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Source: Wildlife Biology, 2020(2)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00650

Wildlife Biology 2020: wlb.00650
doi: 10.2981/wlb.00650

Subject Editor: Peter Sunde. Editor-in-Chief: Ilse Storch. Accepted 6 May 2020

Distribution of mountain hares *Lepus timidus* in Scotland in 2016/2017 and changes relative to earlier surveys in 1995/1996 and 2006/2007

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Mountain hares *Lepus timidus*, incorporating the subspecies *L. t. varronis*, *L. t. hibernicus* and *L. t. scoticus*, have declined in range throughout continental Europe where they face pressures from climate-change, competition and land-management. In Scotland, the absence of a national monitoring scheme, including mandatory reporting of hunting records, means that producing robust estimates of mountain hare population trends is difficult. We repeated questionnaire surveys conducted in 1995/1996 and 2006/2007 to assess the 2016/2017 distribution and hunting records of mountain hares in Scotland and describe regional changes in their distribution over a 20-year period in relation to management for red grouse *Lagopus lagopus scotica* shooting. Comparisons of areas covered in all surveys indicated no net change in the area of Scotland occupied by mountain hares, but within that we found changes in range between regions and sites of differing grouse management intensity. Between 1995/1996 and 2016/2017, range contractions in southern Scotland contrasted with no changes in north-–east Scotland. In north-west Scotland range expanded by 61% in areas practicing driven grouse shooting, declined by 57% in areas practicing walked-up grouse shooting and remained low and stable in areas which did not shoot grouse. A total of 33 582 mountain hares were killed in 2016/2017 representing a 71% and 48% increase from 1995/1996 and 2006/2007 respectively. However, the average kill density in 2016/2017 (12.4 ± 3.3 hares km^{-2}) was comparable to 2006/2007 (10.8 ± 3.0 km^{-2}) and we found no relationship between kill density and contractions in range. Despite increases in numbers of mountain hares killed over the last 20 years, it appears that range contraction may be attributed to factors other than culling, such as changes in habitat and management. Disentangling these factors should be the focus of future research.

Keywords: conservation, grouse moors, habitat, population, wildlife management

The mountain hare *Lepus timidus*, incorporating the subspecies *L. t. varronis*, *L. t. hibernicus* and *L. t. scoticus*, is listed globally as a species of least concern by the International Union for Conservation of Nature (IUCN), but European populations face several pressures at regional levels including climate change (Acevedo et al. 2012, Pedersen et al. 2017), interspecific competition (Caravaggi et al. 2017) and perceived hunting pressure (Watson and Wilson 2018). For member states of the European Union, mountain hares are protected under Annex V of the EU Habitats Directive (92/43/EEC), which requires populations to be maintained in a favourable conservation status. Under Article 17 of the Habitats Directive (92/43/EEC), member states must report every six years on species conservation status based on the assessment of several criteria including population size, habitat suitability and species range. The European range of mountain hares includes isolated populations in the Alps and extends throughout Fennoscandia and the Baltic countries (Angerbjörn and Flux 1995). In the British Isles, the mountain hare is native to Scotland and Ireland and has been introduced to the Peak District in England (Hulbert et al. 2008).

Studies of mountain hare hereafter 'hare' distribution in Scotland show that they are strongly associated with heather moorland, and particularly that managed for red grouse *Lagopus lagopus scotica* shooting (Patton et al. 2010) where hare densities can exceed 200 km^{-2} (Watson et al. 1973). High hare densities on grouse moors are associated with heather habitat management and predator control carried out by gamekeepers, which is thought to benefit hares (Stoddart and Hewson 1984). In comparison, throughout their continental range mountain hares are usually associated with boreal forests and typically occur at much lower densities e.g. 2–3 km^{-2} (Angerbjörn 1986, Newey et al. 2007a, Rehnus and Bollmann 2016). Similar densities (0.5–3 km^{-2}) have been reported in the west of Scotland (Watson and Hewson 1973), where management for grouse shooting is absent or less intensive than in the east (Robertson et al. 2017).

The mountain hare is an important game species throughout much of its European range (Mitchell-Jones et al. 1999). In Scotland, mountain hares are traditionally hunted for sport, especially on moorland managed primarily for red grouse, and killed to protect habitat such as young forests. Over the last two decades, mountain hares have also been killed on some driven grouse moors in an attempt to help control Louping-ill virus carried by sheep ticks *Ixodes ricinus* (Harrison et al. 2010). This is due to the perception that hares are important in the transmission of the virus to red grouse (Laurenson et al. 2003, Harrison et al. 2010). A survey of Scottish landowners and managers estimated that approximately 50% of the number of hares killed in 2006/2007 was for this reason (Patton et al. 2010). These tick-related culls have led to concerns about the justification and sustainability of current mountain hare management practices and their conservation status in Scotland (Thompson et al. 2016, Watson and Wilson 2018).

The 2012–2018 assessment of mountain hares in Scotland downgraded their conservation status from 'Favourable' (JNCC 2013) to 'Unfavourable-Inadequate', describing hunting and management of game as important pressures on mountain hares, together with insufficient data to provide robust population estimates and trends (JNCC 2019). To-date, Scotland lacks a national hare monitoring scheme, including mandatory reporting of hunting records (Brooker et al. 2018) and a standardised method for counting hares is only now being considered (Newey et al. 2018). Thus, available information on conservation status is limited to few studies that rely on incidental and sometimes conflicting data (Massimino et al. 2018, Watson and Wilson 2018, Aebischer 2019, Hesford et al. 2019), further compromised by 4–15-year cyclical fluctuations in hare abundance (Newey et al. 2007b). Distribution data are similarly limited to spatial modelling of hares counted during bird surveys (Massimino et al. 2018) and were used to inform the latest Article 17 reporting (JNCC 2019). However, comparisons of these predictive maps with known distributions (Mathews et al. 2018) showed inconsistent patterns in range (Wheeler et al. 2019).

