Population assessment of the mountain hares (*Lepus timidus*) of England: distribution, abundance and genetics

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PhD 2022

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A thesis submitted in fulfilment of the requirements of
Manchester Metropolitan University for the degree of
Doctor of Philosophy.
Ecology and Environment Research Centre,
Department of Natural Sciences,
Manchester Metropolitan University,
United Kingdom

In collaboration with
Queen's University, Belfast

2022

Image: Mountain hare approaching the author, Rhian Gutter, Margery Hill, Yorkshire, England, UK Date: 12th April 2019. The photo was kindly adopted for the front page of the journal Wildlife Biology, July 2021

TABLE OF CONTENTS

Abstract

In the 1870s a small founder group of mountain hares (*Lepus timidus*) was translocated from Scotland to the Peak District moors, England. They succeeded as a pioneer of rewilding for 150 years, playing important ecological roles within the upland ecosystem,. Nonetheless these mountain hares frequently went unmonitored. From 1971 to 2002 only four formal studies attempted distribution or abundance assessments. Subsequently there were doubts regarding the persistence of the population. In 2008 the species was added to UK Biodiversity Action Plan, which recommended ongoing monitoring.

The aim of the thesis was to provide a fundamental assessment of this mountain hare population, informing conservation status reviews and enabling subsequent potential population viability analysis. The research draws upon a considerable amount of newly collected field observations, citizen science records, geographic information and laboratory investigations. I employ new survey methods, quantitative ecology, geospatial analysis and genetic techniques to describe the distribution, abundance and genetic structure of this population

This work presents evidence that Peak District mountain hares occupy a geographically confined set of hills comprising ~360km^2. They favour cold environments at high elevations and appear completely dependent on heather for food and shelter. Mountain hares frequent different habitats than their sister species, the European brown hare (*L. europaeus*), because of different climatic and dietary preferences. Accordingly, the main threats to mountain hares are climate change which may reduce their range by ~80%; and impending competition with European brown hares.

Surveys of mountain hares are notoriously challenging, since this nocturnal cryptic creature may hide by day to avoid predators. To evaluate day and night time survey methods, I compared daylight transect surveys with night-time thermal imaging and camera traps operating 24 hours per day for 5 months. Census surveys using daylight visual sampling are shown to be highly effective and statistically reliable.

Consequently, some 800km of surveys were conducted, covering much rugged difficult ground, with sufficient encounter rates to enable robust estimation of density, based on high detection probability, observing ~20% of the sampled hares to a range of 520m. These surveys showed the mountain hares as a stable population of ~3,500 individuals (winter adults), with one population centre concentrated on a few square kilometres. Densities are not randomly distributed and appear influenced by anthropogenic land use. Numbers in restored blanket bog areas are highest; upon managed grouse moors numbers are two thirds less. This finding notably contradicts most preceding mountain hare research from the UK.

Research sourced genetic material, mostly roadkill mountain hares, provide matter for DNA extraction and microsatellite sequencing. Owing to technical challenges, results were partial yet appeared to indicate the mountain hare population is mostly randomly mating, having a diverse genetic population structure. There appears to be a low level of hybridisation with European brown hares.

Continued monitoring of this Peak District mountain hare population is necessary to support UK biodiversity conservation goals. The mountain hare population experiences the normal ecological factors that govern natural population fluctuations: weather, food availability, predators, parasites, disease and population cyclicity. There is substantial human caused mortality from roads and persecution. These could be greatly reduced, if society were willing.

This thesis may serve as primary reference for conservation assessments.

Dedication

For Rosie, who believed

Personal acknowledgements

Deep grateful thanks are given to the funders and supporters of this PhD study: Rosie Andersen, Sue Alderman, Jane Russ of Hare Preservation Trust; Nida Al-Fulaij and Gill Nelson of People's Trust for Endangered Species; Neil Reid, Queen's University Belfast; Rodney Hale, Action for Hares South West, Dave Turnbull, Estee Farrar and Catherine Flitcroft, of British Mountaineering Council; Sacha Rogers and Sarah Ross at Penny Anderson Associates.

Help and advice regarding the development of this PhD concept was kindly provided by Roberta Newbury, Caitlin Rice, Rachel Walton, Adele Metcalfe and Stephen Hoon.

I would like to particularly thank Liz Price for providing vital support at the inception of this study. I express special thanks to Richard Preziosi for extensively guiding this work to its conclusion.

The quality, insight and success of this PhD has been wholly enabled by the extensive lagomorph knowledge, practical wildlife monitoring experience and positive encouragement of Neil Reid at Queen's University Belfast. Many thanks to José Melo-Ferreira at University of Porto, who has adopted the Peak District hare genetic studies into a wider European research program.

I would like to thank for academic support my excellent co-supervisor expert team of Ed Harris, Phil Wheeler, Christian Devenish, Elias Symeonakis, David Mallon, Brad Cain, and Huw Lloyd. I would like to thank for professional technical support: Simon Caporn, Martin Jones, Hannah Mossman, Anna Reuleaux, Anita Hashmi, Tom Hughes, Graeme Fox, Liam Hanson, Fraser Baker, Peter Lawrence, Chris Harrison, Oliver Metcalfe, Harry Marshall, Sarah Scott, Grace Ellison, Xaali O'Reilly Berkeley, Guuske Tiktak, Jade Newton-Youens. Thank you to the wonderful MMU students who contributed to field work and developed their own studies: Isabel Commerford, Jack FitzGibbon, Larissa Masterson; and Lowri Thomas of University of Manchester.

This work has been successful thanks to the support, guidance, access and information provision from external parties. Dave O'Hara and Kate Hanley of RSPB Dove Stone; Tia Crouch, Dave Chandler and Tom Aspinall at Moors for the Future; Stephanie Hinde and Chris Wood at National Trust; Ross Evans at United Utilities; James Crowther at Upperwood House. Thank you to the kind people and organisations who provided hare observation data particularly Debbie Alston of Derbyshire Mammals Group; Derek Whiteley and Val Clinging of Sorby Natural History Society. Other kind organisations are also gratefully acknowledged in the ecological niche model chapter. Further kind practical help or contextual advice came at various times from Fiona Mathews, Mammal Society; Scott Newey, James Hutton Institute; Graham Pettigrew; Alex Barlow of Wildlife Network for Disease Surveillance; F. Naden of Victoria Vets Glossop; S. Green and K. Walsh of Natural England.

I would like to thank for help with field work and logistics: Julien Minshull, Dave Hogg, Caitlin Rice, Andy Oliver, CM Shaw. Especial thanks to Kristina Boyd who flew from Montana over 4,000 miles to see these rare English mountain hares. Thank you to many friends who always expressed well wishes and enquiries regarding the well-being of the mountain hares: Rob Taylor, Dave Ward, JoBo, Ian Wolfendale, Paul and Elaine Fleuriot, Dave and Lindsay Palmer, Zoe Barton, Fay Fitch, Shirley Donnelly, Sylvia Humpherston, Andrew Bradley, Andy Holden.

Thank you to those who kindly shared this eventful journey with a wider audience: Simon Hare and Jennifer Harby at BBC; Lisa Dowd at Sky News; Anna Lombardi at The Times.

Many biologists in Montana and Canada provided great inspiration: Mafalda Ferreira and Marketa Zimova; two successful snowshoe hare specialists of University of Montana. Bear experts helped me on my journey, quietly confessing how they love hares as much as bears: Kate Kendall, Wayne Kasworm, Tom Radandt, Tonya Chilton-Radandt, Kim Annis, Justin Teisberg, Madeline Finley, Amy Macleod.

I express thanks to all the mountain hare citizen science recorders, enthusiasts and well wishers who take their own personal time in noting hare occurrences and sharing those with the wider world. Your efforts and enthusiasm are continually appreciated.

The people who may have most appreciated this endeavour are sadly no longer with us, yet constantly remembered: Geoff King, Dennis Powell, John Hewitt, Derek Yalden, Sabine Bedson.

I extend the deepest gratitude for the friendship and support of Jean Powell.

To the reader

The purpose of mountain hare conservation is mountain hare conservation.

They are a keystone species and will tell you much about what is happening on the uplands.

This thesis then acts as formal submission to Manchester Metropolitan University. Yet the document is intended for a wide range of audiences. The original sponsors were Hare Preservation Trust and People's Trust for Endangered Species and so this thesis is for them. The brief was to provide an independent science based investigation of the conservation status of the mountain hares, no matter what the findings.

This thesis may also be referenced by JNCC, Natural England and Defra to inform the conservation status of Mountain hare (*Lepus timidus*) in England. As at July 2021 there are ongoing evaluations of mountain hares for listing on Schedule 5 of 1981 Wildlife and Countryside Act, and for reporting status under Article 17 of the European Community Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC) S1334 - Mountain hare.

However this document also brings much new natural history information, particularly enabled by recent developments in Geographic Information Systems. The material herein is written in the language of the conservation science community. Barring the rather technical statistical analyses, it may be that much new subject matter is of interest to a wider audience.

Included in the thesis are high level distribution maps. Requests for data or locations cannot be fulfilled. Mountain hares are much loved and yet much persecuted.

Interested readers are welcome to contact me with constructive comments.

carlosbedson@outlook.com *Carlos Bedson* *9 August 2021*

Updated 24 April 2022

List of tables

List of Figures

CHAPTER 1 STUDY INTRODUCTION

Image: The Pleistocene winter white English mountain hare lies exposed by camouflage mismatch
Grinah Stones, Bleaklow, Derbyshire, England, UK. Date: 25th February 2021

Chapter 1 Study Introduction

1.1 Background

1.1.1 Mountain hares across the Northern Hemisphere

Lagomorphs are widespread across the globe. Of these there are pika (*Ochotonidae*), rabbits and hares (*Leporidae*) (Macdonald 2001). They are small or medium sized mammals: vegetation browsers and grazers with long-nosed skulls and "peg" teeth and are coprophages, re-ingesting soft faecal pellets to better digest vegetable matter. Many have specific physiological adaptations for different climates, temperatures, habitats and for predator avoidance (Chapman and Flux 1995; Harris and Yalden 2008). As herbivores they play important ecological roles, browsing vegetation, spreading seeds and recycling nutrients. Lagomorphs form the basis of many predator-prey systems, sustaining raptors and meso-carnivores (Macdonald 2001). They persist through high levels of reproduction and yet suffer high levels of mortality from severe climate fluctuations, food limitation, predation and disease (Chapman and Flux 1995).

Mountain hares (*Lepus timidus*) are a species related to Arctic hare (*L. arcticus*), Alaskan hare (*L. othus*) and snowshoe hare (*L. americanus*) (Angerbjörn and Flux 1995; Chapman and Flux 1995). All are adapted or tolerant to cold snow conditions. They are habitat generalists occupying a number of different ecosystems: tundra, boreal forest, bog, heather uplands and browse very frequently each day upon trees and shrubs, and graze upon grasses, thereby recycling nutrients (Harris and Yalden 2008). Mountain hares have brown summer pelage which turns white in winter, affording them camouflage from predators and insulation against cold (Zimova et al. 2018). They breed rapidly with 3 litters of 1 to 6 leverets per summer and live up to 4 years, though up to 9 years is possible (Angerbjörn and Flux 1995; