Natural Heritage Research Partnership

Verification of hybridisation between introduced European and native Irish hares

Quercus Project QU08-14

European hare in Mid-Ulster © Neil Reid

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Executive Summary

1. One of the greatest problems facing conservation in Britain and Ireland is the spread and establishment of introduced species. The European hare (*Lepus europaeus*) is a highly invasive species which has established in Mid-Ulster and west-Tyrone.

2. This study aimed to verify whether introduced European hares can hybridize with native Irish hares (*Lepus timidus hibernicus*) as they can with mountain hares in other areas where both species exist in sympatry, for example, Sweden.

3. Tissue samples were opportunistically collected from 33 hares involved in road traffic accidents in Mid-Ulster from 2003 to 2008. Molecular analysis of a partial region of the transferrin nuclear gene and a segment of mitochondrial DNA was used to establish the genetic identity of each individual.

4. Genetic profiling unambiguously assigned 17/33 samples (c. 51%) as Irish hares, 6/33 samples (c. 18%) as European hares and 6/33 samples (c. 18%) as interspecific hybrids. Four individuals (c. 12%) could not be reliably identified.

5. Bilateral hybridisation of both species has been confirmed. Five interspecific 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 (♂).

6. We make five recommendations for future research and action:

    i. Establishment of a European hare population monitoring programme to determine temporal trends and the trajectory of the species.

    ii. A further genetic study involving systematic sampling to establish the full extent of interspecific hybridisation including the prevalence of backcrossing and introgression.

    iii. Obtain additional European hare samples from Great Britain to establish the origin(s) of the species in Ireland.

iv. Consideration should be given to establishing an experimental approach to assess both individual and population fitness consequences of bilateral hybridisation under captive conditions.

v. The development of a '*European hare eradication strategy*' including an evaluation of the efficacy of management practises and the most effective means by which they can be deployed without compromising the native Irish hare.

Contents

1.0 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). In addition to competition for ecological resources and diseases transmission, interspecific hybridization and subsequent introgression of alien genes can critically compromise the genetic fitness and long-term viability of local populations and species. Hybridisation between introduced and native species is a common problem (Abbott *et al.* 2003). For example, introduced Sika deer (*Cervus nippon*) freely hybridise with native Red deer (*Cervus elaphus*), producing fertile offspring which are at no competitive disadvantage compared to either parental species (Hayden and Harrington, 2000).

The mountain hare (*Lepus timidus*) was once widespread throughout most of northern Europe. Since the end of the last glacial maximum 10,000 years ago, the species range has contracted leaving a scattered and fragmented distribution including Ireland, Scotland, the Alps, eastern Poland, Fenno-Scandinavia, the Baltic and Russia. In addition to climatologically changes, interspecific interactions with the European or brown hare (*Lepus europaeus*) may have an important role in mountain hare population and range declines (Thulin 2003).

The European hare has naturalised successfully in many countries beyond its former range. Its success as an invasive species has resulted in its colonisation of eastern Canada, north-eastern USA, most of South America below 28^{o}S, Australia, Tasmania and New Zealand, as well as many small islands including Barbados, Réunion and the Falklands (Flux and Angermann, 1990).

In Sweden, European hares were introduced in the south of the country during the mid-late 1800s and have now advanced north replacing the native mountain hare over much of its former range (Nilsson, 1820; Lönnberg, 1908; Gerell, 1977; Thulin, 2000). Hybridisation between both species is well known (Lönnberg, 1905; Fraguglione, 1959; Gustavasson, 1965; Gustavasson, 1971; Schröder *et al*. 1987; Thulin and Tegelström, 2002; Thulin *et al*. 2006), with male European hares capable of mating with female mountain hares to produce fertile offspring (Lönnberg, 1905;

Gustavasson, 1965; Gustavasson, 1971; Schröder *et al*. 1987; Thulin and Tegelström, 2002). Mitochondrial DNA (mtDNA) is maternally inherited without male contribution. Thus, identification of nuclear and mtDNA gene transfer has proved an effective means by which to determine the occurrence of interspecific hybridization.

