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NATIONAL HARE SURVEY & POPULATION ASSESSMENT 2017-2019

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An Roinn Cultúir, Oidhreachta agus Gaeltachta
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Main photograph:

Irish Hare *Lepus timidus hibernicus*, Mike Brown

National Hare Survey & Population Assessment 2017-2019

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Executive Summary

- The Irish Hare (*Lepus timidus hibernicus*) is an endemic sub-species of the Mountain Hare (*L. timidus*) and the only lagomorph native to Ireland. There is an invasive population of non-native European Brown Hare (*Lepus europaeus*) in Northern Ireland. The Mountain Hare is listed under the EC Habitats & Species Directive (92/43/EEC) and Article 17 requires that member states regularly undertake national conservation assessments of its status.

- The Irish Hare colonised Ireland after the last ice age, differing from other mountain hares in that it is larger, has a distinctly russet-red coat that does not turn white in winter, and exhibits a highly flexible ecology, being found from the seashore to mountain summits. Its diet is predominately grasses and it prefers heterogeneously structured rough or unimproved grassland, where its dual requirement of good quality forage for nocturnal grazing and daylight shelter for lying-up are provided in a fine grain patchwork at less than 50 hectares in extent; a typical hare's home range. In common with other farmland species, there is evidence that its population declined substantially throughout the 20th century due to agricultural intensification and landscape homogenisation, with a series of recent studies suggesting populations have stabilised at fairly low densities of *c.* three hares/km^2 since 2000.

- The aim of this project was to estimate the current mean population density and the national total population of the Irish Hare and to examine variation in its population across space and time (principally since the Hare Survey of Ireland 2006/07.

- A pilot survey (March to May 2018) compared night-time spotlight surveys of point transects (the methodology used during the last Hare Survey of Ireland 2006/07) with deployment of a national camera trapping array. A total of nine hares was observed at 130 point transect locations within 26 1 km^2 survey squares (one per county with approximately five survey point locations per square) compared to 202 hares at 351 camera trap locations within the same survey squares (14 cameras per square left in situ for one week is 58,968 hours of survey effort equivalent to approximately seven years of continuous observation). Hares were detected in 35% of squares using spotlight surveys compared to 81% of squares using camera traps, with the latter recording +2,144% more individual detections than the former. The chances of detecting a hare within a survey square using spotlight surveys when they were confirmed as present using camera traps was roughly random suggesting that spotlight surveys should be discontinued as the primary survey method for hares in preference for developing a robust camera trapping protocol.

- The full survey (November 2018 to February 2019) involved deploying 596 cameras for 106,026 survey hours (equivalent to approximately 12 years of continuous observation) in 44 1 km^2 survey squares selected throughout Ireland to be statistically representative of the country's overall habitat composition. Cameras were deployed at random within survey squares to avoid any bias induced by association with roads, tracks, paths etc. A total of 253 Irish hare was detected within 85% of survey squares suggesting a highly widespread, common distribution.

- A Species Distribution Model supported heterogeneously structured grassland as the main driver of hare site occupancy, but model predictive success was poor due to the widespread distribution of the species and its generalist habitat requirements. The model suggested that virtually every 10 km^2 square in Ireland contains suitable habitat for the species and should be included within its *Favourable Reference Range* but populations are likely to be locally patchy.

- An additional 1,421 Irish Hare incidental sighting records were submitted by the public via a citizen science web portal hosted by the National Biodiversity Data Centre that also demonstrated the species' widespread ubiquity.

- Aggregating all sources of data (totalling 1,885 species detections) suggested the Irish Hare's *Favourable Reference Range* and *Current Range* are even greater than the 814 hectads, or 10 km^2

squares indicated in the most recent Article 17 assessment. From 2014 to 2019, a total of 522 squares was occupied within its Current Distribution but this number is dependent on the timeframe over which its distribution is assessed (for example, the most recent Article 17 report suggested a Current Distribution of 702 hectads, or 10 km^2 atlas squares, between 2013-2018). In any case the Irish Hare remains widespread and ubiquitous.

- No sightings of the European Brown Hare were recorded during either spotlight or camera trapping surveys and no records of the species have been confirmed as present in the Republic of Ireland.

- Camera traps revealed a detailed account of the Irish Hare's activity pattern with animals showing a bimodal 24-hour crepuscular cycle with peak activity during dawn (05.45 to 09.00) and dusk (17.00 to 18.30) during winter months (November to February).

- Methods were developed to estimate the distance of each hare detected on camera, enabling the use of distance sampling analysis to estimate hare densities. The optimal Distance model assumed a hazard-rate detection function with hares typically detected <5 m from the field edge margin but they were detected up to a maximum distance of 41 m from cameras. However, detections were right truncated at 13 m to improve optimal model fit.

- Mean (± 95% confidence intervals) of Irish Hare density during winter 2018/19 was estimated at 3.19 hares/km^2 (95% confidence intervals: 1.59–6.43) with highest and very comparable densities in the northwest (3.50 hares/km^2) and southwest (3.46 hares/km^2) regions and lowest density in the east (2.66 hares/km^2). The average estimate was 4.5% lower than the 3.33 hares/km^2 estimated during 2006 and 58% lower than the 7.44 hares/km^2 estimated during 2007. Nevertheless, such was the width of the 95% confidence intervals that the current density estimate cannot be said to be significantly lower than the previous survey. Our mean density estimate was comparable to the 20-year mean density from all surveys since 2000 of *c*. 3 hares/km^2 suggesting the population remains stable. The national Irish Hare population was estimated at 223,000 (111,000–449,000) individual hares during 2018/19.

- We review the most recent (2019) Natura 2000 list of threats and pressures, highlighting three concerns of high importance to Irish Hare: i) agriculture, including intensification, mowing and cutting of grassland and habitat restructuring, ii) biological resource use, including illegal poaching and iii) disease, most notably the recent discovery of rabbit haemorrhagic disease virus (RHDV2) in an Irish Hare for the first time during July 2019. Nevertheless, there is no empirical evidence that these or other threats negatively impact the national population.

- The current status of the Irish Hare within the criteria of i) *Range*, ii) *Population*, iii) *Habitat for the species* and iv) *Future prospects* was assessed as Favourable with the overall national conservation assessment stable in common with the two most recent Article 17 reports (dated 2013 and 2019).

- Based on our experience, we make recommendations for future monitoring and surveillance of the Irish Hare including the adoption of camera trapping arrays as a means of collecting standardized data at constant effort monitoring stations; an unchanging network of focal survey squares allowing relative population change to be assessed. With the disease RHVD2 confirmed as present in the Irish Hare population, we support monitoring, at least in the immediate future, on an annual cycle or at least more regularly than every six years to assess the potential impact of the disease on local population abundance and whether any impact on numbers is ephemeral or long-lasting.

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We are grateful to Katie Barbour and Christina Mulvenna who were Research Assistants and helped collect data. We would also like to thank the IDASO Ltd. team for deploying camera traps and for their development of data processing tools. We are grateful to the landowners and farmers who provided access to their land and to members of the public for submitting their sightings online. We would also like to extend our thanks to NPWS staff for submitting animals suspected of having rabbit haemorrhagic disease virus (RHDV2) for testing and Rebecca Jeffrey and Ferdia Marnell for comments on the draft report.

1 Introduction

Ireland is relatively poor in floral and faunal biodiversity (Harrison, 2014; Montgomery *et al.*, 2014). Only a few mammals (e.g. Stoat, Mountain Hare) are considered either endemic or truly native (Searle, 2008; Montgomery *et al.*, 2014). Many species were introduced to the island after human colonisation e.g. Fox, Badger (Searle, 2008; Montgomery *et al.*, 2014) for various reasons, including as sources of food or fur e.g. Rabbit, Pine Marten, or for sport or leisure hunting e.g. Brown Hare (Barrett-Hamilton, 1898). Many others stowed away with human imports e.g. Bank Vole, Greater White-toothed Shrew (Montgomery *et al.*, 2014).

1.1 The Irish Hare

The Irish Hare (*Lepus timidus hibernicus*) is an endemic sub-species of the Mountain Hare (*L. timidus* Linnaeus, 1758) and the only lagomorph native to Ireland (Fairley, 2001; Hamill *et al.*, 2006). However, both the European Rabbit (*Oryctolagus cuniculus* Linnaeus, 1758) and European Brown Hare (*Lepus europaeus* Pallas, 1778) were (first) introduced during the 12th and 19th centuries respectively (Hayden & Harrington, 2000; Fairley, 2001).

The Irish Hare is one of the very few 'paleoendemics' to Ireland; being present since the end of the last glacial maximum 12,900 years ago (Montgomery *et al.*, 2014). Molecular genetic evidence 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), suggesting that Ireland was colonised via a southerly land bridge (Hamill *et al.*, 2006). Further genetic analyses suggests that Irish populations form a unique monophyletic assemblage within mountain hares being more genetically diverse and with more private alleles than any other regional populations (Hughes *et al.*, 2006) representing an 'Evolutionarily Significant Unit'. They are distinguished from other Mountain Hare by genes associated with body size, coat colour and moulting patterns (N. Reid unpublished data). The case for its unique taxonomic position is further substantiated by it differing phenotypically, behaviourally and ecologically from other Mountain Hare (e.g. see Caravaggi *et al.*, 2017).

Historical game bag records collated during the first 'Hare Survey of Ireland 2006/07' suggested that hare populations were likely to have been considerably larger during the mid-19th to early 20th century than at present when the population appeared stable but with significant interannual fluctuations (Figure 1) exhibiting a multiannual periodicity of a *c.* 8 year quasi-cycle (Reid *et al.*, 2007a). The initiation of hare population declines started during the early 20th century (*c.* 1910), synchronous with changes in land management practices associated with early agricultural intensification (Huttman, 1972) and landscape homogenisation (Reid *et al.*, 2007a; 2010). Game bags declined continuously (by - 88%) from 1910 to 1970 with the disappearance of multiannual quasi-cycles.

Standardised daylight direct counts of Irish Hare on day-walked transects during the 'Northern Ireland Rabbit Survey 1985-1995' (conducted by Dr Alan Bell, Agri-Food & Biosciences Institute (AFBI)) suggested that hare population declines were ongoing during the late 20th century (Figure 2; Reid *et al.*, 2007b). Similar daylight surveys in the mid-1990s suggested detection rates had reached an all-time low at around 0.65 hares/km^2 on average throughout Northern Ireland (Dingerkus & Montgomery, 2002).

Recent nocturnal standardised direct counts on night driven-transects during 'Northern Ireland Hare Surveys' from 2002 to 2010 suggested no overall temporal trend, indicating that negative hare population trajectories may have stabilised at relatively low densities (*c.* 3 hares/km^2) during the early 21st century after a long period of substantial decline (Figure 3; Reid & Montgomery, 2010). The last Hare Survey of Ireland (Reid *et al.*, 2007a) reported densities of 3.33 hares/km^2 during winter 2006 and 7.66 hares/km^2 during winter 2007 suggesting that hare populations in Ireland are just as capable of dramatic and short-term fluctuations as hare populations elsewhere. For example, Snowshoe Hare (*L. americanus*) are textbook examples of a species that exhibits fluctuations where peak densities can be

11 times higher than trough densities in the population cycle (Krebs *et al.*, 1995). Despite short-term oscillations, no overall temporal trend in the Irish Hare population during recent decades is supported by sightings data from the British Trust for Ornithology's (BTO's) Breeding Bird Survey (BBS); an analysis of which indicates no overall change in site occupancy (% occurrence) or relative abundance (numbers of sightings per site) throughout Northern Ireland from 1995 to present (N. Reid unpublished data).

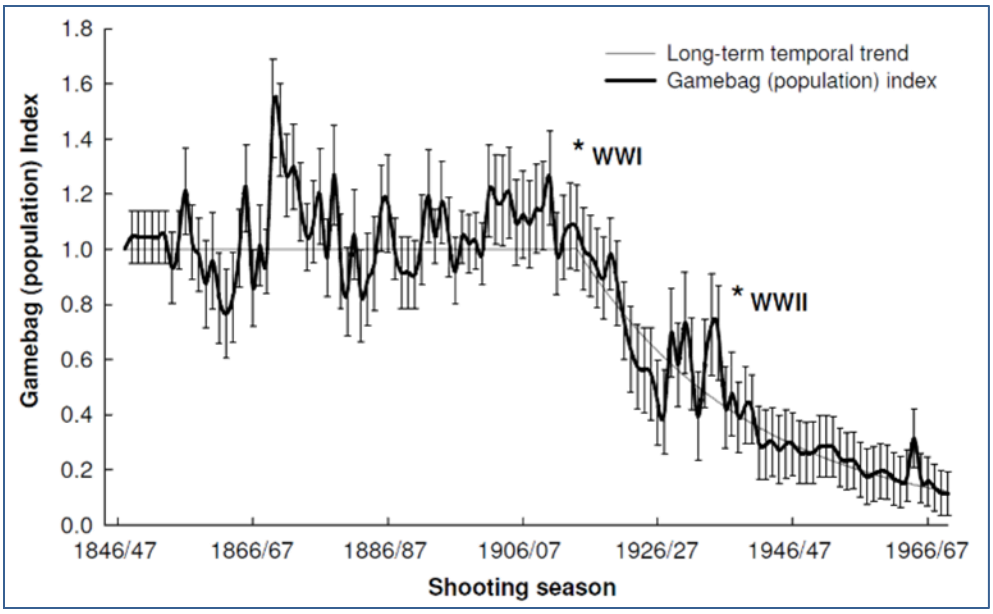


Figure 1 Temporal trend in Irish Hare game bag indices from 14 shooting estates throughout Ireland from 1846-1970 showing a dramatic decline in the number of hares shot annually after WWI (Reid *et al.*, 2007a).

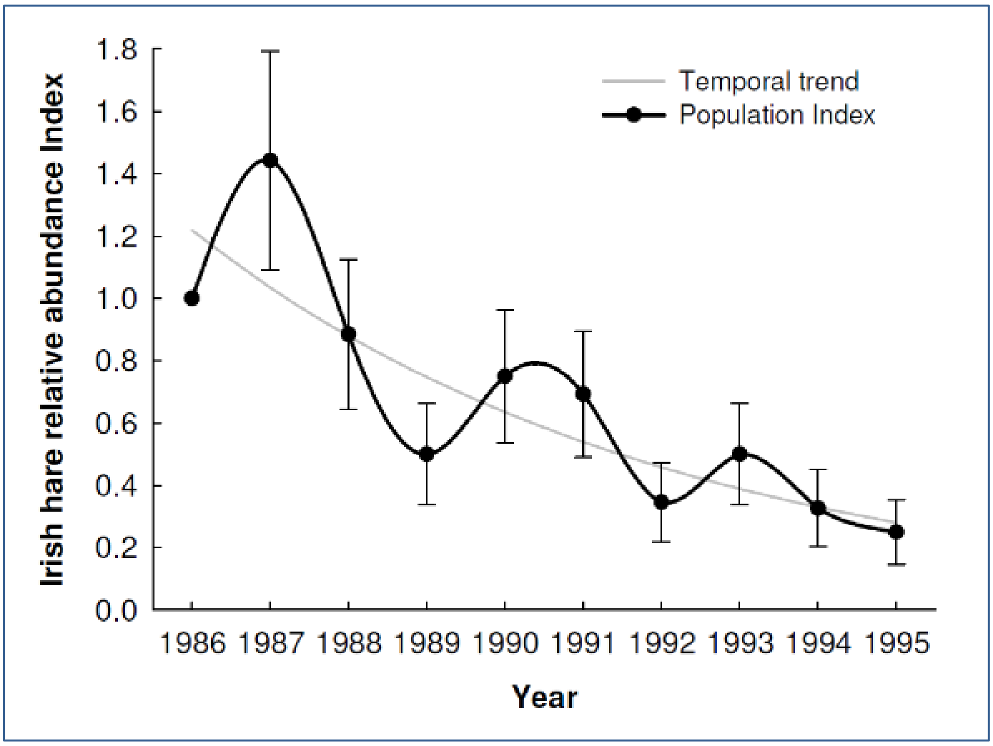


Figure 2 Continuing decline in an index of relative abundance of Irish Hare observed during Northern Ireland Rabbit Surveys between 1986 and 1995 (Reid *et al.*, 2007b).