Questionnaire based surveys are an increasingly used method to quantify species distributions across large geographical areas (White et al. 2005, Thorn et al. 2011, Scott et al. 2014) and have previously been used to describe changes in Scottish mountain hare distribution (Tapper 1996, Patton et al. 2010). We repeated previous surveys to: 1) describe regional changes in mountain hare distribution over a 20-year period in relation to the intensity of grouse moor management, and 2) consider whether changes in distribution are associated with numbers killed. We predicted that changes in hare range would follow patterns of grouse management, with contractions occurring in areas where management of moorland for driven grouse shooting had ceased.

Methods

Data collection

To ensure comparability with previous surveys, we followed the methods of Tapper (1996), repeated by Patton et al. (2010). In January 2018, 4197 questionnaires were mailed to Scottish landowners and managers who were members of either the Game & Wildlife Conservation Trust (GWCT), Scottish Gamekeepers Association (SGA) or Scottish Land & Estates (SL&E), or who had responded to previous surveys. Many private landowners, managers or gamekeepers are members of one or more of these organisations, and it was thought that survey coverage would be maximised by targeting their membership. Reminders were sent out to non-respondents in areas where survey coverage was low. Furthermore, the survey was publicised through social media to encourage members of the public to submit mountain hare sightings. During the 1995/1996 survey, only areas of upland moorland were included (Tapper 1996) despite mountain hares occupying a variety of habitats at a range of altitudes (Newey et al. 2007a, Patton et al. 2010). Recognising this, the 2006/2007 survey was not limited to moorland areas and consequently survey coverage was 3.4 times greater in 2006/2007 than 1995/1996 (Patton et al. 2010). To maximise survey coverage and comparability, we opted to replicate the 2006/2007 survey and did not restrict survey coverage.

Mailed questionnaires were based on those used in the two previous surveys (Supplementary material Appendix 1 Fig. A1) and included a 1:50 000 scale Ordnance Survey map centred on each recipient's postcode. Respondents were asked to outline the boundary of their estate (an area of countryside, owned by a person, family or organisation and ranging in size from <1 km^2 to >300 km^2) on the maps provided and to indicate the 1-km^2 grid squares where mountain hares had been observed within their estate between spring 2016 and receipt of the questionnaire in January 2018. Sightings reported by members of the public and verified data submitted to the National Biodiversity Network (NBN Atlas occurrence download at <https://nbnatlas.org> accessed on Fri Oct 19 10:36:52 UTC 2018) between 2016 and 2017 (Supplementary material Appendix 1, 'NBN_citation_WLB-00650.xlsx'), were similarly used to map mountain hare presence at the 1-km^2 level. The number of mountain hares killed on each estate between March 2016 and February 2017 was also requested thereby enabling us to collect data from one full open season for mountain hare which runs from 1 August to 28 February (Wildlife and Countryside act 1981). Spatial data from returned surveys detailing estate boundaries and mountain hare presence/absence were digitised in ArcGIS and overlaid on a 1-km^2 Ordnance Survey grid square map of Scotland. All survey data was collected and stored in line with EU General Data Protection Regulations.

Survey coverage and distribution

To estimate survey extent, the boundaries of each responding estate were amalgamated into a single continuous shapefile and the total survey area calculated. Though hare presence/absence data for each estate were collected at the 1-km^2 level and analysed at the estate level, confidentiality agreements with respondents required data to be presented at the 10×10-km square level (i.e. 100 km^2). Survey coverage included coastal regions and islands, hence land cover did not total 100 km^2 in all squares. Thematic maps were produced which displayed the area surveyed and area of mountain hare presence as a percentage area of each grid square. Distributional change between surveys is also presented at the 10×10-km square scale and measured as the difference in area where mountain hares were reported between survey periods. As survey coverage also differed between periods, thematic maps presenting distributional change were limited to those estates surveyed in common between the periods being compared.

Regions and estate management

Red grouse shooting is widely practiced across much of the Scottish countryside, especially at higher elevations on heather-dominated moorland (Hudson 1992). Given the positive association between grouse moors and mountain hares (Stoddart and Hewson 1984), we considered that the intensity of grouse moor management may be an important predictor of hare distribution. Grouse shooting is typically categorized into either driven shooting, where grouse are flushed by a line of human beaters towards a stationary line of hunters, and walked-up shooting, where hunters walk in line, often using dogs to help flush grouse (Sotherton et al. 2009, Mustin et al. 2017). Driven shooting requires higher post-breeding densities of grouse than walked-up shooting, is associated with more intensive management of heather habitat and generalist predators (Sotherton et al. 2017), and supports higher densities of mountain hares (Watson and Hewson 1973, Stoddart and Hewson 1984, Hesford et al. 2019). Therefore, following Patton et al. (2010), we categorised the estates of questionnaire respondents into three levels of management based on the predominant grouse shooting type; those where the estate practiced either driven grouse shooting (driven), walked-up grouse shooting (walked-up) or no grouse shooting (not-shot). Typically, grouse estates comprise a mix of land uses, including agriculture, forestry and game shooting (Mustin et al. 2017), but in most cases predator removal, a key component of grouse management, would be applied across all of an estate and not restricted to the heather moorland that supports red grouse. Thus, we believed that shooting type was a good proxy for grouse management intensity.