The European hare 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 19th century when it was introduced for hare coursing (Barrett-Hamilton, 1898). Fourteen introductions took place throughout Ireland from 1848-1890s (Barrett-Hamilton, 1898). In Northern Ireland, introductions occurred at Strabane and Baronscourt, Co. Tyrone; Lurgan Estate, Co. Armagh; Cleenish Island, Co. Fermanagh and on Big Copeland Island, Co. Down. Another release took place in Co. Londonderry but the precise location remains unknown (Barrett-Hamilton, 1898). It remains possible that further unrecorded introductions took place historically or have occurred in recent times.

A systematic survey of each known introduction site during 2005 suggested that only two extant populations remain in Northern Ireland: a substantial population west of Lough Neagh (Mid-Ulster) with a smaller population near Newtownstewart, Co. Tyrone (Fig. 1). Reid & Montgomery (2007) established that Irish and European hares are likely to be strong ecological competitors for habitat space in Mid-Ulster. Moreover, at least one supposed *L. europaeus* x *L.t. hibernicus* hybrid has been recorded in the past (Harting, 1897) and observations of both species sparing and boxing, a typical precopula behaviour of hares (Holley and Greenwood, 1984), and the occurrence of phenotypically ambiguous animals raise suspicions that both species may hybridise in the wild in Ireland (Reid & Montgomery, 2007).

The Irish mountain hare (*Lepus timidus hibernicus*) is the only lagomorph native to Ireland and is morphologically, ecologically, behaviourally and genetically distinct from other mountain hares as a result of speciation in isolation over the last 30,000-65,000 years (Hughes, Montgomery & Prodöhl, 2006). Consequently, the Irish hare has intrinsic conservation value, as it is a unique evolutionary lineage.