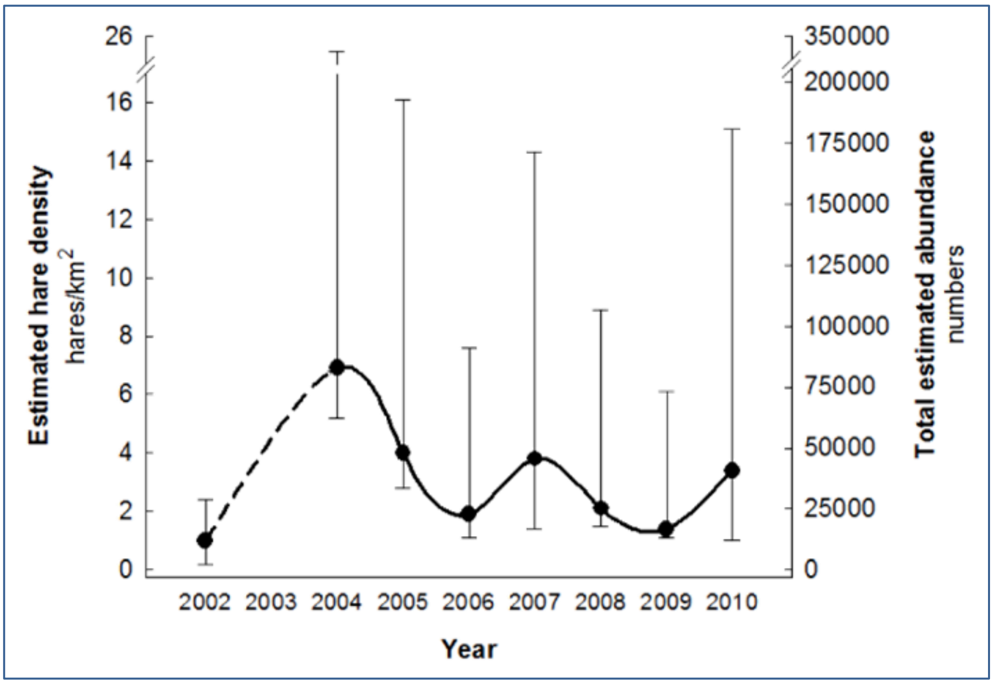


Figure 3 Estimated mean density (left y-axis) and abundance (right y-axis) of Irish Hare derived from customised distance analysis of Northern Ireland Hare Surveys from 2002 to 2010 showing no overall temporal trend. Note i) the low densities *c.* 0.5 - 7.0 hares/km² and ii) extremely wide (and, therefore, not very utilitarian) 95% Confidence Limits.

The Irish Hare had a local Northern Ireland and an All-Ireland Species Action Plan up to 2010 (Anon, 2000; 2005) with conservation measures aimed at maintaining and enhancing hare populations. In the Republic of Ireland, the species is protected under the Wildlife Act 1976 & 2000 whilst it is listed on Appendix III of the Bern Convention (Anon, 1979) and Annex V (a) of the EC Habitats Directive (92/43/EEC), which lists animal *species of community interest whose taking in the wild and exploitation may be subject to management measures* (for example, their licenced use in hare coursing). The species was listed as *Internationally Important* in the first Irish Red Data Book (Whilde, 1993) but the most recent Red List Assessment categorised it as *Least Concern* (Marnell *et al.*, 2009) in common with other Mountain Hare globally. The last three Article 17 reports to the EU Commission assessed the conservation status of the Irish Hare as Unfavourable – inadequate (NPWS, 2007), Favourable (NPWS, 2013) and Favourable (NPWS, 2019), where the apparent improvement in status from 2007 to 2013 reflected improved knowledge/more accurate data rather than actual population change. The species remains widespread across Ireland (Figure 4).

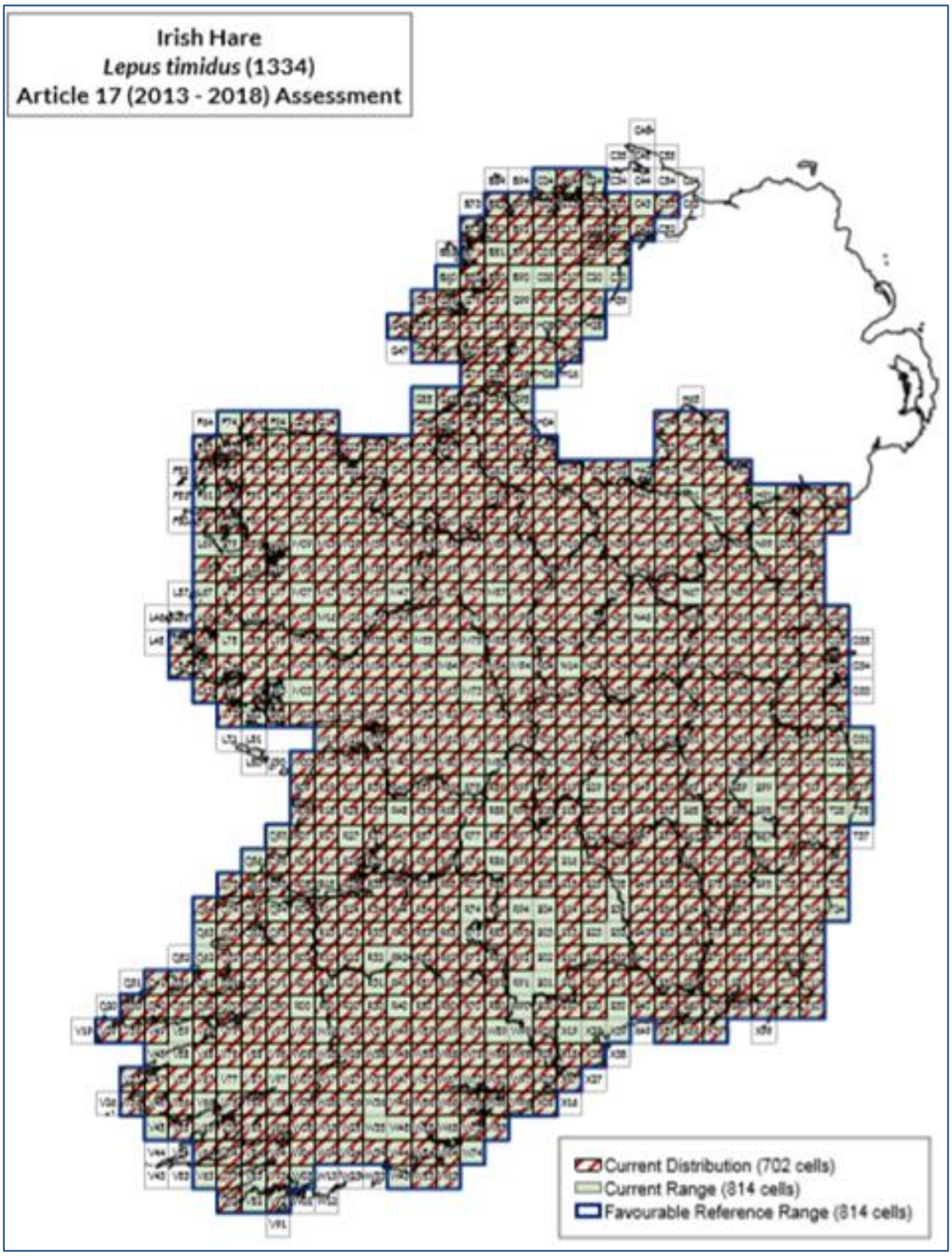


Figure 4 *Favourable Reference Range*, *Current Range* and *Current Distribution* of the Irish Hare throughout the Republic of Ireland as reported in the most recent Article 17 report (NPWS, 2019).

1.2 The European Brown Hare

The European Brown Hare (*Lepus europaeus*) was introduced to Ireland multiple times from the mid-1800s (Barrett-Hamilton, 1898; Reid, 2011) with suspected introductions emerging as recently as the 1970s (Caravaggi *et al.*, 2015). It is native to central mainland Europe but was introduced to Great Britain for food and sport during pre-Roman times where it is now considered a naturalised part of the British fauna (Yalden, 1999). Its much more recent introduction to Ireland, for the purposes of hare coursing (Barrett-Hamilton, 1898), means it is considered a non-native (invasive) species here (Reid, 2011).

The Brown Hare differs from the Irish Hare phenotypically, being sandy-brown rather than russet-red, exhibiting no winter whitening on the flanks or legs; it has a so-called 'thrushy' appearance with dark guard hairs projecting through the undercoat. It also has long ears (equal or longer than the length of the head) and a black dorsal surface to the tail (Figure 5). The Brown Hare competes with the Irish Hare for habitat space and potentially for food, hybridises and introgresses with the native, may support diseases or parasites to which the native is naïve and is likely to expand its range under future climate change scenarios to the detriment of the Irish Hare (Reid, 2011; Caravaggi *et al.,* 2015; 2016; 2017).

Despite many introductions, only two extant populations of Brown Hare is known in Ireland; over 1,000 individuals in south Derry and east Tyrone in Mid-Ulster, which appear to be actively expanding and replacing the Irish Hare locally (Caravaggi *et al.,* 2016), and another, much smaller, population in the vicinity of Baronscourt Estate, west Tyrone, which is disconnected from the eastern population by the Sperrin mountains (Reid, 2011). Brown Hare sightings have been reported in Donegal (Sheppard, 2004), but no extant population has been confirmed in the Republic of Ireland.

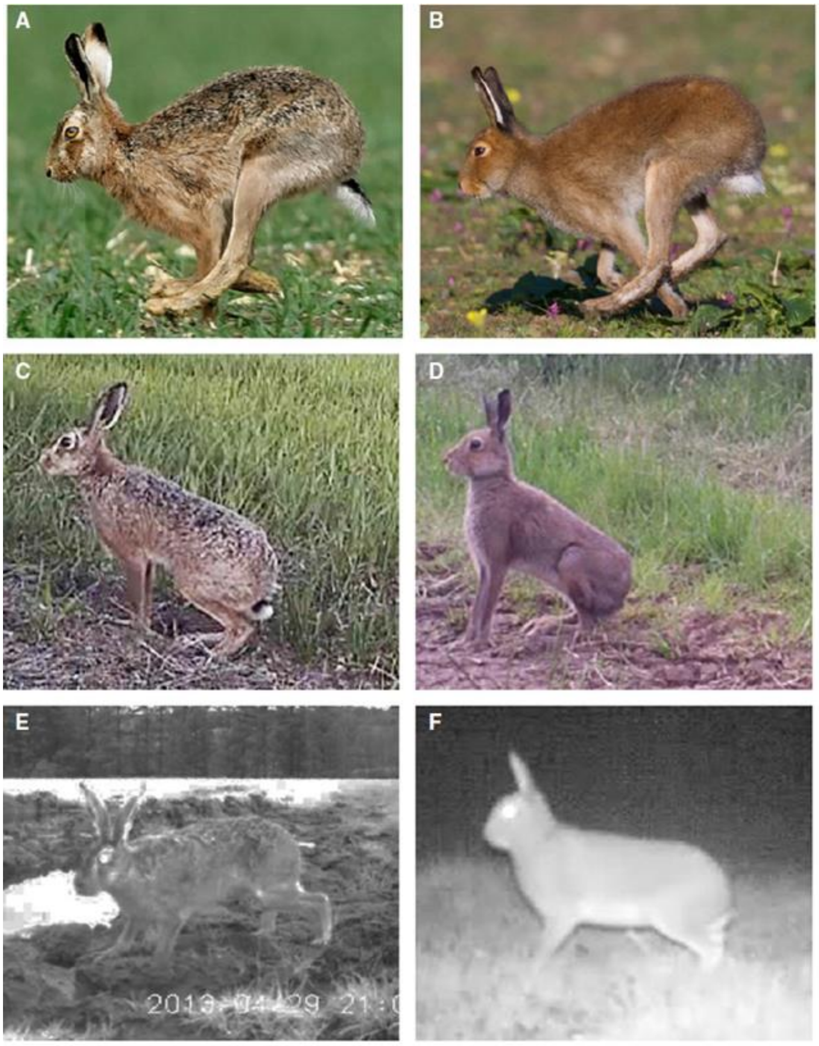


Figure 5 Photographs of **A** European Hare, *Lepus europaeus* (©Nigel Blake) and **B** Irish Hare, *Lepus timidus hibernicus* (©Shay Connolly) extracted with permission from Caravaggi *et al*. (2016), demonstrating clear interspecific differences enabling species ID from both diurnal [**C**, European Hare; **D** Irish Hare] and nocturnal [**E**, European Hare; **F**, Irish Hare)] camera trap footage.

1.3 Current project aims

The broad aim of the current project was to generate data to underpin the next EU Habitats Directive Article 17 report on the conservation status of the Irish Hare and to establish change in the population since the last Hare Survey of Ireland 2006/07 (Reid *et al.*, 2007a). The specific objectives were to:

1. Produce a robust estimate for the mean population density of the Irish Hare (numbers of individuals per km^2 ± confidence intervals) throughout its range in the Republic of Ireland;
2. Provide a robust estimate for the national population of Irish Hare (total number of individuals ± confidence intervals) in the Republic of Ireland;
3. Examine evidence for differences in abundance over space (between regions) and over time (since the last Hare Survey of Ireland 2006/07);
4. Assess the current national conservation status of the Irish Hare throughout the Republic of Ireland;
5. Report any European Brown Hare sightings;
6. Make recommendations for future monitoring and surveillance of the Irish Hare.

1.4 Survey techniques

A number of different survey techniques have been used for hare population enumeration (see Hutchings & Harris, 1996; Langbein *et al*., 1999). Faecal pellet counts are generally only effective at high densities, where pellets are easily found and enumerated in typically open habitats e.g. moorland, and depend on accurately establishing the relationship between the number of animals present and their tracks and signs in the field (e.g. Murray *et al.*, 2002; Newey *et al.*, 2003). This method is unsuitable for low density Irish Hare populations in dense grassland habitats where locating pellets is challenging. Direct counts of individual hares during the day are compromised by hares being predominately crepuscular, with day counts yielding low detection rates (Dingerkus & Montgomery, 2002) that are unlikely to reflect true abundance (i.e. they are underestimates). Direct counts at night (e.g. Preston *et al.*, 2002; Tosh *et al.*, 2004) have previously depended on spotlight surveys looking for the reflection of the animal's eye shine. Conducting night surveys on foot is difficult and dangerous in the Irish landscape due to problems of land access, terrain and small field sizes rendering hedgerows and fences as omnipresent obstacles (N. Reid pers. comm.). Restricting survey points to accessible areas introduces inherent survey bias resulting in underestimates of density (see Reid *et al.*, 2010; Marques *et al.*, 2010; Paxton *et al.*, 2010). Capture-mark-recapture (e.g. Mills *et al.*, 2005) is a robust enumeration technique used elsewhere e.g. Canada, but requires prohibitive staffing levels (to set and check traps daily) necessitating a small focal area, which is, therefore, not suitable for national surveys. It may also present risks to animal welfare from capture and requires specialist licencing and equipment. Moreover, it is most effective in high-density, closed populations (assuming no immigration or emigration). Molecular genetic population estimation by DNA fingerprinting individuals from, for example, faecal pellets, requires representative pellet collection from multiple focal study populations and reliable identification of individuals after DNA extraction by PCR, which can be expensive (especially when large numbers of samples are needed). It also necessitates differentiation of Irish and European Brown Hare faecal pellets. Plant and fungal fragments in herbivore faeces are often PCR inhibitors, making extraction of usable genetic material challenging, requiring large sample sizes. Obtaining fresh faecal pellets requires that tracks are cleared of old pellets before being revisited to collect recent droppings (requiring familiarity with each survey site).

More recent advances, specifically, camera trap technology (or Trail Cams), allows for 24/7 monitoring and surveillance, with cameras erected truly randomly across the landscape, thereby avoiding the issue of methodological bias (e.g. by using roads as survey routes). Newly developed statistical models using camera trap data, for example, the Random Encounter Model (Rowcliffe *et al*., 2008), can provide robust estimation of hare density and abundance with associated 95% confidence intervals and has been used successfully in Ireland (see Caravaggi *et al*., 2016). The latest development is the application of distance sampling analysis for density and abundance estimation from camera trap data (Howe *et al*., 2017) providing a similar analytical approach to that used in the Hare Survey of Ireland 2006-07 (Reid *et al*., 2007a).

1.5 Conservation Assessment

Conservation status is defined in the Habitats Directive as:

> *the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its populations.*

A species is taken as being in favourable conservation status only when:

- *population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and*
- *the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future; and,*
- *there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis;*

Methods for assessing conservation (or population) status of a listed species have been devised by the European Topic Centre for Nature Conservation (ETCNC) in conjunction with EU member states represented on the Scientific Working Group of the Habitats Directive (Evans & Arvela, 2011). The conservation status of a species is assessed on four parameters:

i) *Range*;

ii) *Population*;

iii) *Habitat for the species*; and

iv) *Future prospects*.

Assessment of conservation status results in the application of a traffic-light system, bringing together information on the four parameters. Each parameter is classified as being:

- Favourable (FV or good or green);
- Unfavourable-Inadequate (U1 or inadequate or poor or amber);
- Unfavourable-Bad (U2 or bad or red);or
- Unknown (grey).

