (eds), *Invasive species and biodiversity management*, 103–25. Dordrecht. Kluwer.

DEFRA 2003 Review of non-native species policy—report of the working group. Place of publication. Department for Environment, Food and Rural Affairs DEFRA, London, UK.

Dingerkus, S.K. 1997 The distribution and ecology of the Irish hare *Lepus timidus hibernicus* in Northern

Ireland. Unpublished PhD thesis, Queen's University Belfast.

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.

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

Fairley, J., Gore-Booth, J. and Shiel, C. 2002 The Roe deer of Lissadell. *Deer* **12**, 243, 249.

Fargher, S.E. 1977 The distribution of the Brown hare *Lepus capensis* and the mountain hare in the Isle of Man. *Journal of Zoology, London* **182**, 164–7.

Flux, J.E.C. 1981 Field observations of behaviour in the genus *Lepus*. In K. Myers and C.D. MacInnes (eds), *Proceedings of the World Lagomorph Conference*, 377–94. Guelph, Australia. University of Guelph.

Flux, J.E.C. 1993 Relative effect of cats, myxomatosis, traditional control, or competitors in removing rabbits from islands. *New Zealand Journal of Zoology* **20**, 13–18.

Flux, J.E.C. and Angermann, R. 1990 *The hares and jackrabbits*. In J.A. Chapman, and J.E.C. Flux (eds), *Rabbits, hares and pikas: status survey and conservation action plan*. Oxford. IUCN/SSC Lagomorph Specialist Group, IUCN.

Fraguglione, D. 1959 Les anomalies du pelage chez les lièvres commun et variable. *Diana* **4**, 57–9.

Fuller, R.M., Smith, G.M., Sanderson, J.M., Hill, R.A., Thomson, A.G., Cox, R., Brown, R.T., Clarke, R.T., Rothery, P. and Gerard, F.F. 2002 *Countryside survey: land cover map 2000 final report*. Place of Publication. Centre for Ecology and Hydrology, Natural Environment Research Council, UK.

Gerell, R. 1977 Skånes däggdjur—Resultat från en intervjuundersökning. *Skåne Jakt* **2**, 6–14.

Gibb, J.A. 1981 What determines the numbers of small herbivorous mammals? *New Zealand Journal of Ecology* **4**, 73–7.

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. and Sundt, C.O. 1965 Anwendung von künstlicher befruchtung bei der hybridisierung von zwei hasenarten. *Zeitschrift für Jagdwissenschaft* **11**, 155–8.

Harris, S. and Yalden, D.W. 2004 An integrated monitoring programme for terrestrial mammals in Britain. *Mammal Review* **34** (1/2), 157–67.

Harting, J.E. 1897 A supposed hybrid between the common and the Irish hare. *Zoologist*, 4th series **1**, 95–6.

Hayden, T. and Harrington, R. 2000 *Exploring Irish mammals*. Dublin. Town House and Country House.

Holden, N.M., Brereton, A.J., Fealy, R. and Sweeney, J. 2003 Possible change in Irish climate and its impact on barley and potato yields. *Agricultural and Forest Meteorology* **116** (3–4), 181–96.

Holley, A.J.F. and Greenwood, P.J. 1984 The myth of the mad March hare. *Nature* **309**, 549–50.

