

Implications of 'cyclical' population dynamics for the conservation of Irish hares (*Lepus timidus hibernicus*)

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Abstract

The Irish hare *Lepus timidus hibernicus* is of priority conservation concern in Northern Ireland, based on a perceived decline in abundance during the 20th century and on two surveys in 1994–1996 and 2002 that suggested low densities. We reanalysed a 10-year time series [Northern Ireland Rabbit Survey (NIRS)] that has been key evidence of decline, to derive an annual index of abundance during 1986–1995. This showed a rise to a double peak followed by a trough. We compared these Northern Ireland data with two datasets for *Lepus timidus scoticus*. A 40-year annual index derived from hare bags on Scottish shooting estates [National Game-Bag Census (NGC)] showed strong fluctuations, each lasting several years. Autocorrelation analysis of the NGC data showed elements of cyclical behaviour, with distinct phases and a 16-year period. A previously published 30-year survey of introduced *L. t. scoticus* in northern England also showed large multi-year fluctuations and phasic behaviour, albeit on a shorter time scale. The NIRS index was strongly correlated with NGC data for the same years, suggesting that it too reflected part of a natural population dynamic. The Species Action Plan for *L. t. hibernicus* in Northern Ireland includes the aims of maintaining the existing range and demonstrating increase by 2005, and of doubling the population by 2010. We suggest that these aims and the supporting monitoring strategy are inappropriate for a species that shows multi-annual fluctuations in abundance throughout its geographical range. It is important to distinguish self-correcting population processes from trends requiring remedial conservation action.

Introduction

Cyclical population dynamics are observed in a variety of wildlife populations (e.g. Elton, 1924; Chitty, 1960; Krebs & Myers, 1974; Finerty, 1980; Keith, 1990; Lindström, Ranta & Lindén, 1996). In the literature, 'cyclical' typically refers to a non-random multi-annual wave dynamic, distinct from random year-to-year variation or longer-term trends (Berryman, Lima & Hawkins, 2002). Such patterns in wildlife data generally fail to match the regularity of perfect waveforms, and have therefore been described as 'quasi-cycles' (Nisbet & Gurney, 1982). Nevertheless, authors have sometimes referred loosely to 'cyclicity' where wave characteristics were technically unproven but repeated fluctuations in abundance, each lasting several years, were apparent. Cyclicity clearly involves a number of measurable qualities (autocorrelation, phasic behaviour, amplitude, regularity). Mathematical demonstration of autocorrelation (non-randomness) within the time series, and of periodic regularity, demands long runs of consistently gathered data, which are more commonly available from bag records than from population surveys. A preoccupation with regularity has

been important in trying to understand the causation of cycles. In the context of population monitoring, the occurrence of repeated self-correcting fluctuations of biologically significant amplitude lasting several years (as opposed to random inter-annual fluctuations or one-way long-term trends) is important, whereas their mathematical perfection as cycles is less relevant. In the present paper, we describe such changes in abundance as 'multi-annual fluctuations' and intend this phrase also to imply the repeated and self-correcting nature of these dynamics.

Apparently, cyclical or quasi-cyclical dynamics are known in the mountain hare *Lepus timidus* throughout its geographical range (Angerbjörn & Flux, 1995). In Britain, phase-forgetting quasi-cycles have been demonstrated in bag data (Tapper, 1987, 1992) for both the mountain hare *Lepus timidus scoticus* and the brown hare *Lepus europaeus*. On some but not all Scottish moorland estates, historical bag data for *L. t. scoticus* before World War II showed a roughly 9-year period (Tapper, 1987, 1992). Newey (2005) examined 57 estate series from the same database and concluded that 51% showed evidence of cyclicity (seven truly cyclic, 22 weakly cyclic), with a mean periodicity of

8.7 years (range 5–15 years). Other data series for *L. timidus* show strong multi-annual fluctuations (Middleton, 1934; Mallon *et al.*, 2003). Danell, Willebrand & Baskin (1998) characterize the dynamics of *L. timidus* in boreal forest zones as 'regular fluctuations with low predictability'.