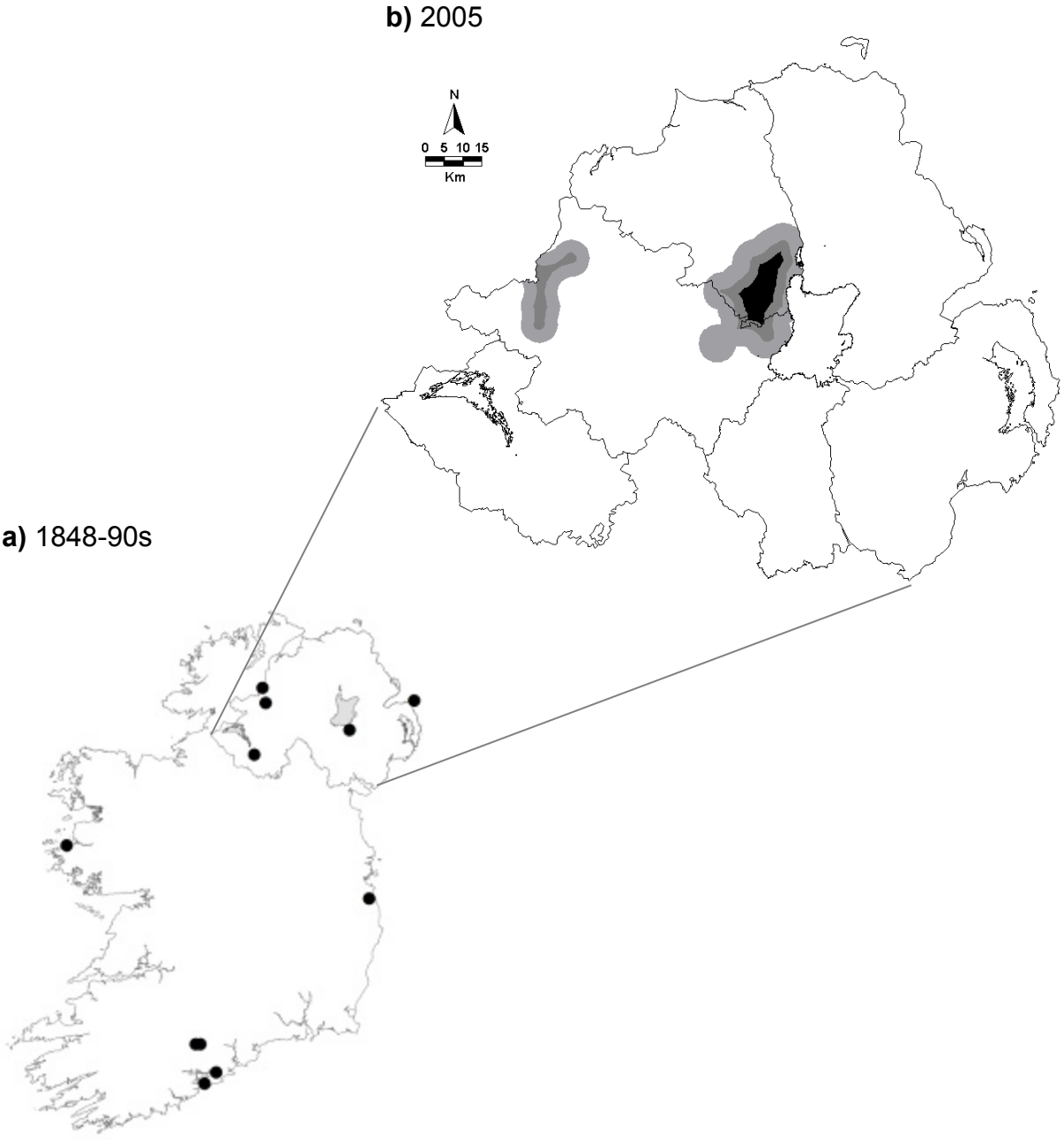

Fig. 1 **(a)** *European hares were introduced on fourteen occasions throughout Ireland between 1848-90s (adapted from Barrett-Hamilton, 1898 by Reid 2006), however, the only extant populations are known in* **(b)** *Mid-Ulster and west Tyrone recorded during 2005 (Reid & Montgomery, 2007).*

Since extant populations of European hare in Northern Ireland may pose a significant risk to the ecological security and genetic integrity of the endemic Irish hare through ecological competition and interspecific hybridisation, this project aimed to:

1. *Verify whether European and Irish hares hybridise spontaneously in the wild in Northern Ireland;*
2. *Establish the minimum prevalence of hybridisation;*
3. *Review the risk to the Irish hare from interspecific hybridisation;*
4. *Develop a rationale and sustainable plan for the future research in logical preparation for any European hare management strategy.*

2.0 Methods

Tissue samples were collected from hares killed in road traffic accidents from 2003 to 2008. Biopsies were taken from the ear of each animal using an 8mm sterile biopsy punch (Robbins Scientific) and preserved in 98% ethanol. In addition, European hare samples were obtained from England (courtesy of Dr. Rebecca Smith, currently at University of Durham) for species reference and comparison to those collect in Ireland. DNA extraction followed protocol described by Taggart *et al.* (1992).

Species identification was based on a sequencing analysis of a 379 base-pair (bp) segment of the mitochondrial DNA (mtDNA) control region (known as the 'D-loop'), and a partial 474bp region, between exons 6 and 7, of the transferrin (*tf*) nuclear gene. Previous investigations on the population genetics of the Irish hare have shown that these regions provide reliable diagnostic genetic markers between Irish and European hares (Hughes, Montgomery & Prodöhl, 2006). Indeed, there are ≥32 fixed genetic differences between Irish and European hares in the chosen mtDNA control region, while both species can be reliably identified on the presence/absence of a single species-specific nucleotide in the partial transferrin gene region.

