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The Irish hare: from the ice age to present

Neil Reid

The Irish hare (*Lepus timidus hibernicus*) is a subspecies of mountain hare (*Lepus timidus*) which colonised Ireland during the last ice age (Montgomery *et al.* 2014). It likely arrived via southerly landmass now submerged below sea level on the continental shelf to the south-west. Cave fossils support its presence as early as 28,000 years before (YBP) present whilst molecular genetic analyses suggest its ancestors split from other mountain hares as early as 363,000 YBP (Hughes *et al.* 2006).

Most mountain hares inhabit high altitudes or latitudes living in snowy montane or tundra habitats where they browse hard woody material, like heather or ground-willow. Isolated as the only endemic lagomorph to Ireland, the Irish hare diverged from its relatives. In the absence of lowland competitors, for example, the European brown hare (*Lepus europaeus*) which is a lowland grassland specialist, the Irish hare could descend from high elevations and adapt to virtually all available habitats. It is found from sea level, where it has been observed swimming and inhabits offshore islands and sand dune systems, through lowland grasslands and forest, up to mountain summits covered by blanket bog. It feeds predominately on grasses, such as Italian rye-grass (*Lolium perenne*) in agricultural systems, or a range of native grasses in natural or unimproved grasslands but can also browse harder woody material such as heather (*Calluna*) species if grasses and herbs are limited.

It differs from the other fifteen subspecies of mountain hare being the largest, with females weighing up to 4.5kg. It shows distinct variation in its skull and jaw morphology; a likely consequence of a change in diet. Despite its size, the productivity of agricultural grasslands allows the Irish hare to have comparatively small home ranges (less than 50 hectares) compared to the other subspecies who range further (up to 200 hectares) in less productive environments. The Irish hare has a distinctly russet red summer pelage and moults to dusky grey-brown in winter but, with a near complete absence of snow, it does not turn entirely white like its relatives. Nevertheless, the ear pinna, flanks and legs can turn partially white with long white guard hairs projecting through the coat resulting in the so-called blue colour morph. The Irish hare possesses the genetic machinery to enable it to turn white (evidenced by some very rare individuals turning entirely white) but moulting is generally not triggered more widely due to a lack of the right combination of changes in daylength and temperature. The Irish hare is genetically distinct from other mountain hares possessing more unique genes than other mountain hare population (Hughes *et al.* 2006).

Species status

The Irish hare is isolated from and differs genetically, ecologically and behaviourally from other mountain hares but differs strikingly in its size and shape and the timing of its life cycle. During 1837, it was originally classified as a full species, *Lepus hibernicus*, by Thomas Bell before being referred to by Charles Darwin in his notebooks, and Gilbert White in the Natural History of Selbourne, as an example of a distinct island fauna. Nevertheless, upon examination of just one specimen, German naturalists Keyserling and Blasius rejected any differences with other mountain hares with Barrett-Hamilton demoting it to a climatic race: *Lepus timidus hibernicus*, in 1900. A classification accepted by Angerbjörn and Flux during 1995 and which has stuck ever since. Whilst it is accepted as an evolutionarily distinct unit of intrinsic conservation value, some suggest it may still warrant full species status (Paulo Prodöhl *pers. comm.*).

Conservation status

After the end of the last ice age, the Irish hare, then more similar to its mountain and Arctic hare ancestors than it is now, likely eked out a living in the open habitats at the edge of the retreating ice sheet. Hares would have been at low densities after the establishment of extensive ancient oak woodlands (the predominant landcover prior to the arrival of man) and likely congregated in open

habitats such as montane bog, upland and lowland heath and coastal sand dunes around the margins of the island. Widespread deforestation and conversion to extensively managed agricultural grasslands *ca*. 5,000 YBP likely benefited ancient Irish hare populations resulting in range expansion and increased densities.

