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# Temporal trends in the Irish hare population

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by

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## **Executive Summary**

1. The Irish hare is one of the highest priority species for conservation action in Northern Ireland. The species attracted major conservation concern following a putative population decline in Northern Ireland during the 1980-90s. The Northern Ireland hare survey started in 2002 and has been conducted at annual intervals since 2004. However, interpretation of short-term changes can only be made in the context of long-term time-series. Hitherto, it has been difficult to place recent Irish hare population estimates in context.
2. Here, we review temporal trends in three time-series datasets representing various measures of Irish hare abundance including; game bag records, diurnal standardised direct counts on walked transects and nocturnal standardised direct counts on driven transects. Taken together, they describe 161 years of change in Irish hare populations from 1846 to 2007.
3. Game bag records suggest that Irish hare populations were likely to have been considerably larger during the mid-19<sup>th</sup> to early 20<sup>th</sup> century than at present. The initiation of Irish hare population decline started during the early 20<sup>th</sup> century, synchronous with changes in land management practices associated with early agricultural intensification. Populations declined continuously from 1914 to 1970.
4. Diurnal standardised direct counts of Irish hares on walked transects during the Northern Ireland Rabbit Survey suggest that hare population declines were ongoing during the late 20<sup>th</sup> century from 1986 to 1995.
5. Recent nocturnal standardised direct counts on driven transects during the Northern Ireland hare surveys exhibit no overall temporal trend. We tentatively suggest that this may indicate that Irish hare populations have stabilised at relatively low densities during the early 21<sup>st</sup> century after a long period of substantial decline.
6. All time-series examined exhibited substantial interannual fluctuations suggesting that the Irish hare has the capacity for short-term variability. Consequently,

interpretation of short-term changes should only be made in the context of long-term time-series.

7. Furthermore, historical data suggest that Irish hare populations exhibit complex multiannual periodicity. Whilst the mechanisms driving long-term fluctuations remain unclear, delayed density dependence, weather conditions and climatic oscillations have been implicated.
  
8. We make the 4 recommendations for action:
  - a. The driving mechanisms of recent interannual variability of the hare population in Northern Ireland are unknown. Without a reliable long-term time-series the factors influencing contemporary population dynamics will remain unclear. Continued annual deployment of standardised field surveys and analytical methods used in the Northern Ireland hare surveys will allow relative temporal change in the hare population of Northern Ireland to be described.
  - b. Research on the population biology of Irish hares remains necessary. There is insufficient information on the most basic aspects of demography such as survival and productivity, their relationship with intrinsic and extrinsic factors and the spatial scale at which these factors affect population change.
  - c. Investigation of the impact of certain aspects of agricultural intensification such as mechanised silage harvest on hare survival will provide valuable information on population recruitment.
  - d. Conservation policies, such as the Irish hare Species Action Plan, would benefit from revision at regular intervals to account for emerging scientific information regarding the biology and status of the species.

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## Introduction

In common with other farmland species, hare populations have declined across Europe since the early 20<sup>th</sup> century (Tapper & Barnes 1986; Slamečka, 1991; Smith *et al.* 2004; Smith, Vaughan-Jennings & Harris, 2005), principally due to agricultural intensification and landscape homogenisation (Smith *et al.* 2004; Smith, Vaughan-Jennings & Harris, 2005). The Irish hare (*Lepus timidus hibernicus* Bell, 1837) is no exception and has attracted major conservation concern following a putative population decline in Northern Ireland during the 1980-90s (Dingerkus 1997; Dingerkus & Montgomery, 2002).

The Irish hare is currently classified as an endemic sub-species of mountain hare (*L. timidus* Linnaeus, 1758) but differs phenotypically, behaviourally, ecologically and genetically from other mountain hares with recent research suggesting that it may warrant full species status (Hughes *et al.* 2006). As the sole native lagomorph in an impoverished mammal fauna (Fairley, 2001; Hamill, 2001), the Irish hare has a greater conservation value than its current subspecies status might suggest.

Early research suggested that the hare population of Northern Ireland had declined to between 8,250-21,000 hares during the mid-1990s (Dingerkus 1997; Dingerkus & Montgomery, 2002). Anecdotal evidence also suggested a decline in hare numbers in the Republic of Ireland (Anon, 2005). Consequently, both a local Northern Ireland and an All-Ireland Species Action Plan (Anon, 2000; 2005) were implemented containing measures aimed at maintaining and enhancing hare populations. Furthermore, the Irish hare is protected under the Wildlife Order (NI) 1985 and annual amendments to the Game Preservation (Special Protection for Irish Hares) Order (Northern Ireland) 2003. It is also listed on Appendix III of the Bern Convention (Anon, 1979) and Annex V(a) of the EC Habitats Directive (92/43/EEC), and is listed as an internationally important species in the Irish Red Data Book (Whilde, 1993). Consequently, the Irish hare is one of the highest priority species for conservation action in Northern Ireland.