We compared mountain hare distribution between three grouse management types (driven, walked-up, not-shot), three survey periods (1995/1996, 2006/2007, 2016/2017) and four Scottish regions (north-west, south-west, north-east and south-east). Regions were defined following Sim et al. (2008) and reflect variation in both topography and management for grouse shooting. Northern regions were separated from southern regions by the central belt of Scotland, an area of low altitude and high human population density that divides the Highlands in the north from the southern Uplands in the south (Hetherington et al. 2008). Regions were further divided from east to west by topographic relief that also reflected differences in the distribution and intensity of management of grouse moors (Robertson et al. 2017) and densities of mountain hares (Watson and Hewson 1973, Tapper 1992), both of which are greater in the east. To reflect the sampling bias for upland estates only during the 1995/1996 survey, we also created a binary variable 'FirstSurvey', which categorised estates according to whether they were first surveyed in 1995/1996 (1) or added in subsequent surveys (0), hereafter referred to as 'Original' and 'Additional' estates respectively.

Statistical analysis

All statistical analyses were performed at the estate level and were restricted to estates greater than 1 km^2. Since the coverage differed between surveys, analyses were limited to estates surveyed in two or more periods when considering changes in distribution over time. When considering the relationship between numbers killed and changes in range, analyses were also limited to estates that reported killing mountain hares during the 2006/2007 survey. All analyses were performed using R (ver. 3.4.3, <www.r-project.org>). Generalized linear mixed models were fitted using the 'lmer' function in the lme4 package (Bates et al. 2015). The percentage ranges presented in the results are actual means (i.e. the observed mean) derived from raw values for the percentage area where mountain hares were reported present at the estate level. Data on numbers killed are self-reported and apply only to those estates that provided this information, therefore they should be treated as minimum values for numbers killed.

Mountain hare range in 2016/2017

Mountain hare range in 2016/2017 was compared (at the estate level) between regions, grouse management types and FirstSurvey category, using general linear models (GLMs) with a normal error distribution. The logit transformed percentage area of each estate where mountain hares were present was included as the response variable and the area of each estate (km^2) was included as a weight. Region, Management type and FirstSurvey were fitted as categorical explanatory variables, together with their two- and three-way interactions. The average mountain hare range varied between management types and FirstSurvey categories (FirstSurvey $\times$ Management type: $\chi^2_2 = 7.9$, $p = 0.02$) which may reflect the sampling bias for upland estates during the 1995/1996 survey. Therefore, we repeated the analysis (without FirstSurvey) for Original and Additional estates separately.

Changes in mountain hare range between survey periods

As the 1995/1996 survey was restricted to upland estates whilst the subsequent surveys were not, we initially assessed whether mountain hare range differed between Original and Additional estates for data collected during the 2006/2007 and 2016/2017 surveys. Comparisons were conducted at the estate level using a generalized linear mixed model with a normal error distribution. The logit-transformed percentage area of each estate where mountain hares were present was included as the response variable, the area of each estate (km^2) was included as a weight and estate ID as a random effect. Survey period and FirstSurvey (first surveyed in 1995/1996 or not) were included as categorical variables, together with their two-way interaction. The average area where mountain hare were reported present on Original estates was 62% greater than on estates added in subsequent surveys, irrespective of survey period ($\chi^2_1 = 42.1$, $p < 0.001$). Therefore, Original and Additional estates were considered separately when testing for changes in mountain hare range between survey periods. In each case, the response variable, error distribution, weights and random effects were as described above, with Survey period, Region and Management type fitted as fixed effects as well as their interactions. If the three-way interaction was significant, the model (without Region) was fitted to the data for each region separately.

Numbers killed and changes in mountain hare range

To determine whether the number of mountain hares killed was related to changes in hare distribution, we produced a kill density index by calculating the number of mountain hares killed per km^2 at the estate level. A GLM was then used to relate kill density in 2006/2007 to changes in mountain hare range between 2006/2007 and 2016/2017. The $\log_e$-transformed change in reported hare range (km^2) was included as the response variable and the area of each estate (km^2) included as a weight. Kill density was included as a covariate and Region as a categorical explanatory variable.

Results

Survey coverage, response rate and mountain hare range in 2016/2017

Survey response rate was 28% (1173) and was comparable to the 2006/2007 survey (27%), but lower than the 1995/1996 survey (41%) (Table 1). This difference may reflect the sampling bias for well-established contacts on moorland estates during the 1995/1996 survey and more duplicate questionnaires sent to different people at the same estate (i.e. to both the estate owner and its manager(s)) in the two most recent surveys (see also Patton et al. 2010). A further 146 records were obtained via the NBN or from members of the public, however, all these were from areas where hares were reported as present by estate respondents, so were discarded. Responses covered 72 612 km^2 of land surface (at the 100-km^2 level), equating to an area equivalent to 92% of Scotland (or 50% of Scotland, 39 562 km^2, at the 1-km^2 level). We resurveyed 99% of the area covered during the 1995/1996 survey and 95% of the area covered during the 2006/2007 survey at the 100-km^2 scale (Fig. 1, Table 2). Of the total survey coverage, 85% was returned from the four mainland regional categories; north-west (40%), south-west (17%), north-east (23%) and south-east (5%).

Mountain hares were widespread in north-east Scotland where they were reported on 46% of the area surveyed by return questionnaires (at the 1-km^2 level), but less in the other regions: north-west (23%), south-east (27%) and south-west (10%) (Fig. 2). Of the respondents, 860 estates had no grouse shooting interest (not-shot) and made up 59% of the survey coverage, whilst estates that were managed for walked-up (77) or driven (138) grouse shooting represented 17% and 24% of the survey coverage respectively. No information was available on grouse management type for <1% ($n = 8$) of the returns and a further 90 responses either did not provide an estate boundary or were duplicate replies. Driven estates accounted for 68% of the total area where mountain hares were reported as present compared to 57% in 2006/2007 and 51% in 1995/1996. Estates that practiced walked-up grouse shooting or did not shoot grouse accounted for 19% and 13% respectively, which was similar to both 1995/1996 (walked-up 12%; not-shot 17%), and 2006/2007 (walked-up 15%; not-shot 19%).

In 2016/2017, for Original estates the mean area occupied by hares on driven grouse moors was 70% ± 6%, compared to only 18% ± 5% on walked-up grouse moors ($\chi^2_1 = 29.9$, $p < 0.001$) and 12% ± 6% on moorland estates which were not managed for grouse shooting ($\chi^2_1 = 27.2$, $p < 0.001$). Additional estates followed a similar pattern where the area occupied by mountain hare on driven grouse moors (55% ± 3%) was greater than on walked-up moors (28% ± 4%; $\chi^2_1 = 55.2$, $p < 0.001$) or on estates with no grouse shooting (5% ± 1%; $\chi^2_1 = 265.8$, $p < 0.001$).

Changes in mountain hare range between survey periods

For Original estates, we found changes in mountain hare range that varied both between regions and grouse management type (Period × Region × Management type: $\chi^2_{12} = 51.2$, $p < 0.001$), however, there was no overall change in mountain hare range between survey periods for either Original ($\chi^2_1 = 3.4$, $p = 0.18$) or Additional estates ($\chi^2_1 = 1.6$, $p = 0.20$) (Fig. 3, Table 3). For Original estates, over the 20-year period 1996–2017, hare range showed an 11% decrease in the south-east ($\chi^2_2 = 7.0$, $p = 0.03$) but was more stable in the north-east ($\chi^2_2 = 5.0$, $p = 0.08$), irrespective of grouse management type. In the north-west, hare range increased by 61% on driven grouse moors ($\chi^2_1 = 70.0$, $p < 0.001$), decreased

Table 1. The number of questionnaires sent and responses received that provided information on mountain hare presence/absence for each of the three survey periods (1995/1996, 2006/2007 and 2016/2017).

Survey period	No. sent	Responses received	Mountain hare presence	Mountain hare absence	No information provided
1995/1996	416	170 (41%)	89 (52%)	38 (23%)	43 (25%)
2006/2007	3390	918 (27%)	328 (36%)	553 (60%)	37 (4%)
2016/2017	4197	1173 (28%)	318 (27%)	765 (65%)	90 (8%)

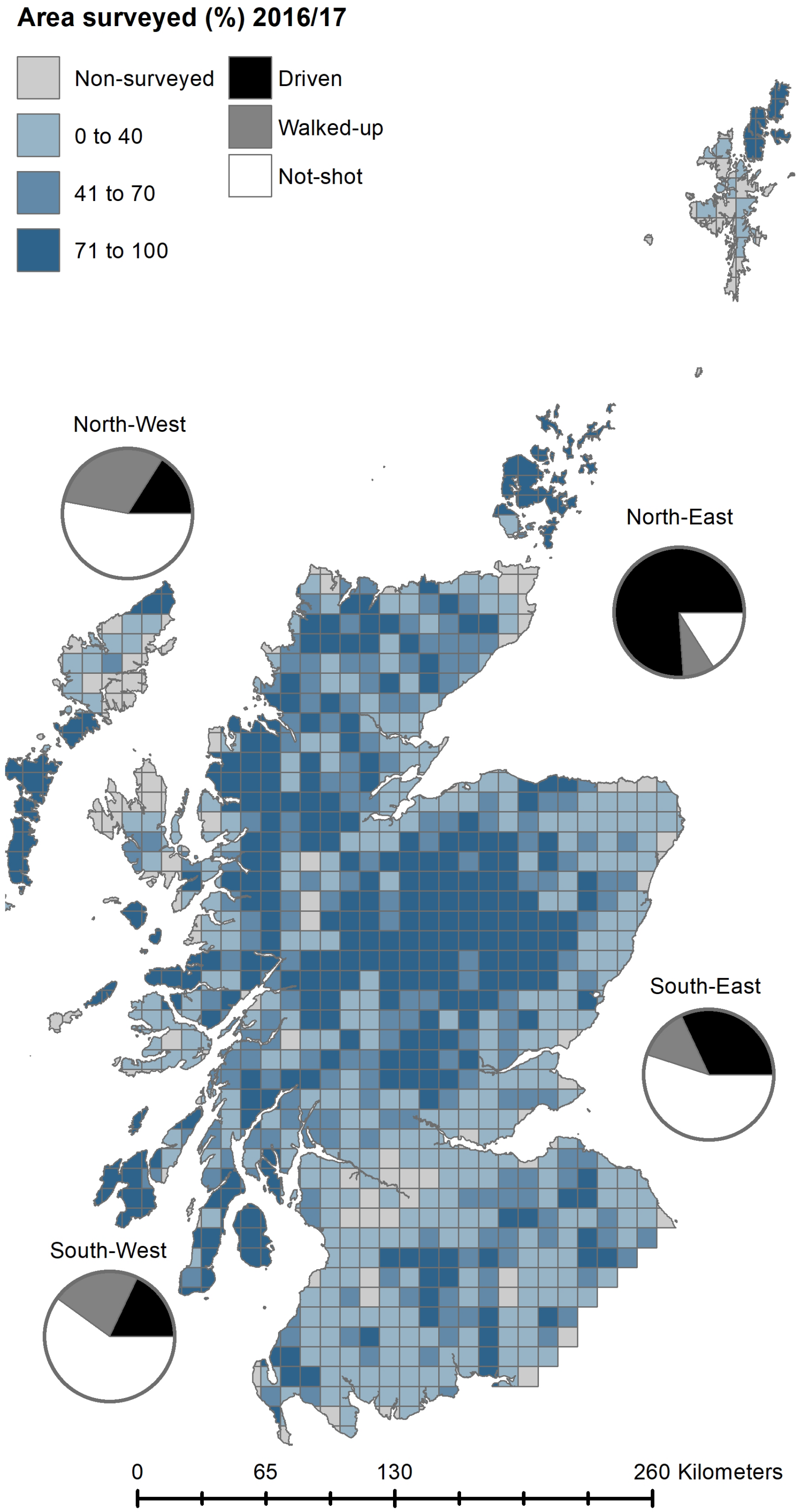


Figure 1. The percentage survey coverage within each 10 × 10-km grid square in Scotland in 2016/2017. Pie-charts represent the percentage survey area within each region categorised according to grouse management type: driven (black) – north-west (16%), north-east (76%), south-west (18%), south-east (32%); walked-up (grey) – north-west (31%), north-east (8%), south-west (22%), south-east (13%); and not-shot (white) – north-west (53%), north-east (16%), south-west (60%), south-east (55%).