Game-bag shooting records collected from 14 estates throughout Ireland from 1848 to 1970 suggest that historical populations existed at much higher densities than today with the population exhibiting long-term stability (oscillating around a stable mean) but with dramatic variation between years showing apparent multiannual fluctuations (Reid et al. 2007). Hare populations the world over are famous for being highly productive and, therefore, exhibit boom-bust dynamics. North American snowshoe hares (Lepus americanus) are ecological textbook examples of exhibiting regular decadal cycles driven by winter snow conditions i.e. food availability and predation by lynx (Lynx canadensis) whose population tracks that of the hare population at but at a lag of 1-2 years. Irish hare game-bags exhibited an approximate 8-year noisy irregular cycle driven by climatic fluctuations; principally the autumn Northern Atlantic Oscillation (NAO) which is associated with local weather conditions. The NAO is a pattern of climate driven by low pressure near Iceland and high pressure near the Azores which drag warm, wet storms across the Northern Atlantic making European landfall on northwesterly shores including Ireland which is sometimes referred to as the Emerald Isle with its 40 shades of green representing the lushness of our grass growth which benefits from such conditions. But just like oscillations of the more famous El Niño phenomenon in the Pacific Ocean, the NAO fluctuates between its normal pattern and a less frequent occurrence where the low pressure systems near Iceland and the Azores shift position deflecting Atlantic storms from northerly latitudes so they make landfall in southern Europe, ordinarily dry, resulting in wet conditions in the Mediterranean basin and cold icy conditions in Ireland. The shift to this latter state historically occurred in one winter out of every eight on average and was loosely associated with the noisy Irish hare population cycle. Specifically, population growth rates were correlated with wet mild autumns which presumably lengthen the growing season making fresh grass available later in the year enabling late born leverets to mature before winter; boosting the breeding population the following spring.

Global climate change, attributed to recent human enrichment of the atmosphere with carbon dioxide, was first detected in historical records by a changepoint in global temperatures which have increased since ca. 1910. The 8-year noisy cycle observed in historical Irish hare populations collapsed and disappeared around 1910 coinciding with a weakening in the correlated cycle observed in the Northern Atlantic Oscillation. Numbers of hares shot dramatically declined by 88% between 1910 and 1970 independent of changes in shooting effort suggestive of a real underlying change in hare availability. Agricultural intensification, specifically landscape homogenisation i.e. the reduction in the number of small, diverse, farms less than 40 hectares in size (the approximate size of typical Irish hare's home range), and increases in large, monocultural, mechanised farms larger than 200 hectares in size, likely drove declines. Mechanical silage harvesting has been posited as one of the mechanisms that caused the long-term decline observed during the 20th century. Irish hares spend their days inactive lying-up in their forms located in tall, dense vegetation used as shelter (typically stands of rushes Juncus spp. in unimproved grasslands) before moving less than 200 metres to adjacent patches of improved grassland to graze during their active period at night. Thus, Irish hares are more abundant in landscapes composed of a habitat patchwork quilt of improved grasslands interspersed with unimproved grasslands and semi-natural habitats where habitat patch size is typically fine-grained.

During summer, Irish hare home ranges dramatically shrink (reducing to about 5 hectares) and animals reside in improved grassland fields during both their active and inactive periods as grass, destined to be cut for silage, grows tall (up to 80cm) providing both shelter and grazing (Reid, McDonald & Montgomery, 2010). This creates an ecological trap as female hares give birth during this period and leverets, being born fully furred on the surface of the ground, lie motionless in the centre of fields where they are deposited to avoid predation by foxes which patrol field boundaries where rabbit warrens are located. Mechanical harvesting is known to cause leveret mortality but there is still a lack of evidence for its role in driving Irish hare population declines. Nevertheless, it has been

hypothesised that a switch from extensive hay making, in which grass is harvested at the end of the summer when leverets are grown, to intensive silage cutting, in which grass is harvested up to 3 times between May and September, may have driven the decline of the Irish hare during the 20th century. Moreover, an increasingly mild climate has resulted in the first silage harvest dates getting earlier and the last later; likely exerting increasing pressure on population recruitment.

