Status of hares in Ireland

- Hare Survey of Ireland 2006/07

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AN ROINN COMHSHAOIL, OIDHREACHTA AGUS RIALTAIS ÁITIÚIL

DEPARTMENT OF THE ENVIRONMENT, HERITAGE AND LOCAL GOVERNMENT

Status of hares in Ireland

Hare Survey of Ireland 2006/07

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Executive summary

The Irish hare (Lepus timidus hibernicus) is an endemic sub-species of mountain hare and is the focus of an All-Ireland Species Action Plan. The Irish Government is required to report on the status of Irish hares under the EC Habitats Directive. Quercus undertook a survey for the National Parks and Wildlife Service in order to report on the current and historical status of hares and to formulate recommendations for monitoring.

Historical game bag data suggest that the Irish hare population is likely to have been considerably larger during the mid-19th to early 20th century than at present. Since then, there has been a substantial decline in the number of hares shot per year. Similar hunting data from Britain and Europe are accepted as evidence of the historical decline of hare populations. Game bags show marked fluctuations and multiannual periodicity in Irish hare populations. Intrinsic density dependence and extrinsic climatic effects influence the scale and period of fluctuations. Coursing records mainly reflect changes in practice, but with information on capture effort, they may be suitable for monitoring changes in hare numbers.

Quercus staff and >80 NPWS personnel surveyed 691 1km² squares across Ireland during 2006 and 2007. To estimate hare densities, novel distance sampling approaches were developed to account for non-uniform distribution of animals with respect to distance from roads. Here, we demonstrate the importance of accounting for this bias when designing and analysing hare surveys.

Assuming that the survey areas were representative and stratifying data analysis by region, the spring density of Irish hares in the Republic of Ireland was estimated to be 3.33 hares/km² in 2006 and 7.66 hares/km² in 2007. Multiplying density estimates by land area, the population of Irish hares in the Republic of Ireland was approximately 233,000 hares in early 2006 and 535,000 in early 2007. The scale of this marked and significant change between consecutive years is consistent with historical data and with recent surveys of Northern Ireland. Approximately 50% and 70% of the Irish hare population were found on pastoral farmland in 2006 and 2007 respectively. The bulk of change in population estimates between years was ascribed to an increase in density on pastoral farmland.

No records of brown hares were confirmed during the survey, suggesting that this non-native and potentially invasive species is mostly, if not entirely, restricted to Northern Ireland.

We make several recommendations:

1. *The aim of future monitoring should be clarified prior to the adoption of a particular survey strategy as there are major implications for cost and analytical complexity;*
   a. *If the main aim is to produce accurate estimates of density, a custom Distance sampling approach similar to that developed here is essential.*
   b. *If the main aim is to establish temporal trends in population change, repeated counts of relative abundance with standardised effort will provide an index of change in numbers over time.*
   c. *Annual counts supplemented with the intermittent collection of distance data could be analysed to establish temporal trends punctuated with reference points of estimated density.*
2. *A pilot investigation should be undertaken to establish to what extent annual coursing records supplemented with capture effort data could contribute to a low cost monitoring strategy.*
3. *Better understanding of the drivers of population change, particularly on pastoral farmland, is required.*

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1 General introduction

The Irish hare (*Lepus timidus hibernicus* Bell, 1837) is an endemic sub-species of the mountain hare (*L. timidus* Linnaeus, 1758) and is the only native lagomorph in Ireland (Fairley, 2001; Hamill, 2001). Both the rabbit (*Oryctolagus cuniculus* Linnaeus, 1758) and the brown hare (*Lepus europaeus* Pallas, 1778) have been introduced (Hayden & Harrington, 2000; Fairley, 2001).

The relationship between the Irish hare and other mountain hare subspecies remains somewhat unclear (Alves *et al*., 2003; Thulin, 2003). Recent evidence (Hamill *et al*. 2006) indicates that the Irish hare is more closely related to mountain hare populations in mainland Europe than its geographically closest neighbour, the Scottish hare (*Lepus timidus scoticus* Hilzheimer, 1906). Furthermore, levels of genetic diversity within Ireland may suggest that the Irish hare may warrant full species status (Hughes *et al*. 2006). Irish hares are larger than other mountain hares (≤4.5kg), possessing a darker pelt that is often distinctly russet in colour and does not turn fully white in winter (Barrett-Hamilton, 1910; Fairley, 2001). Its ears are relatively small and rounded and its tail is predominately white (Barrett-Hamilton, 1910; Fairley, 2001). Mountain hares elsewhere inhabit high mountains, boreal forest and tundra (Thulin, 2003). However, in Ireland the Irish hare is distributed from the inter-tidal zone (Wolfe, Whelan & Hayden, 1996) to mountain summits (Walker & Fairley, 1968).

Whilst remaining widespread (Fig. 1), the status of the Irish hare has attracted concern following a population decline in Northern Ireland (Dingerkus & Montgomery, 2002). Recent studies in Northern Ireland suggest short-term population fluctuations are the norm (O'Mahony & Montgomery, 2001; Dingerkus & Montgomery, 2002; Preston *et al.* 2003; Tosh *et al*. 2004; Tosh *et al.* 2005; Hall-Aspland *et al*. 2006). In the Republic of Ireland, some anecdotal evidence suggests a decline in hare populations (Anon, 2005).

The Irish hare has been legally protected since 1930 in the Republic of Ireland, initially under the Game Preservation Act (1930), more recently by the Wildlife Act (1976) and Wildlife (Amendment) Act (2000). It is listed on Appendix III of the Berne Convention (Anon, 1979), 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). The EC Habitats Directive requires member states to "maintain or restore [mountain hares] to favourable conservation status", necessitating "surveillance" of the population and encouraging scientific research.

Due to its phylogenetic status, distinct morphology and ecology and its cultural value the Irish hare is considered to have intrinsic value. This, in combination with its legal status and suggestions of a population decline, led to the formulation of an Irish hare All-Ireland Species Action Plan (SAP). This aims to maintain the existing range of Irish hares in Ireland, demonstrate a population increase by 2010 and maintain and increase the area and quality of suitable hare habitat (Anon, 2005).

Specifically, the aims of the current project were to:

i) Establish the current distribution of the Irish hare in the Republic of Ireland.
ii) Provide estimates of density of hares according to land class and geographic regions.
iii) Provide the basis for future monitoring of the conservation status of the Irish hare.
iv) Establish the current distribution of the brown hare in the Republic of Ireland.

This project helps fulfill requirements of the EC Habitats Directive in respect of surveillance (Article 11), the assessment of compatibility with exploitation (Article 14) and the promotion of research (Article 18). In turn this information will assist in the demonstration, maintenance and/or restoration of the hare population to “favourable conservation status” (Article 2). Furthermore, the current study partly fulfils section 5.3.1 of the Irish hare All-Ireland Species Action Plan which seeks to “develop a strategy for the conservation and monitoring of the Irish hare” and addresses section 5.5.2 which requires a “base-line survey to determine the current population… in the Republic of Ireland by 2007”. Furthermore, in relation to section 5.5.5 of the SAP, this work assesses “the status of the brown hare”.

Fig. 1 *Distribution of Irish hare detections during badger and habitat surveys from 1989-1993. The species has a widespread distribution throughout Ireland. Data extracted from Feore (1994) and Smal (1995).*

2 Historical data analysis

2.1 Introduction

Agricultural intensification is widely accepted to be the cause of the decline in many European farmland wildlife populations (Donald, 1998; Wilson *et al*. 1999; Preston *et al*. 2002), including hares (Smith *et al*. 2004; Smith *et al*. 2005). Successful management of wildlife populations and implementation of conservation strategies for declining species rely on knowledge of their population dynamics, achieved by long-term assessment of their abundance or density (Langbein *et al*. 1999). However, relatively few data exist on the historical status of the Irish hare.

Game bag time-series have been used to derive indices of hare abundance elsewhere (Strandgaard & Asferg, 1980; Tapper & Parsons, 1984; Tapper, 1987; Smith *et al*. 2005) illustrating declines in populations and regional differences in the timing of declines. In Great Britain, the National Gamebag Census was established in 1961 and has been used to monitor brown hare populations in the UK (Tapper & Parsons, 1984; Tapper, 1992). Elsewhere total catches from clearance netting or driven counts have also been used as hare census methods (Abildgård *et al*., 1972; Pépin, 1985).

Recent primary surveys (O'Mahony & Montgomery, 2001; Dingerkus & Montgomery, 2002; Preston *et al*. 2002; Tosh *et al*. 2004; Tosh *et al*. 2005; Hall-Aspland *et al*. 2006) suggest that Irish hare populations, in common with hare populations elsewhere, exhibit a considerable degree of interannual fluctuation (Krebs *et al*. 2001; Kauhala, 2005), making interpretation of short-term population changes difficult. The scarcity of long term historical data hampers efforts to assess the significance of recently observed population change.

Here we present an analysis of shooting records from Irish estates and netting records from the Irish Coursing Club with the aim of describing long term and recent trends in the Irish hare population.

2.2 Game bag records

2.2.1 Introduction

Hares are an important game species throughout much of Europe and game estates often recorded the number taken in each shooting season. The collection of game bag records was formalised in Great Britain by The Game Conservancy's establishment of the National Gamebag Census and its subsequent use to describe changes in long-term, time-series of brown hare populations (Tapper & Parsons, 1984; Tapper, 1992). It has been suggested that changes to game legislation in the late 1800s coupled with agricultural intensification and changes to land management practises during the early 1900s initiated brown hare population declines (Matheson, 1941; Tapper & Parsons, 1984; Hutchings & Harris, 1993) in England during the early 20th century (Fig. 2). Hare populations continued to decline, not just in Britain but across Europe, throughout the late 20th century (Smith *et al.*, 2004).

Long-term studies of snowshoe hare (*Lepus americanus*) populations derived from hunting records have not only revealed temporal population trends but also complex population dynamics. Canadian snowshoe hares exhibit a decadal cycle of between 9-11 years which is strongly synchronised with fluctuations of their main predator, the lynx (*Lynx canadensis*) (Elton & Nicholson, 1942; Keith, 1963; Krebs *et al.* 1986; Keith, 1990; Krebs *et al.* 2001). Complex dynamics including cyclicity have also been found in mountain hare populations (Ranta *et al.* 1997; Kauhala, 2005). Recent explanations of temporal variability and cyclicity have highlighted the complex interacting roles of density dependence, food supply, direct predation, indirect predator-induced stress, other small mammal populations, parasitism, local weather conditions, climatic cycles and solar activity (Sinclair *et al.* 1993; Krebs *et al.* 1995; Ranta *et al.* 1997; Krebs *et al.* 2001; Korpimaki *et al.* 2004; Newey & Thirgood, 2004; Korpimaki *et al.* 2005; Kauhala *et al.* 2005; Newey *et al.* 2005; Selvas, 2006).

The effects of intrinsic density dependent processes on hare population dynamics are well documented (Krebs *et al.*, 2001). In cyclic snowshoe hare populations, female reproductive output is known to be influenced by the stage of the population phase and thus by population density (Carry & Keith, 1979; Stefan, 1998; Hodges, 2000). Furthermore, juvenile and adult survival, particularly over-winter survival, is affected by intraspecific competition, predation and disease transmission, all mediated by population density (Keith *et al.*, 1984; Boutin *et al.*, 1995; Newey *et al.*, 2005). The synchrony of local hare populations with both terrestrial and aerial predator abundance suggests that density dependent trophic effects are a major influence on the governing dynamics of cyclic population fluctuations (Boutin *et al.*, 1995; Krebs *et al.*, 2001).

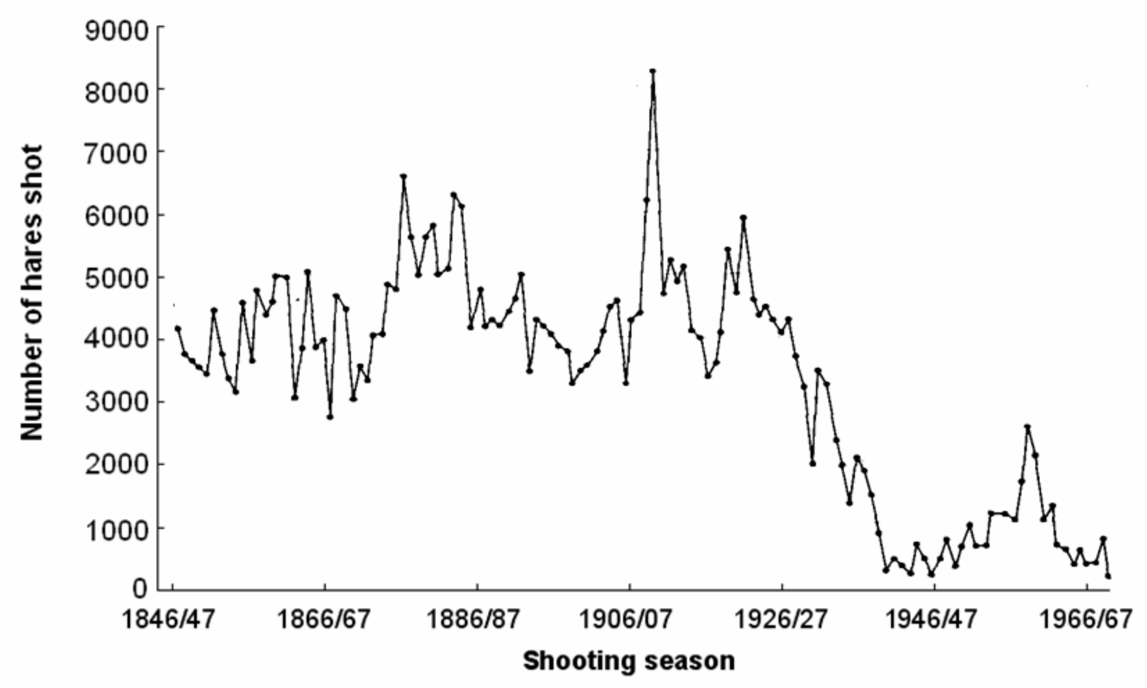


Fig. 2 *An example of the decline in the number of brown hares shot in Great Britain during the early 20th century. These data are from Holkham Estate, Norfolk. After Tapper & Parsons (1984).*

Extrinsic, density-independent processes such as large-scale climatic patterns are also associated with the population dynamics of many terrestrial species (Post & Stenseth, 1999; Patterson & Power, 2001; Stenseth *et al.*, 2002; Stenseth, 2003). Recent studies show that interannual and multiannual hare population fluctuations in some regions are correlated with measures of climatic variation such as the Northern Atlantic Oscillation (NAO) (Schmidt *et al.*, 2004). The NAO is a complex climatic phenomenon characterised by cyclical fluctuations of air pressure and changes in west to east storm tracks across the Northern Atlantic between 40-60°N. The NAO affects temperature, precipitation and wind across most of the northern hemisphere (Lamb & Peppler, 1987; Hurrell & van Loon, 1997), and represents a measure that integrates the effects of a number of abiotic factors that may influence animal population dynamics.

Here we evaluate the use of Irish gamebag records in assessing long-term historical Irish hare population trends. Establishment of trends may enable causal factors of declines to be identified whilst an analysis of hare population dynamics will allow recent population changes to be set in a wider context to better inform conservation strategies.

Specifically we test two hypotheses: 1) that Irish hares have experienced a historical decline in their abundance and that the initiation of such a decline coincided with the agricultural intensification in the early 20th century and 2) that Irish hare populations exhibit multiannual periodicity.

2.2.2 Methods

Record collation

Estate shooting records were acquired from the National Library of Ireland (Dublin), the Public Records Office of Northern Ireland and various private estates. The numbers of hares shot per shooting season (August-February each year) were gathered and a total of 14 time-series were collated spanning 124 shooting seasons between 1846 and 1970. The estates used in analyses were Castle Archdale (Fermanagh), Castlegar (Galway), Crom (Fermanagh), Dromoland (Clare), Favour Royal (Tyrone), Finnebrogue (Down), Headfort (Meath), Kenmare (Kerry), Lissadell (Sligo), Louth Estate (Louth), Oakpark (Carlow), Parkanaur (Tyrone), Shane's Castle (Antrim) and Wicklow House (Wicklow) (Fig. 3).

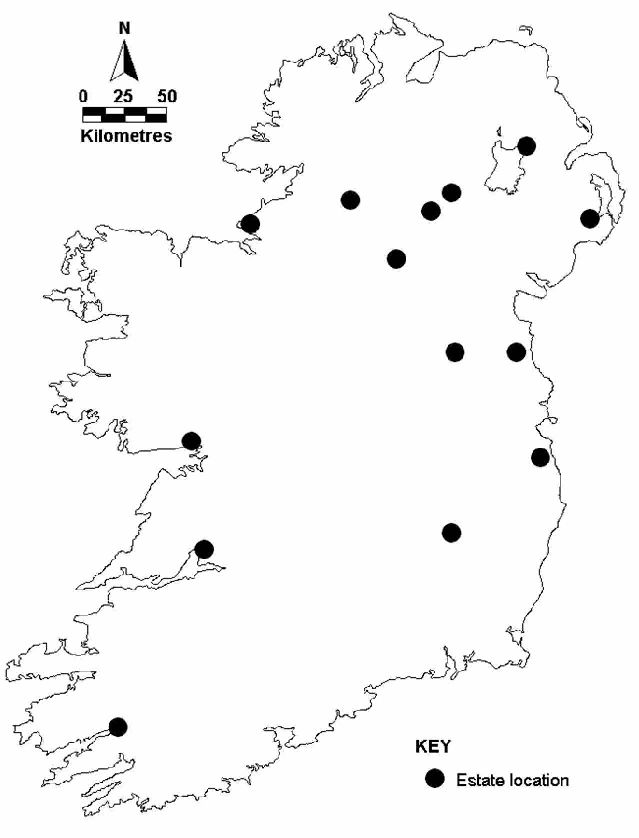


Fig. 3 *The locations of 14 shooting estates from which gamebag records were collated.*

Population indices and growth

Indices of hare gamebag change between 1846-1970 were produced using the specialist software programme TRIM (TRends and Indices for Monitoring data; Pannekoek & van Strien, 2001). Accounting for overdispersion and serial correlation of the data, TRIM interpolates missing observations at each site from changes in all other sites using a Poisson general log-linear model (McCullagh & Nelder, 1989). The technique is particularly useful as it can isolate temporal variation from spatial variation among sites. The first year of the time-series was set to 1 and all subsequent years relative to the first. TRIM allows trends within time-series to be established prior to or after specific events that may have influenced the data; these time points are referred to as changepoints. We identified two potential changepoints: 1914 marked the beginning of World War I (WWI) and the early events precipitating Irish independence, both of which influenced land management and the management of sporting estates, and 1939 was the beginning of World War II (WWII) and the initiation of post-war agricultural intensification.

Gamebag indices have often been used as a proxy for hare abundance and are generally a reflection of hare density (Langbein *et al*. 1999). Hereafter, gamebag indices are also referred to as population indices.

A measure of total population growth was established using the formula:

$$r = \log_e(N_t) - \log_e(N_{t-1})$$

Where *r* is annual population growth, $\log_e$ represents the application of a natural logarithmic algorithm to N_t, the population index at $year_t$ (i.e. the year of interest) and N_{t-1} the population index of $year_{t-1}$ (i.e. the preceding year).