Table 2. The area of Scotland (km^2) occupied by mountain hare during this survey (2016/2017) relative to that in the two previous surveys (1995/1996 and 2006/2007) (measured at the 10×10-km grid square scale).

	Area (km^2)	2016/2017 Present	Absent	Not surveyed
1995/1996				
Present	14 600	12 288 (84%)	2299 (16%)	13 (<1%)
Absent	6336	1394 (22%)	4762 (75%)	180 (3%)
2006/2007				
Present	34 359	23 470 (68%)	9780 (29%)	1109 (3%)
Absent	36 739	5885 (19%)	28 198 (77%)	2656 (7%)

by 57% on walked-up grouse moors ($\chi^2_1 = 14.6$, $p < 0.001$), but showed no change on estates not managed for grouse shooting ($\chi^2_1 = 0.2$, $p = 0.65$). In the south-west, hare range decreased by 52% and 68% on driven ($\chi^2_1 = 4.2$, $p = 0.04$) and walked-up ($\chi^2_1 = 37.7$, $p < 0.001$) grouse moors, but showed no change on estates with no grouse shooting interest ($\chi^2_1 = 1.9$, $p = 0.17$), noting that nevertheless the range on driven shooting estates remained three times higher than on the other types of estate in 2016/2017.

For Additional estates (last two surveys only), temporal changes in mountain hare range varied significantly between regions (Period × Region: $\chi^2_3 = 29.6$, $p < 0.001$) and grouse management types (Period × Management type: $\chi^2_2 = 18.7$, $p < 0.001$). Over the 10-year period 2007–2017, average mountain hare range increased by 5% in the north-east ($\chi^2_1 = 24.6$, $p < 0.001$), decreased by 63% in the south-west ($\chi^2_1 = 14.1$, $p < 0.001$) and showed no change in either the north-west ($\chi^2_1 = 2.1$, $p = 0.15$) or south-east ($\chi^2_1 = 1.0$, $p = 0.31$) irrespective of grouse management type. We also observed an average increase in mountain hare range of 2.5% on estates managed for driven grouse shooting ($\chi^2_1 = 24.9$, $p < 0.001$), but no change on either walked-up estates ($\chi^2_1 = 2.5$, $p = 0.12$) or estates without a grouse shooting interest ($\chi^2_1 = 0.02$, $p = 0.89$) irrespective of region.

Numbers killed and changes in mountain hare range

In 2016/2017, 33 582 mountain hares were killed on 88 estates whose areas totalled 3547 km^2. Of the estates that provided data on numbers killed, 80% (n = 70) were driven grouse moors, 13% (n = 11) were walked-up grouse moors and 8% (n = 7) did not shoot grouse. In 2006/2007, the corresponding values were 72, 7 and 21% respectively. For Original estates (i.e. estates first surveyed in 1995/1996) the number of hares reported killed increased by 71% and 48% in 2016/2017 compared to the 1995/1996 and 2006/2007 surveys respectively (Table 4). For Additional estates, the total number killed increased by 15% between 2006/2007 and 2016/2017. The average kill density in 2016/2017 was comparable to 2006/2007 though greater than in 1995/1996 (Table 4). There was no significant relationship between kill densities in 2006/2007 and changes in mountain hare range at the estate level between 2006/2007 and 2016/2017 ($\chi^2_1 = 0.7$, $p = 0.40$; slope ± SE = −0.002 ± 0.021).

Discussion

Within the last century, mountain hares have declined in range throughout continental Europe (Thulin 2003) with further declines predicted under future climate scenarios (Acevedo et al. 2012). This study describes changes towards the western edge of their European range where it had previously been considered stable (Patton et al. 2010, Mathews et al. 2018). In doing so we highlight the usefulness of questionnaire-based methodologies and importance of practitioner knowledge in advancing our understanding of how land management can influence the distribution of species.

Mountain hare distribution patterns were broadly similar to those previously reported (Massimino et al. 2018, Mathews et al. 2018), with the greatest reported presence in the north-east. Average mountain hare presence was higher on Original compared to Additional estates, reflecting the sampling bias towards hare rich upland moors during the 1995/1996 survey. Across all regions, the area occupied by mountain hare was greater on estates practicing driven grouse shooting than on those where walked-up grouse shooting predominates or where grouse were not-shot, with two-thirds of the mountain hare's range occurring on estates where driven grouse shooting was the main shooting method. This supports previously reported positive associations between grouse management and hares (Watson et al. 1973, Stoddart and Hewson 1984, Patton et al. 2010, Hesford et al. 2019), where it is considered that reductions in generalist predators by gamekeepers, as well as strip burning of older heather, may improve hare habitat and survival (Stoddart and Hewson 1984, Savory 1986, Reynolds and Tapper 1996).