The Irish hare continued to decline through the late 20th century (between 1985 and 1995) reaching a low in the mid-1990s (Dingerkus & Montgomery, 2002) but appear to have stabilised at low densities (approximately 3 hares/km²) during the early 21st century from 2002 to 2010 (Reid & Montgomery 2010). It is, therefore, protected by the EU Habitats Directive, Bern Convention, the Wildlife and Natural Environment Act (Northern Ireland) 2011 and the Wildlife Amendment Act (Republic of Ireland) 2000. The last All-Ireland population estimate suggested there was approximately 500,000 hares in Ireland during 2007 which remained widespread (Reid *et al.* 2007). Despite its decline there are likely more hares in Ireland now than during the pre-human (i.e. pre-grassland) era and it's current abundance and range has resulted in it being regionally IUCN Red-Listed in the category of Least Concern.

Hare coursing

Hunting with Dogs was banned in Scotland under the Protection of Wild Mammals (Scotland) Act 2002, in England and Wales by the Hunting Act 2004 and in Northern Ireland under the Wildlife and Natural Environment Act (Northern Ireland) 2011 but remains widespread throughout the Republic of Ireland where up to 75 local coursing clubs operate, under Government licence. Unlike hare coursing in Great Britain, which was open and occurred in-situ in the wild, Irish hare coursing is 'closed'. Up to 6,000 hares are caught from the wild annually using long-nets and lines of beaters and taken into enclosed paddocks. They are pursued by two dogs, usually greyhounds, where the intention is not to kill the hare; but to test the speed and agility of the two dogs on their ability to turn the hare from its chosen course with bets placed on outcome. There is an escape through which the hare can travel but the dogs cannot pass due to their size. Surviving hares are released back into the wild. Since 1994, Irish Coursing Club (ICC) regulations have imposed the compulsory muzzling of dogs with mortality declining from 15% to 4% before-and-after implementation. Since the implementation of muzzling survival rates have further increased due to improved captive hare husbandry through knowledge transfer between clubs, veterinary attention including eliminating parasites through the use of deworming medications and supplementary feeding throughout the coursing season; coinciding with winter from October to February when conditions in the wild would be challenging. It has been hypothesised that animals may return to the wild in better body condition than when caught. Hare survival rates were over 98% during 2011/12 (Murphy, 2013). Given the overall population size, the impact of mortality due to coursing (now measured in the tens of individuals annually) is likely to be negligible. Each club has a number of areas known as preserves from which they capture and release hares annually. These areas are usually owned by club members and are managed in a sympathetic manner preserving landscape patchiness, predators such as foxes are typically heavily controlled and other forms of hunting, for example, shooting prohibited. Consequently, Irish hare densities are 18 times higher in Irish Coursing Club preserves than the wider countryside (Reid, Magee & Montgomery, 2010). Thus, despite animal welfare or moral and ethical objections, from a conservation perspective, properly managed coursing clubs may well help conserve wild populations.

Biological invasion

It has been said that Irish hares run in the straight line whilst European brown hares run in a jinky or zig-zag pattern. European hares were imported and intentionally released at about 16 locations throughout Ireland from 1848 to the 1890s by coursing enthusiasts who fancied variation in their sport or who intended to create hybrids with optimal coursing characteristics. Some populations established, for example, the introduction at the Powerscourt Estate, Co. Wicklow was so successful animals were harvested and in later years sold in Dublin butcher's shops. Animals were also released

at the Baronscourt Estate, Co. Tyrone were the only surviving recorded introduction is known. All others have since vanished. Nevertheless, there is a population of some 2,000 European hares in Mid-Ulster at a location from which no known historical introduction took place (Reid & Montgomery, 2007). They are spreading by up to 2 kilometres per year and the expansion of their range suggests they may have been introduced as recently as the 1970s (Caravaggi *et al.* 2015). Irish hare densities are depressed in contact with European hares and there some localities within the invader's core range (i.e. where both species have been in contact longest) where the native have locally disappeared. There appears to be an active invasive-native species replacement processes (Caravaggi *et al.* 2016a).