There is a paucity of accurate historical data on mammal population status (Harris *et al.* 1995) with the majority of population trends for British mammals based on limited and unreliable data (Battersby, 2005). Reid *et al.* (2007a) present the only long-term

time-series available for the Irish hare based on game bag data spanning 123 years from the mid-19<sup>th</sup> to mid-20<sup>th</sup> centuries. A medium-term time-series also exists for direct standardised counts of Irish hares spanning a 10 year period during the late 20<sup>th</sup> century taken from Northern Ireland Rabbit Survey 1986-1995.

For species of conservation concern, the importance of contemporary monitoring data and its direct application to management is widely recognised (Choudhury, 1999, 2002; Battersby & Greenwood; 2004). The Northern Ireland hare survey started in 2002 and has been conducted at annual intervals since 2004 (Preston *et al.* 2003; Tosh *et al.* 2004; Tosh *et al.* 2005; Hall-Aspland *et al.* 2006; Reid *et al.* 2007b). The objectives of these surveys were to:

- Establish the density and abundance of Irish hares in Northern Ireland annually.
- Establish temporal data on hare population change.
- Make recommendations for future monitoring of the species' conservation status.

Reid *et al.* (2007a; 2007c) have made substantial improvements in the estimation of absolute hare density over previous hare surveys (Preston *et al.* 2003; Tosh *et al.* 2004; Tosh *et al.* 2005; Hall-Aspland *et al.* 2006) in terms of field methodology and analytical techniques following protocols developed by Marques & Borchers (2006), Paxton *et al.* (2007). Nevertheless, relative temporal change in estimated mean density from previous hare surveys may still be used as a measure of variation in actual hare abundance due to deployment of standardised survey and analytical techniques between 2002 and 2007.

Here we review temporal trends in the three time-series available for the Irish hare to establish relative changes in hare populations from the mid-19<sup>th</sup> century to present.

## Methods

### Long-term historical trends

We review recent work presented by Reid *et al.* (2007a) who reported trends in 340 hare game bag records from 14 shooting estates across Ireland from 1846 to 1970.

### Recent historical trends

The Department of Agriculture commissioned the Northern Ireland Rabbit Survey (NIRS) from 1986 to 1995 to identify temporal trends in the rabbit population of Northern Ireland (Alan Bell pers. comms.). Seventy-two 1km<sup>2</sup> survey squares containing 2.25km long line transects were surveyed annually with 12 survey squares located in each county. Transects followed habitat interfaces including hedgerows, forest edges, river banks and drainage ditches. Each transect was surveyed on foot during daylight hours (9am-5pm) by two observers during January–February each year. Whilst the primary objective was to record field signs of rabbits, sightings and field signs of Irish hares were also recorded. The data for hares have a number of shortcomings but are useful as a repeated-measure standardised relative count.

The NIRS Irish hare data were originally analysed by Dingerkus & Montgomery (2002) who concluded that hare populations had declined significantly between 1986 and 1994. Reynolds *et al.* (2006), in a recent re-analysis of these data, suggested that any population decline may not have been as dramatic as that suggested by Dingerkus & Montgomery (2002) and may have been part of a natural population dynamic, synchronous with similar temporal changes in Scottish mountain hare game bags.

Dingerkus & Montgomery (2002) used a  $\chi^2$  test of association between the presence or absence of hare records over three 3-year time periods (1986-1988, 1989-1991, 1992-1994; data from 1995 were excluded). This analytical approach violated the basic assumption of independence between samples whilst the grouping of the data was arbitrary and may have masked between year variation (Reynolds *et al.* (2006). In contrast, Reynolds *et al.* (2006) used a generalized linear model assuming Bernoulli errors with a logistic link function to model the odds of hare presence for

each year in the time-series and subsequently compared the apparent trends in the NIRS data with trends in the number of mountain hares shot over the same time period on a number of Scottish shooting estates. However, their game bag analysis was based, not on presence or absence as was their NIRS analysis, but on the relative numbers of hares shot modelled using a generalized linear model assuming Poisson errors with logarithmic link function. Therefore, the temporal trends produced by Reynolds *et al.* (2006) from the NIRS data (presence data) and Scottish gamebag data (relative abundance data) were not comparable and may have led to spurious interpretation of temporal change in the Irish hare population. For these reasons, we argue that both of the analytical procedures used by Dingerkus & Montgomery (2002) and Reynolds *et al.* (2006), have inherent shortcomings.