In relatively pristine environments, cyclical dynamics are generally regarded as a natural feature of a species' interaction with its ecosystem. What drives population fluctuations in *L. t. scoticus* in the more human-influenced environments of Britain is unknown. Parallels with hare cycles in North America and Scandinavia, where causation has been better researched, seem inappropriate for two reasons (Tapper, 1992). First, natural predators seem less likely to be important in Britain (Hewson, 1976), as cyclical dynamics are found on shooting estates where a suite of common predator species is heavily culled with the aim of substantially reducing their numbers. Second, whereas cycles in Scandinavian *L. timidus* are synchronized by predators with those in grouse (Lindström *et al.*, 1996), cycles in Scottish *L. t. scoticus* are not synchronous with those in grouse (Tapper, 1992). Factors likely to contribute to cyclical dynamics in Britain include the parasite *Trichostrongylus retortaeformis* (Newey & Thirgood, 2004; Newey *et al.*, 2005) and predation by man (i.e. the harvesting process which itself generates the bag data; Tapper, 1992), but climate also seems a necessary part of the story to explain geographical synchrony (S. C. Tapper, pers. comm.). The latter has not been formally explored, but is implied by the existence of superficially cyclical patterns even in data pooled across large regions like Scotland (Tapper, 1992) or the Komi Republic (Russian Federation; Naumov, 1972). Cyclical population dynamics of red grouse *Lagopus lagopus scoticus* caused by a similar parasite, *Trichostrongylus tenuis*, are thought to be synchronized by wet summers (Cattadori, Haydon & Hudson, 2005). It has been unclear whether long-term fluctuations in abundance occur in the Irish hare *Lepus timidus hibernicus*.

The Irish hare *L. t. hibernicus* is of conservation priority in Northern Ireland for several reasons:

- (1) status as an isolated sub-species;
- (2) status in EU legislation [Annex V(a) of EU Directive 92/43/EEC (Habitats Directive); this annex lists species of community interest whose taking in the wild and exploitation may be subject to management measures];
- (3) a perceived decline in population abundance during the late 19th to late 20th centuries (Dingerkus, 1997; Dingerkus & Montgomery, 2002).

In fact, only in the last decade (1994–1996, 2002, 2004, 2005) have serious attempts been made to survey Irish hares (Dingerkus, 1997; O'Mahony, 2003; Preston *et al.*, 2003; Tosh *et al.*, 2004, 2005). Those in 1994–1996 and 2002 suggested low abundance throughout Northern Ireland, although the 2004 estimate was six times that for 2002. The perception of decline derives particularly from analysis of a less satisfactory medium-term dataset for *L. t. hibernicus* in Northern Ireland by Dingerkus & Montgomery (2002), who concluded that the population of *L. t. hibernicus* in Northern Ireland declined significantly during the mid-1990s. In the present paper, we reanalyse the same data in comparison

with a much longer series of data for *L. t. scoticus* in Scotland, and re-evaluate conclusions about the status of *L. t. hibernicus*.

Materials and methods

The Northern Ireland Rabbit Survey (NIRS)

The NIRS was undertaken by the Department of Agriculture (1986–1995 inclusive) to identify broad trends in the rabbit population of Northern Ireland. It consisted of 72 randomly allocated 1-km² survey plots, with 12 plots distributed in each of the six counties (lat. 54°00'–55°30'N). In each survey plot, a 2.25-km-long transect was defined following habitat interfaces. These were mainly hedgerows, but could also be forest edges, river banks or drainage ditches. Each transect was surveyed on foot by two observers during January–February in each year of the survey, between 09:00 and 17:00 h. The order in which plots were surveyed was constant in all years. During surveys, observers recorded sightings and field signs of rabbits, and sightings of hares.

The NIRS is the only relatively long-term study (10 years) that has used consistent techniques to record Irish hares on survey transects. As a dataset for hares, it has a number of shortcomings. Because the NIRS was primarily a rabbit survey, both high and low rabbit densities could be expected to focus recorders on indirect field signs and to distract them from observing live animals. We had to assume that hares were recorded consistently, and that where hares were not recorded, none were observed (i.e. all zeroes are meaningful). It is also uncertain that all hares encountered were in fact *L. t. hibernicus*, as (introduced) brown hares occur locally in Northern Ireland and the two species are known to hybridize (Thulin & Tegelström, 2002). However, brown hares are thought to be scarce in Northern Ireland (Ni Lamhna, 1979).