Favourable reference values for *Range* and *Population* are set as targets against which future values can be judged. These reference values have to be at least equal to the value provided when the Habitats Directive came into force (in 1994). The *Favourable Reference Range* for a species is the geographic range within which it occurs and which is sufficiently large to allow its long-term persistence. The major pressures and threats perceived to be affecting the species are listed during each assessment and their current status, projected status, and observed impacts are used to determine the species' likely *Future prospects*. If any one of the four parameters is assessed as unfavourable, the overall assessment for the species must also be unfavourable.

2 Methods

2.1 Surveys

2.1.1 Pilot survey

This study consisted of two survey periods:

i) a pilot survey from March to May 2018 (breeding season) and

ii) a full survey implemented from November 2018 to February 2019 (non-breeding season).

The purpose of the pilot survey was to trial the survey methods (nocturnal spotlight surveys and 24/7 camera trapping arrays) and to determine logistical constraints and the time needed to complete data collection (including obtaining permissions from landowners, deployment and collection of camera traps, traversing the landscape etc.). The pilot study was intended as a proof-of-concept demonstration only; it did not aim to derive results i.e. estimated densities etc.

The Hare Survey of Ireland 2006/07 (Reid *et al.*, 2007a) utilised a nocturnal spotlight survey method from point transects located along minor roads with subsequent distance sampling analyses to generate animal densities and abundances. Changing the survey methodology to an entirely camera trap based survey raised concerns about the comparability of results with the original study and the generation of meaningful temporal trends. Thus, one of the principal aims of the pilot survey was to deploy a nocturnal spotlight point transect survey method (identical to that used during 2006/07) alongside camera trapping arrays, to compare species detection rates before proceeding with the optimal method during the full survey.

A total of 26 1 km^2 Irish grid squares was selected for survey during the pilot study (one per county) to provide widespread coverage of the country (Figure 6). Each square was selected at random from those surveyed during 2006/07. Survey squares covered all regions and habitats (Figure 7), being representative of CORINE land cover classifications (EEA, 2018). There was no statistical difference (using a chi-squared (χ^2) test of association) between the composition of the selected survey squares and the composition of the Republic of Ireland as a whole (Table 1).

Each square was surveyed using two methods

i) a nocturnal spotlight survey, and

ii) a camera trapping array (see full details of each method below).

In the pilot study, only the total number of species detected and the total number of detections per species were compared between the two survey methods.

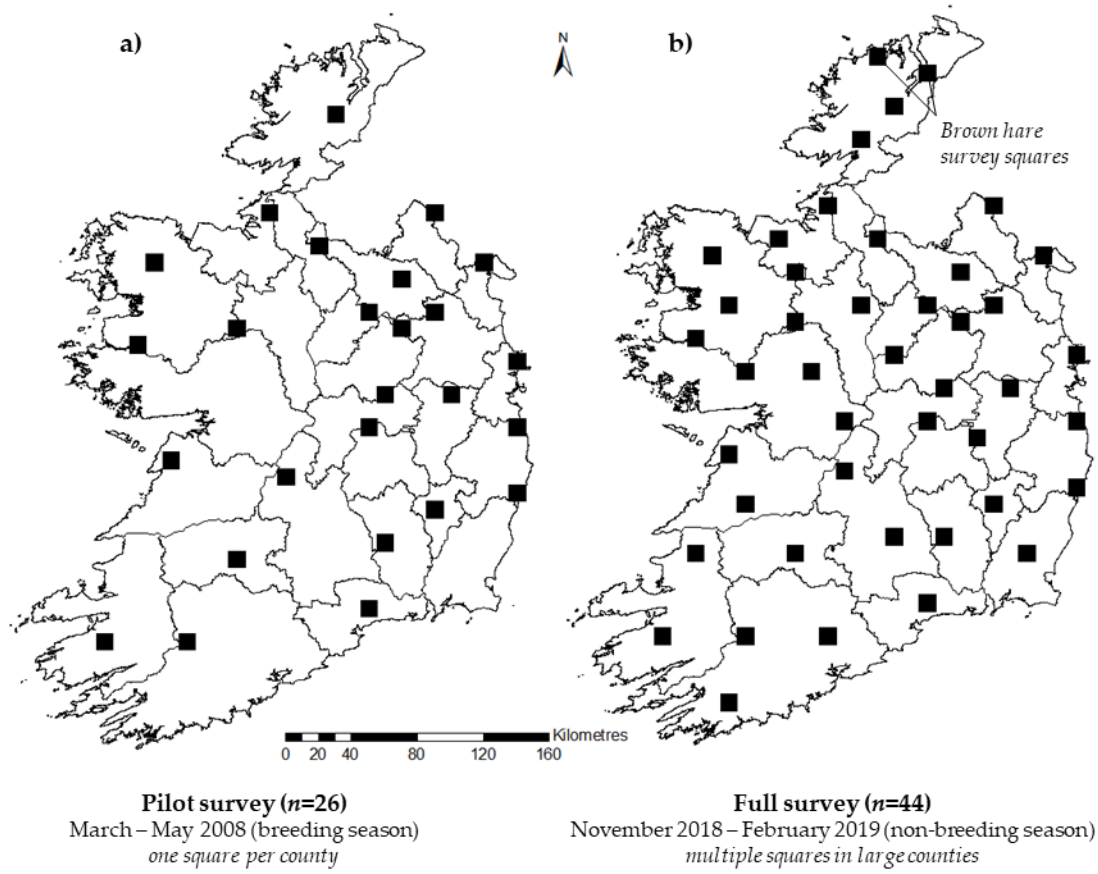


Figure 6 Survey square locations during a) the pilot study (left) and b) full survey providing uniform, widespread coverage (right).

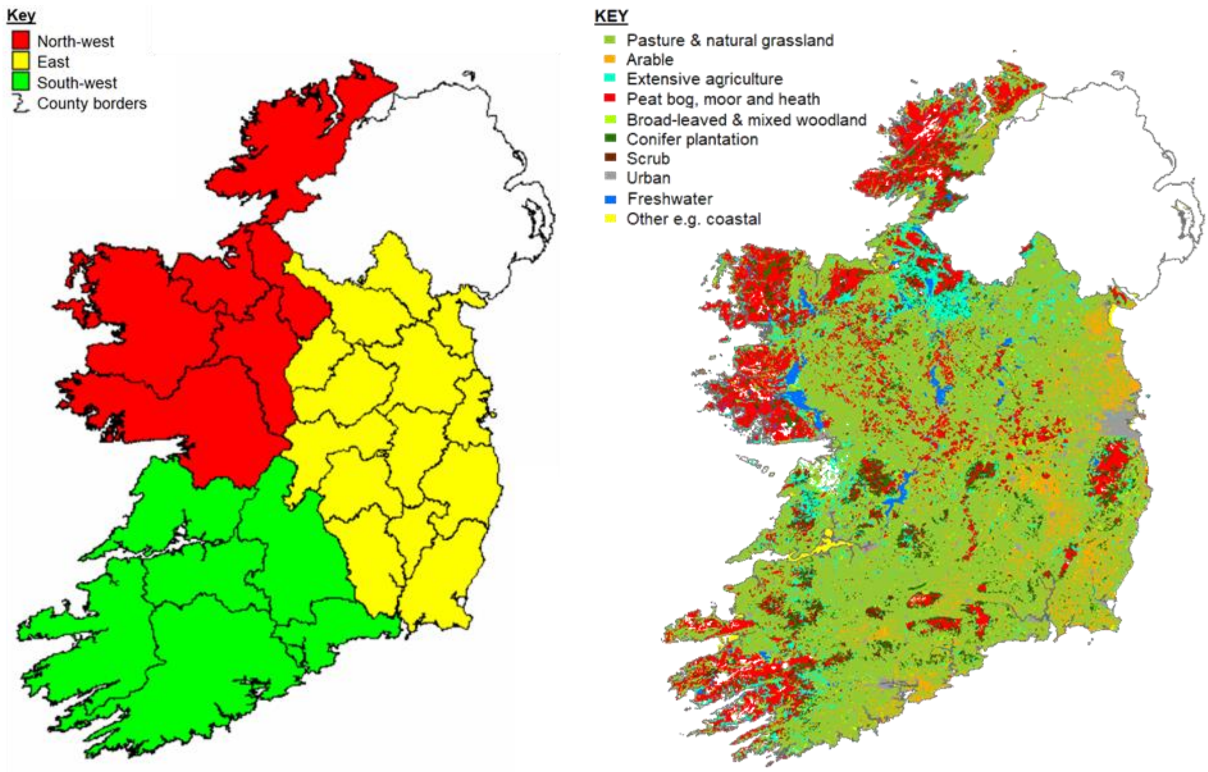


Figure 7 Geographic regions (analytical strata) defining the north-west, east and south-west (left) and CORINE 2018 land cover classifications (EEA, 2018) re-classed into more meaningful categories relevant to wildlife; see key (right).

Table 1 Terrestrial habitat composition (excluding Freshwater) of the Republic of Ireland (also see Figure 7), the pilot survey squares (Figure 6 a) and the full survey squares (Figure 6 b) using CORINE land cover classifications (some combined to create more meaningful categories). All p-values are >0.05 indicating there was no significant difference in survey square composition and that of the wider countryside with % values indicating the comparability within each category. **Inf* indicates the χ^2 statistic was infinite and inestimable given the low values for those categories.

Habitat classification	CORINE code	RoI		Pilot survey (n = 26)				Full survey (n = 44)			
		km²	%	km²	%	$\chi^2_{df=1}$	p	km²	%	$\chi^2_{df=1}$	p
Pasture & natural grassland	231 + 321	39,059	55.6	16.4	63.1	0.335	0.56	26.0	59.1	0.104	0.74
Arable	211 + 242	4,021	5.7	1.0	3.9	1.517	1.00	3.0	6.8	0.829	0.74
Extensive agriculture	243	4,930	7.0	1.4	5.5	1.886	1.00	3.6	8.1	0.754	0.55
Peat bog, moor & heath	322 + 412	11,204	15.9	4.3	16.7	1.043	1.00	6.9	15.7	1.003	1.00
Broadleaved & mixed woodland	311 + 313	988	1.4	0.5	1.9	0.357	0.31	0.6	1.4	0.613	0.46
Conifer plantation	312	2,743	3.9	1.0	3.8	1.015	1.00	1.0	2.4	1.747	1.00
Scrub	324	2,892	4.1	0.7	2.8	1.073	1.00	2.3	5.1	0.901	0.70
Urban	112 + 142	1,330	1.9	0.2	0.7	*Inf*	1.00	0.2	0.4	*Inf*	1.00
Other e.g. coastal etc.	e.g. 421 etc.	3,108	4.4	0.4	1.6	*Inf*	0.63	0.4	1.0	*Inf*	0.27
Total	**231 + 321**	**70,275**	**100**	**26.0**	**100**			**44.0**	**100**		

2.1.2 Full survey

The full survey involved expanding the camera trapping method only (i.e. no nocturnal spotlight surveys were conducted). After accounting for logistical and time constraints (e.g. it took considerably longer identifying and acquiring permissions from each landowner than anticipated), a total of 44 1 km² squares was surveyed. These squares consisted of the same 26 squares used in the pilot survey with a further 18 added (skewed towards larger counties, e.g. Counties Donegal, Galway and Cork, being some of the largest, were allocated three squares each whilst Counties Roscommon, Leitrim and Cavan, being some of the smallest, were allocated one square each). Squares were allocated to provide a roughly uniform, widespread coverage of the country (Figure 6) and, as with the pilot survey, were selected to be representative of the habitats throughout the Irish landscape as a whole (Table 1). In the full survey, the data collected included descriptive data such as the total number of species detected and the total number of detections per species, but also data necessary for estimating Irish Hare densities and abundances (i.e. the distance of each detection from the camera; for full details see below).

2.1.3 Spotlight surveys

The pilot study spotlight surveys commenced approximately 30 minutes after sunset during the hours of darkness and typically concluded before midnight. Within each survey square, a 1 km stretch of minor public road was used as a line transect. Each consisted of five point transects (separated by 200 m), where all points corresponded to the same GPS coordinates surveyed during the 2006/07 survey. A two million candlelight spot-lamp (Tracer, Suffolk, UK) was shone onto the surrounding landscape (360°) from the rear of the vehicle. Animals were detected by the reflection of light from the tapetum (reflective layer at the back of the eye of nocturnal species). For each animal detected, species, number and their radial distance from the observer were recorded (using a ± 1 m Leica Rangemaster LRF 900 Scan rangefinder). Approximately two minutes were spent at each point location, thus (discounting driving transit time); each square was surveyed for approximately ten minutes.

2.1.4 Camera trap surveys

The full survey consisted of deploying 14 camera traps (following Caravaggi *et al.,* 2016) within each of 44 1 km^2 squares (Figure 8). GPS coordinates were generated at random using ArcGIS 10.5 (ESRI, California, USA); thus, unlike spotlight surveys which were biased towards roads, camera traps comprised a truly random sample of the landscape. Prior to camera installation, permission was sought from landowners for access to privately owned land. Initially, this involved posting letters to all houses within each 1 km^2 grid square, identified using the online Eircode finder (https://finder.eircode.ie). The purpose of the letters was to make local residents aware of our presence in the area and to give landowners the opportunity to refuse access or discuss the details of the study. Following the delivery of letters and prior to the installation of cameras, houses in the immediate vicinity of each survey point were visited to confirm permission was granted for land access. Where residents were not at home, a letter was left and neighbours were asked to notify landowners on our behalf. All permissions were granted and cameras were installed. The process of obtaining permission by door-to-door visit varied depending, for example, on the density of houses in the area, how quickly land owners could be located, and the amount of land each individual owned, but, on average, this process took approximately four to six hours per survey square.

The camera traps used were the Bushnell Trophy Cam HD Essential E3 (Bushnell Outdoor Products, Kansas, USA). Cameras were fixed to the nearest vertical structure to each random point (e.g. fence post or tree) at a height of approximately 30 cm above ground level, tilted slightly downwards (20° declination) such that the landscape in front was visible. Cameras were always pointed towards the centre of the selected field, capturing any animals that passed the camera. Cameras were secured in place using a nylon strap and a cable lock (Python Master Lock 8 mm cable lock) to prevent theft. Cameras were set to record 15 second videos when triggered by movement, followed by a one minute pause to avoid double detection of the same animals. In order to reduce damage to cameras and excessive triggering, deployments in fields containing livestock were avoided where possible. In spite of this, livestock were sometimes moved into fields where cameras had been installed so damage and videos of livestock were unavoidable in some instances.

It took approximately one full day (08.30 to 18.00) to install a full complement of 14 camera traps. Cameras were left in situ for a minimum of one week (approximately 168 hours survey effort per camera) before retrieval, which took approximately three to four hours per survey square. Thus, it took 0.5 days to gain permissions, one day for deployment and 0.5 days for retrieval meaning that data collection from each square took approximately two days with a team of two surveyors working together to minimise health and safety concerns associated with lone working. With 14 cameras per square this was approximately 2,352 hours of survey effort per survey square. Across both survey periods (pilot and full survey) two cameras out of 947 deployed (0.2%) were stolen. Damage to cameras generally involved one or both plastic clips on the back being broken and this usually happened during installation when securing them with bicycle locks or by livestock rubbing against cameras in fields.

Figure 8 An example of a 1 km² survey square showing the randomly selected locations of 14 deployed camera traps (centroid of the grey boxes with a unique code per camera). Note the random sample of habitats i.e. pasture, arable and scrub in this case.

2.1.5 European Brown Hare survey locations

Brown Hare sightings were reported in Donegal between 1976 and 2000 (Sheppard, 2004) from Inch Island (Irish grid square C3120) and Creeslough on the north coast of the county (Irish grid C0030), but no extant population has been confirmed in the Republic of Ireland. Two of the 44 1 km² squares selected for the full survey included C3120 and C0030 (see Figure 6 b) in an attempt to ascertain if Brown Hare was still present. Like every other square, each had 14 randomly placed camera traps recording for one week; thus if any Brown Hare was present it was expected that it would have been recorded.

2.2 Distance sampling

In order to derive estimates of animal densities, the distance between the camera and each detected individual as well as the angle (deviation from 0° in front of the camera lens) was required. During deployment, a 4 x 2 m grid was created 1 m in front of each camera by placing spray-painted (bright red) bamboo canes at 1 x 1 m intervals following Caravaggi *et al.* (2016) (see Figure 9). A photograph was captured of this 'reference grid' from the aspect of the camera trap before the canes were immediately removed (i.e. not left in the field) and the camera left in situ.