The partial regions of both the mtDNA D-loop and nuclear *tf* gene were amplified using polymerase chain reaction (PCR) primers using conditions described by Hughes, Montgomery & Prodöhl (2006) and Wallner *et al.* (2001) respectively. Amplified PCR products were purified using Microspin columns (© Roche) and sent for bi-directional commercial sequencing (Macrogen Inc.). Resulting sequences for both mtDNA and nuclear regions were checked and assembled using the software packages Chromas v2.1 (Technelysium Pty Ltd.) and BioEdit v7.0.5.3 Multiple Sequence Editor (Hall, 1999).

In addition to samples collected in Mid-Ulster, mtDNA and *tf* sequences for both mountain and European hares were downloaded from GeneBank to allow further comparisons. Similar sequences specific to Irish hares throughout Ireland were also included in the analysis from Hughes, Montgomery & Prodöhl (2006).

3.0 Results

A total of 33 hare tissue samples were collected and analysed. Chosen nuclear and mtDNA markers used in this study were confirmed as species diagnostic. In all cases, genetic analysis succeeded in unambiguously differentiating Irish hares from European hares.

Nuclear transferrin sequences from European hares in Mid-Ulster were identical to those from European hares from Bristol and the rest of Europe. In contrast, mtDNA sequences from European hares in Mid-Ulster, whilst identical to those from Bristol, differed markedly from those from the rest of Europe. Surprisingly, mtDNA sequences of European hares in Mid-Ulster (including samples from Bristol) match GeneBank sequences of the Yunnan hare (*Lepus comas*). Additional samples from Ireland and Britain are required to clarify the relationship between European hares from Ireland and Great Britain and Yunnan hares. Nevertheless, the mtDNA of European hares in Mid-Ulster was highly divergent from that of Irish hares and other mountain hares from the rest of Europe.

Genetic profiling unambiguously assigned 17/33 samples (c. 51%) as Irish hares, 6/33 samples (c. 18%) as European hares and 6/33 samples (c. 18%) as interspecific hybrids (Table 1). Four individuals (c. 12%) could not be reliably identified due to poor sequencing from either the nuclear or mtDNA markers. Nevertheless, all the available data suggest that these individuals were either European hares or hybrids.

Five interspecific 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 (♂). Both species occur in sympatry in Mid-Ulster and hybrids were distributed throughout the known range of the European hare. There was approximately 20 kilometres between the most northerly and southerly hybrid samples.

Table 1 *The identity of each hare sample analysed using nuclear transferrin and mtDNA 'D-loop' markers. Sampling location, grid reference and genetic identity are given.*

Location	ID	X	Y	mtDNA (D-loop)	Nuclear transferrin (*tf*)	Species Identity
Stewartstown	HR726	287600	371200	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Stewartstown	HR727	344500	367400	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ardroe point	HR728	296700	375800	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballyronan	Loop	291300	384500	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Loup, Coagh	HR785	293120	380120	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballyronan	HR789	294800	386220	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballylifford	HR790	293850	381850	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Coagh road	HR791	288550	376500	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballymaguigan	HR796	295039	389360	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballylifford	HR737	293706	380912	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Randalstown	HR772	309963	389477	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Randalstown	HR773	309963	389477	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Bellaghy	HR820	295790	398297	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballylifford	HR821	293786	381076	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballinderry	HR823	293092	380219	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballinderry	HR825	293204	380358	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Ballinderry	HR830	292936	380071	*L. t. hibernicus*	*L. t. hibernicus*	Irish hare
Stewartstown	HR724	285600	373700	*L. comus*	*L. europaeus*	European hare
Mullaghtironey	HR792	289046	377367	*L. comus*	*L. europaeus*	European hare
Ballymapeake, Bellaghy	HR738	293474	399665	*L. comus*	*L. europaeus*	European hare
Deerpark rd. Bellaghy	HR799	295374	396272	*L. comus*	*L. europaeus*	European hare
Deerpark rd. Bellaghy	HR831	295554	395611	*L. comus*	*L. europaeus*	European hare
Ballymapeake, Bellaghy	HR833	293397	399835	*L. comus*	*L. europaeus*	European hare
Ballyronan	HR787	294700	385100	*L. t. hibernicus*	*L. europaeus*	Hybrid (♂ European hare x ♀ Irish hare)
Ballymaguigan	HR794	295059	389341	*L. t. hibernicus*	*L. europaeus*	Hybrid (♂ European hare x ♀ Irish hare)
Coagh	HR824	291169	379151	*L. t. hibernicus*	*L. europaeus*	Hybrid (♂ European hare x ♀ Irish hare)
Moneymore	HR827	287005	385873	*L. t. hibernicus*	*L. europaeus*	Hybrid (♂ European hare x ♀ Irish hare)
Ballyronan	HR829	294093	382362	*L. t. hibernicus*	*L. europaeus*	Hybrid (♂ European hare x ♀ Irish hare)
Stewartstown	HR725	287500	370600	*L. comus*	*L. t. hibernicus*	Hybrid (♂ Irish hare x ♀ European hare)
Ballinderry	BH-Bally	293000	380200		*L. europaeus*	Unconfirmed
Killyberry, Bellaghy	HR828	294432	395157		*L. europaeus*	Unconfirmed
Rusky road, Loup, Coagh	HR795	291350	384800	*L. comus*		Unconfirmed
Curglasson, Stewartstown	HR832	286743	374049	*L. comus*		Unconfirmed