In our analysis, the response variate was presence or absence of hare records in each survey plot and year (1986–1995 inclusive). This copied the use of the NIRS data by Dingerkus & Montgomery (2002), albeit with one further year of data available. The underlying assumption is that the probability of a record reflects hare abundance. We then used generalized linear modelling (McCullagh & Nelder, 1989) with Bernoulli errors and logistic link function, effectively modelling the odds on occurrence of hares. Survey plot and year were entered as explanatory factors. The significance of year was assessed by dropping the term from the two-way model. From this model, the exponentiated parameter estimates for the different years represent multiplicative effects relative to 1986 and can be interpreted as an annual index of hare abundance (Ter Braak *et al.*, 1994).

The National Game-Bag Census (NGC)

The Game Conservancy Trust's NGC was formally established in 1961 as a historical collection of annual game-bag

records from shooting estates, chiefly in England, Wales and Scotland. Very few estates in Northern Ireland have contributed to the NGC; hence bag records of *L. t. hibernicus* are inadequate for time-series analysis. On Scottish upland estates *L. t. scoticus* is a characteristic game species, and game-bag records allow detailed analysis. Estates were included in the present analysis if *L. timidus* was recorded at any time between 1961 and 2003. Seventy-five per cent of the 214 estates that qualified were situated in the Grampian Highlands, and in individual years these were responsible for 77–85% of the total hare bag for all 214 estates.

We modelled the number of hares shot per estate and year on these 214 Scottish estates from 1961 to 2003 in an analogous fashion to the NIRS analysis, using generalized linear modelling with Poisson errors and a logarithmic link function (McCullagh & Nelder, 1989). Estate identity and year were entered as explanatory factors. Statistical tests were corrected for overdispersion. Because 'zero' records are potentially ambiguous (either no hares shot or no effort made to shoot hares) they were treated as missing values, as any trend should be indicated by non-zero values. This model assumed that the area of each estate was constant throughout the period considered (available data suggested that this was reasonable). To correspond with open seasons for game, NGC years run from 1 February to 31 January. The exponentiated parameter estimates for the different years represented multiplicative effects relative to 1961 and gave an annual index of hare bags across all 214 estates.

The time series of total hare bags from 1961 to 2003 was log-transformed and subjected to autocorrelation analysis using Systat v. 9 (SPSS Inc., 1988). Because the beginning and end of the series were at similar levels (Fig. 1a), no preliminary trend removal or smoothing was carried out.

The Derbyshire Peak District

Lepus timidus scoticus were established in the Derbyshire Peak District (latitude 53°20') in about 1880, by translocation from Scotland (Mallon *et al.*, 2003). Clinging (2003) gives data from a survey by members of the Sorby Natural History Society, repeated annually in March during 1973–2003 inclusive. Although unsophisticated in its methodology, and limited in its coverage, this survey is included for completeness because it gives the only other insight available on the population dynamics of *L. timidus* in mainland Britain. A variable party of observers on foot surveyed a strip transect *c.* 20 km in length, although subject to a number of route revisions. Surveys were repeated within a year if weather conditions were unfavourable at the first attempt. These data are summarized graphically in Fig. 1b (and in Mallon *et al.*, 2003).

Results

In analysis of the NIRS survey data, there was a significant effect of year ($F_{9,647} = 2.90$, $P = 0.002$), indicating changes in the hare abundance index through time. However, this was not a simple decline relative to the starting point of