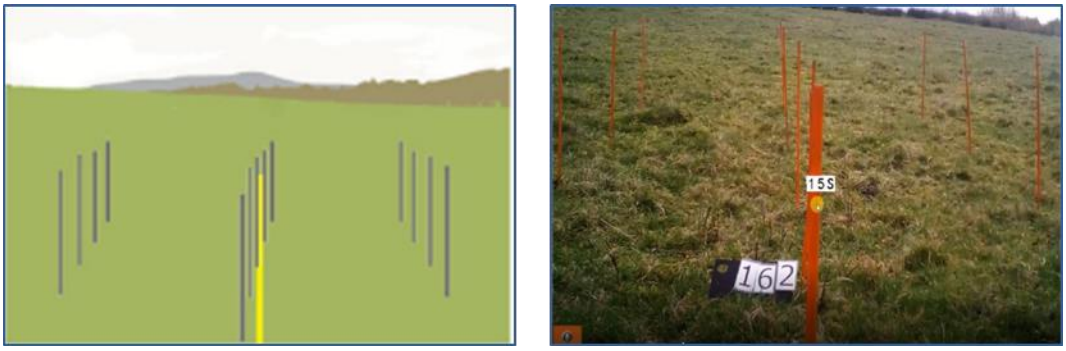


Figure 9 Conceptualised reference photo grid recommended by Caravaggi *et al.* (2016) (left) and an actual example of a reference photo bamboo grid as seen in the field (right).

Upon retrieval of each camera trap, recorded videos were extracted from the memory SD card and uploaded to an online data portal (accessible via http://globalteamcounting.com/signin; operated by IDASO Ltd.). All videos were screened manually (i.e. without the use of computer algorithms) by a single observer (N. McGowan) and the species and number of individuals detected were recorded. Where the identity of a detected species was unclear, videos were referred for expert opinion (N. Reid). With approximately 19,000 videos recorded, each lasting 15 seconds, this process took approximately 80 hours (or 11 working days; though it was not possible to invest such concentration continuously so the task was spread out over a period of weeks among other tasks). For videos containing footage of Irish Hare, the date and time stamp of each video was extracted manually and added to a database spreadsheet against each unique camera ID. The distance and angle to each detected animal was extracted using custom-made software developed by IDASO Ltd. (see Figure 10).

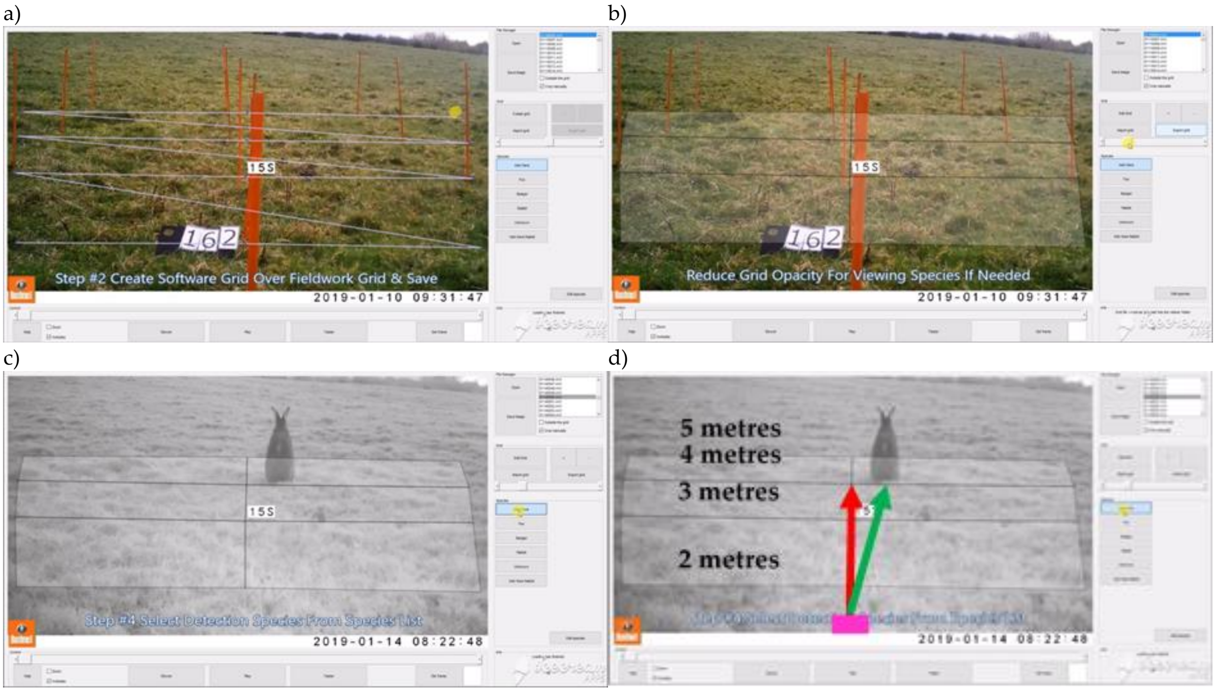


Figure 10 Step-by-step protocol for extracting the distance and angle to each detected animal. a) Select relevant reference photo and create grid, b) make grid transparent, c) overlay grid on species detection, d) use custom software (IDASO Ltd.) to extract distance (green line) calibrated to overlaid grid (to nearest 20 cm) and angle deviation from 0° directly in front of the camera lens. Both parameters were added to the database spreadsheet, generating the data file ready for analysis.

2.3 Data analysis

2.3.1 Spotlight surveys verses camera trap detections (pilot survey only)

Descriptive statistics were used to report the number of species detected, the numbers of individual detections of each species and the percentage difference between spotlight and camera trap results for the pilot survey.

Spearman's correlations were used to determine relationships between the presence/absence (0/1) of each species between each survey method (spotlight and camera traps). They were also used to determine relationships among species (e.g. between Irish Hare and their main predator; the Fox) within surveys (e.g. within spotlights or camera trap survey in isolation). In addition, Spearman's correlations were used to examine the relationships between numbers of individual detections of each species between survey methods and between species within surveys.

Species-specific spotlight survey detection rates were validated with camera trap detections using the Area Under the Curve (AUC) value from the Receiver Operating Characteristic (ROC) curve.

2.3.2 Density and abundance estimation (full survey only)

Camera traps recorded continuously throughout the 24-hour cycle but Irish Hare is predominately crepuscular or nocturnal. Thus, animals are typically inactive during daylight hours and unavailable for detection despite cameras operating during this period. To include all data (from throughout the 24-hour cycle) for the purposes of density estimation would, therefore, erroneously underestimate animal densities due to the inclusion of periods when they were not active. To resolve this problem, Howe *et al.* (2017) restricted data used in distance analysis models to the period during which target animals were available for detection. To replicate this approach, we therefore defined the 'peak period' of activity of hares. A histogram of the frequency of hare detections was plotted across the 24-hour period and a kernel density line was fitted representing the species activity profile. The highest point of the fitted kernel density was assumed to be the period during which 100% of the population was likely to be active (as per Rowcliffe *et al.*, 2014). To define a peak period (as opposed to a single point in time) during which most (i.e. the majority) of the population was active we selected the period when ≥55% of the kernel density was captured. Any detections and all survey effort outside the peak period were discarded and only those detections within the peak period (and corresponding survey effort) were retained for distance analyses.

Density estimates were calculated using conventional distance sampling following Howe *et al.* (2017) who adapted the technique specifically for camera trap data. Density estimates were calculated using Equation 1:

$$\hat{D} = \frac{2t\sum_{k=1}^{K} n_k}{\theta w^2 \sum_{k=1}^{K} T_k \hat{P}_k}$$

Equation 1

Where $\hat{D}$ is the estimated density (animals km^2), t is a pre-determined time interval to divide survey periods into multiple snapshot periods, K is the total number of cameras deployed, k is the individual camera from one to K, n is the number of detections, θ is the angle of view of the camera (radians), w is the truncation distance (m), T is the survey effort within the peak period(s) of activity and $\hat{P}$ is the estimated probability of detection. In order to use this model, a time interval (t) of 15 seconds was selected as it represented the maximum duration of any videos captured from the camera traps.

Detection functions were fitted using Distance version 7.2 software (Thomas *et al.*, 2010) where a range of candidate models were tested including: uniform cosine, half-normal hermite polynomial and hazard rate cosine. Distances to detections were binned into unequal intervals and right truncated as appropriate to optimise the fit of the detection function. First and second order adjustments were applied to each model and the single best detection function selected using Akaike's Information Criterion (AIC) values, with the best model being that with the lowest value. Global (countrywide) density estimates were calculated and subsequently split by regional geographic strata i.e. northwest, east and southwest, allowing spatial variation in density and abundance to be assessed.

Distance models used for regional density estimation used 'design-based 95% confidence intervals' based on inference to extrapolate from the sampled points (camera trap locations) to the entire region. However, the true number of animals in the vicinity of each camera location was unknown so the detection function was used to estimate the true number of hares present. Conventional distance analysis is, therefore, a hybrid approach, blending design-based (extrapolation from points) and model-based (within sample points) inference (following Fewster & Buckland, 2004). At the national (so-called global) level, a fully model-based approach can be employed such that animals are assumed to be uniformly and independently distributed throughout the full survey region; this produces the same mean density but estimates of precision (95% confidence intervals) change and are notably wider than design-based inference. The latter is achieved using a 999-iteration non-parametric bootstrapping method where strata, in this case cluster sampling within 1 km^2 survey squares, taken as the unit of variance (not camera locations within squares) are resampled. This generates so-called 'bootstrapped confidence intervals' associated with the global national estimate which are more conservative with respect to variability of density between sample squares as opposed to between camera locations within squares.

Population change was estimated as percentage change in the mean density estimate compared with the last survey during 2006/07 (Reid *et al.*, 2007a). Such change was deemed statistically significant only if the 95% confidence intervals of the mean estimates did not overlap between time points.

Mean density (numbers of animals per km^2) was converted to abundance (total numbers of animals) regionally and nationally by multiplying densities by the total extent of each region (taken from the previous hare survey report for the purposes of direct comparison:

- Republic of Ireland = 69,878 km^2;
- Northwest = 22,580 km^2;
- Southwest = 24,283 km^2 and
- East = 23,015 km^2).

2.3.3 Species Distribution Models

Maxent 3.4.1 (accessible via: http://biodiversityinformatics.amnh.org/open_source/maxent) was used to predict the probability of hare occurrence throughout Ireland using a 50 ha hexagon pixel size. This scale was chosen for two reasons: i) the maximum home range size of the Irish Hare is approximately 50 ha in size (Reid *et al.*, 2010) and ii) hexagons tessellate in a manner such that they are equidistant from one another and the centre of each cell is equidistant from all edges (not so using square pixels). Unlike many studies that use Maxent or other Species Distribution Modelling platforms, we did not use a presence-only approach i.e. camera locations positive for hares coded as present (=1) and a selection (usually 10,000) randomly selected pixels throughout the country treated as background cells for comparison (=0). Such an approach takes no account of the distribution of survey effort. Rather we used a true presence-absence approach, where locations positive for hare were coded as present (=1) with actual survey locations that failed to detect hares coded as absent (=0). A combination of linear and quadratic species response curves were used to avoid model overfitting using product, threshold or hinged functions. Jackknife resampling analysis was used to determine a heuristic estimate of the relative importance of each environmental variable on hare distribution, based on its contribution to the global model judged using the Area Under the Curve (AUC) value of the Receiver Operating Characteristic (ROC) curve (Liu *et al.*, 2005). Models were built using a 75% training set and a 25% test set of data chosen at random, with four replicate runs to ensure, on average, that most data points were used in building and testing the final averaged model. Response curves of the predicted probability of hare occurrence were plotted for each explanatory variable. A map of landscape favourability was generated to reflect the predicted probability of species occurrence using ArcGIS 10.5 (ESRI, California, USA). The 10^{th} percentile training presence was used as a threshold for continuous probabilities for landscape suitability (a heatmap) (Phillips, 2017) such that likely species presence/absence (a black and white map) was predicted at the 50 ha hexagon level and summarised at the 10 km square level (consistent with the scale commonly used for species atlases. The total extent of the predicted 10 km^2 square distribution could be taken as indicative of the species' *Favourable Reference Range,* i.e. 10 km^2 squares within which suitable habitat exists.

A total of 14 potential explanatory environmental parameters was used in Species Distribution Modelling (Figure 11). Eight represented habitat composition defined by CORINE land cover categories (EEA, 2018) some of which were aggregated to create categories that were more intuitive. For example, improved pasture and natural grasslands (acid, alkaline and neutral) were aggregated into the single category of 'grassland'; broadleaved and mixed woodland were aggregated, whilst coniferous plantations were kept separate. Two parameters captured landscape structure, namely habitat category Shannon's Diversity Index (SDI) and Shannon's Evenness Index (SEI), effectively summarising the variation in habitats relative to their coverage within each pixel. One variable was used to capture the Human Influence Index (HII) that goes beyond urban cover to also incorporate human population density, intensity of agriculture and infrastructure including night-time lights, road networks, railroads, navigable rivers, canals etc. (downloaded from WCS, 2005). Finally, three climatic variables were included: annual mean temperature (Bio1), rainfall (Bio12) and seasonality (Bio4), which was the Bio1 standard deviation*100 (downloaded from www.worldclim.org/bioclim). Animals cannot directly perceive altitude (i.e. their elevation above sea level) but rather perceive its proxies i.e. temperature, precipitation etc., thus, altitude was deliberately excluded from models in preference for climate data which define an animal's direct experience of its environment. Due to the presence-absence approach used, environmental parameters were extracted for each modelled pixel using ArcGIS to create a 'Species with Data' (.SWD) file, upon which the model was constructed before extrapolation to unsurveyed pixels.

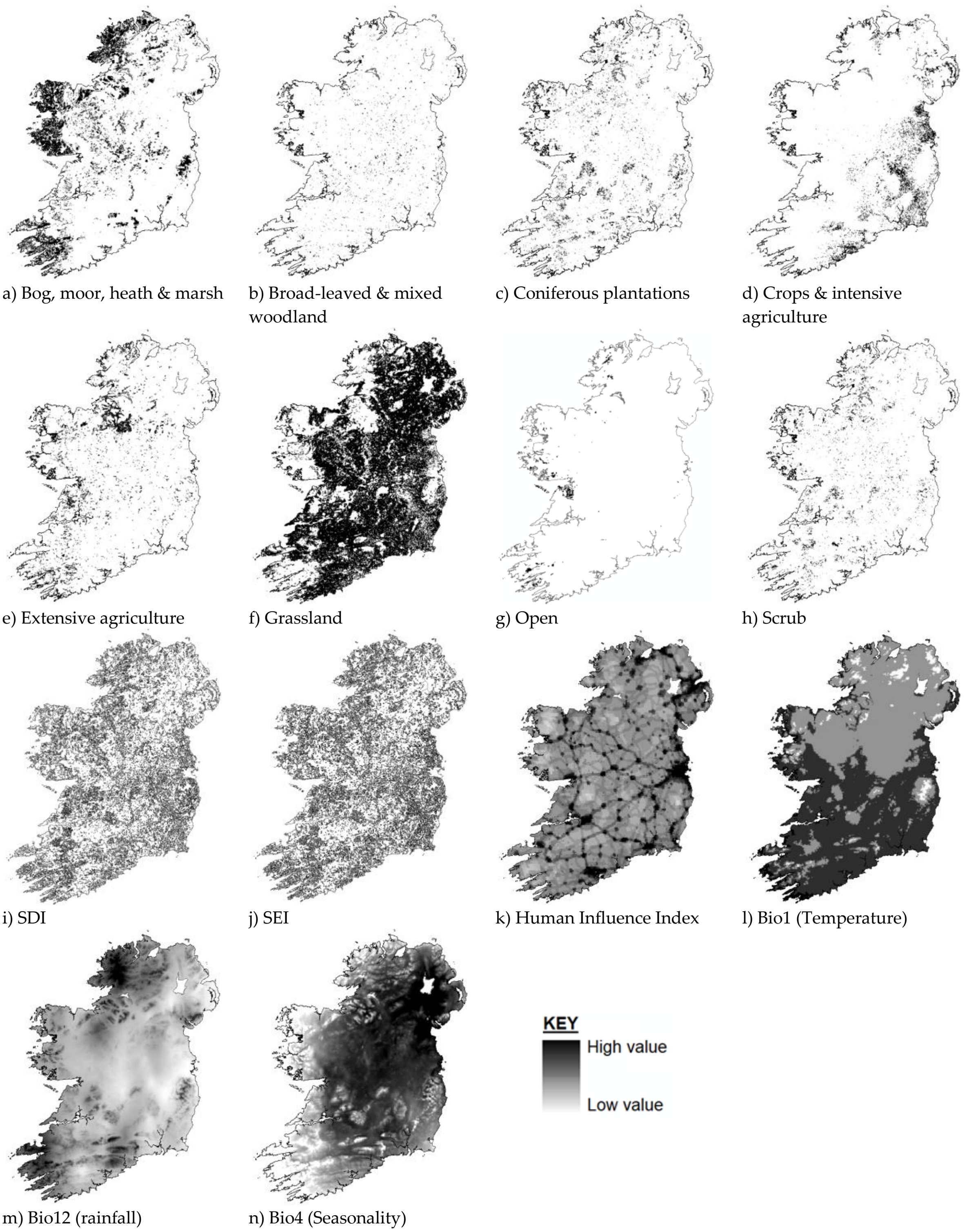


Figure 11 Spatial variation in potentially explanatory variables used in Species Distribution Modelling derived from CORINE 2018 Land Cover categories, their structure (Shannon's Diversity Index and Shannon's Evenness Index), Human Influence Index and three bioclimatic variables from WorldClim.