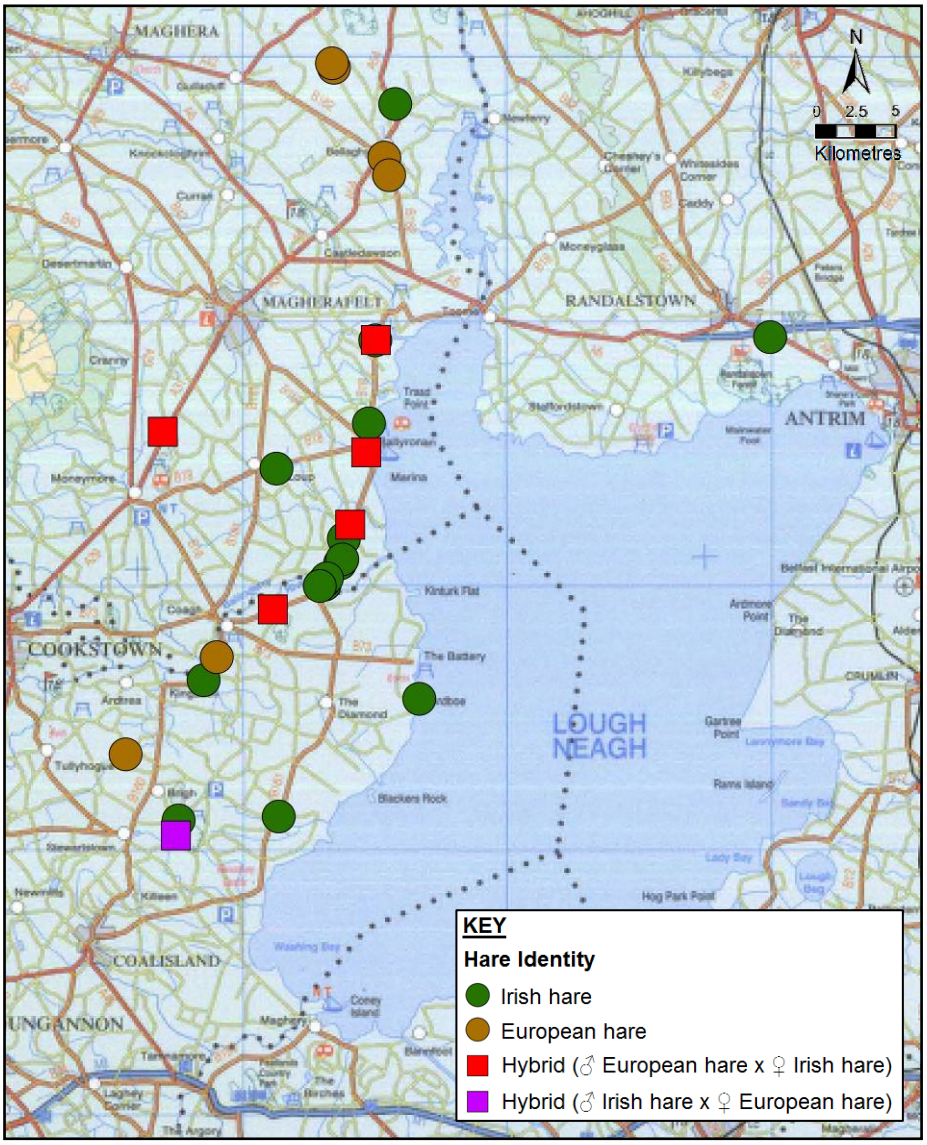

Fig. 2 *Distribution of Irish, European and hybrid hares in Mid-Ulster derived from genetic analysis of tissue samples collected from road traffic accidents from 2003 to 2008.*

4.0 Discussion

This is the first study to demonstrate that introduced European hares hybridise spontaneously with native Irish hares in the wild in Ireland. Hybridisation is bilateral and represented up to 18% of samples examined.

As samples were obtained from road traffic accidents it was not possible to assign an accurate morphological identity to each hybrid. Moreover, given the opportunistic sampling strategy it was not possible to establish whether hybrids were first generation or introgressed backcrosses. However, all indications suggest that hybrids were most likely first generation.

Hughes, Montgomery & Prodöhl (2006) did not detect any evidence of interspecific hybridisation or introgression from more than 100 hares sampled throughout Ireland by examining mtDNA D-loop sequences. Furthermore, analysis of microsatellite DNA data from over 1,100 hares failed to provide any evidence consistent with the presence of European hares throughout Ireland (Hughes, Montgomery & Prodöhl, 2006). Consequently, the restricted geographical distribution of European hare sightings (Reid & Montgomery, 2007) and the restricted distribution of hybridisation suggest that the species has not spread far from its point of introduction. This may indicate that the origin of the European hare in Mid-Ulster was relatively recent or that the native Irish hare is a better ecological competitor than other mountain hares elsewhere, for example, those in Sweden, restricting the spread of the introduced species (Reid & Montgomery, 2007).