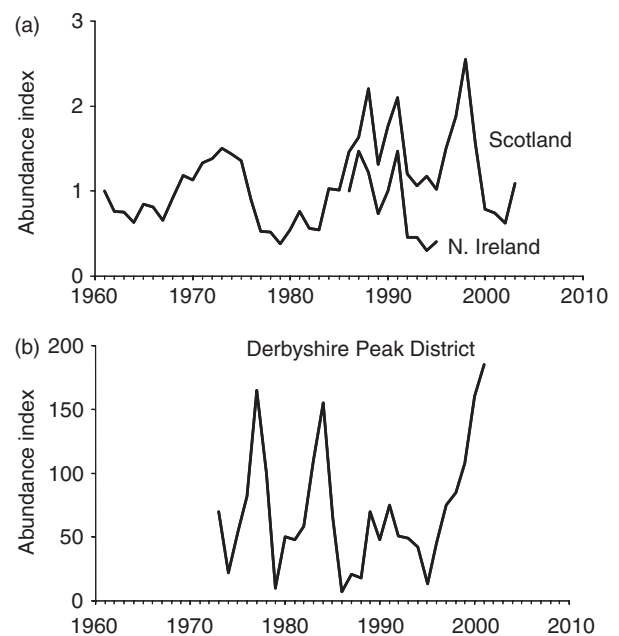


Figure 1 (a) Annual index of the numbers of mountain hares *Lepus timidus scoticus* shot in Scotland between 1961 and 2003 (from the Game Conservancy Trust's National Game-Bag Census, across 214 estates). The shorter series shows a similar index for *Lepus timidus hibernicus* sightings from the Northern Ireland Rabbit Survey, set into context for the period 1986–1995. Index values are expressed relative to the start of each series. (b) Annual index of mountain hare abundance from strip survey counts carried out on foot between 1973 and 2003 in the Peak District in England, redrawn after Clinging (2003).

1986. Rather, it showed a double peak followed by a trough in the hare abundance index (Fig. 1).

The analysis of NGC data also showed a significant effect of year ($F_{42,2204} = 8.32$, $P < 0.001$) as a result of strong fluctuations in abundance over periods of several years. For the years of the NIRS data (1986–1995), the indices calculated for the NGC and NIRS data were closely correlated (Pearson's $r = 0.862$; d.f. = 8; $P = 0.001$).

Time-series analysis of the NGC data (Fig. 2a) showed significant ($P < 0.05$) autocorrelation at lags of 1 and 2 years. These were confirmed by partial autocorrelation coefficients at the same lags. Irrespective of their significance, autocorrelation coefficients fell into a clear pattern, with a well-defined anti-phase. The suggested period was 16 years, although there was strong damping (i.e. the period was not maintained beyond the first cycle).

Survey data from the Derbyshire Peak District showed strong multi-year fluctuations of comparable amplitude. These did not correlate temporally with the other two datasets ($P > 0.05$; Fig. 1b), although 1989 and 1990 were high points in all three series. Time-series analysis for the Derbyshire data again showed a phasic pattern (Fig. 2b). The partial autocorrelation coefficient at a lag of 7 years was significant ($P < 0.05$), suggesting 7-year periodicity.

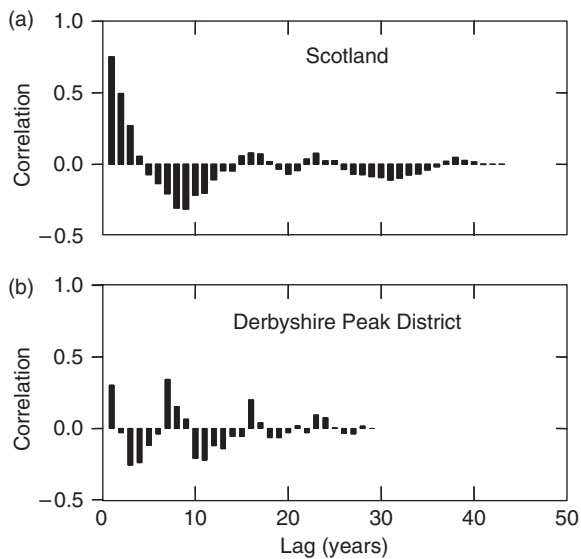


Figure 2 Autocorrelation plots for (a) the Scottish *Lepus timidus scoticus* bag data in Fig. 1a and (b) the Derbyshire Peak District *L. t. scoticus* survey data in Fig. 1b. Vertical bars show Pearson's correlation coefficient for log-transformed data, compared at increasing time lags. Coefficients were significant at $P < 0.05$ at lags of 1 and 2 years in (a), and at lags of 1 and 7 years in (b).