Here we reanalyse the NIRS Irish hare data. However, unlike both Dingerkus & Montgomery (2002) and Reynolds *et al.* (2006), we use relative hare abundance rather than hare presence or absence. Indices of relative hare abundance between 1986 and 1995 were produced using the specialist software programme TRIM (TRends and Indexes for Monitoring data; Pannekoek & van Strien, 2001). Accounting for overdispersion and serial correlation of the data, TRIM uses a poisson general log-linear model (McCullagh & Nelder, 1989) to create a cornerpoint parameterised population index with the first year of the time-series set to 1 and all subsequent years relative to the first. This analysis accounts for spatial variation in relative hare abundance across all sites surveyed and, as a measure of abundance, inherently includes presence and absence. The strength of change in the resultant population index was measured using the log-linear regression coefficient.

### **Contemporary trends**

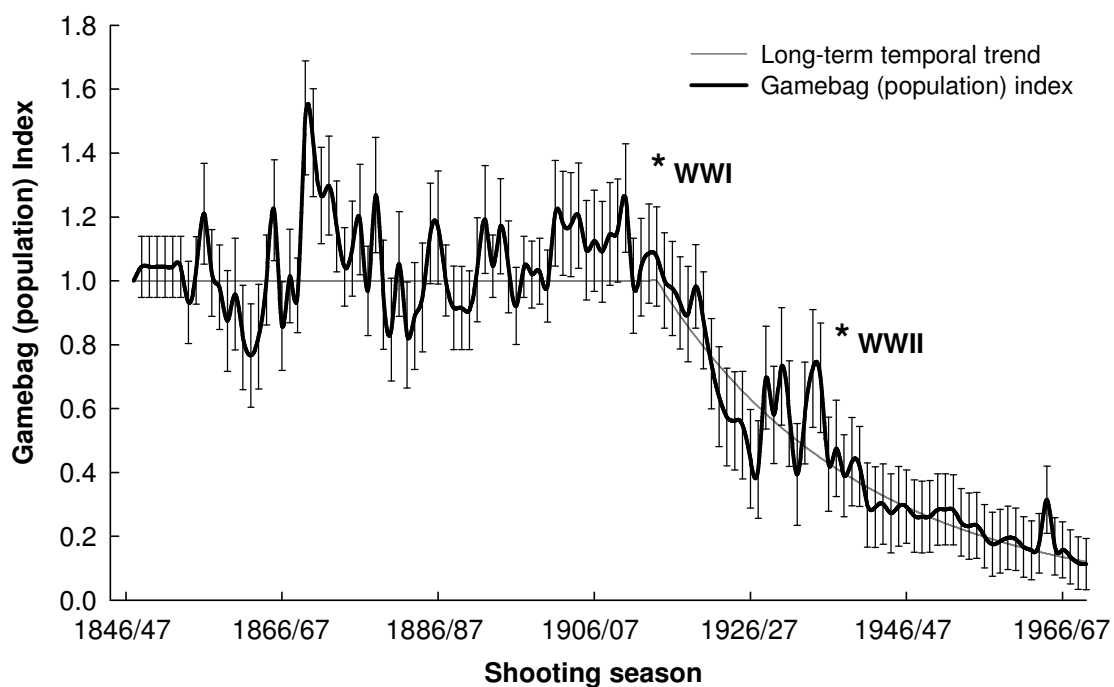
Previous hare surveys have identified a number of problems in obtaining unbiased estimates of hare density when working from survey points located on roads using Distance-sampling methodology (Tosh *et al.* 2005; Hall-Aspland *et al.* 2006; Reid *et al.* 2007a, Reid *et al.* 2007c). Regardless of inherent methodological biases relative temporal change in estimated mean density from previous hare surveys may still be used as a measure of variation in hare abundance between 2002 and 2007. Here, we compare the relative change in density estimates between each of the Northern

Ireland hare surveys since 2002 (Preston *et al.* 2003; Tosh *et al.* 2004; Tosh *et al.* 2005; Hall-Aspland *et al.* 2006; Reid *et al.* 2007b) to illustrate short-term temporal change in hare abundance.

## Results

### Long-term historical trends

Reid *et al.* (2007a) successfully reconstructed trends in the number of Irish hares shot annually throughout Ireland between 1846-1970  $\pm$  standard errors (Fig. 2). Game bag indices have often been used as a proxy for hare abundance and are generally a reflection of hare density (Langbein *et al.* 1999). They concluded that there was no overall change in the number of Irish hares shot across Ireland prior to 1914. However, distinct interannual and multiannual fluctuations were apparent. From 1914-1970 game bag indices declined significantly by -88% (Log-linear  $\beta = -0.039 \pm 0.010$ ,  $p \leq 0.01$ ).