Statistical analysis

Time-series analysis was used to assess the occurrence of periodicity in hare population indices. Autocorrelation coefficients describe the relationship between hare indices at different lagged time periods whilst partial autocorrelation coefficients assess the consistency of the effect throughout the time-series. Only time lags that presented both significant autocorrelation and partial autocorrelation coefficients were deemed statistically meaningful. Where the data were significantly influenced by temporal trends (e.g. population decline) they were first detrended by fitting a curvilinear growth regression and treating the residuals as the population index.

To assess the regulatory factors determining annual hare population growth, multiple regression analysis was conducted using a REML (REstricted Maximum Likelihood) procedure assuming an autoregressive AR(1) error structure (Patterson & Thompson, 1971). Population growth was modelled separately for both the stable (pre-1914) and declining (post-1914) phases of the population. To establish intrinsic density dependent processes the population index in the year preceding that of interest (N_{t-1}) was added as a covariate to models for both phases. To assess extrinsic climatic effects, the mean Northern Atlantic Oscillation Index value for the preceding autumn (NAO_{t-1}) was also entered as a covariate. The NAO is measured by an index of differences in sea-surface pressure between Iceland and the Azores or Iberia. Mean autumn NAO indices were calculated using monthly index data available from the Climate Analysis Section of National Centre for Atmospheric Research, USA (http://www.cgd.ucar.edu/#jhurrell/nao.html).

The importance of inherent periodicity, judged by prior time-series analysis, was tested by including the population index at significant autocorrelated lags. Hence, the population index ten years previous (N_{t-10}) to the year of interest (N_t) was added to the pre-1914 stable phase model, while the population index seven years previous (N_{t-7}) to the year of interest (N_t) was added to the post-1914 declining phase model.

For both study periods all possible models including two-way interactions between population indices at autocorrelated lags and the NAO_{t-1} were created and their performance assessed using the Information-theoretic approach proposed by Burnham & Anderson (2002). Model parsimony was evaluated using the Akaike Information Criterion (AIC) and Akaike weights (w_i). The top set of N models was taken as $\sum_{i=1}^{R} w_i \leq 0.95$ within the whole set of R models (Burnham & Anderson, 2002).

The Akaike weight of each model is the relative likelihood of that model being the best within a set of N models. A model deviance ratio (MDR) test was used to assess the fit of the single best approximating model assuming an F distribution. We ranked the variables according to their relative importance by summing the Akaike weight ($\sum w_i$) from all model combinations where the variable of interested was included (McAlpine *et al.*, 2006). The larger the summed Akaike weight (which varies between 0 and 1), the more important the variable. Finally, multimodel inferencing was used to determine the averaged regression coefficient of each variable across the top set of models (Burnham & Anderson, 2002). To allow for the direct comparison of regression coefficients all variables were standardised to have a $\bar{x} = 0$ and a $\sigma = 1$ prior to analysis (Schmidt *et al.*, 2004).

Statistical analyses were conducted using GenStat© v6 and SPSS© v14.

2.2.3 Results

Of 340 hare game bag records, four estates contributed substantially to the time-series: Castle Archdale (14.8%), Crom (13%), Headfort House (13.5%) and Lissadell (28.8%; Appendix 1). Trends were reconstructed in the number of Irish hares shot annually throughout Ireland between 1846-1970 (Fig. 4). Prior to the first changepoint (1914), there was no overall change in the hare population. However, distinct interannual and multiannual fluctuations were apparent. From 1914-1970 gamebag indices declined significantly by -88% (TRIM $Wald_{1,61}=13.87$, $p<0.001$). The second changepoint (1939) did not significantly alter this trend.

The coverage of the gamebag data, as described by the number of shooting estates represented in each year of the time-series was comparable between the stable and declining phases of the indices. Prior to 1914, each year, on average, had data contributed by 2.71±1.46 estates and after 1914 this remained at 2.76±1.76 estates per year. Eleven of the 14 estates provided a measure of shooting effort, taken as the number of guns used per season, in 109 out of the 340 bag records. This was not accounted for in analyses as it would have substantially reduced the data available, however, mean shooting effort was 1.5 times greater after 1914 (79.3±43.3 guns.estates^{-1}.year^{-1}) than pre-1914 (49.9±32.1 guns.estates^{-1}.year^{-1}).

Time-series analysis suggested that hare gamebags prior to 1914 exhibited a significant positive autocorrelation at a lag of 1 year ($r = 0.43$) and a significant negative autocorrelation at a lag of 10 years ($r = -0.40$, Fig. 5a). Detrended gamebag indices post-1914 exhibited a significant positive autocorrelated lag at 1 year ($r = 0.48$) and a significant negative autocorrelated lag at 8 years, however the effect at 7 years was more consistent throughout the time series ($r=-0.42$, Fig. 5b). Irrespective of their significance, autocorrelation coefficients for both the stable and declining population phases fell into a clear pattern, with a well defined anti-phase. In both time periods the suggested phasic period was 16-17 years, although this was not significant at a $p\leq0.05$ level. All autocorrelated lags were subject to strong damping and were not maintained beyond the first cycle.

During the stable phase of the population indices, annual hare population growth was influenced negatively by the population index in the preceding year (N_{t-1}) and ten years previously (N_{t-10}) (Figs. 6a & 7a) but positively by the autumn Northern Atlantic Oscillation Index value for the preceding autumn (NAO_{t-1}, Figs. 6a & 7a). During the declining phase of the population indices, annual hare population growth was influenced negatively by the population index in the preceding year (N_{t-1}) and seven years previous (N_{t-7}) but no effect of the autumn Northern Atlantic Oscillation Index value for the preceding autumn (NAO_{t-1}) could be discerned (Figs. 6b & 7b).

For the stable phase of the time-series, five variables were retained within the top set of models and were taken as those most likely to explain variation in annual Irish hare population growth prior to 1914. Direct interannual density dependence, demonstrated by the population index at $year_{t-1}$ (N_{t-1}) and inherent decadal periodicity demonstrated by the population index at $year_{t-10}$ (N_{t-10}) had consistently strong negative effects on population growth. The autumn NAO index during $year_{t-1}$ (i.e. NAO_{t-1}) also contributed to interannual variation in population growth (Fig. 6).

For the declining phase of the time-series, only two variables were retained within the top set of models describing annual Irish hare population growth post-1914. Direct interannual density dependence (N_{t-1}) and inherent periodicity on a 7 year (N_{t-7}) anti-phase (Fig. 6).

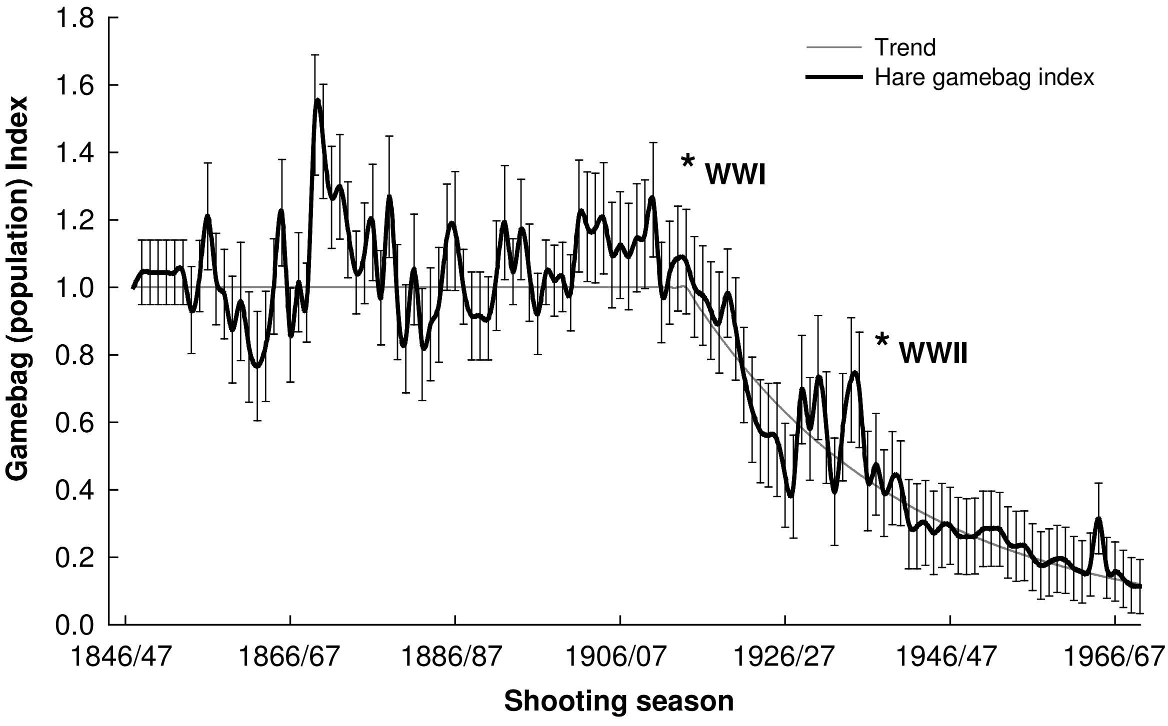


Fig. 4 *Trends in Irish hare gamebag indices from 14 shooting estates throughout Ireland from 1846-1970 produced using TRIM software analysis. Analysis changepoints are shown at the beginning of WWI (1914) and WWII (1939).*

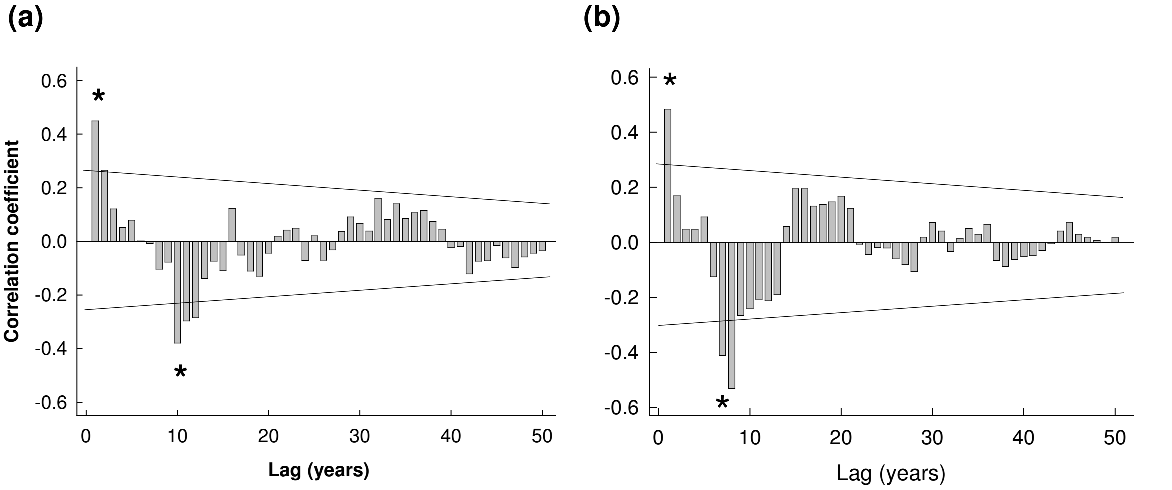


Fig. 5 *Time-series autocorrelation coefficients of* ***(a)*** *pre-1914 hare population indices and* ***(b)*** *post-1914 detrended hare population indices. Lines indicate lags that are significant at p≤0.05 and * indicates lags that have significant autocorrelation and partial autocorrelation coefficients.*

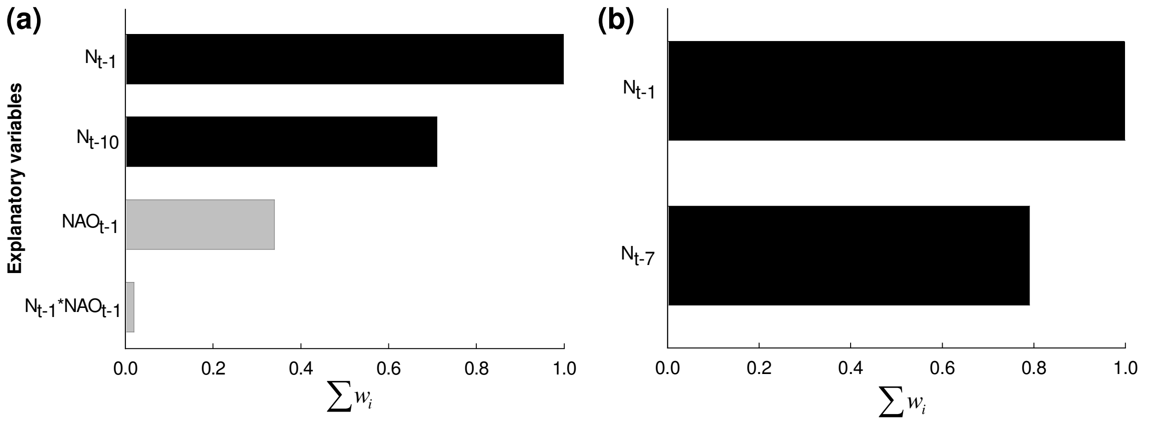


Fig. 6 *Relative importance of factors in explaining variation in the annual Irish hare population growth* ***(a)*** *pre-1914 and* ***(b)*** *post-1914. Variables are ranked in the order of their summed Akaike weight ($\sum w_i$) within the top set of models. Black bars indicate those variables that were retained in the best single approximating model i.e. that with the lowest AIC value, and grey bars indicate variables included in all other models within the top set.*

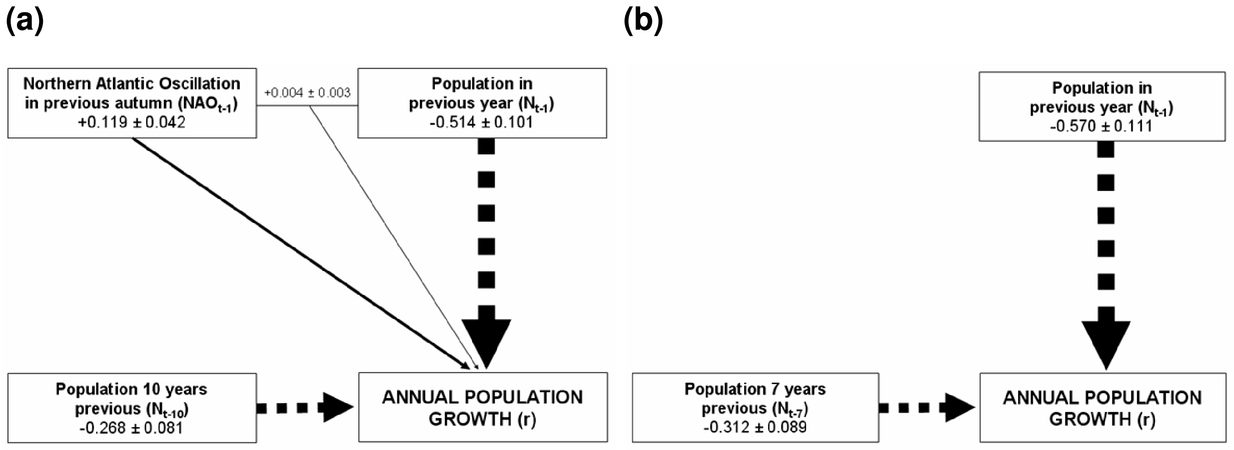


Fig. 7 *Path diagram showing the model averaged regression coefficient ± standard error for each explanatory variable retained within the top set of models that explain variation in annual Irish hare population growth for **(a)** 1846-1913 and **(b)** 1914-1970. Line width represents the scale of the effect while dashed lines indicate negative effects and solid lines indicate positive effects.*

2.2.4 Discussion

We have established long-term historical trends in Irish hare game bags and demonstrated the prevalence and influence of some factors governing interannual and multiannual population growth. From localities throughout Ireland, 124 years are represented within Irish game bag records and long-term trends are clear (Fig. 4). Prior to 1914, hare game bags fluctuated markedly but there was no overall trend. Thereafter, the annual hare index declined markedly reflecting a major decline in the number of hares shot. Although the sample of estates is small, the consistency of coverage and shooting effort between the stable and declining phases of the game bag indices suggest that the trend observed after 1914 represents a real change in the hare population of Ireland. If the abundance of hares differed between game estates and the wider countryside the results presented here may be biased. Nevertheless, game bag indices have often been used as a proxy for hare abundance and are generally accepted to reflect real changes in hare density over time (Strandgaard & Asferg, 1980; Tapper & Parsons, 1984; Tapper, 1987; Langbein *et al*. 1999; Smith *et al*. 2005). The observed decline in the numbers of hares shot in Ireland is consistent with declines in game bags across Great Britain (Fig. 2) and elsewhere in Europe (Bröekhuizen, 1982; Tapper & Parsons 1984; Pielowski, 1990; Tapper, 1992; Mitchell-Jones *et al*., 1999; Smith *et al*., 2005).

A number of factors may have played an important role in this decline. The loss of gamekeepers in Britain during WWI and WWII which has been linked to the decline in the brown hare population (Tapper, 1992) may also have been experienced in Ireland. Significant changes in land ownership patterns were also underway in Ireland at this time, namely the sub-division of numerous large estates into smaller holdings. As a result, practises that would have enhanced hare populations, such as predator control and habitat management, were discontinued. Furthermore, in common with the rest of

Europe, agricultural intensification in Ireland during the early 20[th] century may also have contributed to declines in hare populations.

Time-series analysis suggested that density dependence may be a strong factor determining Irish hare population fluctuations. Prior to the start of the long-term population decline, multiannual fluctuations were evident with a distinct anti-phase at a lag of 10 years, whilst a 16 year phasic period was suggested. During the long-term decline of Irish hare population, multiannual fluctuations exhibited a shortened anti-phase at 7 years, whilst a 17 year phasic period was suggested. Decadal fluctuations are well known from snowshoe hare populations in North America (Keith, 1963; Krebs *et al.*, 2001), whilst recent analysis of Scottish gamebag records suggest that *Lepus timidus scoticus* may exhibit a 16 year quasi-cycle and mountain hare populations in the Peak District have been shown to have a strong 7 year periodicity (Reynolds *et al.*, 2006).

Explanations of the cause of multiannual fluctuations vary widely (Middleton, 1934; Tapper, 1987, 1992; Mallon *et al*, 2003; Newey, 2005). Krebs *et al.* (2001) supported the 'predator-prey-winter food' or 'tri-trophic' hypothesis for explaining hare population regulation (Krebs *et al.*, 1986; Trostel *et al.*, 1987; Sinclair *et al.*, 1988) suggesting that hare cycles are largely predator-prey oscillations influenced by winter food availability. Delayed density dependence of one or more years is a common characteristic in these processes (Carry & Keith, 1979; Boutin *et al.*, 1995).

Large scale climatic processes may be capable of synchronising populations over large geographical areas (Stenseth *et al.*, 1999, 2002). Geographic synchrony of hare populations elsewhere is poorly understood but other large scale influences such as solar activity have been implicated (Ranta *et al.* 1997; Sinclair, 1993; Smith, 1983). Solar activity and the NAO exhibit roughly decadal variations that have been shown to be closely associated (Lamb & Peppler, 1987; Hurrell & van Loon, 1997; Angell, 2001; Tourpali *et al.*, 2005; Versteegh, 2005), especially in autumn and winter (Ogi *et al.*, 2003; Lukianova & Alekseev, 2004; Koder & Kuroda, 2005; Bochnicek & Heida, 2006). It is possible that the influence of the NAO on Irish hare population growth may have been responsible for the decadal periodicity evident prior to 1914.