2.4 Empirical distribution data

Whilst Species Distribution Modelling provided a prediction of likely habitat suitability and thus the likelihood that any 10 km atlas square could support Irish Hare, we also collated incidental observations of Irish Hare. A web-based citizen science project was launched, supported and hosted by the National Biodiversity Data Centre, Waterford. Members of the public were invited to submit species records online (Figure 12) using a bespoke web portal (accessible via https://records.biodiversityireland.ie /record/national-hare-survey#7/53.455/-8.016). The availability of the portal was advertised in an article published in The Irish Times newspaper (https://www.irishtimes.com/news/environment/can-coursing-be-good-for-hares-the-strange-answer-is-yes-1.3738552) and in the magazine, Biodiversity Ireland (http://www.biodiversityireland.ie/wordpress/wp-content/uploads/Biodiversity_Ireland_Issue _18_web.pdf), as well as widely on social media (Twitter, Facebook etc.). All hare records since the 2013 Article 17 report (NPWS, 2013) i.e. January 2014 to March 2019 (the most recent record in present survey) were collated and added to the pilot and full survey results and mapped at a 10 km^2 square resolution. The 10 km^2 occupancy records were compared regionally using chi-squared (χ^2) tests with pairwise post-hoc comparisons incorporating a Bonferroni correction. Collated occupancy records (2014-2019) were compared to those reported in the most recent Article 17 report (NPWS, 2019).

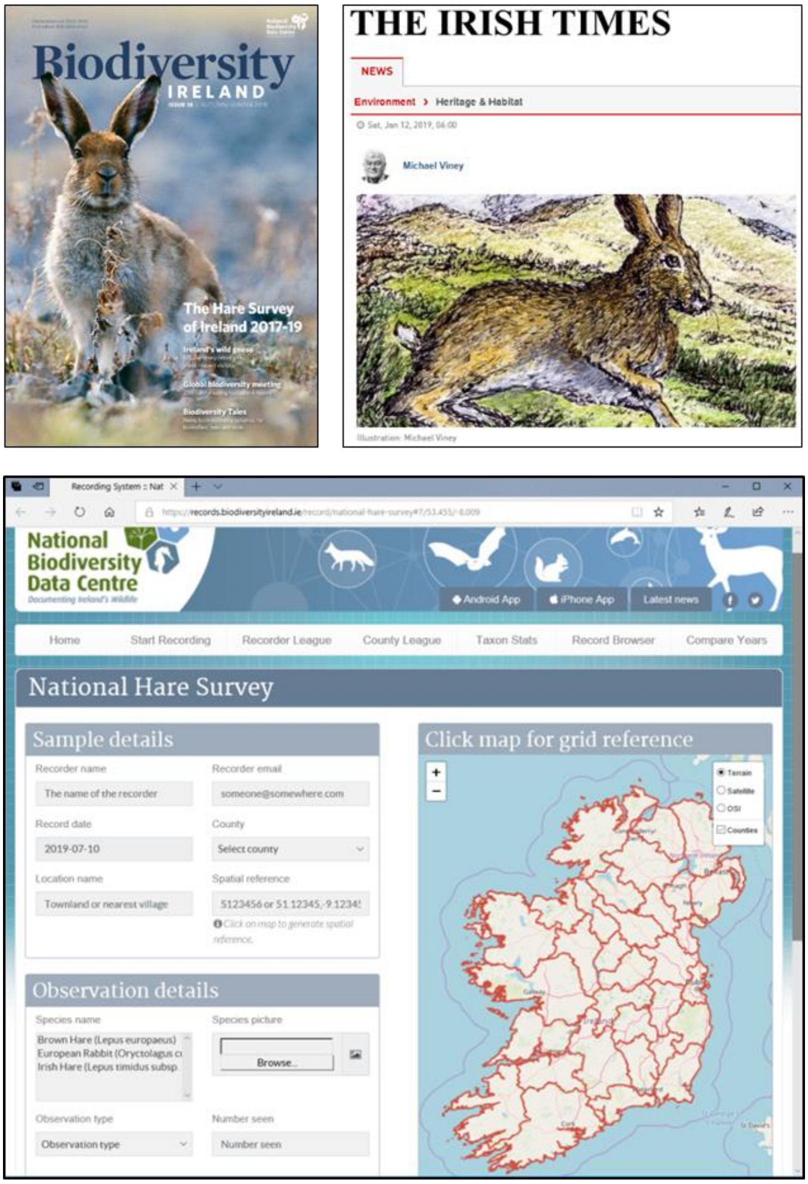


Figure 12 Media articles advertising the National Hare Survey (above) and the online National Biodiversity Data Centre portal set-up to capture species records from the public.

3 Results

3.1 Pilot survey

3.1.1 Species detection rates

From 130 point transect locations within 26 squares (totalling 4.3 spotlight survey hours), a total of 84 individuals belonging to four wild mammal species was detected during the pilot survey using the nocturnal spotlight method: Irish Hare, Rabbit, Fox and Badger. In contrast, a total of 2,604 individuals of twelve species was detected by camera traps in the same survey squares (58,968 survey hours from 351 camera deployments; Table 2; Figure 13). In addition to wild mammals, farmland birds were detected in approximately 1,500 videos (3% of approximately 48,000 videos), which were not analysed as it was beyond the scope of the current survey. The species present in 20 videos could not be determined. Grey Squirrel was detected only during the pilot survey (spring/summer) and Red Deer was detected only during the full survey (winter). All species detections and their Irish grid spatial coordinates have been submitted to the National Biodiversity Data Centre, Waterford. Across all species, camera traps yielded 3,000% more detections than spotlight surveys including over 2,000% more Irish Hare detections (Table 2).

Table 2 Species inventory, number of detections and percentage occurrence at survey points and within survey squares comparing spotlight surveys to camera trap surveys during the pilot survey. *+Inf* indicates that no confidence intervals were estimable for an increase from 0.

Species	Number of detections (% occurrence within squares, at points)		Difference (% increase using cameras)
	Spotlight	Camera trap	
Irish Hare	9 (35, 7)	202 (81, 20)	+193 (+2,144%)
Fox	2 (8, 2)	255 (100, 41)	+253 (+12,650%)
Badger	3 (4, 1)	133 (77, 19)	+130 (+4,333%)
Rabbit	70 (27, 10)	1,827 (35, 12)	+1,757 (+2,510%)
Wood Mouse	0 (0, 0)	85 (50, 7)	+85 (+*Inf*)
Sika Deer	0 (0, 0)	66 (8, 1)	+66 (+*Inf*)
Fallow Deer	0 (0, 0)	25 (4, 1)	+25 (+*Inf*)
Hedgehog	0 (0, 0)	5 (19, 1)	+5 (+*Inf*)
Grey Squirrel	0 (0, 0)	2 (8, 1)	+2 (+*Inf*)
Pine Marten	0 (0, 0)	2 (8, 1)	+2 (+*Inf*)
Rat	0 (0, 0)	1 (4, 0.3)	+1 (+*Inf*)
Red Squirrel	0 (0, 0)	1 (4, 0.3)	+1 (+*Inf*)
Total	**84 (50, 18)**	**2,604 (100, 65)**	**+2,520 (+3,000%)**

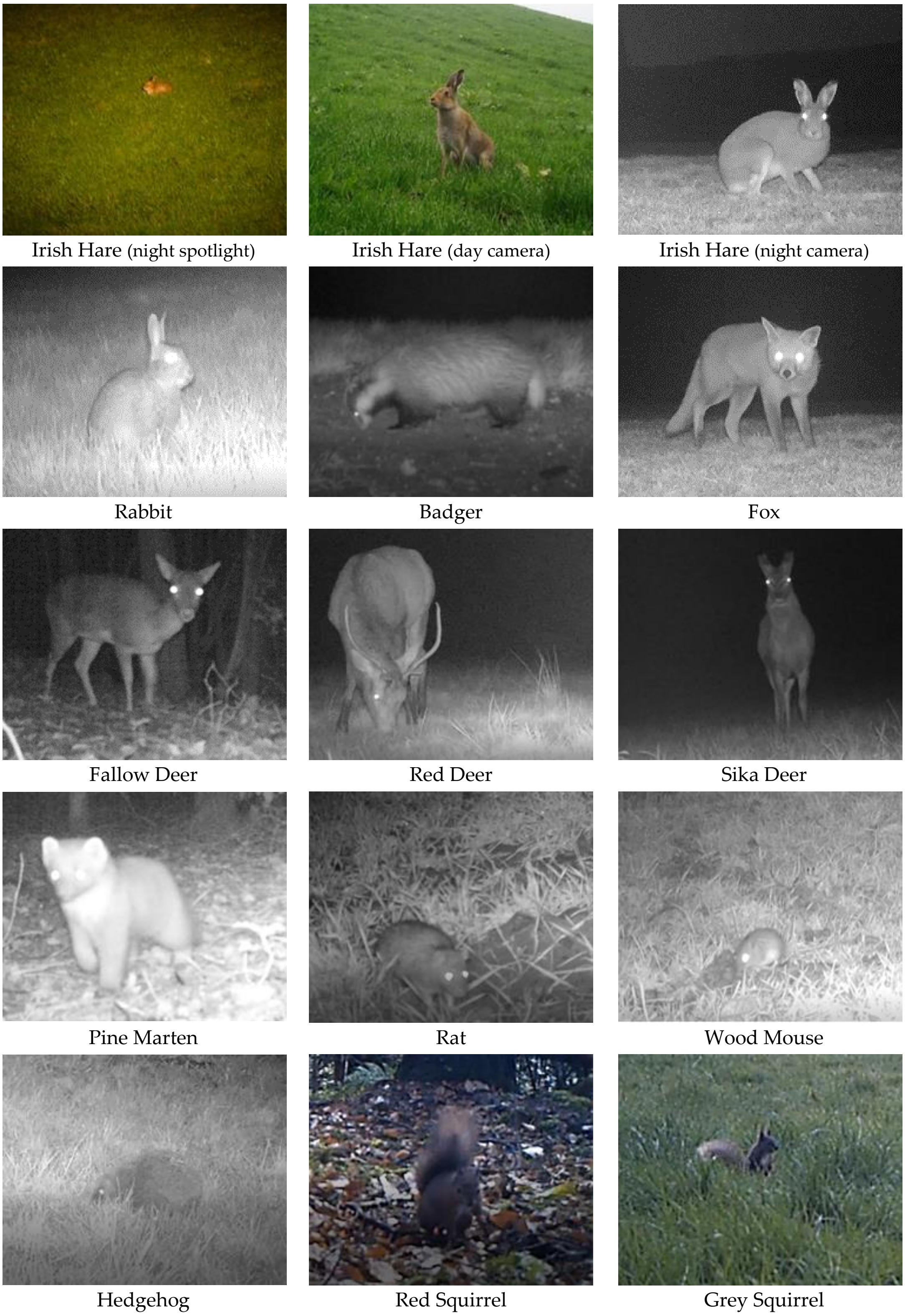


Figure 13 Images of species detected during camera trap surveys including an example of an Irish Hare during the pilot spotlight survey and on camera traps during both day (colour) and night (black and white).

During the pilot study, Irish Hare was detected in 35% of squares (9/26) using spotlight surveys and 81% (21/26) of the same squares using camera traps (Table 3). Species detections matched (both positive and negative results) between spotlight and camera trap surveys in 46% of squares (Table 3). The AUC value for spotlight surveys cross-validated against camera trap surveys was close to 0.5 and the associated 95% confidence interval spanned 0.5 (Table 3), suggesting that the likelihood of detecting a hare using nocturnal spotlight surveys when confirmed as truly present by camera trap surveys was near random.

Table 3 Two-by-two contingency table for hares cross-tabulating positive and negative detections from pilot study spotlight surveys (columns) and camera trap surveys (rows) reporting the Area Under the Curve (AUC) value from the Receiver Operating Characteristic (ROC) curve for each using both occurrence (presence/absence) and relative activity (numbers of detections). CI are 95% confidence intervals.

		Spotlight surveys			AUC (95% CI)
		-ve	+ve	Total	
Camera trap surveys	-ve	4 (15%)	1 (4%)	5 (19%)	
	+ve	13 (50%)	8 (31%)	21 (81%)	
	Total	17 (65%)	9 (35%)	26 (100%)	0.590 (0.322 - 0.859)

Fox occurrence (presence/absence) was positively associated with Rabbit and hare occurrence within spotlight survey data (rs = 0.48, p = 0.01 and rs = 0.40, p = 0.05 respectively). Fox detections (number of sightings) was also positively associated with hare detections within spotlight surveys (rs = 0.40, p = 0.05). Rabbit detections were positively associated between spotlight and camera trap surveys (rs = 0.46, p = 0.02), as were Fox detections (rs = 0.41, p = 0.04). Additionally, Rabbit detections from spotlight surveys were positively associated with Fox detections using camera trap surveys (rs = 0.49, p = 0.01).

3.2 Full survey

3.2.1 Species detection rates

From 596 camera locations within 44 squares (totalling 106,026 survey hours), a total of 1,236 detections of twelve species was made during the full survey; yielding a total of 3,840 mammal detections of 13 species across both the pilot and full surveys (Table 4). The apparent decline in detections between the pilot and full survey, despite increasing the number of squares surveyed from 26 to 44, is accounted for by the difference in Rabbit detections. During the pilot survey several cameras within the Co. Carlow survey square were mounted (unknowingly) directly adjacent to a Rabbit warren, resulting in 1,488 detections at that one site (accounting for 81% of all Rabbit detected during the pilot study). Care was taken during the full survey to avoid placing cameras right next to warrens; thus, Rabbit detections (and overall detections) declined between the two surveys despite higher survey effort in year two. It should be noted that the pilot survey occurred during the breeding season for most species (March to May) when young animals were more likely to be detected, whilst the full survey occurred during the non-breeding season (November to February), which may have also contributed to a decline in total detections. In addition to mammals, approximately 2,000 videos (11% of the approximately 19,000 videos) contained footage of birds, which have not been analysed here. Species detections were indeterminable in 52 videos.

Survey effort (number of hours of camera deployment) varied between the geographic regions resulting in varying numbers of hare detections, yet the detection rate (detections standardised by survey effort) was largely comparable between the east and southwest and higher in the northwest (Table 5).

Table 4 Comparison of numbers of detections (% of total detections) for each species between the pilot and full survey using camera traps.

Species	Pilot survey		Full survey		Overall detections	
	n	%	n	%	n	%
Irish Hare	202	8%	253	20%	455	12%
Fox	255	10%	335	27%	590	15%
Badger	133	5%	108	9%	241	6%
Rabbit	1,827	70%	274	22%	2,101	55%
Fallow Deer	25	1%	17	1%	42	1%
Red Deer	0	0%	3	0.2%	3	0.1%
Sika Deer	66	3%	19	2%	85	2%
Pine Marten	2	0.1%	8	1%	10	0.3%
Rat	1	0.04%	9	1%	10	0.3%
Wood Mouse	85	3%	191	15%	276	7%
Hedgehog	5	0.2%	12	1%	17	0.4%
Red Squirrel	1	0.04%	7	1%	8	0.2%
Grey Squirrel	2	0.1%	0	0%	2	0.1%
Total	**2,604**	**100%**	**1,236**	**100%**	**3,840**	**100%**

Table 5 Regional and national hare detection rates and survey effort

Region	Detections n	Survey effort (hours)	Detection rate (detections/ week)
Northwest	121	44,104	0.46
Southwest	52	25,403	0.34
East	80	36,519	0.36
Total	**253**	**106,026**	**0.40**

3.3 Spatial patterns

3.3.1 Site occupancy

Irish Hare was recorded at 38/44 (85%) of survey squares with a widespread distribution (Figure 14 a).

3.3.2 Species distribution models

Prediction of the occurrence of Irish Hare was relatively poor with correct classifications in training and test datasets varying from *c*. 61-66% (Figure 15). Irish Hare occurrence was most strongly influenced by the extent of grassland (a quadratic response with lowest occurrence when landscapes were *c*. 50% grass and highest occurrence in simpler landscapes either with a lot or very little grassland) and negatively associated with habitat Shannon's Evenness Index favouring less even, more heterogeneous, environments (Figure 15).

Predicted probabilities of Irish Hare occurrence (represented as a continuous heatmap) suggest a high degree of heterogeneity (Figure 14 b & c). Irish Hare was predicted to occur in all but one 10 km^2 grid square (Figure 14 d) and is therefore likely to be highly widespread. However, its predicted distribution throughout the landscape is a fine-grain mosaic of hotspots (corresponding with high habitat suitability) and coldspots (corresponding with low habitat suitability), resulting in a patchwork of high and low density areas within a general landscape of average suitability (likely corresponding to average density).

3.3.3 Additional incidental records

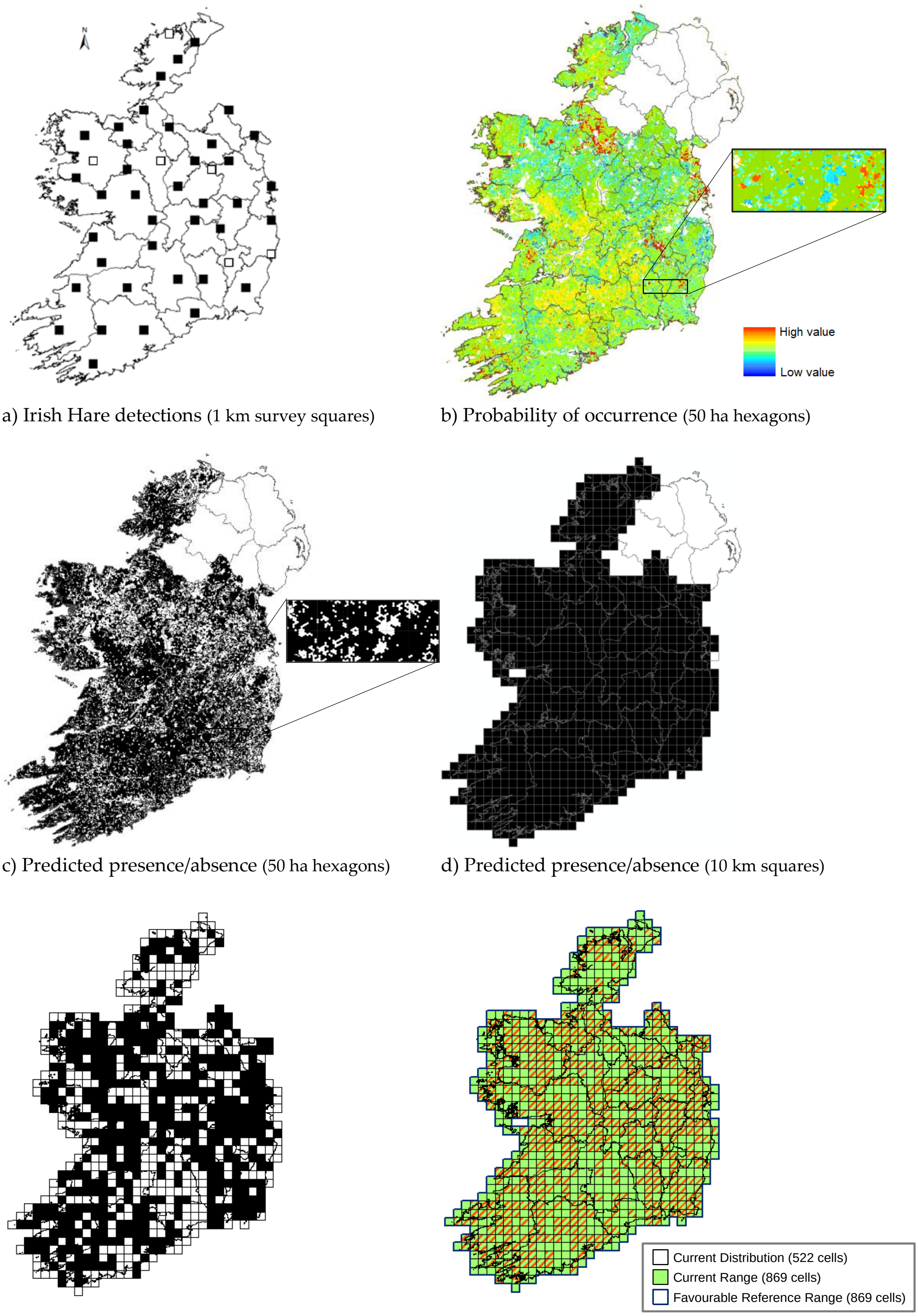
Citizen science public records submitted to the National Biodiversity Data Centre from January 2014 to March 2019 collated 1,421 records of Irish Hare, whose sightings were widespread (Figure 14 e). In total, Irish Hare was reported in 482 of 837 (58%) of 10 km squares throughout Ireland. It was most commonly reported in the east of the country, with 180 of 282 (64%) of 10 km^2 squares positive, and 56% (169/300 squares) and 53% (167/316 squares) of squares positive in the northwest and southwest respectively. When the 2014 to 2019 data gathered by the National Biodiversity Data Centre were collated with the current survey data, a total of 39/44 (88%) of survey squares was found to be occupied by Irish Hare.

3.3.4 Current Distribution, *Range* and *Favourable Reference Range*

The widespread occurrence of suitable habitat (derived from the Species Distribution Model) plus the widespread distribution of sightings from both the National Biodiversity Data Centre and the survey results suggest that the *Favourable Reference Range* and *Current Range* of the Irish Hare should include all 10 km^2 squares in the Republic of Ireland, i.e. 869 x 10 km squares representing a significant increase ($p < 0.001$) since 2007 (Table 6). From 2014 to 2019, a total of 521 squares was occupied within its C*urrent Distribution,* but this number is dependent on the timeframe over which its distribution is assessed (for example, there was a significant ($p < 0.001$) increase in the *Current Range* from 2007 to present but any change is indicative of improved knowledge/more accurate data than actual range expansion (Table 6)). In any case the Irish Hare remains widespread and ubiquitous (Figure 14 f).

Table 6 Comparison of number of 10 km^2 squares (n = 869 throughout ROI) included in the Irish Hare's *Favourable Reference Range*, *Current Range* and *Current Distribution* for each Article 17 report (NPWS, 2007; 2013; 2019) and those data generated independently during the current study (2014-2019) showing statistical change.

	Article 17 reports			Current study & statistical change		
	NPWS 2007	NPWS 2013	NPWS 2019	2014-2019	$\chi^2_{(df=3)}$	*p*
Favourable Reference Range	749 (86.2%)	780 (89.8%)	814 (93.7%)	869 (100.0%)	130.0	< 0.001
Current Range	749 (86.2%)	780 (89.8%)	814 (93.7%)	869 (100.0%)	130.0	< 0.001
Current Distribution	619 (72.1%)	490 (56.4%)	702 (80.8%)	522 (60.1%)	145.0	< 0.001



a) Irish Hare detections (1 km survey squares)

b) Probability of occurrence (50 ha hexagons)

c) Predicted presence/absence (50 ha hexagons)

d) Predicted presence/absence (10 km squares)

e) NBDC public records (10 km squares)

f) Composite map *Jan 2014 – Jul 2019* (10 km squares)

Figure 14 a) Detection of Irish Hare in survey squares, b) species distribution model predicted probability of occurrence (or habitat suitability), c) predicted presence/absence at 50ha scale and d) summarised at the 10 km^2 scale, e) citizen science public records submitted to the National Biodiversity Data Centre and f) a composite map defining the *Current Distribution*, *Current Range* and *Favourable Reference Range*.

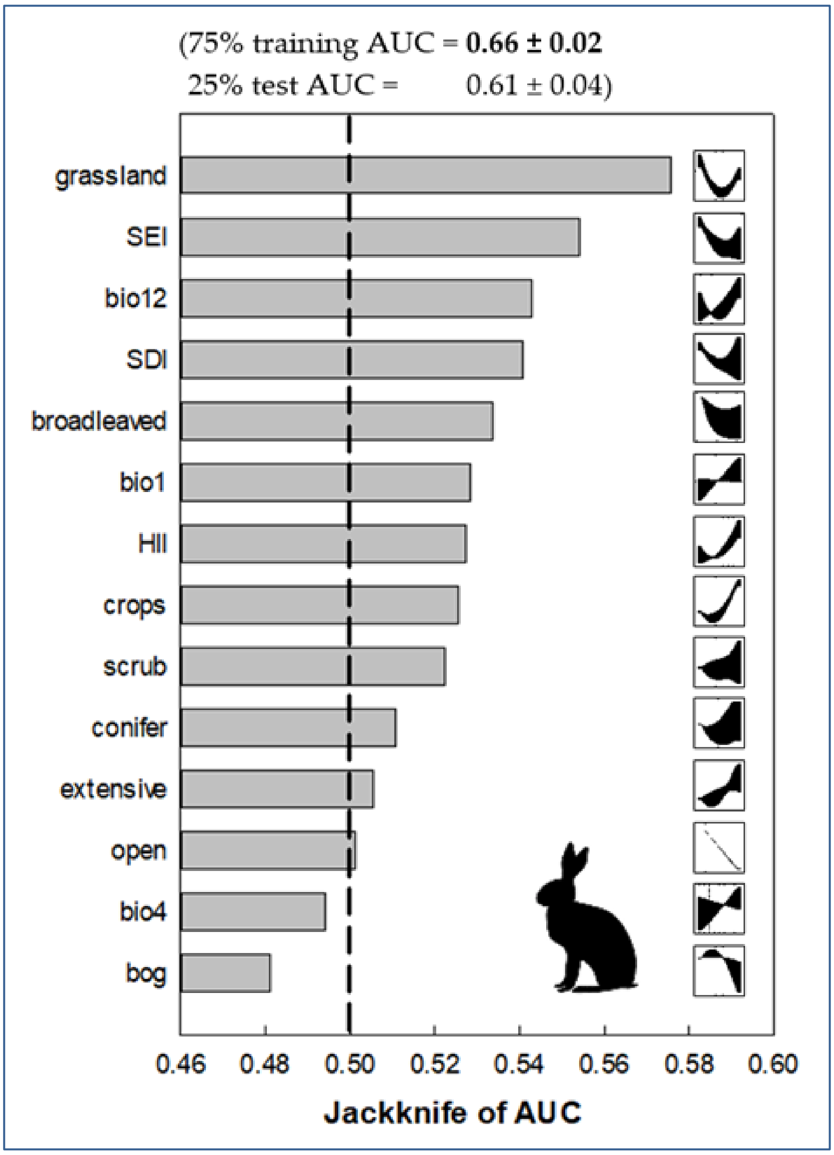


Figure 15 Jackknife test of variable importance (ranked descending from most (top) to least (bottom) important on y-axis) using model AUC values (x-axis). Values are averages over four replicate runs using a 75:25% partitioning of the data into training:test sets. Insert plots show the 95% confidence intervals (black shading) of the species response curves for each variable (the average line passing through the centre of each CI), where the x-axis shows variation of the predictor variable (from lowest value left to highest value right) and the y-axis shows the predicted probability of species occurrence (from lowest value bottom to highest value top). Actual axis numbering has been omitted for simplicity. Broad confidence intervals indicate uncertainty in the species response to that variable; direction of the curve indicates positive, negative or quadratic responses

3.3.5 Species activity cycles

Irish Hare exhibited a bimodal activity pattern having been recorded most commonly on camera traps during dawn (05.45 to 09.07) and dusk (17.07 to 18.26), corresponding to a crepuscular activity profile (Figure 16). All distance analyses were restricted to the peak periods of activity for each species (hatched periods within Figure 16) to ensure mean maximum density was estimated.

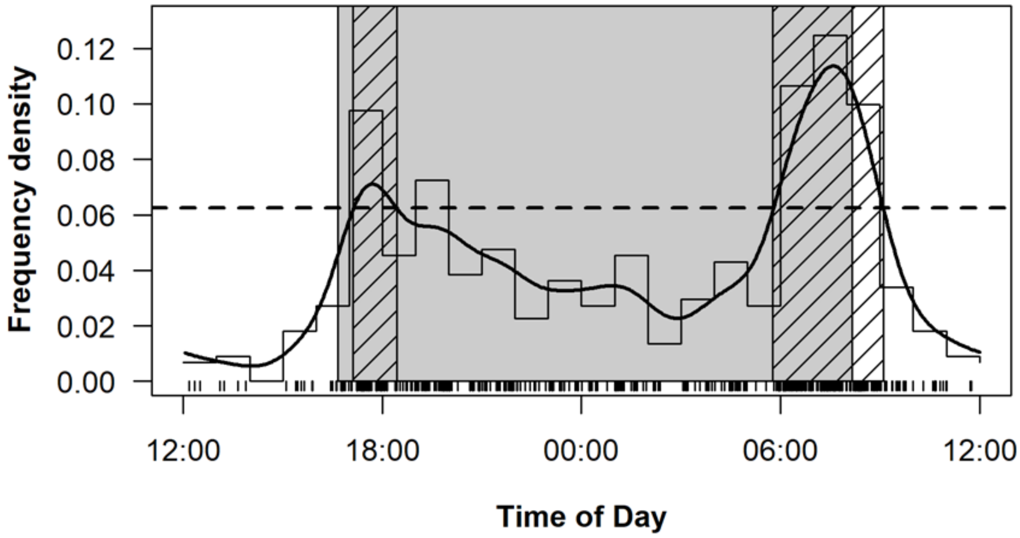


Figure 16 Diel (24-hour) activity pattern for the Irish Hare showing the frequency density (bold black line) fitted to hourly camera trap detections (bars) and their 'peak period' of activity (hatched area), defined as ≥ 55% of records (dashed line) within the overall nocturnal dark period (grey shading). The density of detections is shown as ticks along the x-axis (Image produced using 'activity' package (Rowcliffe, 2019), using R version 3.5.3 (R Core Team, 2019)).

3.3.6 Distance analysis detection functions

The Distance model assumed a hazard-rate detection function (Figure 17) right truncated at 13 m with variable bin sizes (initially in 1 m bins from 0-1 m, 1-2 m and 2-3 m but subsequently in larger bins from 3-5 m and 5-13 m). Hare activity was typically <5 m from the field edge margin but detections were made up to 41 m from the camera. Records >13 m were right truncated to improve model fit.

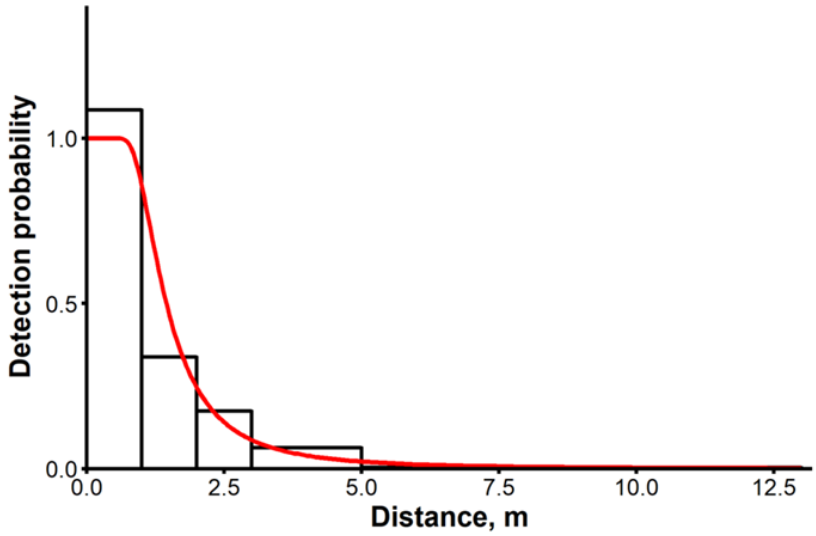


Figure 17 Distance detection functions for camera trap detections of Irish Hare.

3.3.7 Density and abundance estimates

Mean Irish Hare density (Table 6) was estimated to be 3.19 hares/km² (95% confidence intervals: 1.59–6.43) (though the more conservative global bootstrapped confidence limits suggest densities could vary from 0.86 - 17.14 hares/km²), with highest mean regional densities (and very comparable figures) for the northwest (3.50 hares/km²) and southwest (3.46 hares/km²) and lowest density in the east (2.66 hares/km²). The average density estimate was 4.5% lower than the 3.33 hares/km² estimated during 2006 and 58% lower than the 7.44 hares/km² estimated during 2007. Nevertheless, such was the width of the 95% designed-based confidence intervals that the current density estimate cannot be said to be significantly lower than the last survey.

Scaled up by the area of each geographic region, the national Irish Hare population was estimated at 223,000 (95% confidence intervals: 111,000–449,000) hares throughout the Republic of Ireland during winter 2018/19. The more conservative bootstrapped confidence limits suggested that the population could vary from 60,000 to 1.2 million individuals (Table 7).

Table 7 Distance analysis density estimates for Irish Hare density and total population, restricted to species-specific peak period of activity (see Figure 16) which accounted for variation in sampling effort. The extent of each region was assumed to be the same as the last survey with Republic of Ireland = 69,878 km², northwest = 22,580 km², southwest = 24,283 km² and east = 23,015 km².