- Homolka, M. 1987 A comparison of the trophic niches of *Lepus europaeus* and *Oryctolagus cuniculus*. *Folia Zoologica* **36**, 307–17.
- Hughes, M., Montgomery, W.I. and Prodöhl, P. 2006 Population genetic structure and systematics of the Irish Hare. Unpublished report prepared by Quercus for the Environment and Heritage Service DOE, N.I.
- Hurlbert, S.H. 1978 The measurement of niche overlap and some relatives. *Ecology* **59**, 67–77.
- Hutchings, M.R. and Harris, S. 1996 *The current status of the brown hare Lepus europaeus in Britain*. Peterborough. Joint Nature Conservation Committee.
- Klansek, E., Kalivodová, E., Šimonovic, V. and Kürthy, A. 1998 Landscape-ecological evaluation of the flood plain of the river March Morava with regard to hare *Lepus europaeus* Pallas and roe deer *Capreolus capreolus* L. *Ekológia Bratislava* **17**, 201–207.
- Krebs, C.J., Boonstra, R., Boutin, S. and Sinclair, A.R.E. 2001 What drives the 10-year cycle of snowshoe hares? *Bioscience* **51**, 25–35.
- Lönnberg, E. 1905 On hybrids between *Lepus timidus* L. and *Lepus europaeus* Pall. from southern Sweden. *Proceedings of Zoological Society of London* **1**, 278–87.
- Lönnberg, E. 1908 Några villebrädsarters nutida utbredning i Skåne. *Svenska Jägarförbundets Tidskrift* **46**, 7–16.
- MacCracken, J.G. and Hansen, R.M. 1982 Herbaceous vegetation of habitat used by Blacktail Jackrabbits and Nuttall Cottontails in Southeastern Idaho. *America Midlands Naturalist* **107**, 180–84.
- Mack, R.N. 1981 The invasion of *Bromus tectorum* L. into western. North America: an ecological chronicle. *Agro-Ecosystems* **7**, 145–65.
- Manly, B.F.J. 1997 *Randomisation, bootstrap and Monte Carlo methods in biology*. 2nd edn. London. Chapman and Hall.
- Morris, P.A. 1993 *A Red Data Book for British Mammals*. London. The Mammal Society.
- Nilsson, S. 1820 *Skandinavisk Fauna Del 1: Däggande Djuren*. Lund. Berlingska boktryckeriet.
- O'Mahony, D. and Montgomery, W.I. 2001 The distribution, abundance and habitat use of the Irish hare *Lepus timidus hibernicus* in upland and lowland areas of Co. Antrim and Co. Down, Northern Ireland. Unpublished report prepared by Queen's University Belfast for the Environment and Heritage Service DOE, N.I.
- Pianka, E.R. 1973 The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**, 53–74.
- Preston, J., Prodöhl, P., Portig, A. and Montgomery, W.I. 2003 The Northern Ireland Irish Hare *Lepus timidus hibernicus* Survey 2002. Unpublished report prepared by Queen's University of Belfast for the Environment and Heritage Service DOE, N.I.
- Reid, N., Dingerkus, K., Montgomery, W.I., Marnell, F., Jeffrey, R., Lynn, D., Kingston, N. and McDonald, R.A. 2007 Hare Survey of Ireland 2006/07. *Irish Wildlife Manuals*, No. 32. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.
- Rhymer, J.M. and Simberloff, D. 1996 Extinction by hybridization and introgression. *Annual Review in Ecology and Systematics* **27**, 83–109.
- Schröder, J., Soveri, T., Soumalainen, H.A., Lindberg, L.-A. and van der Loo, W. 1987 Hybrids between *Lepus timidus* and *Lepus europaeus* are rare although fertile. *Hereditas* **107**, 185–9.
- Sheppard, R. 2004 Brown hares *Lepus europaeus* Pallas in N.W. Ireland. *Irish Naturalists' Journal* **2712**, 484–5.
- Smith, R.K., Vaughan-Jennings, N., Robinson, A. and Harris, S. 2004 Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? *Journal of Applied Ecology* **41** (6), 1092–1102.
- Smith, R.K., Vaughan-Jennings, N. and 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 Review* **35** (1), 1–24.
- Stokes, K., O'Neill, K. and McDonald, R.A. 2006 Invasive species in Ireland. Unpublished report to Environment and Heritage Service and National Parks and Wildlife Service by Quercus, Queen's University. Environment and Heritage Service, Belfast and National Parks and Wildlife Service, Dublin.
- Tapper, S. and Parsons, N. 1984 The changing status of the brown hare *Lepus capensis* L. in Britain. *Mammal Review* **14**, 57–70.
- Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H. and Bishop, J.R.B. 2004 Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance/> (11 July 2007).
- Thulin, C.G. 2000 Hybridisation between introduced brown hares and native mountain hares in Sweden. Unpublished PhD thesis, Uppsala University.
- Thulin, C.G. 2003 The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown hares *L. europaeus*? *Mammal Review* **33** (1), 29–42.
- Thulin, C.G. and 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? *Journal of Zoology, London* **258**, 299–306.
- Tosh, D., Towers, R., Preston, J., Portig, A., McDonald, R.A. and Montgomery, W.I. 2004 Northern Ireland Irish hare survey 2004 Unpublished report prepared by Quercus for the Environment and Heritage Service DOE, N.I.
- Tosh, D., Brown, S., Preston, J., Montgomery, W.I., Reid, N., Marques, T.A., Borchers, D.L., Buckland, S.T. and McDonald, R.A. 2005 Northern Ireland Irish hare survey 2005. Unpublished report prepared by Quercus for the Environment and Heritage Service DOE, N.I.

- Vaughan, N. Lucas, E.-A., Harris, S. and White, P.C.L. 2003 Habitat associations of the European hare *Lepus europaeus* in England and Wales: implications for farmland management. *Journal of Applied Ecology* **40**, 163–75.
- Yalden, D.W. 1971 The mountain hare in the Peak District. *Naturalist* **918**, 81–92.
- Yalden, D.W. 1999 *The history of British mammals*. London. Poyser Natural History.
- Warwick, T. 1940 A contribution to the ecology of the muskrat in the British Isles. *Proceedings of the Zoological Society of London*, Series A, **110**, 165–201.
- Watson, A., Hewson, R., Jenkins, D. and Parr, R. 1973 Population densities of mountain hares compared to red grouse on Scottish moors. *Oikos* **24**, 225–30.
- Wolfe, A. and Hayden, T.J. 1996 Home range sizes of Irish mountain hares on coastal grassland. *Biology and Environment* **96B**, 141–6.
- Wolfe, A., Whelan, J. and Hayden, T.J. 1996 The diet of the mountain hare *Lepus timidus hibernicus* on coastal grassland. *Journal of the Zoological Society of London* **240**, 804–10.