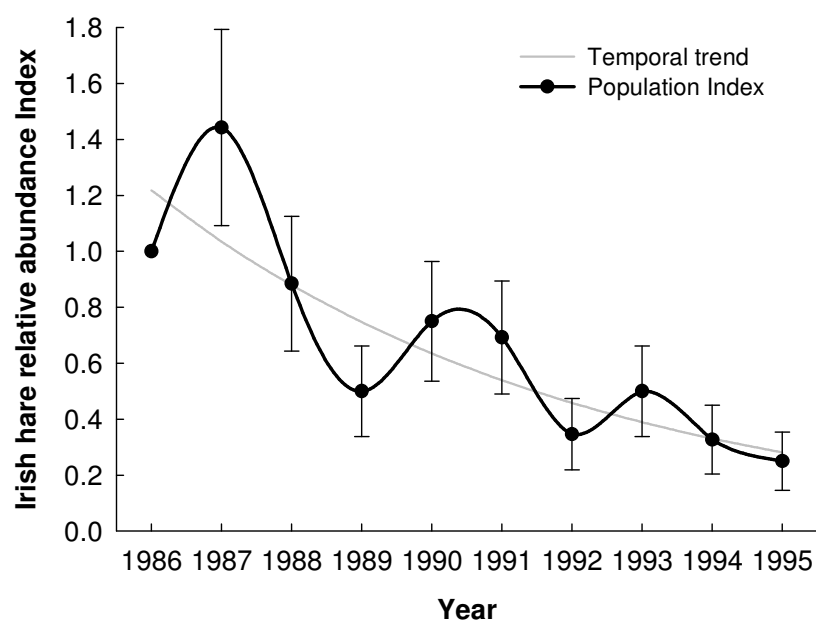


**Fig. 2** Temporal trends in Irish hare game bag indices from 14 shooting estates throughout Ireland from 1846-1970 showing a dramatic decline in the number of hares shot annually after 1914 [\*extracted from Reid *et al.* 2007a].

Reid *et al.* (2007a) suggest that fluctuations in Irish hare numbers, as a product of population growth rate, was influenced by delayed density dependence at a lag of one year, periodicity with a quasi- anti-phase of decadal intervals prior to the population decline and seven year intervals after the decline and autumn temperatures and rainfall as described by the Northern Atlantic Oscillation Index. They suggest climatic forcing may have been a dominating factor in the decadal cycles observed in hare numbers prior to the population decline but, this may have been lost due to the overriding influences of agricultural intensification and a weakening of the periodicity observed in the Northern Atlantic Oscillation.

### **Recent trends**

Trends were reconstructed in the relative number of Irish hares observed annually from 1986-1995 during the Northern Ireland Rabbit Survey  $\pm$  standard errors (Fig. 3). Whilst there was a degree of interannual variation, relative abundance indices declined significantly by -75% over the ten year study period (Log-linear  $\beta = -0.161 \pm 0.027$ ,  $p \leq 0.01$ ).



**Fig. 3** Decline in relative annual abundance index of the number of Irish hares observed during the Northern Ireland Rabbit Survey between 1986 and 1995 produced using the software TRIM.

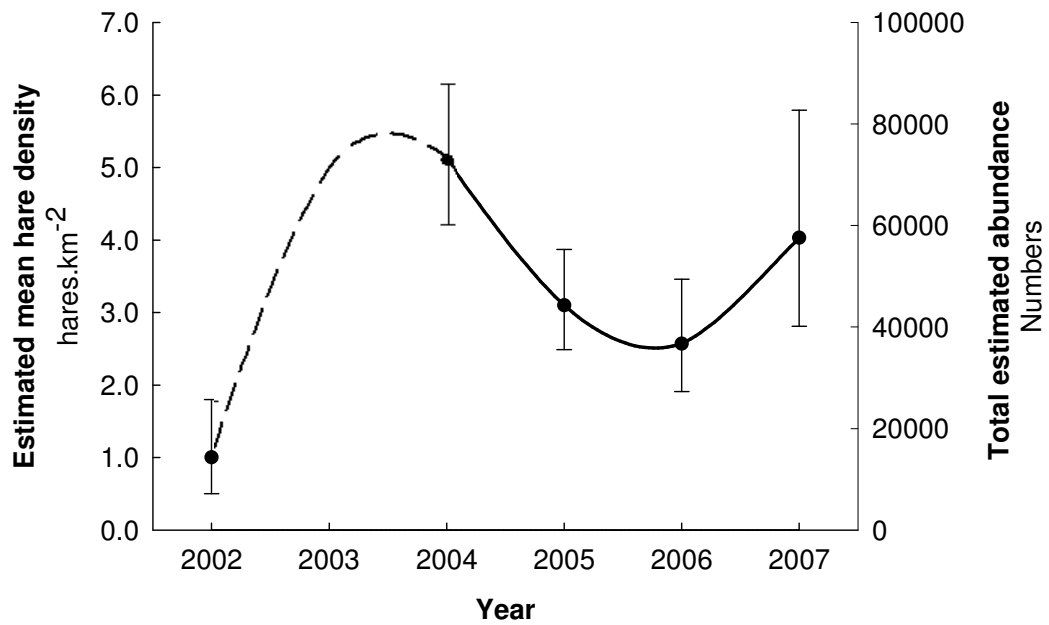
**Contemporary trends**

Hare density estimates from the Northern Ireland hare surveys may be underestimated by 50-70% (Reid *et al.* 2007a; Reid *et al.* 2007b). Nevertheless, standardised methodology should result in standardised bias. Consequently, relative change can be described over time despite the estimates of absolute density being potentially erroneous.

The estimated mean density of hares during 2007 was significantly higher than that for 2002 (Table 1). The 95% confidence intervals for the estimates during 2004, 2005 and 2006 overlapped substantially with those for 2007, but the mean estimate was lower than 2004 and higher than both 2005 and 2006 (Table 1; Tosh *et al.* 2004; Tosh *et al.* 2005; Hall-Aspland *et al.* 2006). There is a degree of interannual variability in estimated densities between 2002 and 2007 but no overall temporary trend was evident (Fig. 4).

**Table 1** *Estimated density and abundance of Irish hares in Northern Ireland from 2002-2007*

<b>Study</b>	<b>Year of fieldwork</b>	<b>Mean estimated density hares/km<sup>2</sup> (CI)</b>	<b>Total estimated abundance N (CI)</b>
Preston <i>et al.</i> (2003)	2002	1.00 (0.50-1.80)	14,000 (7,000 - 25,200)
Tosh <i>et al.</i> (2005)	2004	5.11 (4.23-6.16)	72,000 (59,700 - 86,900)
Tosh <i>et al.</i> (2005)	2005	3.10 (2.49-3.87)	43,700 (35,000 - 54,400)
Hall-Aspland <i>et al.</i> (2006)	2006	2.57 (1.91-3.46)	42,600 (28,600 - 63,400)
Reid <i>et al.</i> (2007b)	2007	4.03 (2.81-5.79)	57,100 (39,800 - 82,000)



**Fig. 4** Trends in Irish hare density and abundance estimates  $\pm$  95% confidence limits during Northern Ireland hare surveys from 2002 to 2007 (Preston et al. 2003; Tosh et al. 2004; Tosh et al. 2005; Hall-Aspland et al. 2006; Reid et al. 2007b). The line through 2003 was interpolated using a cubic regression.

## Discussion

This is the first study to draw together all available time-series data on Irish hare abundance in an attempt to reconstruct likely temporal changes in hare populations in Ireland over the last 161 years.

As a cursorial grazing species that avoids predation by concealment, hares have two basic requirements; food and refuge (Frylestam 1980; Tapper & Barnes 1986; Lewandowski & Nowakowski, 1993; Vaughan *et al.*, 2003; Hiltunen, Kauhala & Linden 2004; Smith *et al.*, 2004; Smith, Vaughan-Jennings & Harris 2005). Therefore, habitat heterogeneity appears to be important to hares, particularly in pastoral landscapes (Smith *et al.* 2004; Smith, Vaughan-Jennings & Harris, 2005). Irish hares have been shown to be associated with landscapes supporting a 'patch-work quilt' of improved grasslands interspersed with *Juncus*-dominated rough pasture or scrub (Reid *et al.* 2007d). Loss of hedgerows, amalgamation of fields and temporal and spatial synchronicity of farm management processes are major contributing factors to biodiversity loss (Benton *et al.*, 2003) including hare species declines (Smith *et al.*, 2004; Smith, Vaughan-Jennings & Harris 2005).

Game bag time-series have been used to derive indices of hare abundance across Europe and the UK (Strandgaard & Asferg, 1980; Tapper & Parsons, 1984; Tapper, 1987; Langbein *et al.* 1999) illustrating population declines (Smith, Vaughan-Jennings & Harris, 2005). By an analysis of game bag data, Reid *et al.* (2007a) suggest that Irish hare populations were likely to have been considerably larger during the mid-19<sup>th</sup> to early 20<sup>th</sup> century. In common with hare populations elsewhere (Smith *et al.* 2004; Smith, Vaughan-Jennings & Harris, 2005), the decline of the Irish population was synchronous with land management changes brought by agricultural intensification and increasing landscape homogenisation during the early 20<sup>th</sup> century (Reid *et al.* 2007a).