Throughout Europe, European brown hares generally occur at lower elevations than mountain hares with both contacting one another at intermediate altitudes. Where European hares have been introduced into the range of mountain hares elsewhere, for example, to southern Sweden, they have replaced the native species, in this case the Heath hare (*Lepus timidus slyvaticus*), over an area larger than the entire land area of Ireland within 200 years (Caravaggi *et al.* 2016b). The Irish hare has a climatic and habitat niche distinct from other mountain hares which is closer to that of the European hare. Thus, it is particularly vulnerable to invasion and negative impacts from the European hare.

Climate change

Two-thirds of species within the Order Lagomorpha (the group to which rabbits and hares belong) are vulnerable to changes in their distribution and range due to global climate change altering temperature and precipitation patterns (Leach *et al.* 2015). The mountain hare's suitable climatic space is predicted to decrease by 10% with a ~4° shift in their ranges towards the Arctic. Comparable models for the Irish hare suggest its suitable climatic space will contract by 75% over the next 50 years in a north-westerly direction retreating from the warmer, drier more agriculturally intense south-east of Ireland (Caravaggi *et al.* 2016b). European hare models suggest that climate change may further facilitate the replacement of the Irish hare favouring the invader which is predicted to expand its range from the north to the south-west with Ireland becoming more suitable for the invader than the native by 2070. It may be that in a century's time, offshore islands in the north-west of Ireland may be the only refuge of the Irish hare from both warming temperatures and biological invaders. Thus, in the future we may talk of Irish and European hares in the same way as we currently discuss the disappearance of native red squirrels due to invasion by Northern American grey squirrels.

Conservation

Hare life histories are remarkably like those of ground-nesting birds. Hares give birth on the surface of the land, usually farmland, where their young remain motionless. This is not dislike the grey partridge, skylark, lapwing or curlew which lay their eggs in a shallow scrape or nest in open farmland. It is not surprising declines in ground-nesting birds mirror those of the Irish hare due to agricultural intensification. The corollary is that conservation action which benefits ground-nesting birds appears to support hares also. Land management sympathetic to raising grey partridges as game birds, such as leaving winter stubble in place, less intensive grassland management (fewer reseeding events and less frequent harvests), and having field edge margins including wildflower strips, provides hares with suitable grazing adjacent to rougher vegetation for shelter increasing the carrying capacity of the land. Agri-environment schemes, where farmers are paid to not conduct activities harmful to the environment or to introduce conservation measures, do not necessarily deliver benefits for hares unless the measures taken increase fine-scale habitat patchiness (Reid, McDonald & Montgomery, 2007). Oddly, Dublin and Belfast International Airports, as well as many golf courses, are well known as Irish hare hotspots. Such sites have areas of rough grass which is typically cut only once annually and doesn't undergo reseeding or extensive herbicide treatment. If the habitat is suitable, hares can habituate to any amount of disturbance hardly twitching an ear as a jet screams to a halt only metres away or weaving in-and-out of the crowds lining the fairways at the Irish Open! Thus, despite tales of decline associated with farming or threats from invaders facilitated by climate change, it is difficult not to be optimistic about an animal which seems so adaptable and capable of tolerating so much disturbance (referred to by scientists as 'behavioural plasticity'). The current conservation status of the Irish hare is being assessed under the 'Hare Survey of Ireland 2017-19' project funded by the National Parks & Wildlife Service (NPWS) which aims to produce an up-to-date population estimate and distribution whilst assessing current threats and pressures. The Irish hare has gone from being virtually unknown prior to the mid-1990s to being one of the best studied and well understood mammals on the island of Ireland.

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