Regional changes in mountain hare range may reflect patterns of grouse management intensity and changes in management between surveys, as well as underlying environmental gradients (e.g. geology and weather, Watson and Hewson 1973) which interact with the distribution of grouse moor management (Picozzi 1968). For example, mountain hare range remained relatively stable or increased on estates in north-east Scotland, an area of intensive grouse management (Anderson et al. 2009), but contracted in south-west Scotland, where numbers of grouse shot had declined since 1980 (Robertson et al. 2017). Recent spatial models of mountain hare distribution did not cover the south-west but showed significant declines in abundance indices across 34% of the considered part of their range (Massimino et al. 2018), including in areas of north-west Scotland, where we found concurrent range reductions. However, their data were collected during surveys primarily designed for birds, which are known to perform poorly when estimating hare numbers (Brooker et al. 2018, Newey et al. 2018, Wheeler et al. 2019), and we show that declines occurred on walked-up estates whilst estates managed for driven grouse shooting showed recent range increases in the north-west.

Distribution maps presented here and in Massimino et al. (2018), were produced using data collected by citizen science survey methods and may be limited by the reliability of

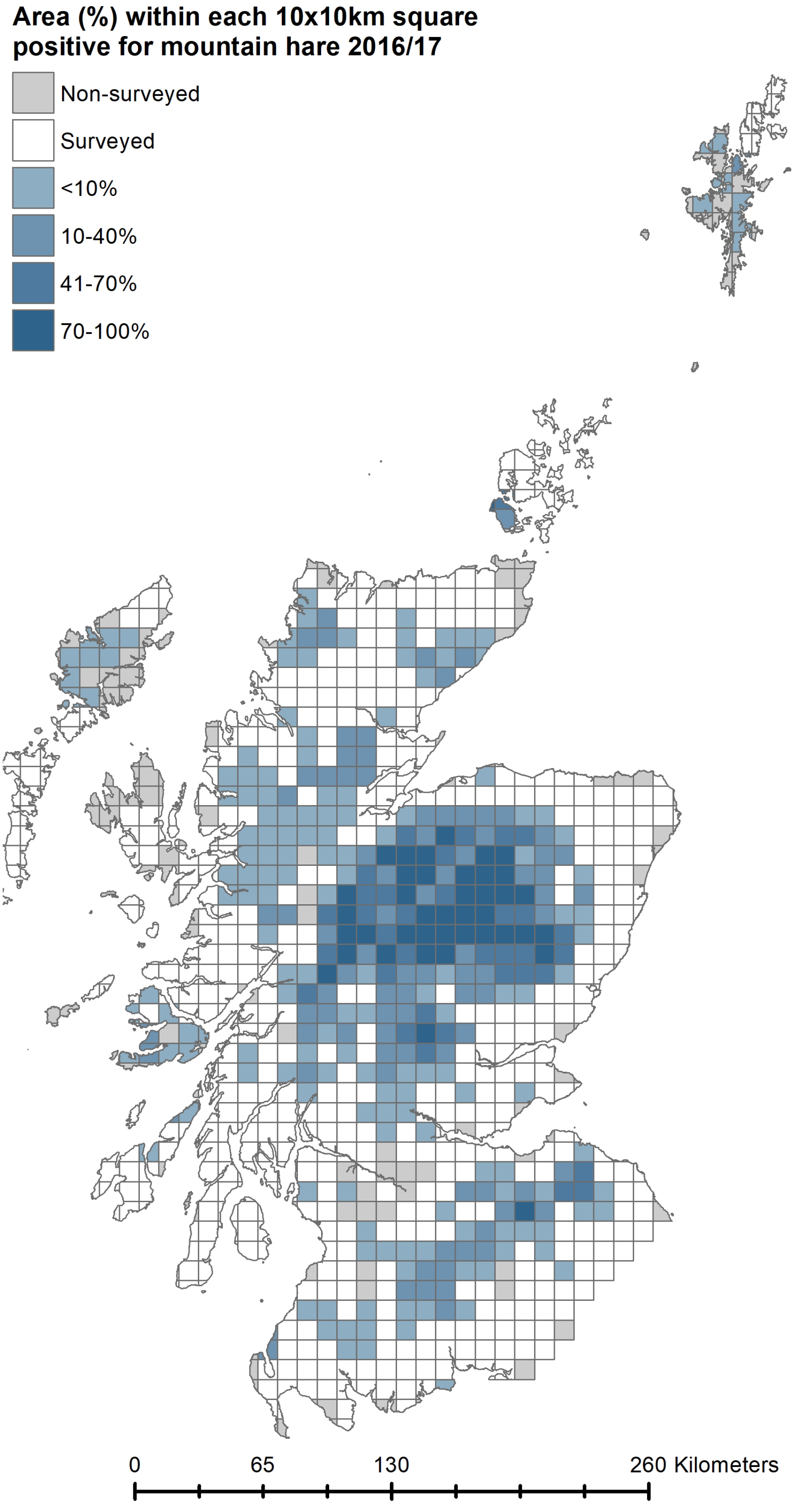
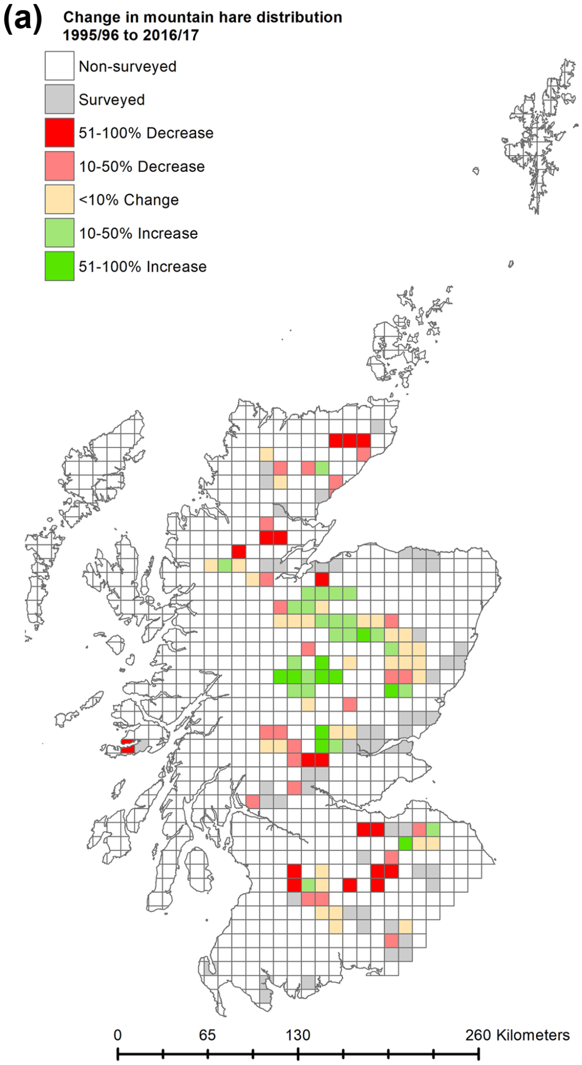