High seasonal NAO indices are associated with increased rainfall and mild temperatures in Great Britain and Ireland (Butler *et al.*, 1998; Benner, 1999). During cyclical fluctuations in small mammals such as voles, lemmings, mice and hares it has been suggested that survival rather than reproductive rate drives population increase (Korpimaki *et al.*, 2004). Here we suggest that over-winter survival of adults may be aided by extended grass growth whilst survival and maturation of leverets, particular by those born late in summer, may be assisted by the mild autumns that occur during high NAO index years. Furthermore, Irish hares may breed throughout the autumn and winter during mild years (Neil Reid, pers. obs.). Greater survival of adults and leverets from the previous year provides a greater founder population for reproduction in the year of the shoot from which gamebag indices were calculated. Consequently, we suggest that interannual fluctuations of Irish hare populations prior to population decline were partly mediated by autumn temperatures and rainfall determined by the Northern Atlantic Oscillation. Similar influences of the NAO on brown hare populations have been demonstrated in Denmark (Schmidt *et al*., 2004).

Schmidt *et al*. (2004) noted that the steady increase in NAO indices during the latter 20th century should have brought increases in hare populations. However, such increases were unable to reverse declines caused by ongoing agricultural intensification. This may explain the disappearance of the NAO as a major influence on Irish hare population growth after 1914. Some authors have suggested that lagged density dependent processes, such as variation in reproductive success are sufficient to induce periodicity or regular cyclicity alone (Royama, 1992). Consequently, it may be that despite the apparent disappearance of climatic decadal forcing, the Irish hare population still maintained a regular cycle, albeit with a shortened period.

The present study provides evidence from game bag data that supports the hypothesis that Irish hare populations began to decline during the early 20th century. Irish hare populations exhibit multiannual periodicity prior to and after the population decline. This may suggest that the processes that naturally regulate hare populations continued to influence their dynamics despite overriding anthropogenic factors.

2.3 Coursing records

2.3.1 Introduction

The Irish Coursing Club (ICC) is the official body responsible for organising hare coursing meetings in Ireland. Coursing is licensed under the Wildlife Acts (1976 and 2000) and as a condition of this licensing the ICC has collated records of the number of hares netted for coursing and released back into the wild since 1988. Catches of hares from clearance netting and driven counts have previously been used as successful hare census techniques (Andrzejewski & Jerierski, 1966; Abildgård *et al.*, 1972; Gross *et al.*, 1974; Pépin, 1985). In contrast to historical game shooting records we hypothesised that coursing records might reflect more recent trends in the Irish hare population.

While it is likely that coursing records indicate hare availability to some extent, clearly the number of hares caught will also reflect the scale of club needs for meetings and a related effect of hare survival rates in captivity, both of which may change over time. A comprehensive review of hare mortality during coursing in Ireland is provided by Reid *et al*. (2007). For example, in 1993 the ICC introduced a directive for improving hare survival that included compulsory muzzling of dogs. As part of our investigation of the factors affecting the number of hares caught and released for coursing, we were therefore obliged to consider the contribution of such changes in practice to variation in the number of hares caught and released.

Our analytical approach was to account for as many "practice-related" variables as possible and isolate the remaining component of variance that could then be ascribed to temporal trends. This variance could, nonetheless, still be alternatively ascribed to trends in the hare population or in the scale of coursing activity.

2.3.2 Methods

Records were examined for all coursing club meetings in Ireland between 1988/89 and 2003/04. The numbers of active clubs per season and the number of hares taken from and released back into the wild were collated. Approximately 13% of records were missing data on the numbers of captures but data on the numbers of releases were always present. Capture data were missing entirely for 1995/96 and 1997/98. The reasons for missing data are not known. For descriptive purposes only, i.e. not for statistical analysis, missing capture data were interpolated using the number of hares released and mean mortality for the specific season. For 1995/96 and 1997/98 data were interpolated using mean hare mortality after 1993, i.e. after the implementation of muzzling.

Statistical analyses

Factors affecting the number of hares released per club were analysed by fitting a model using the REML procedure (Patterson & Thompson 1971). Yearly records were treated as repeated measures of the same club, the use of muzzled or unmuzzled dogs was a fixed factor, club was treated as a random factor and the number of captures was treated as a covariate. Factors affecting variation in hare survival, i.e. the proportion of hares released into the wild, was therefore indicated by significant interactions with the numbers of hares captured. All two-way interaction terms were fitted initially, but subsequently removed if found to be non-significant. Prior to analysis all variables were tested for colinearity using correlation, ensuring that none of the variables were significant bivariates i.e. $r > 0.7$ (Fielding and Haworth 1995). The influence of each term in the final model was taken as the Wald statistic generated when the term of interest was fitted last (Kruuk *et al.* 1999), divided by the degrees of freedom (Quinn & Keough 2002). Statistical tests were preformed using GenStat© (v6).

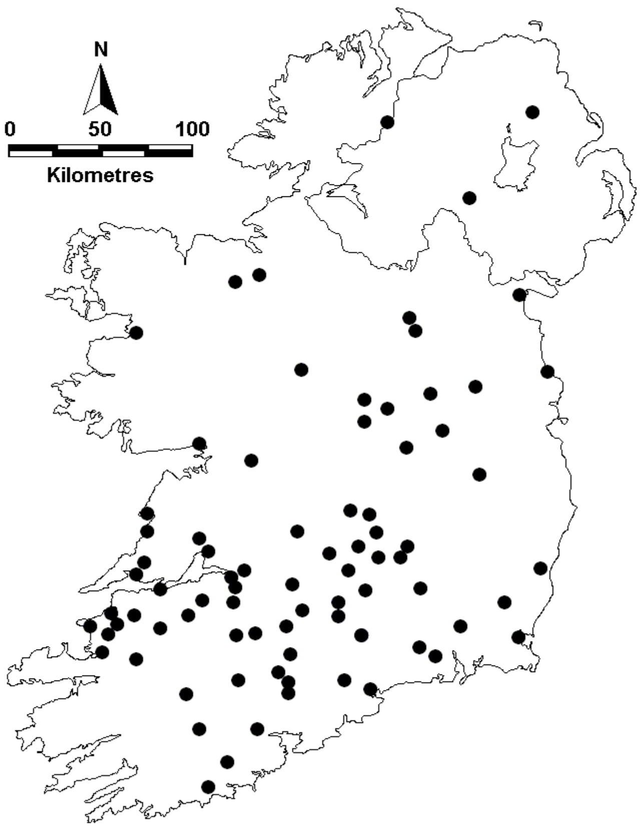


Fig 8 *Distribution of coursing clubs in Ireland for which records between 1988/89 and 2003/04 were analysed.*

Table 1 *Summary of Irish Coursing Club records between 1988/89-2003/04.*

Status of dogs	Year	Number of hares captured	Number of hares released	Number of hares not released	Number of active clubs	Mean number of hares captured per club ± s.d.	Mean % mortality of hares per club ± s.d.
Unmuzzled	1988/89	*6644	5590	*1054	79	84.1 ± 17.2	16.0 ± 8.8
	1989/90	*6709	5636	*1073	79	84.9 ± 16.0	16.0 ± 9.7
	1990/91	6373	5315	1058	77	82.8 ± 17.6	17.3 ± 1.8
	1991/92	6569	5617	952	77	85.3 ± 15.9	14.5 ± 7.4
	1992/93	6756	5722	1034	78	86.6 ± 15.6	15.2 ± 6.7
Sub-total	**-**	**33051**	**27880**	**5171**	**390**	**84.7 ± 16.5**	**15.8 ± 9.1**
Muzzled	1993/94	*5866	5427	*439	73	80.4 ± 14.9	7.6 ± 4.9
	1994/95	5921	5650	271	76	77.9 ± 14.6	4.7 ± 5.9
	1995/96	*6265	6006	*259	77	81.4 ± 16.7	4.2 ± 0.7
	1996/97	6224	6024	200	74	84.1 ± 13.7	3.4 ± 0.5
	1997/98	*6133	5882	*251	78	78.6 ± 14.4	4.1 ± 0.1
	1998/99	6050	5804	246	76	79.6 ± 17.8	4.4 ± 0.9
	1999/00	6507	6294	213	78	83.4 ± 18.2	3.4 ± 0.5
	2000/01	5877	5570	307	76	77.3 ± 13.9	5.5 ± 1.4
	2001/02	6005	5823	182	76	79.0 ± 15.6	3.3 ± 0.5
	2002/03	5877	5720	157	75	78.5 ± 15.9	2.7 ± 0.4
	2003/04	5751	5608	143	71	81.0 ± 17.4	2.3 ± 0.6
Sub-total	**-**	**66476**	**63808**	**2668**	**830**	**80.1 ± 15.9**	**4.1 ± 5.9**
Total	**-**	**99527**	**91688**	**7839**	**1220**	**81.6 ± 16.2**	**7.9 ± 8.9**

** partially incomplete records are interpolated*

2.3.2 Results

The records of 81 clubs (Fig. 8) conducting 1220 coursing meetings (390 with unmuzzled dogs and 830 with muzzled dogs) over 16 seasons were analysed. The number of active clubs decreased over the period of study reflecting a decrease in general levels of coursing activity (Table 1).

The main effects of hare captures and club were statistically substantial but biologically trivial, since they accounted for variation in the scale of coursing operations (Table 2).

The relationship between the number of hares released and the number captured was greatly affected by the introduction of dog muzzling, i.e. hare survival was greater when dogs were muzzled (Fig. 9). The relationship between the number of hares released and those captured varied with time and when the analysis was run for each year the slope increased over time (Fig. 10), indicating that hare survival increased for reasons that could not be accounted for by muzzling alone. The relationship between the number of hares released and the number of hares captured varied among clubs, indicating that hare survival varied among clubs. Muzzling also affected the number of hares released and this effect varied significantly among clubs.

Finally, the number of hares released varied among years and this effect varied among clubs. These two components of the total variance in the number of hares released could not be accounted for by the modelled changes in coursing practice but could be alternatively ascribed to changes in the scale of coursing activity and/or trends in the hare population, either or both of which also varied among clubs or club localities.

Table 2 *Factors affecting the number of hares released by coursing clubs, from a REML model.*

Explanatory variables	Interpretation of effect	$F_{d.f.}$	p
Captures*muzzling	The number of hares caught plus the affect of muzzling substantially affects the number of hares released.	$228.07_{1,902}$	<0.001
Captures	Number of hares released is related to number of hares caught	$139.45_{1,902}$	<0.001
Captures*year	Hare survival improves with time due to factors other than muzzling	$88.03_{1,902}$	<0.001
Muzzling	Number of hares released affected by muzzling of dogs	$72.29_{1,902}$	<0.001
Year	Temporal trend in hare availability and/or scale of coursing	$10.61_{1,902}$	<0.001
Club	Number of hares released varies among clubs	$4.65_{80,902}$	<0.001
Club*year	Variation among clubs in hare availability trends and/or scale of coursing	$3.28_{79,902}$	<0.001
Club*muzzling	Effect of muzzling dogs varies among clubs	$2.78_{76,902}$	<0.001
Captures*club	Hare survival varies among clubs	$1.73_{79,902}$	<0.001

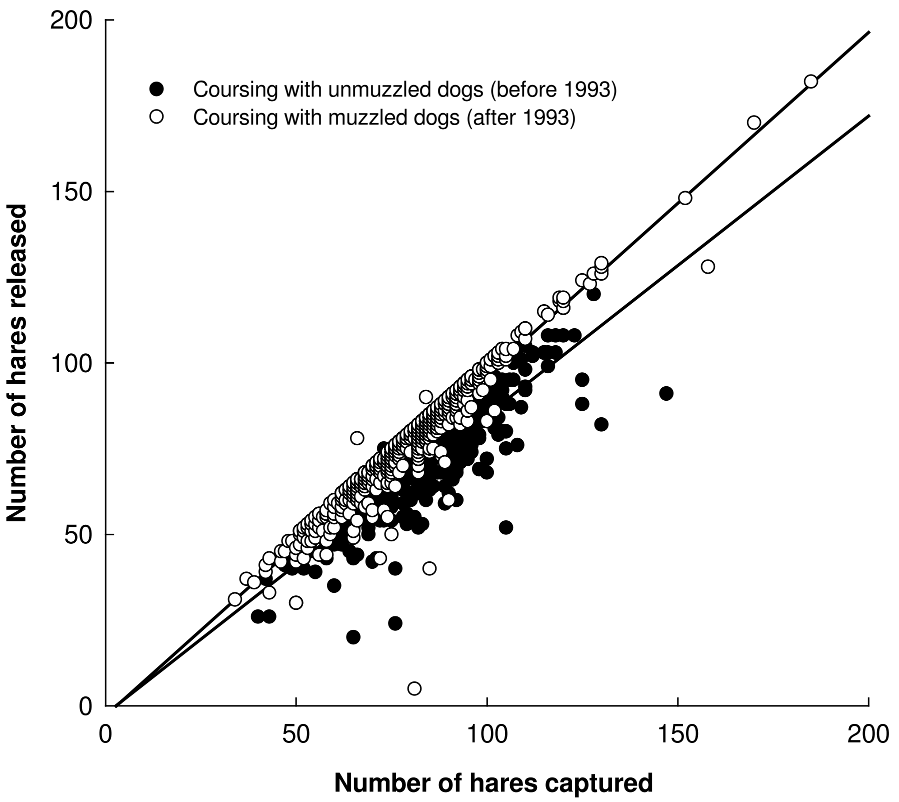


Figure 9 *The relationship between the number of hares captured and the number of hares released was closer during courses using muzzled dogs (r^2=0.91, n=675 club-years) than those using unmuzzled dogs (r^2=0.78, n= 386 club-years).*

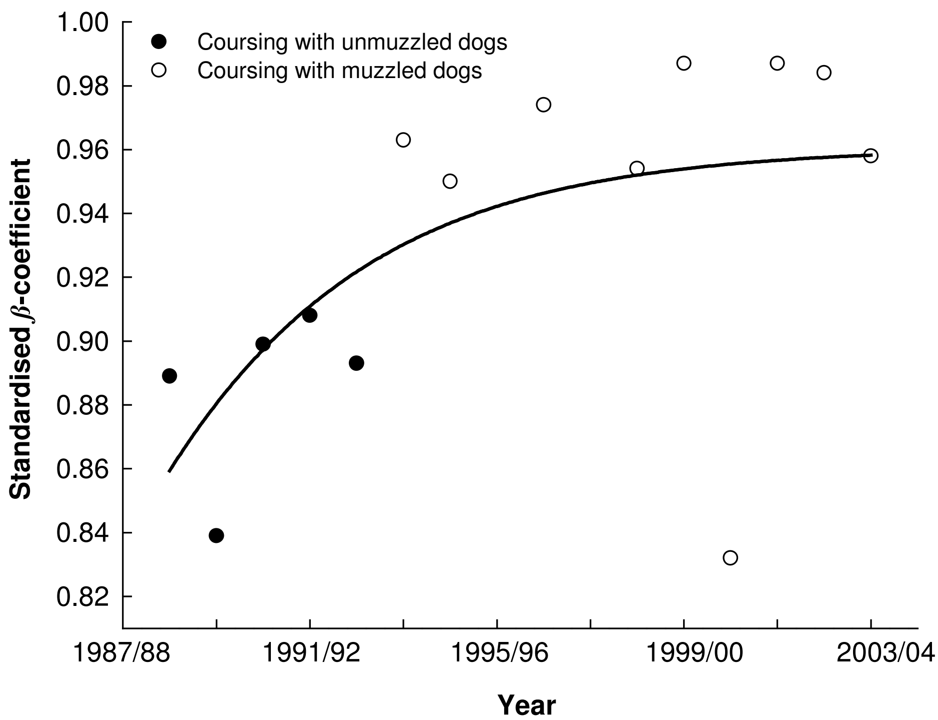


Figure 10 *Slopes of the relationship between the numbers of hares released and numbers captured in each year between 1988/89 and 2003/04. During 2000/01, two out of 76 clubs experienced unusually high rates of hare mortality.*

2.3.3 Discussion

The number of hares caught for coursing reflects the availability of hares to a limited extent, but is a substantial effect of the scale of club needs and, over the period of this study, of changes in the survival of animals while in captivity. Therefore, to control for these confounding factors we investigated variance in the number of animals released, while controlling for scale, changes in practice and resulting changes in survival.

A large part of variation in the numbers of hares released by coursing clubs was explained by declining rates of hare mortality, due to the introduction of dog muzzling and other ongoing enhancements of hare husbandry. Such improvements in husbandry appear to have resulted in fewer hares being needed for meetings and, therefore, fewer hares being caught.

A relatively small component of variance could not be accounted for by known scale or practice-related factors, and was potentially a useful measure of changes with time (year effect) and variation in this temporal effect among clubs (year*club interaction). To resolve the proportion of these temporal trends that is due to variation in hare availability, i.e. may reflect changes in hare populations, and to changes in the scale of coursing club needs, it is necessary to understand the effort put into capturing hares.

Without measures of effort, ICC records are not appropriate for monitoring changes in the status of the hare population. If effort was known, this could be added to the models used above. The main statistical effect of effort would be biologically trivial, i.e. it would indicate that if you tried harder you would catch more hares. However, with understanding of the relationship between effort and numbers caught over a relevant range of hare populations, the slopes for each year in the interaction between effort and year could be interpreted as a measure of changing hare availability. Put simply, in years when less effort is required to catch the same number of hares, this suggests that more hares are available for capture. The standard error of the slope could be taken as a measure of confidence. In principle, a similar approach to the interaction between club (or region) and effort would reflect spatial patterns of hare abundance.

We recommended that, for a pilot period, coursing clubs should record some measure of capture effort. This would ideally take the form of a quantitative measure, such as net-metre-days or at least the number of netting days, number of beaters and/or area netted. Such recording would enable the ICC to make a valuable contribution to the monitoring of the status of the Irish hare and provide a relatively simple and cost effective tool to help NPWS fulfil its surveillance requirements under the EC Habitats Directive.

3 Hare Survey of Ireland 2006/07

3.1 Introduction

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). This is especially pertinent for species that are exploited for hunting (Perez *et al*., 2002; Reeves, 2002; Baghli & Verhagen, 2003) where an understanding of demography is essential to establish sustainable harvest rates. For mammals in particular, such data are usually limited and often unreliable (Harris *et al*., 1995). In Great Britain the need for a comprehensive national mammal monitoring network to provide robust data on population trends has long been recognised (Toms, Siriwardena & Greenwood, 1999; Macdonald & Tattersall, 2001; Battersby & Greenwood; 2004) and recently established by the Tracking Mammals Partnership (Battersby, 2005). A Bat Monitoring Programme has been in place in the Republic of Ireland since 2003 (McAney, 2006) and major efforts have been made in recent years to establish standardised monitoring methodologies for other mammal species of conservation concern such as pine martens, cetaceans, otters, seals and in the current study, Irish hares. Ideally, mammal surveillance programmes should emulate the success of bird monitoring programmes, generating annual trend data (Battersby & Greenwood; 2004).