Measure	Region	Estimated number	Design-based confidence intervals LCL	Design-based confidence intervals UCL	Bootstrapped confidence intervals LCL	Bootstrapped confidence intervals UCL
Density (individuals/km²)	Northwest	3.50	1.41	8.69		
	Southwest	3.46	1.24	9.64		
	East	2.66	1.01	7.02		
	Total	**3.19**	**1.59**	**6.43**	**0.86**	**17.14**
Population (total individuals)	Northwest	79,030	31,838	196,220		
	Southwest	84,019	30,111	234,088		
	East	61,220	23,245	161,565		
	Total	**222,911**	**111,106**	**449,316**	**60,095**	**1,197,709**

4 Discussion

4.1 Pilot study

The Hare Survey of Ireland 2006/07 (Reid *et al.*, 2007a) used a nocturnal spotlight survey methodology with distance analysis to generate density and abundance estimates for the Irish Hare. Whilst a range of potential survey methods are available (see Section 1.4 for a review of techniques), the most pertinent development since the last survey was the widespread adoption of camera traps to collect data on terrestrial mammals. Thus, the central aim in conducting a pilot study was to assess the relative detection rate of Irish Hare using traditional nocturnal spotlight versus camera trapping methods, in addition to assessing survey time investment and the difficulties in identifying landowners and gaining permission to access land.

Camera traps generated substantially higher species richness and several orders of magnitude more individual detections than spotlight surveys of the same 1 km^2 survey squares. This was a function of the relative survey effort of each technique. When undertaking spotlight surveys the observer sweeps a circle around their location on a minor road to detect eye shine before moving on to the next survey point. Excluding driving time, each 1 km^2 square was directly observed for probably less than ten minutes each, making detection of a hare within such a short observation window virtually random when compared to camera trap detections, where cameras ran continuously for seven days (168 hours) per camera location, of which there were 14 locations per square (2,352 hours of survey effort per square). Thus, during the pilot study camera traps generated +3,000% more detections of wildlife, with +2,144% more Irish Hare detections than spotlight surveys. Furthermore, spotlight surveys at half of the survey sites resulted in Type II errors (i.e. false negatives; failing to detect hares when they were, in fact, present). In terms of logistics, spotlight surveys were biased towards roads, which animals may avoid, whereas camera locations were a demonstrably random selection of habitats. Spotlight surveys were conducted after sunset when, as we now know from camera trap detections, hares are less active compared to dawn. Given that several factors may have affected the variability and reproducibility of the spotlight survey data (e.g. Edwards *et al.*, 2000; Gehrt, 2002; Thorn *et al.*, 2010), it was pragmatic that the full survey should abandon spotlight surveys as labour intensive with little return, in favour of rolling out a nationwide array of camera traps.

The pilot survey suggested that Fox detections were positively associated with those of Rabbit and Hare, indicative of their relationship as predator and prey.

4.2 Full study

4.2.1 Species detection rates

Despite the increase in survey effort and distribution of squares between the pilot and full survey, the total number of animal detections declined. Whilst some reduction might have been expected as the pilot survey occurred during the breeding season (March to May 2018) whereas the full survey occurred during the non-breeding season (November 2018 to February 2019), with an associated reduction in young animals in the population due to winter mortality, the majority of the differences in detections were due to a fall in Rabbit records. Rabbits are highly overdispersed in the countryside (i.e. missing from many sample locations but present in large numbers where they occur) meaning that they are strongly spatially autocorrelated, with a large number of individuals associated with, and not straying far from, their warren. Thus, any camera erected (accidentally) close to a warren captures huge numbers of Rabbit records due to their coming and going whilst cameras placed away from warrens capture fewer records. A few cameras placed within a single survey square in Co. Carlow, close to a highly active warren, generated the vast majority of Rabbit records during the pilot survey. A decision was taken to avoid placing cameras directly adjacent to warrens during the full survey, resulting in a dramatic reduction in Rabbit detections and a lower number of overall animal detections.

4.2.2 Hare detections

Totals of 202 and 253 Irish Hare were detected during the pilot and full surveys, respectively (total of 455 hares), representing a robust sample size from which to generate a distance sampling detection function for the purposes of estimating density and abundance. A minimum of approximately 60 detections is recommended as a rule-of-thumb when fitting a detecting function (Buckland *et al.*, 1993).

European Brown Hare was not detected during this study despite two of our survey squares (Irish Grid C3120 and C0030) having been selected specifically to test the hypothesis that it may still exist at locations in Donegal where it was previously reported (Sheppard, 2004). Moreover, a genetic study that screened some 3,000 or so hares throughout the island of Ireland during the early 2000s failed to detect any European Brown Hare DNA in any of the sampled animals (Hughes *et al.*, 2006), which might be expected if it had previously been present and hybridised with the native Irish Hare. Whilst an extant Brown Hare population has been well studied in Northern Ireland (Reid & Montgomery, 2007; Reid, 2011; Caravaggi *et al.*, 2016), the species appears to be absent from the Republic of Ireland.

4.2.3 Spatial patterns

Hares occur widely throughout Ireland (Lysaght & Marnell, 2016; NPWS, 2019) occupying a range of habitats from coasts (Wolfe *et al*., 1996) to mountains (Walker & Fairley, 1968). The National Biodiversity Data Centre's public records from 2014 to 2019 suggest the species distribution and range remains stable and widespread throughout Ireland (Figure 14e). The greatest number of public reports was submitted from the east of the country, followed by the northwest, with the fewest received from the southwest. This may be due to variation in range within each region but more likely due to recording effort, i.e. the east has a higher human population density.

Our Species Distribution Model of Irish Hare occurrence had relatively poor predictive power. Similar models (using the software Maxent) have been built in Ireland for rare, highly localised species (those by extension with highly specific habitat requirements), for example, the distribution of the freshwater pearl mussel (*Margaritifera margaritifera*) was predicted with an accuracy of 97% (Wilson *et al.*, 2011). It makes sense that common and widespread species, such as hares, are not range restricted and thus have weaker habitat associations and, thus, cannot be modelled with such a high degree of accuracy. Nevertheless, the ecological relationships from our species distribution model appeared broadly sensible, with hare occurrence driven by heterogeneously structured grasslands. Hares require grassland for foraging within a short distance of rough vegetation for lie-up (Reid *et al.*, 2010). Such is the prevalence of grassland throughout Ireland that hares were predicted to occur in virtually every 10 km^2 grid square. When surveying hares using traditional spotlight survey methods it has often been remarked that hare detection is frequently clustered i.e. multiple detections (often groups) close together prior to driving several kilometres with no detections before encountering another cluster, despite the landscape often not appearing to visually change in the eyes of the observer (N. Reid pers. obs.). Our species distribution model replicated this apparent fine scale patchy structure with hotspots and coldspots of habitat suitability embedded in a matrix of average suitability; meaning hares can be found virtually anywhere but are typically clustered in localised patches; i.e. those habitats that deliver their fine scale requirements of forage and lie-up.

4.2.4 Activity patterns

Camera traps operated continuously day-and-night during their deployment. Thus, the frequency distribution of time stamps from video detections allowed the activity profile or diel (24-hour) activity pattern (temporal niche) of the Irish Hare to be accurately defined. We present data which robustly demonstrates that the Irish Hare to have a bimodal activity pattern, being largely crepuscular (active at dawn and dusk). Thus, methods to estimate density and abundance need to be cognisant that data should be drawn from the peak periods of activity (ensuring average maximum density is estimated). Traditional spotlight survey methods used in 2006/07 surveyed hares from one hour after sunset until about 12 midnight, roughly corresponding to one of their peak periods of activity (however, it should be noted that their dawn peak activity was higher than their dusk peak, suggesting dawn as the single best time to observe hares being active).

4.2.5 Density, abundance and population trends

Whilst we adopted camera trapping as a different survey method from the previous Hare Survey of Ireland 2006/07 we used a consistent analytical method, distance sampling, to estimate densities. Despite contrasting survey methods, our estimate of mean density of 3.2 hares/km^2 during winter 2018/19 was very close to (less than 5% different from) the estimate of 3.3 hares/km^2 during 2006, with virtually complete overlap in the 95% confidence intervals, indicative of no significant trend in the population between these two years. Moreover, our density in 2018/19 was virtually identical to the grand long-term mean of all Irish Hare density estimates obtained since 2000 where most, regardless of varying survey methods, were close to 3.0 hares/km^2 (Figure 18).

Two years in the time-series of Irish Hare density estimates are notably unusual: during 2004 the mean density in Northern Ireland was estimated at 6.9 (5.2 - 25.0) hare/km^2, whilst during 2007 the mean density in the Republic of Ireland was estimated at 7.7 (4.8 – 14.3) hares/km^2. Thus, our estimate for 2018/19 was 54% and 58% lower than 2004 and 2007 respectively, however, such is the width of the 95% confidence intervals during 2004 and 2007 that we cannot be certain the population significantly differed from the estimate in 2018/19. Given that hares are used as textbook examples (literally) of wildlife whose populations exhibit extreme amplitude; varying by up to a factor of 11 between peak and trough densities, it may not be unexpected that some years in our time-series are either unusually high or low (Krebs *et al.*, 1995). However, we can be certain that there was no clear trend across densities obtained during the last 20 years or between the last Hare Survey of Ireland 2006/07 and the current survey, suggesting the population is largely stable.

Spatial variation suggested similar hare densities in the northwest (3.5 hares/km^2) and southwest (3.5 hares/km^2) but lower in the more agriculturally intense east (2.7 hares/km^2) where arable crop farming may make the landscape marginally less suitable for a grassland specialist species (Reid & Montgomery, 2007). This spatial pattern contrasts to that reported in the Hare Survey of Ireland 2006/07 where estimated densities were highest in the east and lowest in the northwest. It seems likely that spotlight survey detection during 2006/07 was compromised by the landscape. Detection of a hare in a field of rushes (*Juncus* spp.), common in western regions, using spotlight surveys is low, not because hares are absent, but because the tall vegetation obscures any animals such that detections are few in number and detection distances are very short. By comparison, hare detection in agricultural grassland fields in the east using spotlight surveys was comparatively high as any hares present in short vegetation in flat landscapes were detected. Thus, spotlight surveys may over or underestimate densities depending on the vegetation of the surveyed habitat, whilst camera traps, erected largely at random and running 24/7, are likely subject to fewer biases in detection. Thus, we are inclined to accept that hare populations are genuinely at higher density in the west of Ireland compared to the agriculturally intense east.

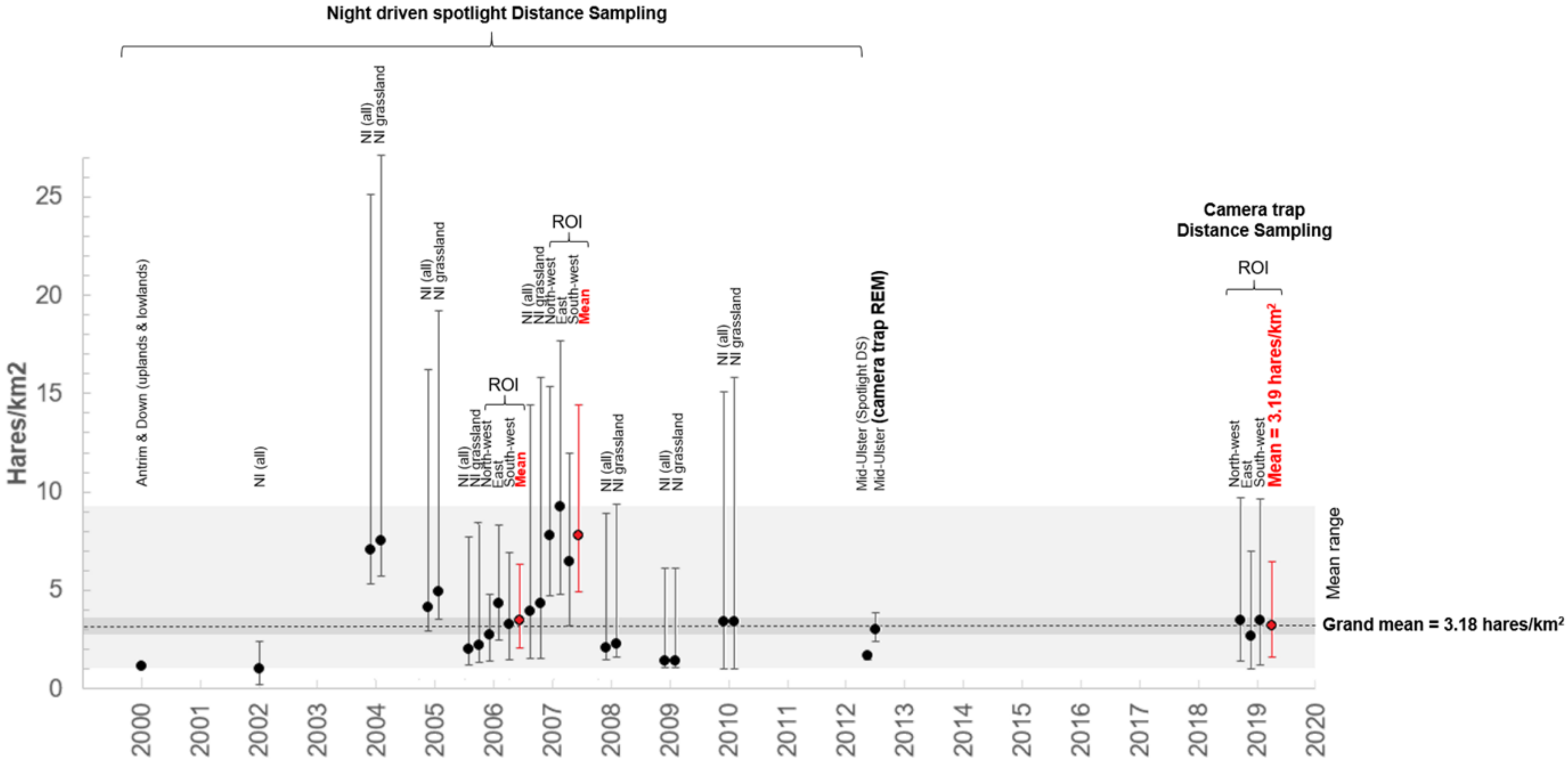


Figure 18 Irish Hare density estimates collated from surveys spanning the last 20 years compared to the results of the full survey here (2018/19). Mean estimates generally ranged (light grey shading) from 1-9 hares/km² (error bars = 95% confidence intervals 0.2-27.0) with the range of mean estimates for 2018/9 (dark grey shading) comparable to those for ROI in 2006 and 2007 and almost identical to the grand mean over the last 20 years (dashed line).

When interpreting the results of this or similar surveys we must be mindful of what the metrics produced mean 'in-the-real-world'. Reducing temporal and spatial variation in populations to one number: the average, or mean, population density can result in subsequent misinterpretation. Focusing on an average can obscure the variation present in the population. Those that spend time in the outdoors may see hares frequently or can probably think of times or places where they have encountered several sightings of hares. A mean density of 3.0 hares/km^2 will be perceived as low in comparison to anecdotal knowledge of such locations. Certainly, there are locations where Irish Hare densities can be considerably higher than the average density of 3.0 hares/km^2. For example, densities at Dublin and Belfast International Airports are up to 10 times higher at up to 30 hares/km^2 (N. Reid unpublished data) and there are locations in the wider countryside that support a similarly high abundance (usually offshore islands with no predators). Moreover, there are locations where hare populations are at very low densities or have been locally extirpated (0 hares/km^2), usually due to a combination of farming practices and persistent illegal poaching often using lurchers (N. Reid pers. obs.). Whilst estimates of density are accompanied by 95% confidence intervals, which capture a lot of this variation (e.g. the bootstrapped range of 0.86-17.14 hares/km^2 during 2018/19), even 5% of potential observations may lie outside this range, for example, 0 or up to 30 hares/km^2. Thus, the average density hides large spatial variation and 3.0 hares/km^2 may not even be the most commonly occurring density. Moreover, such is the spatial variation between camera locations, survey squares and regions that the width of confidence intervals makes it difficult to detect temporal change or trends over time. The variation in the population would have to move substantially and consistently either positively or negatively for the mean density to show any shift away from the overall estimate of about 3.0 hares/km^2. In those years where the population estimates suggested such shifts (for example, 2004 and 2007), the width of the associated 95% confidence intervals still precluded interpreting such change as 'statistically significant' at the usual 95% level of confidence. Thus, whilst assessing the absolute Irish Hare population size and its change is required by the Habitats Directive every six years, the meaningfulness of expressing this as change in the average density is questionable in terms of the statistical resolution this provides. Direct comparison of simple detection rates (not converted to density) using a test of difference where survey methods remain consistent, for example, between standardised camera trapping sessions, would be the most powerful means to assess relative population change but would not generate an absolute density or abundance estimate (for further discussion see Section 4.5 below).