Discussion

Comparison with earlier interpretation

An earlier analysis of the NIRS by Dingerkus & Montgomery (2002) used a χ^2 test of association between the presence or absence of hare records and three 3-year time periods (1986–1988, 1989–1991, 1992–1994; 1995 data were not included). The authors found proportionally fewer records in the third period and concluded that a statistically significant decline in the Irish hare population in Northern Ireland had occurred between 1986 and 1994. Taking into account their own estimate of hare abundance in 1994–1996 and ancillary (mostly anecdotal) records, they also concluded that the population now existed at low density in Northern Ireland compared with the early 20th century (Dingerkus & Montgomery, 2002). Use of a χ^2 analysis on the NIRS data was inappropriate for two reasons. First, by using the same survey squares in successive time periods (3-year categories), the analysis violated the basic assumption of independence between samples, resulting in pseudo-replication (Hurlbert, 1984). Second, the grouping of data into three time periods was arbitrary, and masked year-to-year fluctuations.

Our reanalysis of the NIRS investigated year-to-year changes, allowing for site differences. This indicated that although overall a significant decline occurred during the period 1986–1995, this was not a simple dynamic as suggested by Dingerkus & Montgomery (2002), but a double peak followed by a trough. The striking correlation between these dynamics and simultaneous changes in *L. t. scoticus* in

Scotland (at comparable latitudes) put the Northern Ireland data into an importantly different context, because the Scottish data form part of a long-term series in which cyclical dynamics have been identified (Tapper, 1992; Newey, 2005) and where large multi-annual fluctuations have been a striking feature (Tapper, 1992).

Population fluctuations in *L. timidus*

The NGC bag data for Scottish *L. t. scoticus* showed marked fluctuations with peaks spaced several years apart. Autocorrelation analysis showed that correlation coefficients were organized into distinct phase (+ve values) and anti-phase (–ve values). The full period suggested was 16 years. Thus from a peak year, one would have to wait about 16 years before numbers were likely to reach comparable levels again, whereas from any start date the population was likely to be substantially different in just a few years' time. The damping effect in subsequent oscillations indicates lack of regularity, as in phase-forgetting quasi-cycles. It is not important in the present context because we are not so much interested in the causation of fluctuations or their mathematical regularity, as in the time scale on which fluctuations occur. It is this time scale that should set the perspective for conservation decisions.

Because the shooting of *L. t. scoticus* – like most harvesting – is probably a density-dependent process, fluctuations in bag data may exaggerate the scale of population dynamics (Finerty, 1980). Survey index data from the Derbyshire Peak District (Fig. 2b) are valuable here to compare an unshot British population. The Derbyshire counts were the least standardized of the three datasets, with changes in route length, no replication, and influenced by changes in visibility because of weather. Peaks and troughs in the Derbyshire data were not synchronous with those in the Northern Ireland and Scottish series, although the period 1989–1990 was a high point in all three series. Nevertheless, in Derbyshire too multi-annual fluctuations of comparable magnitude (four- to fivefold) occurred, albeit on a shorter period.

From another perspective, the fact that a clear autocorrelative pattern with phase and anti-phase is produced from an analysis of bag data across 214 Scottish estates suggests that considerable geographical synchrony in bag size exists among estates, even though shooting is organized estate by estate. If bag records from most estates showed no cyclical dynamics, or if cycles existed in different parts of Scotland but were out of phase, then the data would be expected to be far more chaotic than shown here. Ranta *et al.* (1997) showed that population dynamics of *L. timidus* in Finland were synchronized over hundreds of kilometres. Overall, it therefore also seems unlikely that shooting itself causes the observed patterns in bag data.