Figure 2. Reported percentage presence of mountain hares within each 10 × 10-km grid square in Scotland in 2016/2017. Squares were marked as surveyed if responses were provided for that square but where mountain hare were not reported as present.

the information received (Hunter et al. 2013). For instance, confusion with European hares *Lepus europaeus* by inexperienced observes within upland/lowland ecotones, may have impacted the accuracy of reporting leading to false positives. In contrast, failure to detect mountain hares may have led to false negatives, therefore absences in this study should be treated as pseudo-absences only. Moreover, mountain hare range may be under reported in areas where reported hare



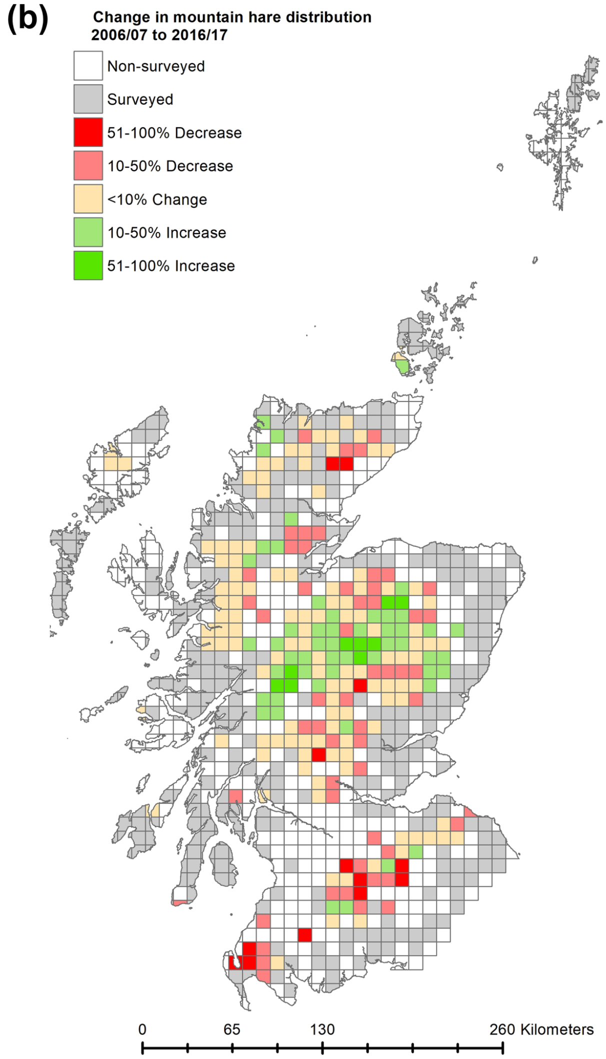


Figure 3. Change in mountain hare distribution in Scotland: (a) from 1995/1996 (Tapper 1996) to 2016/2017 and (b) from 2006/2007 (Patton et al. 2010) to 2016/2017. Distribution compared at a 10×10-km grid square scale, limited to the area surveyed in common between the time periods being compared. Areas were marked as surveyed if mountain hares were reported absent in both survey periods and were marked as 'Non-surveyed' if <10% of the grid square had been surveyed in common. For a comparison of 1995/1996 to 2006/2007 see Patton et al. (2010).

presence was low due to lower participant engagement (Patton et al. 2010). Thus, spatiotemporal clustering as a result of measurement bias may also be a limiting factor (Bird et al. 2014). Nonetheless, by using a questionnaire-based methodology we surveyed over 90% of Scotland and were able to identify areas where mountain hare range has contracted within the last two decades.

Described reductions in mountain hare range were consistent with those of moorland birds, including golden plover *Pluvialis apricaria*, curlew *Numenius arquata*, black grouse, *Lyrurus tetrix* and red grouse, over a similar time period (Balmer et al. 2013). Declines in these bird species have been attributed to large-scale changes in upland land-use, where heather moorland has been either afforested or lost to over-grazing, predominantly by sheep (Fuller and Gough 1999, Douglas et al. 2014, White et al. 2015, Robertson et al. 2017). These changes have resulted in fragmentation of remaining moorland habitats, especially in south–west Scotland, where management of moors for driven grouse shooting has largely ceased and generalist predators have increased accordingly (Douglas et al. 2014, Robertson et al. 2017). We found greatest reductions in hare range in this region and it is likely that changes in land management have significantly contributed to their decline (Hulbert et al. 1996, Watson and Wilson 2018) as illustrated by the last record of mountain hares from Langholm Moor in 2002 (S. Ludwig unpubl.), a moor previously managed for driven grouse shooting, following the cessation of fox control by gamekeepers in 1999 (Ludwig et al. 2017). Over the next decade, further land-use change is expected in southern Scotland in line with Government afforestation targets (Scottish Government 2019), which may present a challenge for mountain hare conservation in this region.

Table 3. Average percentage area (± SE) reported positive for mountain hares on Scottish estates in each survey period (1995/1996, 2006/2007 and 2016/2017), in relation to regions (north-east, north-west, south-west and south-east) and grouse management type (driven, walked-up and nt-shot). Data is presented for Original estates only. Values are calculated from actual means at the estate level (n = number of estates). Percentage change is the overall change for the 20-year period (1995/1996 to 2016/2017).

Region	Grouse management	n	1995/1996	2006/2007	2016/2017	% change
	driven	65	49.0% ± 4.5	65.5% ± 5.1	64.3% ± 4.5	31.3% ($\chi^2_1 = 2.4$, $p = 0.119$)
North-east	walked-up	11	15.5% ± 5.9	21.0% ± 7.5	46.0% ± 10.3	198% ($\chi^2_1 = 32.7$, $p < 0.001$)
	not-shot	22	16.7% ± 7.0	35.8% ± 10.1	12.4% ± 6.9	−25.9% ($\chi^2_1 = 0.8$, $p = 0.378$)
	driven	31	50.7% ± 6.7	84.1% ± 4.8	81.6% ± 5.4	61% ($\chi^2_1 = 70.0$, $p < 0.001$)
North-west	walked-up	30	42.1% ± 7.3	24.9% ± 6.7	18.0% ± 5.4	−57.1% ($\chi^2_1 = 14.6$, $p < 0.001$)
	not-shot	30	26.3% ± 6.7	20.6% ± 7.0	20.7% ± 7.1	−21.2% ($\chi^2_1 = 0.2$, $p = 0.649$)
	driven	14	84.9% ± 5.6	71.5% ± 13.0	76.6% ± 8.8	−9.8% ($\chi^2_1 = 1.4$, $p = 0.236$)
South-east	walked-up	5	64.9% ± 20.4	50.1% ± 23.9	42.6% ± 13.9	−34.3% ($\chi^2_1 = 2.5$, $p = 0.117$)
	not-shot	8	22.7% ± 15.0	38% ± 23.3	19.9% ± 16.3	−12.6% ($\chi^2_1 = 4.8$, $p = 0.026$)
	driven	8	68.2% ± 12.3	56.5% ± 15.4	32.9% ± 12.1	−51.8% ($\chi^2_1 = 4.2$, $p = 0.041$)
South-west	walked-up	8	22.6% ± 11.3	9.9% ± 8.3	7.2% ± 7.2	−67.9% ($\chi^2_1 = 37.7$, $p < 0.001$)
	not-shot	27	12.0% ± 4.5	7.8% ± 5.5	12.5% ± 5.4	4.1% ($\chi^2_1 = 1.9$, $p = 0.165$)
overall		259	39.0% ± 2.6	46.0% ± 3.1	43.6% ± 2.9	11.8% ($\chi^2_1 = 3.4$, $p = 0.18$)

Table 4. Number of mountain hares reported killed and the average kill density (i.e. the number of hares harvested per km² of hare presence ± SE) for estates surveyed in common between periods (1995/1996, 2006/2007 and 2016/2017) (n = number of estates).

Periods surveyed		Total killed		
		1995/1996	2006/2007	2016/2017
1995/1996, 2006/2007 and 2016/2017	no. killed	5646 (n = 18)	6515 (n = 18)	9673 (n = 18)
	kill density	*6.4 ± 2.0 km^{-2}*	*10.8 ± 3.0 km^{-2}*	*12.4 ± 3.3 km^{-2}*
2006/2007 and 2016/2017	no. killed		13 703 (n = 43)	15 770 (n = 43)
	kill density		*12.2 ± 2.2 km^{-2}*	*12.0 ± 2.2 km^{-2}*
2016/2017	no. killed			8139 (n = 29)
	kill density			*10.7 ± 2.2 km^{-2}*

In north-east Scotland, tick-related culls of mountain hares have recently been associated with severe declines in hare indices on grouse moors (31% per annum from 1999 to 2017) (Watson and Wilson 2018). Declines in species abundance are often accompanied by shifts in range (Lawton 1993, Fuller et al. 1995), however, we show that mountain hare range has remained stable or increased in this region. Although increased hunting pressure can sometimes cause shifts in species range and could explain the apparent mountain hare range expansion in the north-east (Verdade 1996), we found no relationship between kill density and changes in range. Whilst we observed increases in the number of mountain hares killed over the last two decades, the average kill density changed little over the last 10 years, suggesting that changes in reported hunting records probably reflect cyclical fluctuations in mountain hare densities (Reynolds et al. 2006, Aebischer 2019, Hesford et al. 2019), a well-described pattern observed in mountain hare populations across Europe (Newey et al. 2007b). Managed grouse moors generally support high densities of mountain hares and appear likely to be population sources rather than sinks (Watson et al. 1973, Hesford et al. 2019). Despite increases in numbers of hares killed over the last 20 years, it appears that the range contractions may be unrelated to culling, and instead other changes such as moorland habitat loss and reductions in management effort might be more important. Disentangling the ecological drivers determining occupancy and density patterns should be the focus of future research.

Acknowledgements – We thank all those who responded to the questionnaire and who provided mountain hare data, including Scottish Gamekeepers Association and Scottish Land and Estates who assisted with mailing to their memberships. Kayleigh Hogg, Kim Morrison, Amy Butterfield, Charlene Shaw and Colin Shaw helped with the initial mailing, whilst Carol Anderson, Tony Stevenson and Irene Johnston helped co-ordinate responses. Hannah Weald and Megan Roberts assisted with digitising and data entry. We are also grateful to Nicholas Aebischer who provided statistical advice and Kathy Fletcher who commented on early drafts.

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Supplementary material (available online as Appendix wlb-00650 at <www.wildlifebiology.org/appendix/wlb-00650>). Appendix 1.