Irish hare population declines were ongoing during the latter 20<sup>th</sup> century with the current analysis of the Northern Ireland Rabbit Survey Irish hare data supporting the conclusions of Dingerkus & Montgomery (2002) demonstrating a strong decline between 1986 and 1995. The analytical methods used to demonstrate change in

observed abundance of hares during the NIRS overcome many of the problems inherent to previous analyses carried out by both Dingerkus & Montgomery (2002) and Reynolds *et al.* (2006). Comparison of temporal trends exhibited by Irish populations and Scottish mountain hare populations by 'eye-balling' (Reynolds *et al.* 2006) should be avoided. Brown hare populations across Great Britain underwent dramatic declines from the 1960s to the 1980s (Smith *et al.* 2004). Here we demonstrate a markedly similar decline in Irish hare numbers.

In common with brown hare populations in Great Britain that appeared to stabilise between the mid-1990s to 2003 (Battersby, 2005), Irish hare densities determined by Northern Ireland hare surveys from 2002 to 2007 exhibited no overall temporal trend. Whilst recent surveys in Northern Ireland cover an insufficient period to reliably establish statistically significant population trends, we tentatively suggest that Irish hare populations in Northern Ireland, synchronous with brown hare populations in Great Britain, appear to have stabilised during the early 21<sup>st</sup> century after a long period of substantial decline.

A number of other estimates of Irish hare density have been made throughout the past (Whelan, 1985; Jeffery, 1996; Dingerkus 1997; O'Mahony & Montgomery, 2001; Reid, 2006). Each used different field methods and statistical analyses with little is known about the biases inherent to each. Consequently, they are neither comparable to one another or the time-series review here and have not been considered in this study.

Marked interannual variability is a common feature of all three population time-series available for Irish hares. Scottish mountain hare populations have been shown to fluctuate between 2-59 times the minimum density (Watson & Hewson, 1973). In common with hare populations elsewhere (Watson & Hewson, 1973; Krebs *et al.*, 2001), the Irish hare has the capacity for substantial short-term population change.

Historically, Irish hare populations also exhibited marked multiannual fluctuations with a 7-10 year quasi- anti-phase (Reid *et al.* 2007a). Complex dynamics corresponding to roughly decadal periodicity have been observed in other hare species across Europe and North America (Elton & Nicholson, 1942; Keith, 1963; Krebs *et al.* 1986;

Keith, 1990; Ranta *et al.* 1997; Krebs *et al.* 2001; Kauhala, 2005). Whilst the driving forces of population cyclicity are little understood, climatic oscillations have been implicated (Reid *et al.* 2007a). Whilst there are little empirical data to support the existence of recent multiannual variation, there is little reason to discount the potential influence of climate and related periodicity in contemporary hare dynamics (Reynolds *et al.* 2006; Reid *et al.* 2007a). Reynolds *et al.* (2006) suggest that evaluation of conservation measures and strategies such as those set out by the Irish hare Species Action Plan (Anon, 2002; Anon, 2005) should be mindful of the complex population dynamics exhibited by the target species. General population declines can be ongoing, despite short term increases. Interpretation of short-term changes can only be made in the context of long-term time-series.

## **Recommendations**

Variation in the Irish hare population can be substantial over a short period of time. The degree of contemporary interannual and multiannual variation is not known. When fluctuations are pronounced populations must be monitored more closely and for longer to determine trends than when fluctuations are insignificant. The current Northern Ireland hare survey method allows relative temporal change in the hare population of Northern Ireland to be described annually. If a full understanding of contemporary trends is required, continued annual population monitoring will be necessary.

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## References

- Anonymous (1979) *Convention on the conservation of European wildlife and natural habitats*. Bern Convention. Council of Europe, Strasbourg.
- Anonymous (2000) *Biodiversity in Northern Ireland: Species Action Plans - Irish Hare, Chough & Curlew*. Environment and Heritage Service NI. pp 6-9, Department of Environment. Belfast. UK.
- 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 & Heritage Service, Department of Environment, Northern Ireland and the National Parks & Wildlife Service, Department of Environment, Heritage and Local Government, Republic of Ireland.
- Battersby, J. & Greenwood, J.J.D. (2004) Monitoring terrestrial mammals in the UK: past, present and future, using lessons from the bird world. *Mammal Review*, **34**: 3-29.
- Battersby, J. (Ed) & Tracking Mammals Partnership. (2005) *UK Mammals: species Status and Population Trends. First Report by the Tracking Mammals Partnership*. JNCC / Tracking Mammals Partnership, Peterborough.
- Bell, T. (1837) *History of British Quadrupeds, including the cetacea*. 1st ed. pp 341. London. UK.
- Benton, T.G. Vickery, J.A. & Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**:182-188.
- Choudhury, A. U. (1999) Status and Conservation of the Asian Elephant *Elephas maximus* in north-eastern India. *Mammal Review*, **29**(3), 141-173.
- Choudhury, A. U. (2002) Distribution and conservation of the Gaur *Bos gaurus* in the Indian Subcontinent. *Mammal Review*, **32**, 199–226.
- Dingerkus, S.K. (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, S.K. & Montgomery, W.I. (2002) A review of the status and decline in abundance of the Irish hare (*Lepus timidus hibernicus*) in Northern Ireland. *Mammal Review*, **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, C. S. & Nicholson, M. (1942). The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology*, **11**: 215-244.
- Fairley, J. (2001) *A basket of weasels*. Privately published, Belfast. UK.
- Frylestam, B. (1980) Utilization of farmland habitats by European hares (*Lepus europaeus*, Pallas) on southern Sweden. *Viltrevy*, **11**:271-284.
- Game Preservation (Special Protection for Irish Hares) Order (Northern Ireland) 2003*. Statutory Rule 2003 No. 114. Government Printer for Northern Ireland. ISBN 0337964181.

- Hall-Aspland, S., Sweeney, O., Tosh, D., Preston, P., Montgomery, W.I. & McDonald, R.A. (2006) *Northern Ireland Irish hare survey 2006*. Report prepared by Quercus for the Environment and Heritage Service (DOE, N.I.). UK.
- 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., Morris, P., Wray, S. & Yalden, D.W. (1995) A review of British mammals: population estimates and conservation status of British mammals other than cetaceans. Joint Nature Conservation Committee, Peterborough, UK.
- Hiltunen, M., Kauhala, K. & Linden, H. (2004) Habitat use of the mountain hare *Lepus timidus* in summer: the importance of different vegetation layers. *Acta Theriologica*, 49, 479-490.
- Hughes, M., Montgomery, W.I. & Prodöhl, P. (2006) *Population genetic structure and systematics of the Irish Hare*. Report prepared by Quercus for the Environment and Heritage Service (DOE, N.I.). UK.
- Jeffery, R.J. (1996) *Aspects of the ecology and behaviour of the Irish hare Lepus timidus hibernicus on lowland farmland*. Unpublished PhD thesis, Trinity College Dublin. Ireland.
- Kauhala, K., Helle, P. & Hiltunen, M. (2005) Population dynamics of mountain hare *Lepus timidus* populations in Finland. *Wildlife Biology*, 4: 299-307.
- Keith, L. B. (1963) *Wildlife's Ten-Year Cycle*. Univ. of Wisconsin Press, Madison.
- Keith, L. B. (1990) Dynamics of snowshoe hare populations. *Current Mammalogy*, 2: 119–195.
- Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. (1986) Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon. *Journal of Animal Ecology*, 55: 963–982.
- Krebs, C. J., Boonstra, R., Boutin, S. & Sinclair, A. R. E. (2001) What drives the 10-year cycle of snowshoe hares? *Bioscience*, 51, 25–35.
- Langbein, J., Hutchings, M.R., Harris, S., Stoate, C., Tapper, S.C. & Wray, S. (1999) Techniques for assessing the abundance of brown hares *Lepus europaeus*. *Mammal Review*, 29, 93-116.
- Lewandowski, K. & Nowakowski, J.J. (1993) Spatial distribution of the brown hare *Lepus europaeus* populations in habitats of various types of agricultural. *Acta Theriologica*, 38:435-442.
- McCullagh, P. & J.A. Nelder. (1989) *Generalized Linear Models*. Chapman and Hall: London.
- Marques, T.A. & Borchers, D.L. (2006) *Report on estimation of Irish hare density from the Hare Survey of Ireland 2006*. Report prepared by the Research Unit for Wildlife Population Assessment (RUWPA) within the Centre for Research into Ecological and Environmental Modelling (CREEM), University of St. Andrews, Scotland for Quercus, Queen's University Belfast.

- O'Mahony, D. & 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*. Report prepared by Queen's University Belfast for the Environment and Heritage Service (DOE, N.I.). UK.
- Pannekoek, J. & van Strien, A. (2005) *TRIM 3 Manual: Trends & Indices for Monitoring data*. Statistics Netherlands.
- Paxton, C.G.M., Marques, T.A. & Borchers, D.L. (2007) *Report on estimation of Irish hare density from the Hare Survey of Ireland 2007 with revised estimates for the Hare Survey of Ireland 2006*. Report prepared by the Research Unit for Wildlife Population Assessment (RUWPA) within the Centre for Research into Ecological and Environmental Modelling (CREEM), University of St. Andrews, Scotland for Quercus, Queen's University Belfast.
- Preston, J., Prodöhl, P., Portig, A & Montgomery, W.I. (2003) *The Northern Ireland Irish Hare *Lepus timidus hibernicus* Survey 2002*. Report prepared by Queen's University of Belfast for the Environment and Heritage Service (DOE, N.I.). UK.
- Ranta, E., Lindstrom, J., Kaitala, V., Kokko, H., Linden, L. & Helle, E. (1997) Solar activity and hare dynamics: a crosscontinental comparison. *American Naturalist*, **149**, 765-775.
- Reid, N. (2006) *The conservation ecology of the Irish hare (*Lepus timidus hibernicus*)*. Unpublished PhD thesis. Queen's University Belfast.
- Reid, N., Dingerkus, K., Montgomery, W.I., Marnell, F., Jeffrey, R., Lynn, D., Kingston, N. & McDonald, R.A. (2007a) *Status of hares in Ireland: Hare Survey of Ireland 2006/07*. In Marnell, F. and Kingston, N. (eds) *Irish Wildlife Manuals*, No. 30. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland. ISSN 1393 6670.
- Reid, N., Sweeney, O., Wilson, C., Preston, S.J., & Montgomery, W.I. (2007b) *Northern Ireland Irish hare survey 2007*. Report prepared by Quercus for the Environment and Heritage Service (DOE, N.I.). UK.
- Reid, N., Sweeney, O., Wilson, C., Preston, S.J., Montgomery, W.I. & McDonald, R.A. (2007c) *Developments in hare survey methodology - as applied to the NI Irish hare survey 2007*. Report prepared by Quercus for the Environment and Heritage Service (DOE, N.I.). UK.
- Reid, N., McDonald, R.A. & Montgomery, W.I. (2007d) Mammals and agri-environment schemes: hare haven or pest paradise? *Journal of Applied Ecology*. **44**(6), 1200-1208.
- Reynolds, J.C., O'Mahony, D.O. & Aebischer, N.J. (2006) Implications of 'cyclical' population dynamics for the conservation of the Irish hare (*Lepus timidus hibernicus*). *Journal of Zoology*, **270**(3); 408-413.
- Slamačka, J. (1991) *The influence of oecological arrangements on brown hare population*. In: *XXth Congress of the International Union of Game Biologists*. (eds. Csányi, S. & Ernhaft, J.), pp 340-346. Hungary.
- Smith, R.K., Vaughan-Jennings, N., Robinson, A. & Harris, S. (2004) Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? *Journal of Applied Ecology*, **41**, 1092-1102.

- Smith, R.K., Vaughan-Jennings & 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.
- Strandgaard, H. & Asferg, T. (1980) The Danish bag record II. Fluctuations and trends in the bag record in the years 1941-76 and the geographical distribution of the bags in 1976. *Danish Review of Game Biology*, **11**, 1-112.
- Tapper, S. & Parsons, N. (1984) The changing status of the brown hare *Lepus capensis* L. in Britain. *Mammal Review*, **14**; 57-70.
- Tapper, S.C. & Barnes, R.F.W. (1986) Influence of farming practices on the ecology of the brown hare (*Lepus europaeus*). *Journal of Applied Ecology*, **23**, 39-52.
- Tapper, S.C. (1987) Cycles in game bag records of hares and rabbits in Britain. *Symposia of the Zoological Society of London*, **58**, 79-98.
- Tosh, D., Towers, R., Preston, J., Portig, A., McDonald, R.A. & Montgomery, W.I. (2004) *Northern Ireland Irish hare survey 2004*. Report prepared by Quercus for the Environment and Heritage Service (DOE, N.I.). UK.
- Tosh, D., Brown, S., Preston, J., Montgomery, W.I., Reid, N., Marques, T.A., Borchers, D.L., Buckland, S.T. & McDonald, R.A. (2005) *Northern Ireland Irish hare survey 2005*. Report prepared by Quercus for the Environment and Heritage Service (DOE, N.I.). UK.
- Vaughan, N. Lucas, E.-A., Harris, S. & 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**; 163-175.
- Watson, A., R. Hewson, D. Jenkins, & P. Parr. (1973) Population densities of mountain hares compared with red grouse on Scottish moors. *Oikos*, **24**; 225-230.
- Whelan, J. (1985) The population and distribution of the mountain hare (*Lepus timidus* L.) on farmland. *Irish Naturalists' Journal*, **21**; 532-534.
- Wilde, A. (1993) *Threatened mammals, birds, amphibians and fish in Ireland. Irish Red Data Book II: Vertebrates*. HMSO, Belfast. UK.
- Wildlife Order (Northern Ireland) 1985*. Statutory Rule 1985 No. 171. Government Printer for Northern Ireland.