Population fluctuations and density of *L. t. hibernicus* in Northern Ireland

For the limited period of their availability, the NIRS data match fluctuations in the Scottish hare index, indicating that

fluctuations take place on a similar time scale and may even be synchronized. It is conceivable that climatic fluctuations could tend to synchronize population dynamics between *L. t. hibernicus* in Northern Ireland and *L. t. scoticus* in Scotland and England, given that these are nearby regions with overlapping latitudinal ranges. Tantalizingly, the series ended at a low value. Did the Northern Ireland hare population subsequently recover to the levels of 1987, as the NGC index suggested was the case for Scotland? In 2000, regional surveys in Antrim and Down (O'Mahony, 2003) estimated density at between 0.5 and 3.0 hares km⁻², the higher figures representing upland areas with rough grazing. Surveys in all six counties of Northern Ireland in 2002, 2005 and 2006 (Preston *et al.*, 2003; Tosh *et al.*, 2004, 2005) estimated average densities at 1.0, 5.1 and 3.1 km⁻², respectively. Despite differences in methodology, it would appear that hare densities increased by a factor of at least five during the period 2000–2005.

Previous authors (Dingerkus & Montgomery, 2002) suggested that *L. timidus* was currently at low density in Northern Ireland. The densities quoted above are indeed low by comparison with managed heather moors with predator control in Scotland, where bags can exceed 50 hares km⁻² even on estates of more than 100 km², indicating that density can touch at least this level in peak years (unpublished NGC data; for 2443 non-zero bags, median = 1.4 hares km⁻²; upper 95 percentile = 30 hares km⁻²). In Sweden, however, natural density in an area of fragmented boreal forest was estimated at only 3.3 hares km⁻² (Lindlöf & Lemnell, 1981). In the temporary absence of foxes due to epidemic disease, hare densities in this habitat rose to approximately six times normal levels (Lindström *et al.*, 1994).

In Northern Ireland, only 36% of land area is semi-natural habitat (Northern Ireland Countryside Survey, 2000). Low hare density here may well imply a landscape that is degraded from the hare's point of view, where the better patches of habitat are isolated and where natural predators are common. But it does not imply unsustainability. To make that case, one needs evidence of a biologically significant decline in abundance, which the NIRS does not provide.

Implications for management

The natural occurrence of multi-annual fluctuations in abundance has important implications for management strategy. For Irish hares, we must consider whether the NIRS data reflect a fluctuation that is likely to be reversed without intervention or whether there is evidence for population change demanding remedial management. In the latter case, a further crucial question is whether any feasible course of action will remedy the situation.

Current management strategy for *L. t. hibernicus* in Northern Ireland, notably the Species Action Plan (SAP; Environment & Heritage Service, 2000), is clearly hampered by a shortage of good quality data and relatively little

scientific study of the sub-species anywhere in Ireland. The first two objectives of the SAP are

- to maintain the existing range and demonstrate a population increase by 2005 and
- to double the present population by 2010 over as much of the range as possible.

These targets do not allow for the possibility of strong multi-annual fluctuations as a characteristic of the species. In Scotland, the English Peak District, and Northern Ireland, fluctuations in abundance indices (this study) or estimated abundance (Tosh *et al.*, 2004, 2005) easily exceeded the doubling in 10 years envisaged by the Northern Ireland SAP targets. Such fluctuations could have satisfied or frustrated SAP targets, irrespective of any conservation action.

Furthermore, the detection of trends requiring remedial management is more demanding in species that show such natural dynamics. Obvious hazards are that short time series of annual surveys illustrating part of a natural 'cycle' could be misinterpreted (as we suggest was the case with the NIRS) or that more widely spaced surveys catching the population at different phases of its 'cycle' could suggest an overall trend where none was present. A key strategy of the SAP is to monitor *L. t. hibernicus* at 3–5-year intervals to seek evidence of population change. Both the appropriateness of that strategy and the targets themselves seem questionable in the light of the present analysis.

Conservation (SAP) targets should certainly be revised to make them biologically meaningful and measurable. We should also reconsider whether existing evidence justifies the priority conservation status given to *L. t. hibernicus* in Northern Ireland, and what further data might be gathered to improve the 'fit' of conservation plans to actual population status? Those concerned with the conservation of this species must consider extinction risk and meta-population effects as well as population trend, but none of these can be assessed without a sustained monitoring strategy suited to the possibility of large-magnitude multi-annual fluctuations in abundance.

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