Article 11 of the European Habitats Directive (92/43/EEC) requires that member states "undertake surveillance of [mountain hare] conservation status" giving Ireland a statutory obligation to monitor changes in the Irish hare population. Hellawell (1991) defines surveillance as repeated and standardised observations of abundance over time, using methods that enable changes in numbers to be detected. Whilst no data exist on the current conservation status of the Irish hare in the Republic of Ireland, previous studies, notwithstanding varying methodologies, suggest that Irish hare population densities may have varied markedly in Northern Ireland over the last 13 years (Table 3).

Table 3 Estimated density of Irish hares in Northern Ireland from 1994-2006.

Study	Year of fieldwork	Mean estimated density hares/km^2 (range)
Dingerkus & Montgomery (2002)	1994-96	0.65 (0.20-1.54)
O'Mahony & Montgomery (2001)	2000	1.18* (0.27-2.86)
Preston *et al*. (2003)	2002	1.00 (0.50-1.80)
Tosh *et al*. (2005)	2004	5.11 (4.23-6.16)
Tosh *et al*. (2005)	2005	3.10 (2.49-3.87)
Reid (2006)	2005	3.01 (2.02-4.48)
Hall-Aspland *et al*. (2006)	2006	2.57 (1.91-3.46)

*Density calculated using the published total abundance divided by the land area of Northern Ireland c. 14,043km^2.

One of the greatest problems facing conservation, particularly on islands is the spread and establishment of introduced species (Harris & Yalden, 2004; Stokes *et al*., 2006). Reid & Montgomery (2007) demonstrate that the brown hare is well established in Northern Ireland and suggest that its naturalisation may represent a significant risk to the future ecological security and genetic integrity of the Irish hare. Ireland has international obligations under the Convention on Biological Diversity (Anonymous, 1992), the Berne Convention (Anonymous, 1979) and the European Habitats Directive (EEC 43/92) to address invasive species issues. It is, therefore, desirable that adequate monitoring is established to document the spread and impact of alien species (Anonymous, 2003; Harris & Yalden, 2004), including the brown hare in Ireland.

Population estimation techniques

Lagomorphs have been surveyed using almost every census technique available for terrestrial mammals (Hutchings & Harris, 1993). Night-driven, spotlight surveys have become a favoured method of estimating relative abundance of nocturnal mammals due to their efficiency, repeatability, and lack of interference with the subject (Langbein *et al*., 1999). A measure of true density and abundance can sometimes be more informative to conservation strategies than simpler measures of relative abundance. Distance sampling, using the software programme Distance, enables estimates of true density to be modelled by relating count data to the distribution of animals relative to the observer (Fig. 11; Buckland, *et al*., 2004). Distance sampling assumes that all animals at the point of survey are detected (i.e. 100% of animals on the survey transect or point). The further the surveyor looks from the survey point the less likely it becomes that a target animal will be detected. Assuming uniform distribution of animals

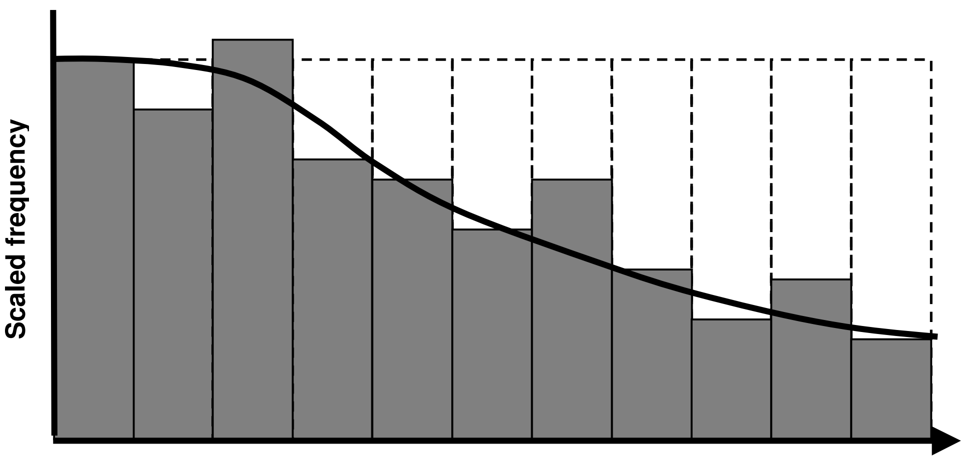


Fig 11 *Hypothetical example of detection function estimation. The grey bars represent the (scaled) counts of hares detected within each of distance interval; the dashed bars represent the (scaled) expected number of hares; the curve represents the estimated detection function fitted to the observed counts. (Counts have been scaled to take account of the fact that more hares are expected at greater distances because there is more area at greater distances from a point.)*

in the area searched, the probability of detecting an animal at any distance from the surveyor can be estimated using the distances to observed animals. This is then used to convert the number of animals seen into an estimate of the number of animals present within the area searched. Animal density is estimated by dividing the estimated number of animals present by the area of the region searched. Finally, if the area searched is representative of the country as a whole, the density estimate can be multiplied up by the total land area of the Republic of Ireland to provide an estimate of the total abundance of hares.

Distance sampling provides robust estimates of absolute abundance only when the study population and survey design conform to the key assumptions of the analyses. Previous research demonstrates that surveys of hares conducted from roads do not conform to the assumptions of distance sampling and biased estimates are common (Tosh *et al.*, 2004; Tosh *et al.,* 2005). However, by identifying biases in hare survey methodologies and developing means of accounting for them we aimed to develop a strategy that will provide a robust basis for future monitoring.

3.2 Methodology

Survey design

Forty survey teams involving >80 people (Appendix 2) surveyed the most south-westerly 1km^2 Irish grid square in each 10km Irish grid square. In cases where the most south-westerly 1km^2 square was not bisected by 1km of suitable minor road the next nearest 1km^2 square that was suitable was selected. To ensure uniform coverage an attempt was made to survey each 10km grid square each year. Square selection was made with a geographic information system (GIS). Squares that proved unsurveyable during 2006 due to issues such as access or health and safety were abandoned in 2007 and replaced with the next nearest suitable square.

Surveyors were trained in the identification and differentiation of Irish and brown hares and rabbits. Data were also gathered for foxes. Surveys were conducted during winter (January-March) when ground vegetation was minimal, maximising the detectability of animals. Furthermore, it is generally better to assess pre-breeding mammal populations due to the variability in juvenile recruitment between years (Macdonald *et al.*, 1998). A 2 million candlepower spotlight was used from the back of a high clearance vehicle or from a step ladder such that the observer's head height was approximately 3m from ground level, i.e. above most hedgerows (Fig. 12). Five points were surveyed along each 1km transect spaced at approximately 200m intervals (Fig. 13). Both sides of the road were swept twice with the light beam to ensure that all target animals were detected. For each cluster of animals observed, the species, cluster size (i.e. number in the group) and the angle and radial distance (measured by laser rangefinder) of the cluster from the observer was recorded. During both survey years, survey effort was taken as the number out of the eighteen 20° sectors of a 360° circle, i.e., swept by the light beam that were visible without obstruction (measured using a custom-made protractor; Appendix 3). During 2007, data were also collected on the frequency at which each 20° sector of the 360° field of view were visible (Appendix 3). Surveys were conducted between one hour after sunset and midnight.

To describe patterns of hare distribution with respect to field boundaries, "transfield" transects were walked perpendicular to the road at a random selection of points in 2007. These transects extended to the first field boundary or 250m in cases where a boundary was not met. For each cluster of hares detected, the species, cluster size (i.e. number) and perpendicular distance of the cluster from the transect (and by inference, from the road and field boundary) was recorded.

To describe hare distribution, data were collated from hare surveys during both years supplemented by incidental sightings from surveyors, sightings submitted by members of the public via e-mail and sightings recorded on the biology.ie database (www.biology.ie).

Fig. 12 *Survey being conducted from the back of a pickup truck* ©*Mathieu Lundy*

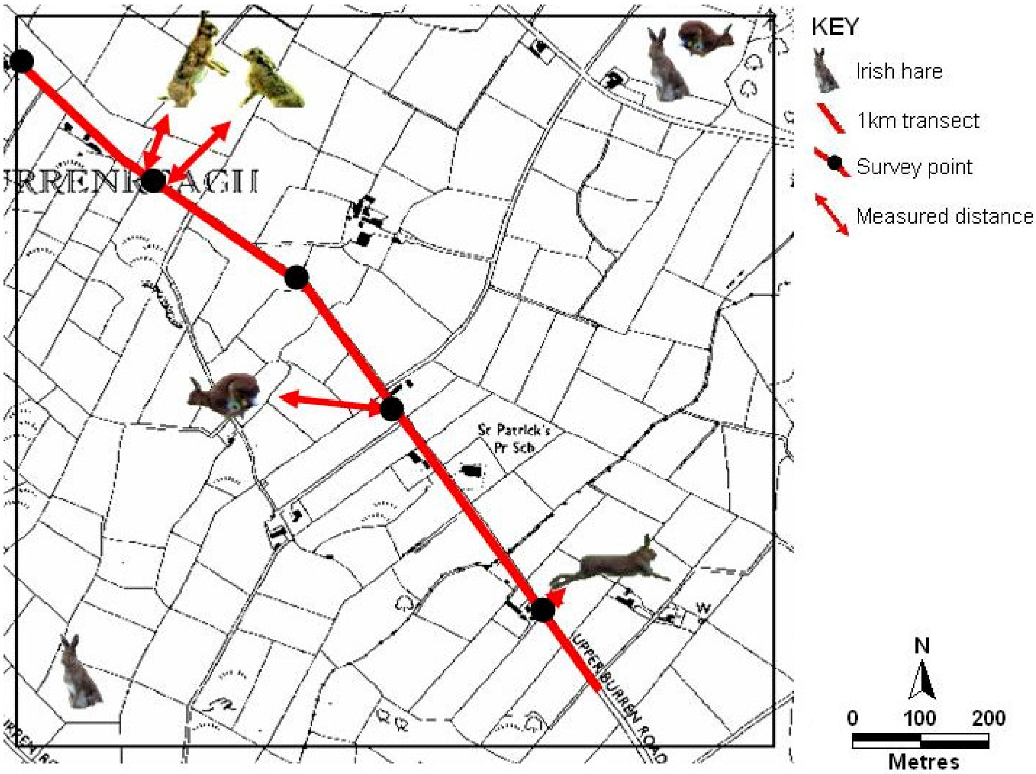


Fig. 13 *A typical 1km² survey square containing a 1km transect on which 5 survey points were placed approximately 200m apart from which the number and distance of each hare cluster was recorded. Note that not all hares within each square will have been detected.*

Habitat data

ArcView GIS 3.3 (ESRI, California, USA) was used to compute landscape and habitat variables using the CORINE land cover map (EEA, 2000). Spatial Analyst 2.0 and Patch Analyst 3.1 extensions were used to describe the proportion of the landscape made up of four landclass types:

i) bog, moor, heath and marsh
ii) mixed farmland
iii) pastoral farmland
iv) other habitats

Each landclass was measured at three spatial scales measured from the centre of each survey square; 1km^2 (radius = 0.56km), 10km^2 (radius = 1.78km) and 100km^2 (radius = 5.64km). Landclass categories were chosen intuitively based on landscape characteristics that were likely to influence the patterns of abundance of a predominately grassland species (e.g. area of pastoral agriculture).

Statistical analyses

The effect of habitat on Irish hare sightings was assessed by building a set of univariate generalised linear models assuming a Poisson error distribution with a logarithmic link function using the number of hares counted per survey square as the dependent variable and the proportional cover of each habitat type as independent variables at each of three spatial scales (1km^2, 10km^2 and 100km^2). The spatial extent within each variable was chosen as that which had the highest Akaike weight value within each set of three models (Akaike, 1983; Burnham and Anderson, 2002). Variance in the frequency of Irish hare sightings was then investigated by fitting generalised linear models assuming a Poisson error distribution with a logarithmic link function using the habitat variables at the appropriate spatial scale and any parameters that may have confounded their effects including survey effort, year and region (Table 4). Proportional data were arcsine square-root transformed (Hosmer & Lemeshow 2000). As the primary focus was to investigate the explanatory power of the independent variables rather than building a predictive model, interaction terms were omitted. Furthermore, their inclusion would have limited resolution for some variables if the data were further divided with respect to nominal factors.

Table 4 *Explanatory variables used to predict Irish hare abundance. Habitat variables were obtained from the CORINE database (EEA, 2000).*

Variable category	Variable name	Units	Description
Dependent variable	Irish hare abundance	Count	1km^2 frequency of hare sightings
Species data	Rabbit abundance	Count	1km^2 frequency of rabbit sightings
	Fox abundance	Count	1km^2 frequency of fox sightings
Factors	Year	Categorical	2006 or 2007
	Region	Categorical	East, North-west and South-west
Confounding covariate	Survey effort	Proportion	Product of the number of survey points and the number of visible sectors per 1km^2 survey square
Habitats	Bog, moor, heath & marsh	Proportion	Area of each 1km^2, 10km^2 and 100km^2 area around each survey square classed as inland marsh, moor, heath or peat bog
	Mixed farmland	Proportion	Area of each 1km^2, 10km^2 and 100km^2 area around each survey square classed as arable horticulture, complex cultivation patterns or heterogeneous agricultural areas including areas dominated by agriculture with significant areas of natural vegetation
	Pastoral farmland	Proportion	Area of each 1km^2, 10km^2 and 100km^2 area around each survey square classed as improved pasture or natural grassland
	Other	Proportion	Area of each 1km^2, 10km^2 and 100km^2 area around each survey square classed as bare rock, beaches, burnt areas, salt marsh, sand dunes, scrub, sparely vegetated areas or woodland

Model parsimony was evaluated using the Akaike Information Criterion (AIC) and Akaike weights (w_i), while multimodel inference was used to assess the contribution and effect of each covariate (for full explanation of model selection procedures see *Statistical Analyses* on page 8, Section 2.2.2). To allow for the direct comparison of regression coefficients all variables were standardised to have a $\bar{x}$ = 0 and a σ = 1 prior to analysis (Schmidt *et al.*, 2004). Statistical analyses were conducted using GenStat© v6.

Density estimation

Conventional Distance Sampling (CDS) point transect methods require that:

i) Points are placed randomly with respect to animals.
ii) All animals at distance zero are detected.
iii) Distances are measured accurately to the initial position of detected animals.
iv) The fraction of a circle about each point which is searched is either the same at each point transect or is measured.

The terrestrial environment does not always fulfil the analytical assumptions of Distance-sampling. First, hares are surveyed at night. Travelling to randomly located points throughout the countryside during darkness is unsafe, logistically impractical and disturbing to those living in the countryside. Therefore, sample points were placed on roads. Whilst this facilitates the survey, locating samplers on roads will introduce bias into the data, as hares may avoid field boundaries or avoid roads in particular due to human disturbance. Consequently, the highest proportion of animals may be some distance from the observer. An additional complication is that survey effort at different points was not always the same because obstacles, such as hedgerows and trees, sometimes obscured a portion of the area being surveyed. Also not all survey squares contained 5 survey points leading to highly variable levels of survey effort per survey square.

Consequently, CDS was not appropriate to estimate absolute density of hares when using data from surveys located on roads and specialist methods were developed by the University of St. Andrews, Scotland to account for non-uniform distribution of animals with respect to roads and variable survey effort (Marques & Borchers, 2006; Paxton *et al*. 2007) using the programme language R (CRAN, 2007).

In 2007, a measure of angular sampling bias was achieved by recording the number and direction of 20^o sectors visible within a 360^o circle around each survey point (Appendix 3). This bias was accounted for during custom analysis. In addition to this directional bias, variation in total survey effort per square was taken into account by using the number of points surveyed in each 1km^2 survey square.

The data from night-walked transfield transects were used to provide additional information for estimating hare density gradients relative to field boundaries, in this case, the road. Three models were used to estimate the hare density gradient away from roads; (1) half-normal, (2) hazard-rate and a (3) modified Gaussian.

Density and abundance estimates were obtained for the Republic of Ireland as a whole during 2006 and 2007, with estimates stratified by geographic region (Fig. 14a) comprising i) East (Leinster plus Cavan and Monaghan), ii) North-west (Connaught plus Donegal) and iii) South-west (Munster) and by landclass (Fig. 14b): i) bog, moor, heath & marsh, ii) mixed farmland, iii) pastoral farmland and iv) other habitats. Upper and lower 95% confidence limits were produced using a non-parametric bootstrapping procedure.

3.3 Results

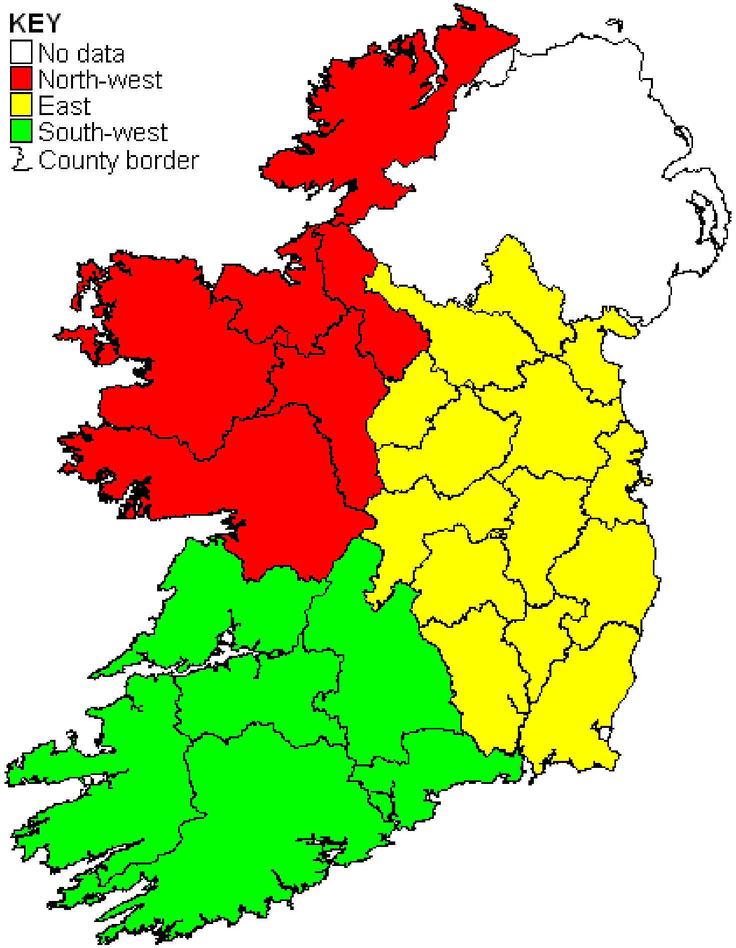
Over both survey years a total of 691 out of 833 (c. 83.0%) of the 10km Irish grid squares in the Republic of Ireland were successfully surveyed for hares (Fig. 15). Of those that were not surveyed, the majority were missed because they were mostly sea with a relatively small area of land. This under-sampling of the coastline may cause bias if density is different on the coast than elsewhere. However, the pattern of detections suggest that this is not the case (Fig. 16). A total of 365 Irish hares (in 240 groups), 1209 rabbits (in 669 groups) and 198 foxes (in 191 groups) were recorded. The number of hares observed increased from 141 hares in 2006 to 224 in 2007 (Table 5). The Irish hare is widespread throughout the Republic of Ireland (Fig. 16a). Rabbit and fox sightings were greater in the eastern and south-western regions (Fig. 16b & 16c). A detailed analysis of rabbit and fox sightings will be the subject of a later publication.

No confirmed reports of brown hare were made in either survey year. However, a number of anecdotal reports suggest that a small population of brown hares may exist between Julianstown, Co. Meath (53^{0}40’21”N, 06^{0}17’07”W) and Balbriggan, Co. Dublin (53^{0}36’28”N, 06^{0}11’03”W) and may extend as far north as south Co. Louth.

Landclass type exerted varying influences on Irish hare counts at different spatial scales (Fig. 17). The effect of pastoral farmland was most evident within immediate vicinity (1km^2); bog, moor, heath & marsh and other habitats exerted most influence on hare abundance at the local scale (10km^2), while mixed farmland dominated by arable horticulture had its greatest effect at the landscape scale (100km^2).

Multimodel inference produced a summary of the competing set of models accounting for variance in frequency of Irish hare sightings. As expected, survey effort had the greatest effect on the number of hares seen (Fig. 18). The area of pastoral farmland in the immediate vicinity (1km^2) and the area of bog, moor, heath & marsh at the local scale ($10km^2$) had positive influences on hare abundance, whilst rabbit relative abundance appeared negatively to affect the number of hares observed (Fig. 18). Accounting for the effects of survey effort, landscape type and rabbit abundance the frequency of Irish hare sightings was significantly higher in the eastern region than either of the two western regions during both survey years and the total frequency of hare sightings increased between 2006 and 2007 (Fig. 19).

(a) Geographic regions



(b) Landclass categories

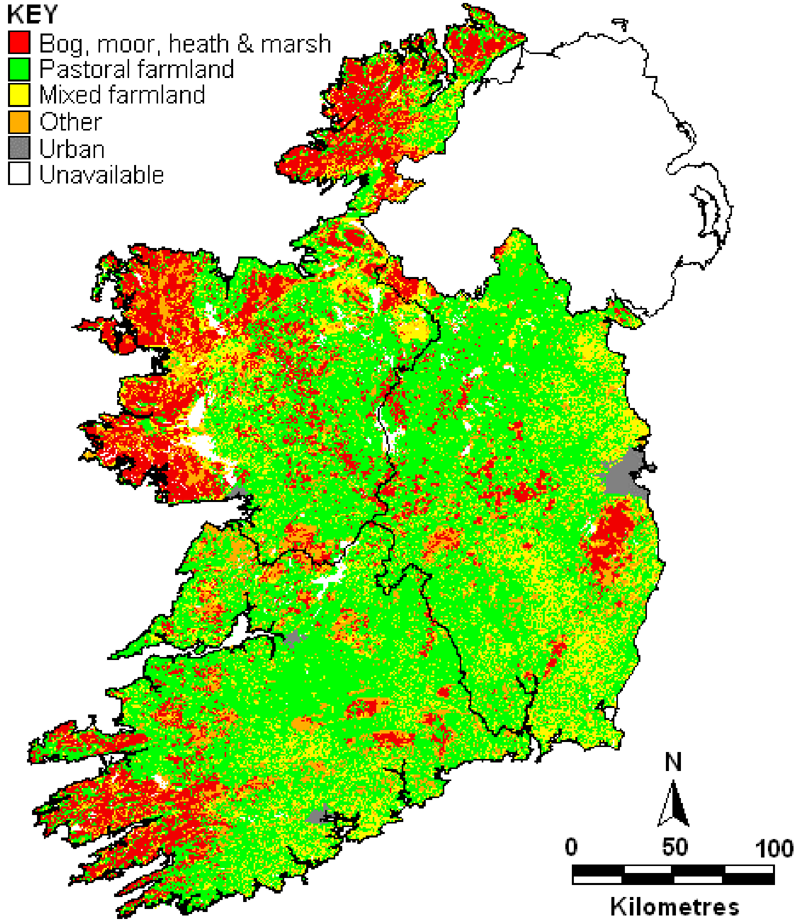


Fig. 14 *Stratification of Ireland into **(a)** geographic regions and **(b)** landclass categories for use in analyses.*

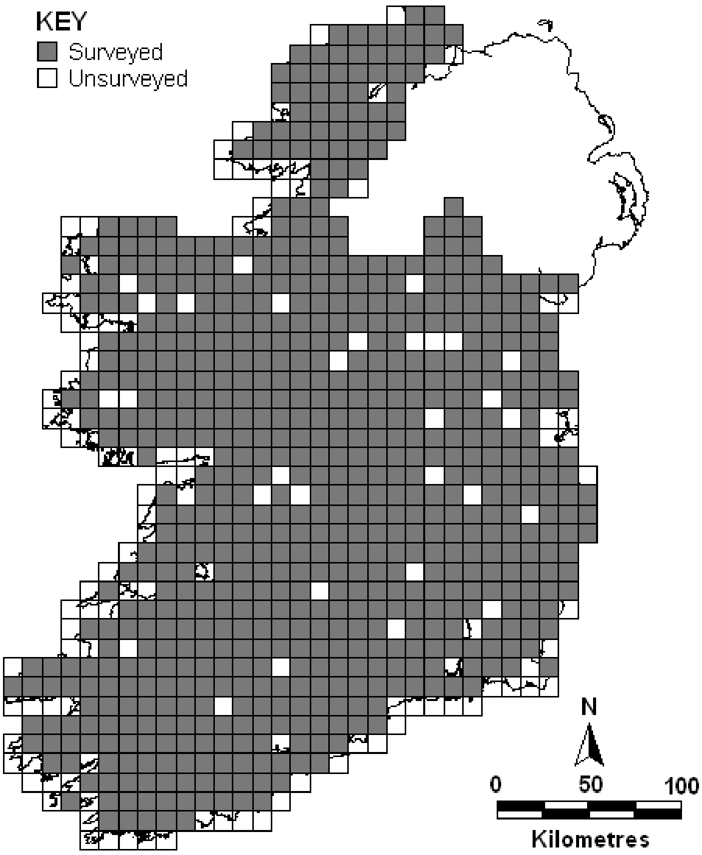


Fig. 15 *The distribution of 10km Irish grid squares that were surveyed during the Hare Survey of Ireland 2006/07.*

Table 5 *Descriptive summary for 1km² squares surveyed during the Hare Survey of Ireland in a) 2006 and b) 2007.*

a) Region	**2006**				
	n	**Number with survey effort >0**	**Number with Irish hare detections**	**Detected % occurrence** (confidence intervals)	**Total number of Irish hares seen**
Republic of Ireland	603	525	72	13.71 (11.60-15.90)	141
East	200	150	24	16.00 (13.60-17.80)	52
North-west	181	165	19	11.51 (9.50 - 13.50)	35
South-west	222	212	29	13.68 (11.80-15.90)	54

b) Region	**2007**				
	n	**Number with survey effort >0**	**Number with Irish hare detections**	**Detected % occurrence** (confidence intervals)	**Total number of Irish hares seen**
Republic of Ireland	647	638	92	14.42 (12.30-16.60)	224
East	195	194	26	13.40 (11.40-15.40)	77
North-west	214	209	36	17.22 (14.90-19.70)	80
South-west	238	237	30	12.66 (10.80-14.80)	67

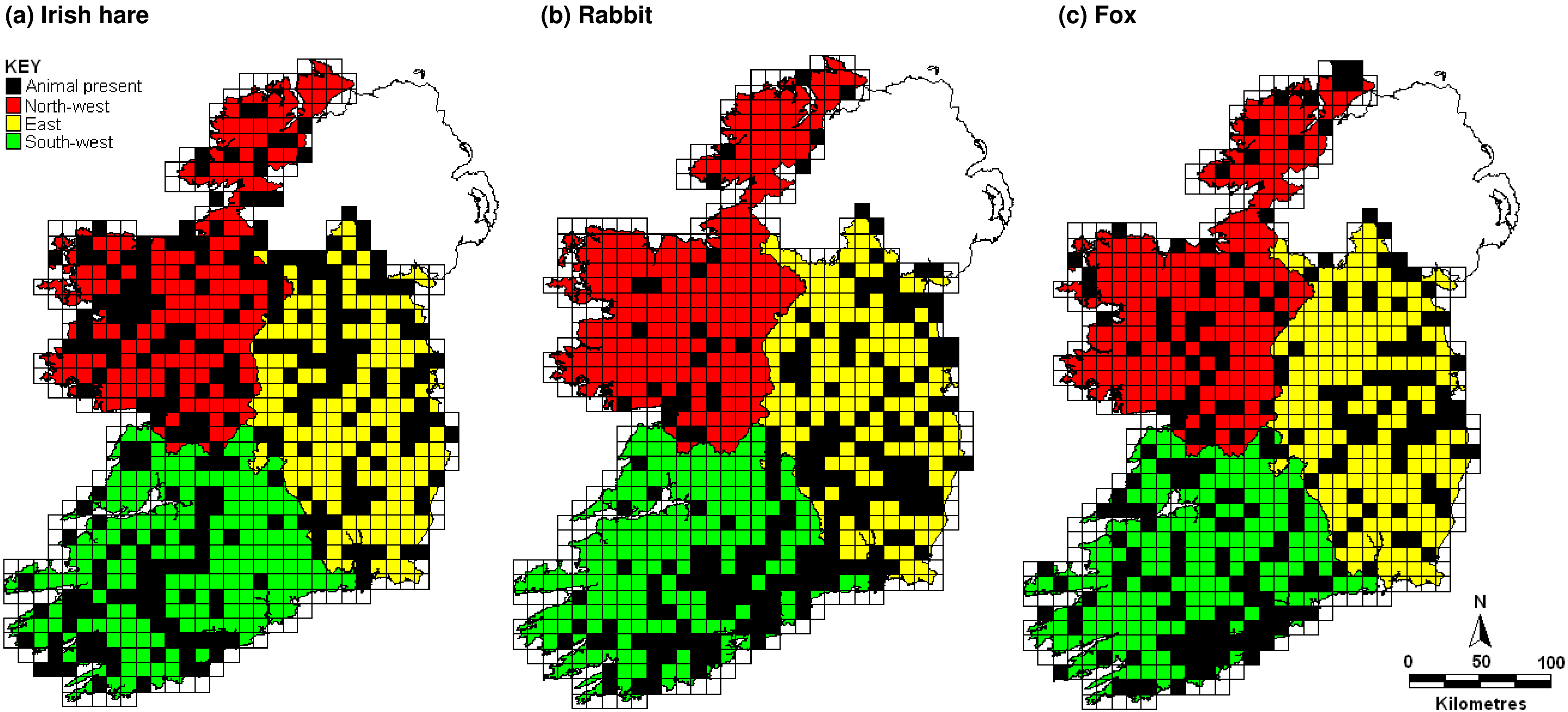


Fig. 16 *Sightings of **(a)** Irish hare, **(b)** rabbit and **(c)** fox in the Republic of Ireland during 2006/07. *[Data were extracted from the Hare Survey of Ireland 2006/07 (including incidental sightings submitted by e-mail) and <u>www.biology.ie</u>.*

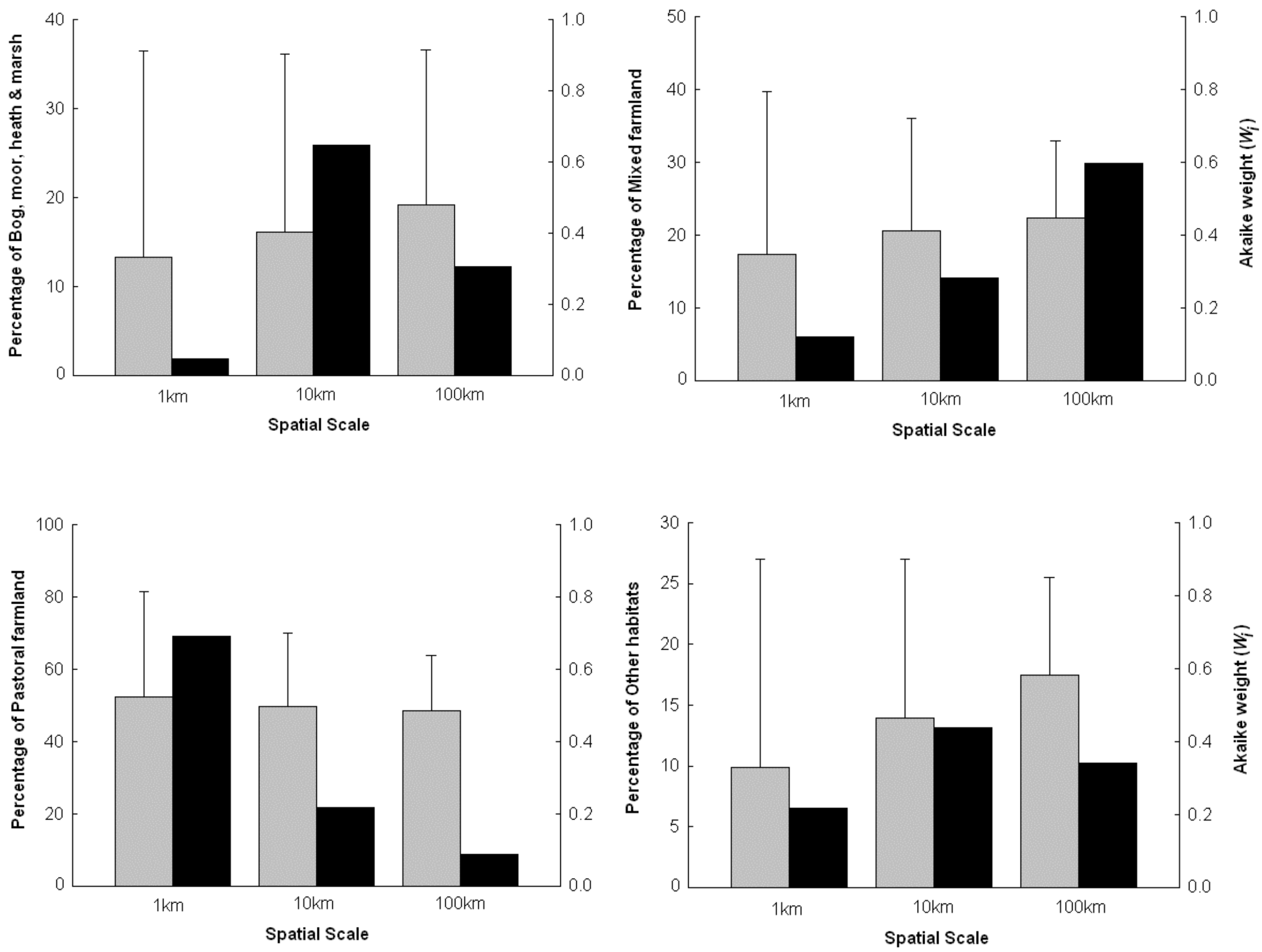


Fig. 17 *Selection of appropriate spatial scale for* ***(a)*** *bog, moor, heath & marsh,* ***(b)*** *mixed farmland,* ***(c)*** *pastoral farmland and* ***(d)*** *other habitats. The scale at which each variable was taken to operate was chosen as that which had the highest Akaike weight (black columns). Mean values ± standard deviations are shown as grey columns.*

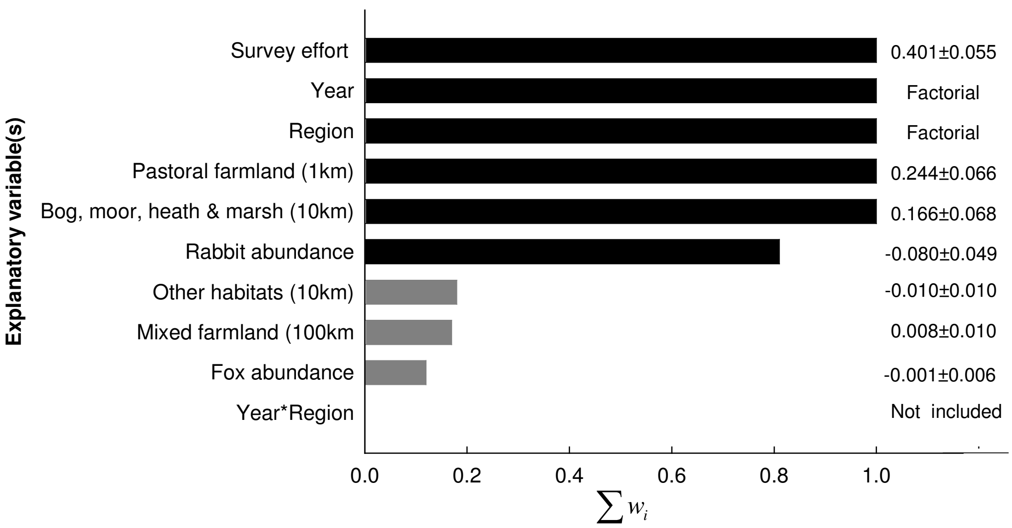


Fig. 18 *Relative importance of factors in explaining variation in the frequency of Irish hare sightings. Variables are ranked in order of the sum of their Akaike weights ($\sum w_i$) within the top set of models i.e. models with dAIC≤2. Black bars indicate those variables that were retained in the best single approximating model (i.e. that with the lowest AIC value) and grey bars indicate variables included in all other models within the top set. Notation to the right indicates the strength of the slopes for each standardised covariate.*

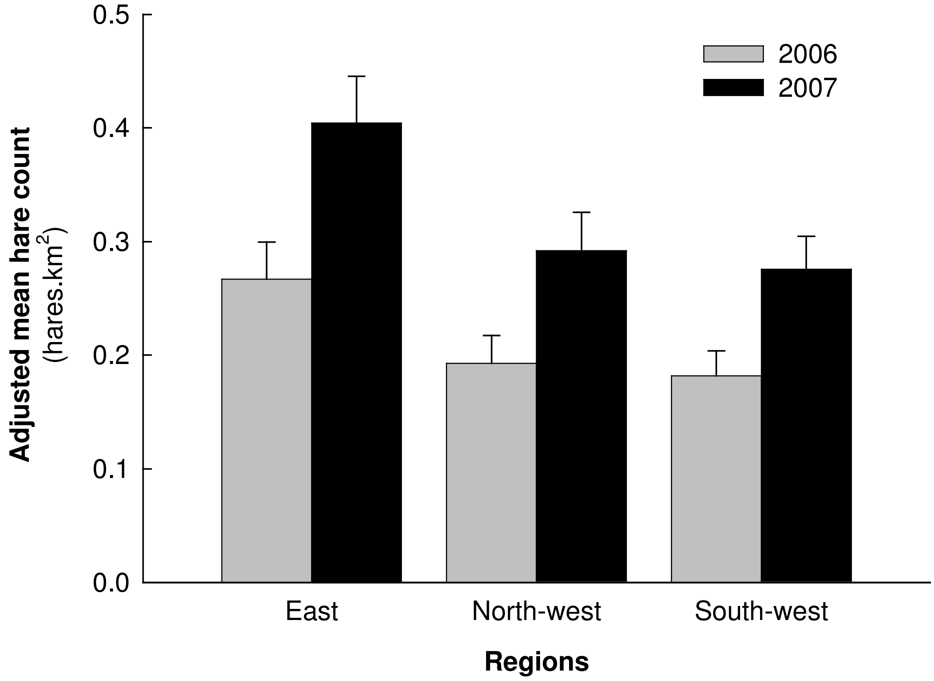


Fig. 19 *Adjusted mean frequency of hare sightings per survey square controlling for the effects of survey effort, habitat and rabbit abundance.*

Survey points located on the same transect are related and therefore not independent, for this reason the survey square, not the survey point, was taken as an independent sampling unit for variance estimation during Distance analyses. Most survey squares in both years contained 5 survey points, but some had less (Fig. 20). Survey effort was further affected by the angular bias anticipated by the sampling procedure (Fig. 21). The distribution of visible 20^o sectors around each survey point was non-uniform ($\chi^2_{df=17}$ = 356.00, $p<0.001$), with less search effort in segments lying more parallel to the road (Fig. 22). Partly as a consequence of this, and partly because of non-uniform hare distribution, the observed density of hares relative to the survey point exhibited a highly non-uniform distribution with respect to angle from road, with lower frequencies close to the road and greatest numbers being observed directly perpendicular to the road from the survey points. Using measured radial distances from the survey point (Fig. 23a) and calculated perpendicular distances from the road (Fig. 23b), the distribution of hare clusters exhibited a pronounced shoulder.

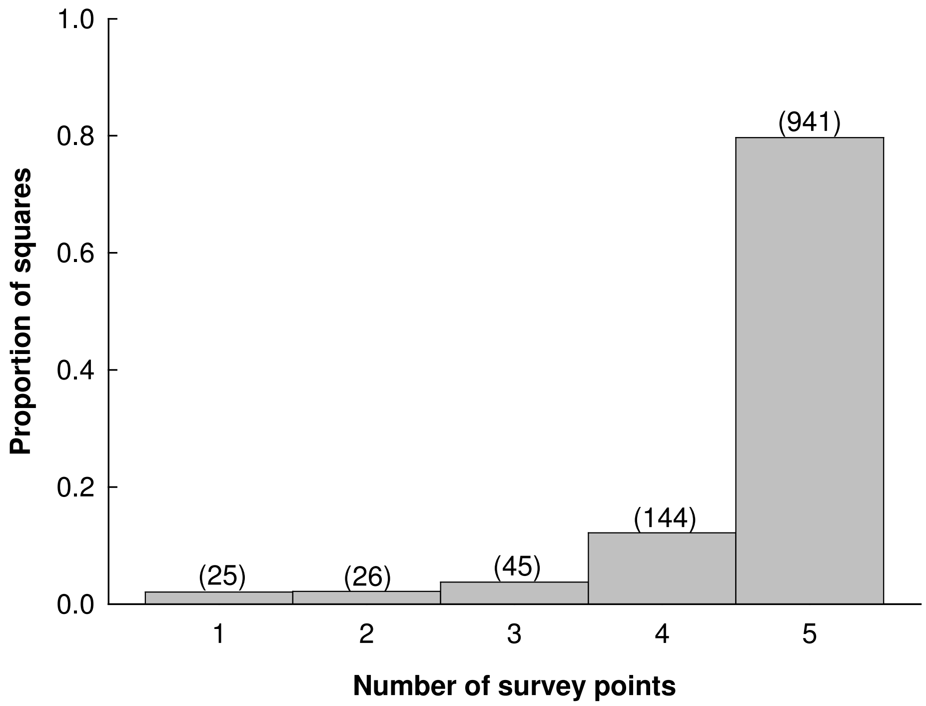


Fig. 20 *Distribution of the number of survey points within each survey square. Data from 2006 and 2007 combined and the sample size (n) in each case is shown in parentheses above the bars.*

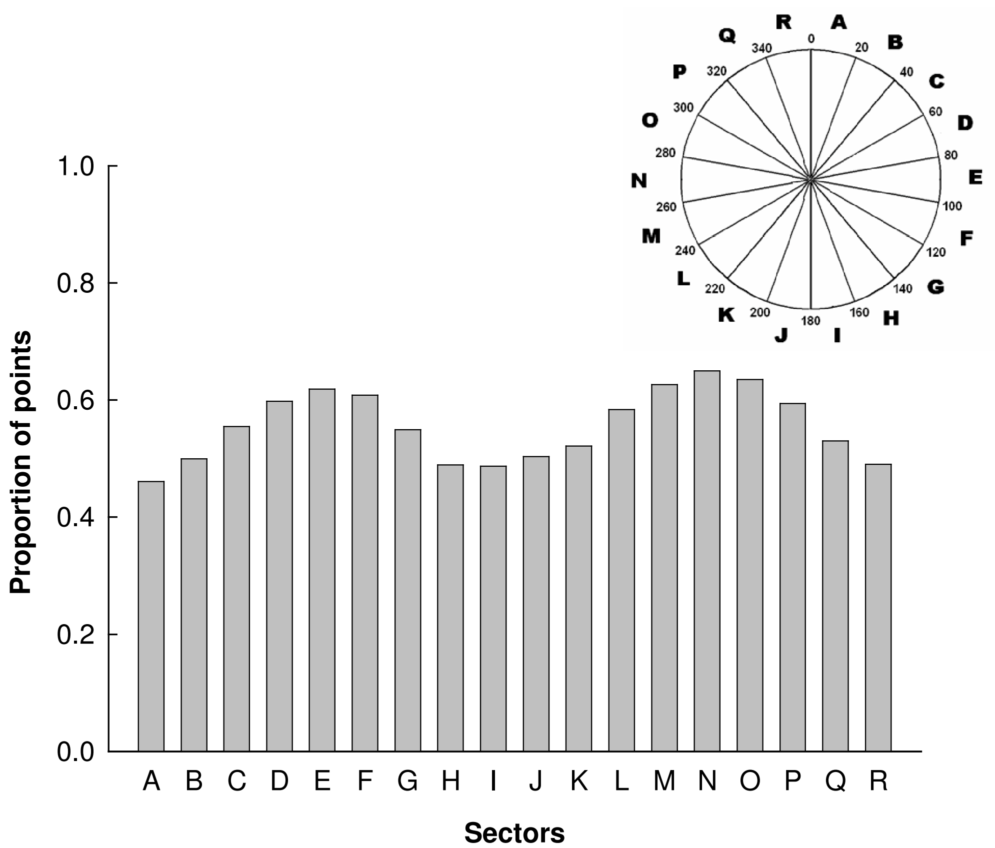


Fig. 21 *Proportion of survey points where each sector was visible across all field sectors. Sectors 'E' is perpendicular to the surveyor on the right side of the road (90-100^o) and sector 'N' is perpendicular to the surveyor on the left side of the road (260-280^o).*

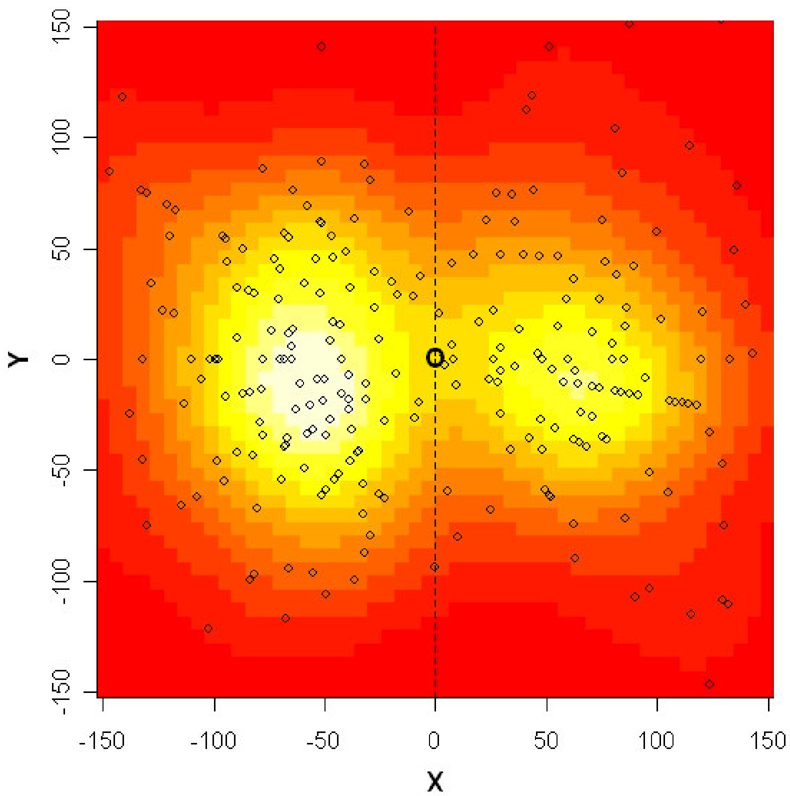


Fig. 22 *The positions of detected hares (small open circles) relative to the survey point (bold open circle at 0,0) and the road (dashed line). The intensity of colour is a smooth representation of the density of hare detections in space, with highest relative densities being white and lowest being red. Note that if the assumptions of conventional Distance sampling had been met a single hotspot of density would lie directly over the observed at co-ordinates 0,0.*

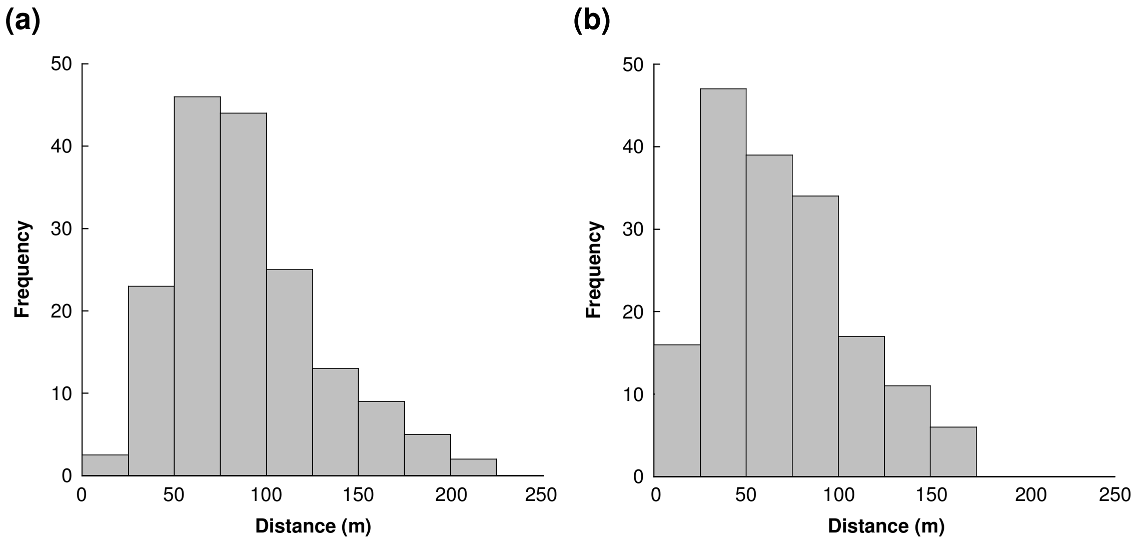


Fig. 23 *Frequency of distances of hare clusters measured* ***(a)*** *radially from survey points and* ***(b)*** *perpendicularly from the road for the 2007 survey.*

Customised Distance Sampling methods were used to estimate the parameters of both the detection function and density gradient of hares, while simultaneously accounting for the non-uniform angular sampling bias. Angular bias was not measured in 2006, however, data from 2007 were used to correct the 2006 data. A half-normal detection function was used with three models of density gradient including (a) half-normal, (b) hazard-rate and (c) Gaussian-based (Fig. 24). All models were right-truncated at a distance of 250m. These models assume that true hare density in each sector is independent of that sector being visible.

One troubling issue was that there was a subset of survey points where overall survey effort was noted, but the visibility in each sector was not recorded. This subset of data had a significantly higher median total field of view value (0.67 per survey square) than those squares in which the field of view breakdown was known (0.55 per survey square; Mann-Whitney W = 1281504, two-tailed $p<0.001$). Without data on the field of view broken down by sector, models of density gradient assume that effort distribution is the same for all survey points; this is evidently not the case. This may have introduced further bias, but additional data would be required to determine this.

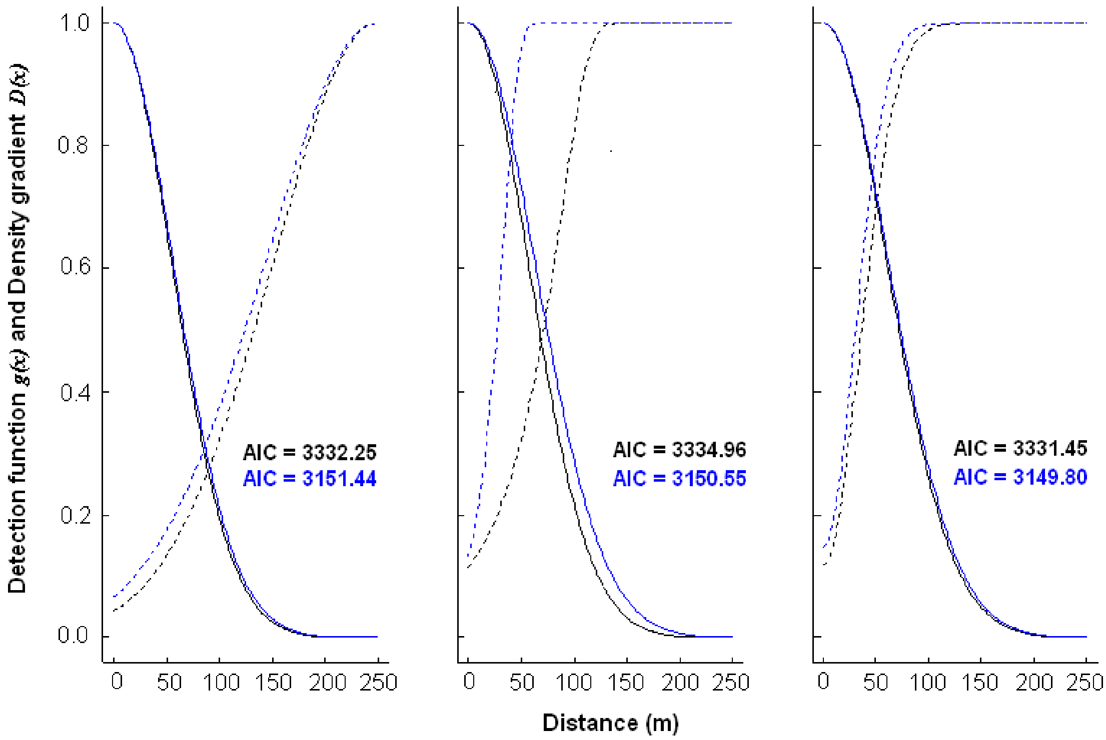


Fig. 24 *Estimated detection function (lines peaking at the left) and density gradient (lines peaking at the right) ignoring angular sampling bias (black lines) and accounting for it (blue lines) estimated using a (a) half-normal, (b) hazard-rate and (c) Gaussian based model showing the AIC value used for model selection.*

When using data from the points alone, all three models used to estimate the perceived density gradient of hares from the road in both years had similar AIC values implying they were equally good representations of the density gradient (Fig. 24). This is a concern because the models lead to very different estimates of density and abundance. The point transect data were, however, supplemented by the data on perpendicular distance of hare detections from the road from the night walked transfield transects. Use of these data which establish the extent to which hares actually avoid roads, allowed the Gaussian-based model to be chosen above others on the basis of AIC.

A total of 59 hares (in 42 groups) were observed on 432 night-walked transfield transect surveys. Six hare detections were made beyond 250m from the road and were excluded from further analyses as these would have been undetectable to any point surveys from the road. Unlike the point transect data, in which animals farther from the road are sampled with lower probability, transfield transect data can provide a direct sample from the distribution of distances of hares from roads (Fig. 25). As the total length of walked transfield transects varied (transects were walked perpendicular to the road until the first boundary was met), transfield data actually over-sample close distances relative to further distances. We refer to this decline in relative sampling intensity with distance as the "attenuation effect", and this was taken into account in the analysis (Fig. 26).

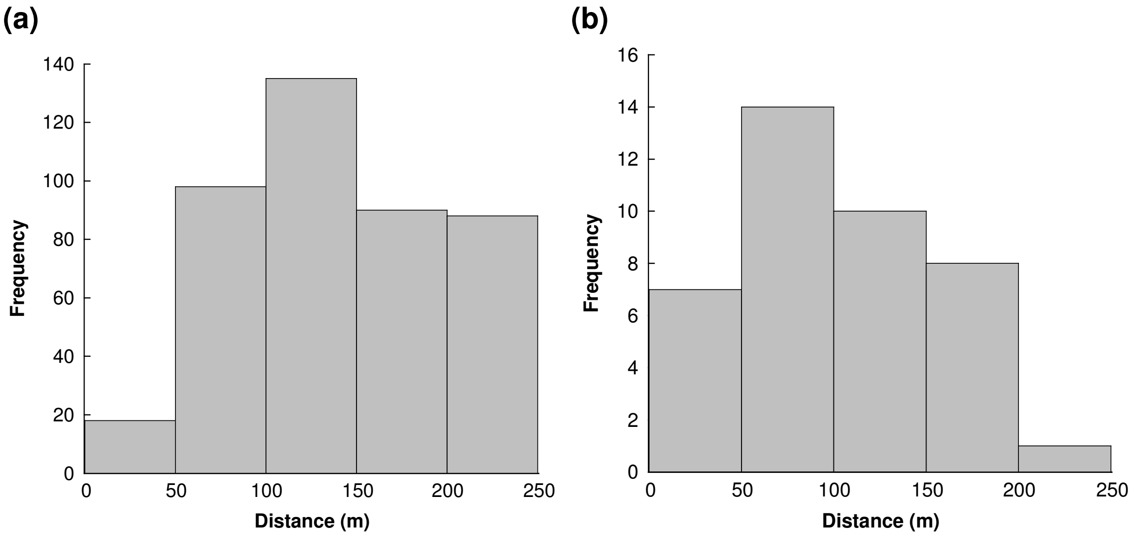


Fig. 25 *Frequency of **(a)** night-walked transfield transects length and **(b)** perpendicular distances of detected hare clusters from the road during 2006 and 2007 combined.*

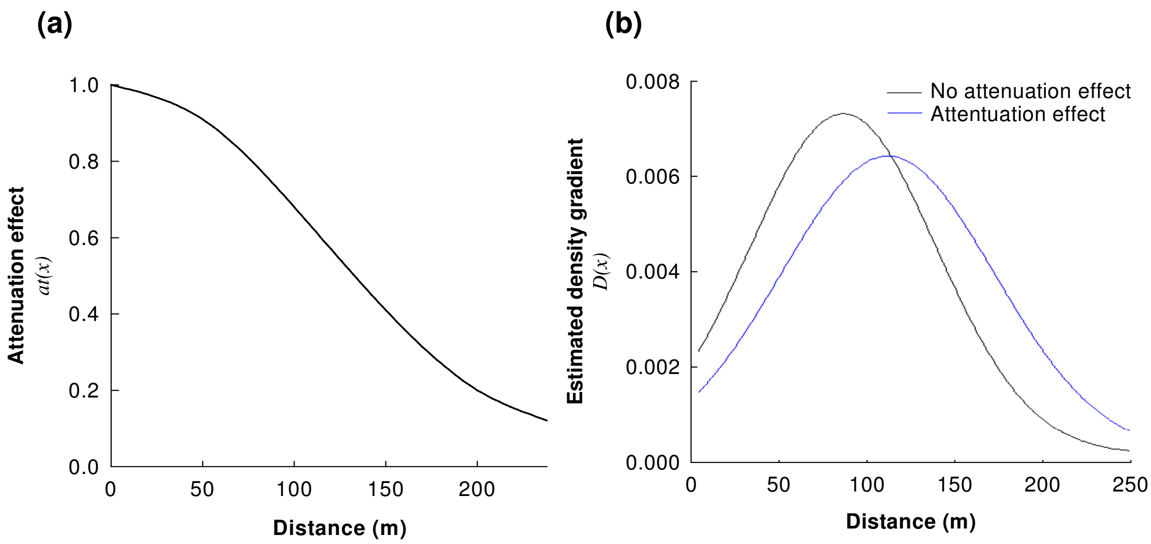


Fig. 26 **(a)** *The attenuation effect due to the varying lengths of transfield transects and* **(b)** *its effect on the estimated density gradient of hares from on-road point surveys.*

The estimated density gradient obtained from both the transfield transect data with attenuation and the point transect data (taking account of non-uniform angular effort) in the analysis is shown in Fig. 26 (using a Gaussian-based model for density gradient). The estimated modal density of hares occurred at 130m (Fig. 27), not 250m as was estimated in models that did not include the transfield transect data.