Thulin (2003) suggested that in Sweden the loss of species-specific litters, as a result of male competitive dominance and interbreeding, persistently erodes mountain hare population densities enabling European hares to become dominant. If European hares were introduced to Northern Ireland recently, it follows that hybridization represents a significant threat to sympatric Irish hares. However, if extant European hare populations are descendant from individuals introduced during the late 1800s, their geographically restricted range indicates that hybrids have a reduced reproductive fitness. Thus, despite hybridization, both sympatric species

may be able to maintain their own genetic integrity. There are no data by which to evaluate each hypothesis; consequently, more work is required to fully establish the threat that interspecific hybridisation poses to the native 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 for cost-effective eradication (Stokes *et al.* 2006).

5.0 Recommendations

We make five recommendations for future research and action:

1. Monitoring of European hare populations in Mid-Ulster and west-Tyrone is essential to establish an accurate distribution for the species and determine temporal trends and the trajectory of the species.

2. A further genetic study involving systematic sampling of hares from Mid-Ulster, taking morphometric criteria into consideration, is required to establish the full extent of interspecific hybridisation including the prevalence of backcrossing and introgression.

3. Obtain additional European hare samples from Great Britain to establish the origin(s) of the species in Ireland.

4. Individual and long-term population fitness consequences of bilateral hybridisation are unknown and difficult to quantify in the wild. Any further 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.

5. A '*European hare eradication strategy*' is required to prevent any loss of Irish hare genetic integrity. Such a strategy should include an evaluation of the efficacy of potential management practises and the most effective means by which they can be deployed. Immediate action is often the only opportunity for cost-effective eradication.

6.0 Acknowledgements

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