Adopting the camera trap locations used here for future surveys of terrestrial mammal relative abundance and relative population change is recommended. The same squares were originally used by Smal (1995) for the first national Badger survey, generating a range of biological records. They were subsequently used during the first Hare Survey of Ireland (Reid *et al.*, 2007a) and continuing their use establishes a network of survey sites for direct comparison over time, about which a large volume of data has been now been collected.

4.3 Pressures and threats

There is a paucity of data on threats and pressures that impact the Irish Hare due mainly to the cost and difficulty of collecting local population biology parameters to build models of drivers of change. Thus, the collection of empirical data on threats and pressures was beyond the scope of this study.

Nevertheless, reviewing the most recent (2019) list of Natura 2000 Standard Data Form threats and pressures under EU Habitat Directive codes (available from http://cdr.eionet.europa.eu/help/habitats_art17) we suggest a list of the most pertinent threats and pressures to the conservation status of the Irish Hare (Table 8).

Of the threats and pressures listed, we suggest three are of highest importance: i) agriculture including intensification, mowing and cutting of grassland, and habitat restructuring, ii) biological resource use including illegal poaching and iii) the introduction of disease, most notably the recent discovery of rabbit haemorrhagic disease virus (RHDV2) in the Irish Hare for the first time.

Within the <50 ha of their usual home range, Irish Hares require a heterogeneous mix of good quality grassland, providing nocturnal foraging, and diffuse rough vegetation, usually stands of rushes (*Juncus* spp.) to take shelter in during daytime lie-up (Reid *et al.*, 2010). Agricultural intensification is the most likely cause of hare population declines (Smith *et al.*, 2005) with landscape homogenisation (Reid *et al.*, 2010) and mechanization, most notably the rolling of grass and silage harvesting (Kaluziński & Pielowski, 1976; McLaren *et al.*, 1997) being the principal threats.

During the course of field work for this survey (whilst gaining permission to access land and during camera deployment and collection) we received multiple landowner, farmer and local reports of illegal hare poaching; where animals are hunted without a Government license by long dogs, usually lurchers, often at night using spotlights. Camera traps captured videos of long dogs being walked off-the-leash during daylight hours but no direct evidence of poaching activity occurring was captured. Fieldwork was conducted by three survey teams, each broadly covering one region (east, southwest and northwest). All teams received such reports, suggesting the problem is at least perceived as widespread. Illegal poaching of hares using lurchers is known to cause local population extirpations if persistent (N. Reid pers. obs.), but there are few objective data by which to quantify its prevalence and impact, as many landowners fail to report the activity and the number of prosecutions is low.

Rabbit haemorrhagic disease virus (RHDV2) was recorded in the wild Rabbit and Hare population in Ireland for the first time during July 2019 (NPWS Press Release available at www.npws.ie/news/deadly-disease-found-irish-hares-and-rabbits-%E2%80%93-public-asked-report-any-sightings-irish-coursing). RHDV first emerged in China during the early 1980s and became a global panzootic, killing millions of domestic (farmed) rabbits within nine months (Liu *et al.*, 1984; Xu, 1991). In 2010, a new more virulent strain of virus (RHDV2) emerged in domestic rabbits in France (Le Gall-Reculé *et al.*, 2011). It causes death within a few days of infection with sick animals often showing partial paralysis, emerging from cover into the open and convulsing or fitting often screaming or moaning for prolonged periods before dropping dead. If found dead the animals typically show no visible external symptoms yet have died from massive internal bleeding (le Gall-Reculé *et al.*, 2013). The disease was first detected in Ireland during July 2019. A National Parks & Wildlife Service (NPWS) Conservation Ranger found a dead Rabbit on Scattery Island in the Shannon estuary while at much the same time a colleague 140 miles away picked up another in Wicklow after a report by a couple living in the town of Avoca. Both animals tested positive for RHDV2. Testing was carried out by the Department of Agriculture, Food & Marine Laboratories (DAFM), Kildare. Subsequently the disease was confirmed as infecting an Irish Hare found dead at the Wexford Slobs, resulting in the suspension of the Irish Coursing Club's license to take hares from the wild for the purposes of coursing. The virus is widespread throughout Europe, not just in rabbits but in four species of hare: the Sardinian Cape Hare (*Lepus capensis mediterraneus*), the Italian Hare (*Lepus* corsicanus), the European Brown Hare (*Lepus europaeus*) and the Mountain Hare (*Lepus timidus*) (Puggioni *et al.*, 2013; Camarda *et al.*, 2014; Bell *et al.*, 2019; Neimanis *et al.*, 2018), and seemingly unrelated species including voles and shrews (including the Greater White-toothed Shrew *Crocidura russula* (Calvete *et al.,* 2019)) also present in Ireland. It remains to be seen whether the disease causes declines in either Rabbit or Hare populations in Ireland as has been observed in Great Britain (Diana Bell, University of East Anglia, pers. comm.) and continued monitoring and surveillance of the situation is needed.

Table 8 List of pressures and threats (available from http://cdr.eionet.europa.eu/help/habitats_art17) with justification of their relevance to the Irish Hare based on expert opinion.

Code	Pressure/threat	Description
A	**Agriculture**	
A01	Conversion into agricultural land (excluding drainage and burning)	Irish Hare prefers extensive grassland agriculture (Reid, 2006) and is generally threatened by intensification (Smith *et al.*, 2005), with grass rolling and mechanical harvest of silage threatening leveret survival (McLaren *et al.*, 1997) throughout the breeding season. Removal or conversion of natural, unimproved or semi-improved grassland to other land use categories may perturb local populations. Fertilisation reduces floristic diversity and thus impacts diet as well as reducing cover (e.g. rushes). Hedges, copses and scrub may provide lie-up sites whose removal will affect animals locally.
A02	Conversion from one type of agricultural land use to another (excluding drainage and burning)	
A03	Conversion from mixed farming and agroforestry systems to specialised (e.g. single crop) production	
A05	Removal of small landscape features for agricultural land parcel consolidation (hedges, stone walls, rushes, open ditches, springs, solitary trees, etc.)	
A06	Abandonment of grassland management (e.g. cessation of grazing or mowing)	
A08	Mowing or cutting of grasslands	
A09	Intensive grazing or overgrazing by livestock	
A13	Reseeding of grasslands and other semi-natural habitats	
E	**Development and operation of transport systems**	
E01	Roads, paths, railroads and related infrastructure (e.g. bridges, viaducts, tunnels)	Irish Hare is vulnerable to road traffic collisions but the overall impact of road mortality is unknown.
G	**Extraction and cultivation of biological living resources (other than agriculture and forestry)**	
G07	Hunting	Irish Hare is threatened by illegal (unlicensed) hunting using lurchers. This can cause local population extirpations (N. Reid *pers. obs.*).
G10	Illegal shooting/killing	
G11	Illegal harvesting, collecting and taking	
I	**Alien and problematic species**	
I02	Other invasive alien species (other than species of Union concern)	The Irish Hare is threatened by the invasive European Brown Hare. The latter can replace the native through competition and hybridisation/introgression (Reid, 2011; Caravaggi *et al.*, 2016).
L	**Natural processes (excluding catastrophes and processes induced by human activity or climate change)**	
L06	Interspecific relations (competition, predation, parasitism, pathogens)	Rabbit haemorrhagic disease virus 2 (RHDV2) was confirmed in the wild Rabbit and Hare populations of Ireland during July 2019 raising concerns that it may negatively impact Irish Hare populations.
N	**Climate change**	
N01	Temperature changes (e.g. rise of temperature & extremes) due to climate change	Hare population dynamics have been closely associated with climatic oscillations with the Irish Hare's population size historically associated with the Northern Atlantic Oscillation (autumn weather). Studies predict that the Irish Hare's range will contract in a south-easterly to the north-westerly direction under global climate change as Irish mean temperatures rise and the southeast becomes drier (Leach *et al.*, 2015; Caravaggi *et al.*, 2017).
N03	Increases or changes in precipitation due to climate change	

4.4 National conservation assessment

Whilst we suggest that the *Favourable Reference Range* could be updated in future Article 17 assessments to include all 10 km^2 squares in the Republic of Ireland and despite an apparent increase in the *Current Range* and *Current Distribution*, such changes are likely to be the result of improved knowledge and/or better data quality than actual range expansion or contraction. Thus, we can be fairly confident there has been little or no distribution or range contraction since the first Article 17 report (NPWS, 2007), suggesting that, within the assessment criterion of *Range*, the Irish Hare is Favourable and its status has remained stable since 2013 (NPWS, 2013; NPWS, 2019).

In addition, there was no significant difference in Irish Hare densities or abundances between the last Hare Survey of Ireland 2006/07 (Reid *et al.*, 2007a) and the current study indicating its *Population* is Favourable and stable.

As the Irish Hare is highly widespread and exhibits no strong habitat preferences or avoidance (as inferred by Species Distribution Modelling), mostly inhabiting agricultural land that covers *c*. 70% of the Republic of Ireland (CORINE Land Cover data; EEA, 2018), it can be assumed that, within the assessment criterion of *Habitat for the species*, its status is Favourable and has remained stable (NPWS, 2013; NPWS, 2019).

We listed a large range of potential threats and pressures (see Table 8) but there are few or no data by which to empirically assess the impact of these perceived issues on the population biology of the species but given the stability of the species' *Range*, *Population* and *Habitat* it was assumed its *Future prospects* are also Favourable (Table 9). Nevertheless, a number of key issues could impact its status in future, most notably range retraction from the southeast to northwest given the likely changes in temperatures and rainfall in Ireland (Leach *et al.*, 2015; Caravaggi *et al.*, 2017). Expanding population(s) of European Brown Hare in Northern Ireland (or should they be confirmed as present in the Republic of Ireland) may, in the long-term, replace Irish Hare populations due to competition and hybridisation (Reid, 2011; Caravaggi *et al.*, 2016; Caravaggi *et al.*, 2017). Finally, rabbit haemorrhagic disease virus 2 (RHDV2) has the potential to cause widespread mortality in Ireland but its impact on the Irish hare population remains unknown at this point. This study, having been completed just before the presence of the disease was confirmed in Ireland, will act as an appropriate baseline ('before') survey to which short-term changes due to the impact of RHDV2 can be compared ('after' any outbreak); should data be collected. Thus, whilst we currently judge *Future prospects* for the species as Favourable, we encourage vigilance with respect to the potential impacts of climate change, invasive species and disease.

With criteria on *Range*, *Population*, *Habitat for the species* and *Future prospects* Favourable, we propose an overall national conservation assessment of Favourable status for the Irish Hare resulting in its status remaining stable since 2013 (NPWS, 2013; NPWS, 2019), whereby i) population data on the species indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats; ii) the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future; and, iii) there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis.

Table 9 Summary of the current (2018/19) conservation status of the Irish Hare

Criteria	**Status (2018/19)**
Range	Favourable (FV)
Population	Favourable (FV)
Habitat for the species	Favourable (FV)
Future prospects	Favourable (FV)
Overall assessment	Favourable (FV)
Overall trend in conservation status	**Favourable (FV)**

The current IUCN Red Listing for the Mountain Hare (*Lepus timidus*) is Least Concern (Smith & Johnston, 2019) and the last regional assessment for the Irish Hare (*L.t. hibernicus*) was listed as Least Concern (Marnell *et al.*, 2009) with the current conservation assessment supporting the continuation of that status.

4.5 Recommendation for future surveillance and monitoring

Despite changing survey methods between the last Hare Survey of Ireland (2006/07) and the current study (2017/19), in order to adopt the most up-to-date methods, we recognise that consistency of methods provides the most robust basis for comparison. The squares selected for the current survey were drawn from those examined in the previous survey (Reid *et al.*, 2007a). Within each 10 km^2 square, the southwest most 1 km^2 area was surveyed, replicating the selection methodology adopted by Smal (1995) for the first nationwide Badger survey. We recommend that future surveys should use the same 1 km^2 survey squares, not just for comparability, but to assemble a nationwide network of intensively monitored squares, yielding a wide range of biodiversity data that can be reliably monitored over time.

> ***Recommendation 1:*** Adopt a standardised network of 1 km survey squares common to past surveys to establish a monitoring network building time-series data survey-upon-survey.

We strongly recommend using camera traps for future surveys as data on all terrestrial mammals can be collected, allowing change in multiple species to be assessed (including those of policy relevance such as Badger).

> ***Recommendation 2:*** Integrate analysis of camera trap data to non-target species (e.g. Badger) enabling changes in range and abundance of other common terrestrial mammals (and their interactions) to be monitored.

Given the high degree of spatial variation in the Irish Hare population, establishing temporal trends with any precision over a long (6-yearly) monitoring cycle is challenging. Annual fluctuations in some animal populations, notably hares (see Reid *et al.*, 2010), mean that comparing any two years is problematic with any trends more reflective of the points within the oscillations that were sampled rather than actual population change. We advocate regular (preferably annual) surveys, at least until the contemporary dynamics of the Irish Hare population can be established. This is particularly important against the current backdrop of the unknown impact of RHDV2 and the species' listing under Annex V(a) of the EC Habitats Directive (92/43/EEC), which lists animal *species of community interest whose taking in the wild and exploitation may be subject to management measures* (for example, their licenced use in hare coursing). Annual surveys would necessitate sampling a smaller number of sites and the effort required to undertake this may require the coordination of NPWS and/or volunteer effort in deploying and collecting camera traps, as well as in processing the imagery. We would not advocate attempting to estimate densities each year but rather compare relative detection rates to establish short-term change in the population at focal sites.

> ***Recommendation 3:*** Establish a limited network of constant effort monitoring sites, surveyed more regularly than the Article 17 six-yearly reporting cycle, requiring its support by NPWS/volunteer effort to establish interannual Irish Hare population dynamics.

Determining the sample size needed for future surveys is challenging. If the required outcomes are density and abundance estimates, then data must undergo specific and specialised analyses, for example, distance sampling, to translate detection rates into population estimates with associated 95% confidence intervals. Population change over time is determined by whether such confidence intervals overlap. Translating the effects of varying sample sizes (either sample points, i.e. camera locations, or survey squares) on the resulting width of any population confidence intervals is problematic as there is no direct one-to-one relationship due to the spatial variability in hare detections and the effect of subsampling detections within specific timeframes, i.e. different periods of activity, differences in detection rates between seasons etc. We are therefore reluctant to suggest a proposed future sample size when estimating density and abundance.

If the required outcome is, however, an assessment of relative rather than absolute change, it can be tested using a paired comparison of mean detection rates (not translated into density or abundance) between the same squares sampled at two time points (now and the future). This is more straightforward and *a priori* Power Analysis can be used to suggest minimum sample sizes. A two-tailed test of difference between matched pairs (e.g. a paired t-test or equivalent) with a Power (1-β error probability) of 0.8 (the minimum power typically accepted in the published literature) at the usual 95% significance level ($\alpha = 0.05$) can detect an effect size w = 0.5 (a large i.e. 50% difference) with a sample size of n = 34. Thus, it is recommended that if temporal change in the relative detection rate of Irish Hare (not density and abundance) is acceptable then any future study should select a minimum of 34 1 km^2 survey squares from those used here, comparing the summed total detections within each square between each time point. Any subsample of the squares used here should be tested *a priori* to ensure they remain representative of the Irish landscape and effort should be made to ensure roughly uniform distribution of squares throughout the country. Given that data collection during the current study took approximately two full days for each square we might expect that 34 squares would require a minimum of 68 working days to survey (three to four months) plus contingency. Given the need to collect data during the non-breeding season (October to February annually) and the appeal of having a short survey window so data are contemporaneous, we might suggest a need for multiple surveyors or survey teams (e.g. NPWS Conservation Rangers covering their own areas and/or volunteer support). It took approximately three to four months to watch all videos from the full survey period (n = 44) and to analyse the associated data (to generate distances, angles, dates and times of detections, obtain and extract peak activity periods, and to build distance sampling models). As such, one would expect the same process to take two to three months for a sample size of 34 squares. Therefore, the entire data collection process and analysis of 34 survey squares using camera traps should take approximately five to seven person/months.

> ***Recommendation 4:*** Adopt a minimum number of necessary survey squares (e.g. n = 34) to allow change in relative detection rates to be assessed using simple statistics avoiding the technical complexity of density and abundance estimation.

We identify here a range of potential threats and pressures to Irish Hare populations but there is a paucity of empirical data to quantify their actual impact on population dynamics. Data on the impact of agriculture (e.g. the impact of mechanised silage harvest), illegal poaching and disease on local population persistence and change in abundance are lacking. These are key knowledge gaps, which limit our ability to fully assess the species conservation status.

> ***Recommendation 5:*** Further research is required on the drivers of population biology in the Irish Hare that would be facilitated by a network of constant effort monitoring sites augmented by local level collection of empirical threats and pressure data i.e. change in agriculture, prevalence of illegal hunting etc.

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