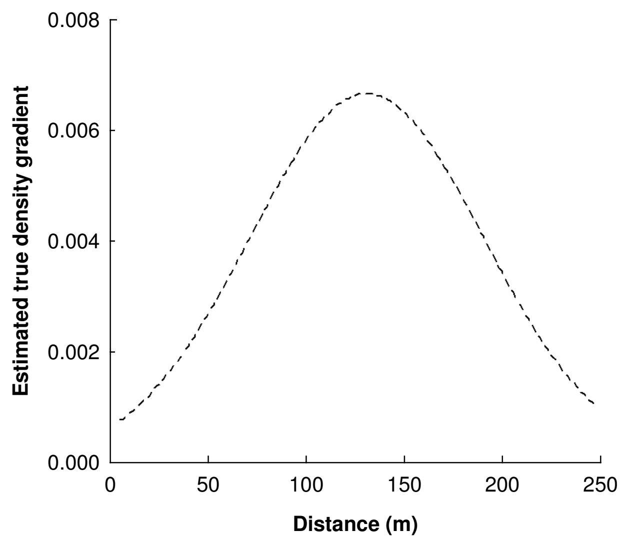


Fig. 27 *The estimated density gradient derived from on-road point surveys and walked transfield transect surveys with respect to distance from the road. Note modal density occurs at 130m from the road.*

Without taking any biases into account and using conventional distance analyses, estimated hare density would have been 1.72 hares/km^2 in 2006 and 2.29 hares/km^2 in 2007. Accounting for the sources of bias identified above and using custom Distance-analysis methods, hare density was estimated to be 3.33 hares/km^2 in 2006 and 7.66 hares/km^2 in 2007. Hare density increased significantly between 2006 and 2007 (pairwise comparison p<0.01, Table 6). Hare densities did not vary significantly between geographic regions in either year (pairwise comparison p=NS). During 2006, hare density did not differ significantly among habitats. During 2007, hare densities were significantly higher on pastoral farmland than both bog, moor, heath & marsh and other marginal habitats (pairwise comparison p<0.01, Table 7) but did not differ from mixed farmland.

Table 6 *Density and abundance estimates with 95% confidence intervals in parentheses for Irish hares during 2006 and 2007 stratified by geographic region. The total area of Republic of Ireland = 69,878km^2, West and North-west = 22,580km^2, East = 23,015km^2 and South-west = 24,283km^2.*

Region	2006		2007	
	Mean density (hares/km^2)	**Mean abundance**	**Mean density** (hares/km^2)	**Mean abundance**
West and North-west	2.62^a (1.30-4.67)	59,000 (29,000-105,000)	7.63^a (4.58-15.19)	172,000 (104,000-343,000)
East	4.20^a (2.32-8.20)	97,000 (53,000-189,000)	9.13^a (4.66-17.56)	210,000 (107,000-404,000)
South-west	3.16^a (1.35-6.78)	77,000 (33,000-165,000)	6.31^a (3.08-11.81)	153,000 (75,000-287,000)
Republic of Ireland (All regions)	**3.33* (1.97-6.21)**	**233,000 (138,000-434,000)**	**7.66* (4.83-14.29)**	**535,000 (338,000-999,000)**

^{a} Superscript lower case letters indicate no statistically significant difference between estimates. Pairwise comparison are only between regions within years.
**Overall density significantly different between 2006 and 2007*

Table 7 *Density and abundance estimates with 95% confidence intervals in parentheses for Irish hares during 2006 and 2007 stratified by habitat type. The total area of Bog, moor heath & marsh = 12,159km^2, Mixed farmland = 10,873km^2, Pastoral farmland = 37,315km^2 and Other marginal habitats = 9,531km^2.*

Habitats	2006		2007	
	Mean density (hares/km^2)	**Mean abundance**	**Mean density** (hares/km^2)	**Mean abundance**
Bog, moor, heath & marsh	5.11^a (1.62-12.47)	62,000 (20,000-152,000)	2.89^b (1.27-6.53)	35,000 (15,400-79,500)
Mixed farmland	3.06^a (1.51-5.41)	33,000 (16,000-59,000)	7.96^{a,b} (2.96-17.49)	87,000 (32,000-190,000)
Pastoral farmland	2.97^a (1.57-5.36)	111,000 (59,000-200,000)	9.18^a (5.96-17.11)	343,000 (223,000-641,100)
Other marginal habitats	2.64^a (0.79-5.07)	25,000 (7,500-48,000)	3.58^b (<0.001-8.14)	34,100 (0-77,800)
Republic of Ireland (All habitats)	**3.29 (1.94-6.06)**	**231,000 (137,000-425,000)**	**7.19 (5.46-11.07)**	**499,000 (326,000-966,000)**

^{a,b} Superscript lower case letters indicate no statistically significant difference between estimates. Pairwise comparison are only between habitats within years.

3.4 Discussion

Recognising that the task of estimating terrestrial mammal abundance is fraught with difficulties, particularly if the study species is predominantly nocturnal and exhibits complicating behaviour such as non-random animal distribution patterns (e.g. avoidance of roads); we have developed novel field survey techniques and innovative analytical solutions to the challenges of hare surveys.

The number of hares seen in survey squares could, with consistent sampling effort at repeated sites, be adopted as a rough index of hare abundance. However, many authors have highlighted problems associated with analyses of relative abundance due to sampling biases caused by variation in visibility and animal behaviour (Mahon, Banks & Dickman 1998; Edwards *et al.*, 2000). It is therefore necessary to interpret differences in sighting frequencies with caution. Hare abundance was positively influenced by the extent of pastoral grasslands within the immediate vicinity (within the 1km survey square) provided the local landscape (defined as the surrounding 10km grid square) was interspersed by rough areas such as bog, moor, heath and marsh. These results are to some degree consistent with previous work in Northern Ireland suggesting that hares require a patchwork of grassland habitats and rough rushy habitats to provide both quality grazing and suitable shelter (Reid *et al.*, 2007). Rabbit abundance had a negative relationship with the number of hares seen. Grazing affects the availability of herbaceous vegetation (MacCracken & Hansen, 1982) and competition between sympatric leporids is known (Homolka, 1987; Chapuis, 1990; Flux, 1993).

By using distance-sampling it was possible to estimate absolute density of hares and thereby improve on simple encounter rate indices. The level of detail and analysis was, however, rather involved because many of the central assumptions of distance-sampling theory are broken by point surveys of hares conducted from roads. Assumptions relating to measurement of distances and angles were fully met. Critically, however, hares do not distribute themselves uniformly with respect to roads. Furthermore, roadside hedges (a typical feature of the Irish landscape) obscured vision in the portions of the point transects immediately adjacent to the road. Previous researchers have dealt with these biases by left truncation and/or grouping animal detections into bins. Whilst these techniques are commonly applied they are inadequate for dealing with the major biases identified here and would have resulted in flawed estimates of hare abundance. We developed novel distance sampling estimation methods to deal with the particular nature of these surveys.

Despite the analytical complications of working from roads, for Irish hare surveys, spotlight counts from minor roads is the only realistic way of surveying enough land to obtain the minimum number of sightings required to estimate density with some degree of precision. In Ireland, particularly rural areas, both road density and traffic volumes are low, especially at night, and recent radio-tracking experience suggests that minor roads were neither avoided nor used preferentially by Irish hares during either the day or night (Neil Reid, pers. obs.). It seems likely that the avoidance behaviour observed was in reference to field boundaries in general rather than roads in particular. However plausible this argument may be, the calculation of general hare abundance based on surveys within the 250m strip either side of roads rests on the untested assumption that the density of hares in this strip is not significantly different from that in the wider countryside. If this assumption is wrong, and there is higher or lower hare density outside of this area, the densities provided here will be biased for the area beyond the immediate vicinity of roads.

If the underlying assumptions of our survey and analytical methods hold, the abundance of Irish hares in the Republic of Ireland is in the order of several hundred thousand albeit with wide confidence limits. The estimated density of 7.66 hares/km^2 (95% CI 4.83-14.29) in the Republic of Ireland is entirely consistent with the estimate for Northern Ireland of 7.99 hares/km^2 (95% CI 4.18-14.46) during early 2007 (Reid, *et al.* 2007b), using comparable survey methods and analytical techniques. The estimated abundance of hares in the Republic of Ireland taken together with the results of the Northern Ireland hare survey in 2007 (Reid, *et al.* 2007b), suggest that there were 649,000 hares (95% CI 432,000-1,198,000) in Ireland as a whole during early 2007. Irish hare densities have been reported to range from 1.0-126.6 hares/km^2 (Fairley, 2001; Jeffrey, 1996), with current estimates being comparable to that recorded on mixed farmland during winter in Kildare (6.8 hares/km^2; Whelan, 1985). 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 dramatic short-term population change and it is plausible that the population could have more than doubled between 2006 and 2007. Local weather conditions and climatic events have been suggested as driving forces for mountain hare population change (see *Section 2.2 Game bag records*). It is noteworthy that most of the change in populations between 2006 and 2007 was ascribed to change in densities on pastoral farmland. This may reflect the importance of grassland habitats to Irish hares, particularly with regards to management practices. Specifically, a delay in silage cutting during 2006 caused by unusually wet conditions during late spring and early summer may have facilitated leveret maturation, survival and recruitment during that year. Furthermore, 2006 was one of the highest North Atlantic Oscillation Index years in the last decade with mild autumn and winter conditions. An extended period of grass growth may have extended hare reproduction and aided over-winter survival of adults.

Between-year comparisons of densities within different habitats could not be made. Estimates for bog, moor, heath and marsh in 2006 are based on few sightings and have extremely wide confidence intervals so should be treated with caution. It is possible that under-sampling of habitats with respect to vegetation height may have biased detection rates. Densities in 2007 are more reliable than 2006 due to an increased number of sightings. The prevalence of suitable pastoral grassland throughout the three geographic regions was similar; consequently, regional differences in mean hare densities are unremarkable.

In relation to Article 2 of the EC Habitats Directive, without temporal data comparable to the current survey there is little information by which to define “favourable conservation status” for the Irish hare. All that can be said with certainty is that total abundance of Irish hares in Ireland is higher than expected based on previous Northern Ireland hare surveys and that given favourable environmental conditions the population appears robust enough to undergo an apparent doubling within one year. It seems likely that the greatest potential for successful anthropogenic intervention in hare populations, in line with the objectives of the Irish hare Species Action Plan (Anon, 2005), is in areas of extensive pastoral farmland.

The brown hare is well established in Northern Ireland (Reid & Montgomery, 2007). Whilst not confirmed as present in the Republic of Ireland during these surveys, its presence cannot be ruled out. Given the difficulty in distinguishing the brown hare from the native Irish hare and the frequently localised nature of introduced populations, further work is required, particular in those areas in which anecdotal reports have been made.

In conclusion, the custom Distance-sampling methods developed here are useful for demonstrating differences in hare density over time, regions and landclasses. The current study is not directly comparable to previous work on Irish hare distribution in the Republic of Ireland (Ni Lamhna, 1979; Smal, 1995; Fig. 1.2), however, the species remains widespread and common, and has been shown to exhibit substantial interannual fluctuations in density.

4 General discussion

This is the first study to establish long-term historical population trends and provide robust estimates of current and recent density and abundance of Irish hares in the Republic of Ireland. Historically, Irish hare populations may have been many times higher than the current population and, based on game-bag analysis, a long-term decline in abundance of hares in Ireland coincided with similar declines in Great Britain and Europe. Changes in land management practises during the early 20th century and ongoing agricultural intensification throughout the mid-late 20th century are the most influential amongst factors that have contributed to historical declines of hares (Smith *et al*. 2005).

Irish populations, similar to hares elsewhere, exhibit marked interannual and multiannual fluctuations. Intrinsic density dependence and extrinsic climatic factors clearly influence annual population growth. Interannual fluctuations remain a feature of the contemporary hare population with total estimated abundance in the Republic of Ireland increasing significantly from 233,000 to 535,000 hares between 2006 and 2007. Such dramatic short-term change is consistent with the fluctuations observed in historical game bag indices, suggesting that substantial changes in the hare population are not unusual.

Interpretation of short-term changes should be made in the context of long-term time-series. General population declines can be ongoing, despite short term increases. In this case, there are no reliable data to establish recent population trends. Despite the likelihood that recent studies of Irish hare population status in Northern Ireland contain negative bias, the interannual fluctuations identified are likely to reflect genuine change in the hare population. The current All-Ireland population of Irish hares is estimated at 649,000 hares (95% CI 432,000-1,198,000; this study; Reid *et al*. 2007b).

The Distance-sampling methodologies, both field surveys and statistical models, developed in this study have proven useful and robust tools for demonstrating hare population change over time. However, we have to stress that care must be taken to account for biases introduced not only from sampling protocols but also animal behaviour, when assessing hare abundance using these methods and surveying from roads. Further work is desirable to verify the assumption that the density of the hare population is similar in the area adjacent to roads and the rest of the countryside.

Establishing a population increase by 2010, as required by the Irish hare Species Action Plan, needs to be evaluated carefully as a target. Given what is known of fluctuations in the Irish hare population, a doubling, or indeed a halving of the population from one year to the next may not be unusual and cannot be interpreted as a measure of success or failure of conservation strategies. Consequently, regular continued surveillance of the population is necessary to establish long-term population trends.

5 Recommendations

Variation in the Irish hare population can be substantial over a short period of time. When fluctuations are pronounced populations must be monitored for longer to determine trends. Multiannual cycles complicate monitoring further and would require a much longer time-series. If a full understanding of contemporary trends is required, annual population monitoring in some considerable detail will be required. Undertaken at the scale applied here, such monitoring would place considerable strain on existing resources and manpower. Consequently, it will be necessary to carefully evaluate the purpose of monitoring in order to design a cost-effective approach.

For comparability between surveys over time, a standard methodology must be adopted that is repeatable and provides widespread coverage with a large number of statistically independent replicates. Simple counts are labour intensive and relatively easy but are wholly inadequate for the calculation of national population estimates. Repeated observations by NPWS personnel of the same points over time, together with recording of certain other metrics (distance and visibility) that would allow analysis by specialist contractors when resources permitted, may prove a compromise strategy for routine determination of trends. No advantage is gained by adopting a simple count method, with no measurements of distance or visibility, over a Distance-sampling method as labour is only reduced marginally but potential biases are greatly enhanced. Consequently, future data collection should be based on the survey and analytical methods developed here.

A cost effective tool to provide further information for monitoring the Irish hare population, particularly in areas where the species is exploited, would be to pilot the collection of capture effort data by coursing clubs.

The precise mechanisms that drive interannual and multiannual hare population change remain unknown. Evidently, such drivers can have a substantial impact on population change. Without a better understanding of factors affecting hare population growth, it is not possible to develop or implement measures for enhancing hare populations.

Conservation policies, such as the Irish hare SAP, would benefit from revision at regular intervals to account for emerging scientific information regarding the biology and status of the species. The success of conservation strategies in increasing the Irish hare population should account for natural variation and periodicity exhibited by the species. Care must be taken not only to establish realistic conservation targets, with some supportable means of achieving these, but also to ensure that the success or failure of SAP measures can be properly evaluated. One potential area of future research is to evaluate the efficacy of the REPS scheme in maintaining and improving suitable hare habitat within areas of pastoral farmland.

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7 References

Abildgård, F., Andersen, J. & Barnorff-Nielsen, O (1972) The hare population (*Lepus europaeus*, Pallas) of Illumø Island, Denmark. A report on the analysis of the data from 1959 to 1970. *Danish Review of Game Biology*, **6**, 1-31.

Akaike, H. (1983) Information measure and model selection. *Bulletin of the International Statistical Institute*, **50**(1), 277-291.

Alves PC, Ferrand N, Suchentrunk F, Harris DJ (2003) Ancient introgression of *Lepus timidus* mtDNA into *L. granatensis* and *L. europaeus* in the Iberian Peninsula. *Molecular Phylogenetics and Evolution*, **27**, 70–80.

Andrejewski, R. & Jezierski, W. (1966) Studies on European hare. XI. Estimation of population density and attempt to plan the yearly take of hares. *Acta theriologica*, **11**; 433-488.

Angell, J.K. (2001) Relation of size and displacement of the 300 mbar north circumpolar vortex to QBO, El Nino, and sunspot number, 1963-2000. *Journal of Geophysical Research – Atmospheres*, **106**(D23): 31787-31794.

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

Anonymous (1992) *Convention on Biological Diversity*. Rio de Janeiro. Brazil.

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

Baghli A. & Verhagen R. (2003) The distribution and status of the polecat *Mustela putorius* in Luxembourg. *Mammal review*, 33; 57-68.

Barrett-Hamilton, G.E.H. (1910) *A History of British Mammals*. Vol. **2**, pp 325-348. London. UK.

Battersby, J.E. & 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.

Bearzi, G. (2003). *Delphinus delphis* (Mediterranean subpopulation). In: IUCN 2006. *2006 IUCN Red List of Threatened Species.* www.iucnredlist.org

Bell, T. (1837) *History of British Quadrupeds, including the cetacea*. 1st ed. pp 341. London. UK.

Benner, T.C. (1999) Central England temperatures: long-term variability and teleconnections. *International Journal of Climatology*, **19**(4):391-403.

Bochnicek, J. & Hejda, P. (2006) Connections between the distribution of prevailing winds in the winter Northern Hemisphere, solar/geomagnetic activity and the quasi-biennial oscillation (QBO) phase. *Studia Geophysica Geodaetica*, **50**(2): 299-318.

Boutin, S., Krebs, C. J., Boonstra, R. (1995). Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos*, **74**: 69–80.

Bröekhuizen, S. & Masskamp, F. (1982) Movement, home range and clustering in the European hare (*Lepus europaeus* Pallas) in the Netherlands. *Zeitschrift fur Saugetierkunde*, 47;22-32.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas (2004) *Advanced Distance Sampling*. Oxford University Press. UK.

Burnham, K.P., Anderson, D.R. (2002) *Model selection and Multimodel Inference: A practical information-theoretic approach*, 2nd edn. Springer, New York, USA.

Butler, C.J., Coughlin, A.D.S. & Fee, D.T. (1998) Precipitation at Armagh Observatory 1838-1997. *Biology and Environment, Proceedings of the Royal Irish Academy*, **98B**(2): 123-140.

Cary, J.R., and Keith, L.B. (1979). Reproductive change in the 10-year cycle of snowshoe hares. *Canadian Journal of Zoolog*y, **57**: 375–390

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**; 176–185.

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.

CRAN (2007) *The Comprehensive R Archive Network*. http://cran.r-project.org/

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.

Donald, P.F. (1998) Changes in the abundance of invertebrates and plants on British farmland. *British Wildlife*, **9**, 279–289.

Edwards, G.P., de Preu, N.D., Shakeshaft, B.J. & Crealy, I.V. (2000) An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildlife Research*, **27**, 143–149.

EEA (2000) *Corine Land Cover map 2000* – digital data. European Environment Agency. http://www.eea.europa.eu/

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.

Feore, S.M. (1994) *The distribution and abundance of the Badger Meles meles L. in Northern Ireland*. Unpublished PhD thesis. Queen's University Belfast.

Fielding, A.H. & Haworth, P.F. (1995) Testing the generality of bird-habitat models. *Conservation Biology*, **9**, 1466-1481.

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.

Gross, J. W., L. C. Stoddart, and F. H. Wagner. (1974). Demographic analysis of a northern Utah jackrabbit population. Wildlife Monographs Number **40**:1–68.

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.

Hamill, R.M., Doyle, D. & Duke, E.J. (2006) Spatial patterns of genetic diversity across European subspecies of mountain hare, *Lepus timidus* L. *Heredity,* 1-11.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) *A Review of British Mammals: population estimates and conservation status of British mammals other than cetaceans*. JNCC, Peterborough. UK.

Harris, S. & Yalden, D.W. (2004) An integrated monitoring programme for terrestrial mammals in Britain. *Mammal Review*, **34** 1/2; 157-167.

Hayden, T. & Harrington, R. (2000) *Exploring Irish mammals.* Town House and Country house Ltd, Dublin. Ireland.

Hellawell, J.M. (1991) *Development of a rationale for monitoring. In Goldsmith B., Ed., Monitoring for conservation and ecology*. Chapman and Hall, London, pp 1-14.

Hodges, K.E. (2000) *Ecology of snowshoe hares in southern boreal and montane forests*. *In* Ecology and conservation of lynx in the United States. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-30WWW, 163–206.

Homolka, M. (1987) A comparison of the trophic niches of *Lepus europaeus* and *Oryctolagus cuniculus*. *Folia Zoologica,* **36**; 307–317.

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.

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

Hurrell, J. W., & H. van Loon (1997) Decadal Variations in Climate associated with the North Atlantic Oscillation. *Climate Change*, **36**, 301-326.

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

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., J. R. Carey, O. J. Rongstad & M. C. Brittingham (1984) Demography and ecology of a declining snowshoe hare population. *Wildlife Monographs*, **90**:1-43

Keith, L. B. (1990) Dynamics of snowshoe hare populations. *Current Mammalogy,* **2**: 119–195.

Kodera, K. & Kuroda, Y. (2005) A possible mechanism of solar modulation of the spatial structure of the North Atlantic Oscillation. *Journal of Geophysical Research – Atmospheres,* **110**(D2): D02111.

Korpimaki, E., Brown, P.R., Jacob, J. & Pech, R.P. (2004) The puzzles of population cycles and outbreaks of small mammals solved? *Bioscience*, **54**(12): 1071-1079.

Korpimaki, E., Norrdahl, K., Huitu, O. & Klemola, T. (2005) Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proceedings of the Royal Society B-Biological Sciences*, **272** (1559): 193-202.

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., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K., and Turkington, R. (1995) Impact of food and predation on the snowshoe hare cycle. Science (Washington, D.C.), **269**: 1112–1115.

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.

Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guiness, F.E. (1999) Population density affects sex ratio variation in red deer. *Nature*, **399**: 459-461.

Lamb, P.J., & R.A. Peppler (1987) North Atlantic Oscillation: concept and application. *Bulletin of Amercian Meterological Society*, **68**; 1217-1225.

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.

Linnaeus, C. (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* 10th edn. Stockholm. Sweden.

Lukianova, R. & Alekseev, G. (2004) Long-term correlation between the NAO and solar activity. *Solar Physics*, **224**(1): 445-454.

MacCracken, J.G. & Hansen, R.M. (1982) Herbaceous vegetation of habitat used by Blacktail Jackrabbits and Nuttall Cottontails in Southeastern Idaho. *America Midlands Naturalist,* **107**; 180–184

Macdonald, D.W., Mace, G. & Rushton, S.P. (1998). *Proposals for Future Monitoring of British Mammals*. Department of the Environment, Transport and the Regions / Joint Nature Conservation Committee.

Mahon, P.S., Banks, P.B. & Dickman, C.R. (1998) Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. *Wildlife Research*, **25**, 11–22.

Mallon, D., Wheeler, P., Whiteley, D. & Yalden, D.W. (2003). Mountain hares in the Peak District. *British Wildlife*, **15**; 110–116.

Matheson, C. (1941) The rabbit and the hare in Wales. *Antiquity*, **1941**; 371-381.

McAney, K. (2006) A conservation plan for Irish vesper bats. *Irish Wildlife Manuals* No. 20. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland.

McCullagh, P. & J.A. Nelder. (1989) *Generalized Linear Models*. Chapman and Hall: London.

Middleton, A.D. (1934). Periodic fluctuations in British Game. *Journal of Animal Ecology*, **3**; 231–249.

Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V. & Zima, J. (1999) *Atlas of European Mammals*. Academic Press, London.

Newey, S. & Thirgood, S. (2004) Parasite-mediated reduction in fecundity of mountain hares. *Proceedings of the Royal Society B-Biological Sciences*, **271**(Suppl.); 543-545.

Newey, S., Shaw, D.J., Kirby, A., Monteith, P., Hudson, P.J. & Thirgood, S.J. (2005) Prevalence, intensity and aggregation of intestinal parasites in mountain hares and their potential impact on population dynamics. *International Journal of Parasitology*, **35**, 367-363.

Ní Lamhna, E. C. (1979) *Provisional distribution Atlas of Amphibians, Reptiles and Mammals in Ireland*. 2nd Edition. An Foras Forbatha. Ireland.

Ogi, M., Yamazaki, K. & Tachibana, Y. (2003) Solar cycle modulation of the seasonal linkage of the North Atlantic Oscillation (NAO). *Geophysical Letters*, **30**(22): Art. Number 2170.

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.

Patterson, H.D. & Thompson, R. (1971) Recovery of interblock information when block sizes are unequal. *Biometrika*, **58**: 545-554.

Patterson, B.R. & Power, V.A. (2001) Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. *Oecologia*, **128**, 244–255.

Pépin, D. (1985) Spring density and day time distribution of the European hare in relation to the habitat in an open field agrosystem. *Zeitschriff für Säugetierkunde*, **51**, 79-86.

Perez, J.M., Granados, J.E., Soriguer, R.C., Fandos, P., Marquez, F.J., and Crampe, J.P. (2002) Distribution, status and conservation problems of the Spanish ibex, *Capra pyrenaica* (Mammalia: Artiodactyla). *Mammal Rev.* **32**(1):26-39.

Pielowski, Z. (1990) Über die Abhängigkeit der Besatzdichte und anderer Populationsparameter des Hasen von der Agrarstruktur und landwirtschaftlichen Aktivitäten. *Beiträge Zur Jagd- und Wildforschung*, **17**, 147–156.

Post, E. & Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**(4): 1322-1339.

Preston, C.D., Telfer, M.G., Arnold, H.R., Carey, P.D., Cooper, J.M., Dines, T.D., Hill, M.O., Pearman, D.A., Roy, D.B. & Smart, S.M. (2002) *The Changing Flora of the UK.* DEFRA: Department for Environment, Food & Rural Affairs , London. UK.

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.

Quinn, G.P. & Keough, M.J. (2002) *Experimental design and data analysis for biologists*. Cambrigde University Press, Cambridge, UK.

Ranta, E., Lindstrom, J., Kaitala, V., Kokko, H., Linden, L. & Helle, E. (1997) Solar activity and hare dynamics: a crosscontinential comparison. *American Naturalist*, **149**, 765-775.

Reeves, R.R. (2002) The origins and character of 'aboriginal subsistence' whaling: a global review. *Mammal Review,* **32**: 71-106.

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

Reid, N., Montgomery, W.I. & McDonald, R.A. (2007) Mammals and agri-environment schemes: hare haven or pest paradise? *Journal of Applied Ecology*, doi: 10.1111/j.1365-2664.2007.01336.x

Reid, N. & Montgomery, W.I. (2007) Is naturalisation of the brown hare in Ireland a threat to the endemic Irish hare? *Biology and Environment: Proceedings of the Royal Irish Academy*, **107**B, 1-10.

Reid, N., Sweeney, O., Wilson, C., Preston, S.J., Montgomery, W.I. & McDonald, R.A. (2007b) *Northern Ireland Irish hare survey 2007.* Report prepared by Quercus for the Environment and Heritage Service (DOE, N.I.). UK.

Reid, N., Montgomery, W.I. & McDonald, R.A. (2007) Factors associated with hare mortality during coursing. *Animal Welfare*, **16** (4).

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.

Royama, T. (1992) *Analytical population dynamic*s. Chapman & Hall, New York. USA.

Schmidt, N.M., Asferg, T. & Forchhammer, M,C. (2004) Long-term patterns in European brown hare population dynamics in Denmark: effects of agriculture, predation and climatic. *BMC Ecology*, **4**(15).

Selvas, V. (2006) UV-B-induced plant stress as a possible cause of ten-year hare cycles. *Population Ecology*, **48**(1): 71-77.

Sinclair, A.R.E., Gosline, I.M., Holdsworth, G., Krebs, C.J., Boutin, S., Smith, I.N.M., Boonstra, R. & Dale, M. (1993) Can the solar-cycle and climate synchronize the snowshoe hare cycle in Canada - Evidence from tree rings and ice cores. *American Naturalist*, **141**(2): 173-198.

Sinclair, A. R. E., Krebs, C.J., Smith, J. M. N. & Boutin, S. (1988) Population biology of snowshoe hares. III. Nutrition, plant secondary compounds and food limitation. *Journal of Animal Ecology* **57**: 787–806.

Smal, C. (1995) *The badger and habitat survey of Ireland*. Report to NPWS, Department of Environment, Heritage and Local Government. Government Publications, Dublin. ISBN 0-7076-1604-2.

Smith, C.H. (1983) Spatial trends in Canadian snowshoe hare, *Lepus americanus*, population cycles. *Canadian Field Naturalist*, **97**: 151-160.

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.

Stefan, C.I. (1998) *Reproduction and pre-weaning juvenile survival in a cyclical population of snowshoe hares.* MSc. thesis, University of British Columbia, Vancouver. Canada.

Stenseth, N.C., Chan, K.-S., Tong, H., Boonstra, R., Boutin, R., Krebs, C.J., Post, E., O'Donoghue, M., Yoccoz, N.G., Forchhammer, M.C. & Hurrell, J.W. (1999) Common dynamic structure of Canada lynx populations within three climatic regions. *Science* **285**, 1071-1073.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S., Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**(5585): 1292-1296.

Stenseth, N.C., Ottersen, G., Hurrell, J.W. Mysterud, A., Lima, M., Chan, K.S., Yoccoz, N.G. & Adlandsvik, B. (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Nino Southern Oscillation and beyond. *Proceedings of the Royal Society of London B-Biological Series*, **270**(1529): 2087-2096.

Stokes, K., O'Neill, K. and McDonald, R.A. (2006) *Invasive species in Ireland.* 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.

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. (1987) Cycles in game bag records of hares and rabbits in Britain. *Symposia of the Zoological Society of London*, **58**, 79-98.

Tapper, S.C. (1992) *Game Heritage: an Ecological Review from Shooting and Gamekeeping records.* Game Conservancy, Fordingbridge, UK.

Thulin, C.G. (2003) The distribution of Mountain Hares (*Lepus timidus*, L. 1758) in Europe: A challenge from Brown Hares (*L. europaeus*, Pall. 1778)? *Mammal Review*, **33**: 29-42.

Toms, M.P., Siriwardena, G.M. & Greenwood, J.J.D. (1999) *Developing a mammal monitoring programme for the United Kingdom.* BTO Research Report Number 223. British Trust for Ornithology, Thetford. UK.

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.

Tourpali, K., Schuurmans, C.J.E., van Dorland, R., Steil, B., Bruhl, C. & Manzini, E. (2005) Solar cycle modulation of the Arctic Oscillation in a chemistry-climate model. *Geophysical Research Letters*, **32**(17): L17803.

Trostel, K., Sinclair, A. R. E., Walters, C. & Krebs, C.J. (1987). Can predation cause the 10-year hare cycle? *Oecologia* **74**: 185–193.

Versteegh, G.J.M. (2005) Solar forcing of climate 2: Evidence from the past. *Space Science Reviews*, **120**(3-4): 243-286.

Walker, J. & Fairley, J.S. (1968) Winter food of Irish hares in County Antrim, Northern Ireland. *Journal of Mammalogy,* **49**, 783-785.

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.

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

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. & Bradbury, R.B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture Ecosystems & Environment*, **75**, 13–30.

Wolfe, A. Whelan, J. & Hayden, T.J. (1996) Dietary overlap between the Irish mountain hare, *Lepus timidus hibernicus* and the rabbit *Oryctolagus cuniculus* on coastal grassland. *Biology and Environment: Proceedings of the Royal Irish Academy*, **96B**, 89-95.

Appendices

Appendix 1 Contribution of records from each shooting estate to the gamebag database.

Estate name	County	Province	Years represented	Percentage of total years (%)	Percentage of total hare count (%)
Castle Archdale	Fermanagh	Ulster	1859-1867 1899-1941	14.6	14.8
Castlegar	Galway	Connaught	1854-1856 1858-1860 1865-1875 1878-1890 1917-1921	8.8	5.2
Crom	Fermanagh	Ulster	1858-1865 1895-1896 1924-1956	13.0	13.0
Dromoland	Clare	Connaught	1875-1884	2.9	1.8
Favour Royal	Tyrone	Ulster	1928-1932	1.3	0.1
Finnebrogue	Down	Ulster	1875-1886	3.6	5.8
Headfort	Meath	Leinster	1865-1892	7.8	13.5
Kenmare	Kerry	Munster	1897-1898 1902-1907 1909-1910	0.6	0.2
Lissadell	Sligo	Connaught	1846-1847 1853-1863 1890-1895 1900-1934 1938-1945	16.9	28.8
Louth House	Louth	Leinster	1900-1901	0.3	<0.1
Oakpark	Carlow	Leinster	1878-1891 1894-1895 1897-1899 1946-1949	5.8	2.7
Parkanaur	Tyrone	Ulster	1876-1902 1919-1954	12.0	0.6
Shane's Castle	Antrim	Ulster	1921-1927 1929-1937 1956-1970	8.8	9.7
Wicklow House	Wicklow	Leinster	1874-1886	3.6	3.7

Appendix 2 Survey teams that participated in the Hare Survey of Ireland 2006/07.

Survey teams	Number of points surveyed
40 teams	
Barry O'Donoghue & Penny Bartlett	165
Brian Haran, John Higgins & Eoin McGreal	179
Cameron Clotworthy, Maurice McDonald & Denis Strong	71
Carl Byrne *et al.*	148
Ciara Flynn & Roy Thompson	141
Ciarán Foley *et al.*	171
Clare Heardman & Paddy Graham	226
Cyril Saich & Sean Breen	197
Danny O'Keeffe & Donal Scannell	261
David Lyons & Emma Granville / Sinead Biggane	160
David McNamara & Miriam Crowley	241
Declan O'Donnell & Michael O'Sullivan	57
Denis O'Higgins *et al.*	64
Enda Mullen *et al.*	275
Eva Sweeney & Tim Burkitt	219
NPWS Research (Ferdia Marnell & Rebecca Jeffrey / Naomi Kingston / Deirdre Lynn)	268
Ger O'Donnell, Robert Holloway & Aonghus O'Donaill	114
Irene O'Brien, James Kilroy & Denis Strong	144
Jerry Higgins & Robert Steed	69
John Mathews *et al.*	104
Judit Kelemen *et al.*	128
Kathryn Freeman & Padraig O'Sullivan	10
Liam Lenihan & Seamus Hassett	261
Lorcan Scott & Jimi Conroy	170
Mark Byrne & Rebecca Teesdale	112
Maurice Eakin *et al.*	294
Neil Reid & Karina Dingerkus	142
Noel Buglar & Colm Malone	197
Paddy O'Sullivan & Tony Murray	57
Padraig O'Donnell & Denis O'Higgins	54
Pat Smiddy & Brian Duffy	361
Pat Vaughan *et al.*	61
Robert Lundy & Anthony Prins	82
Roy Thompson & John Carroll	152
Stefan Jones & Denis Ryan	193
Sue Moles *et al.*	49
Tim O'Donoghue & Paschal Dower	266
Tim Roderick *et al.*	146
Tony Murray & Paddy O'Sullivan	90
Tríona Finnen, Ciarán Foley, Sue Moles & Andrea Webb	42
TOTAL	**6141**

Appendix 3 Hare Survey of Ireland form.

Hare survey of Ireland 2006/07
Point record sheet

Survey Square ID ______ **Grid ref of point** ______

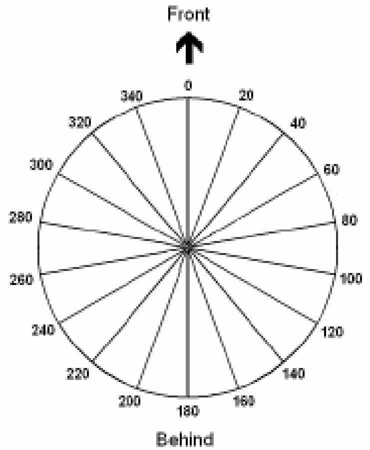
Date ______ **Time of survey** ______

Rain (0=none 1=light 2=heavy) ______ Cloud (0=none 1=partial 2=complete) ______

Species (Irish hare, brown hare, rabbit and/or fox)	**Number of animals** (0-?)	**Distance** (m)	**Angle** (X°)	Activity when spotted	Reaction to spotlight
Other comments:					

Field of view (0-18)
(the total number of compass sectors in which you **CAN** see, that is you have a clear line of sight) ______

Sectors not visible
(please shade those compass sectors in which you **CANNOT** see, in which your view is obscured)



* The number of sectors shaded plus the value for the FOV should equal 18.

KEY
Species: Irish hare, brown hare, rabbit or fox
Number of animals: number (1-?)
Distance: exact distance in metres to animals (use Rangefinder)
Angle: exact angle to animal(s) from observer (use your compass)
Activity when spotted: 0= crouching 1= sitting upright 2=moving
Reaction to spotlight: 0= no reaction 1= yes stayed still 2= yes moved away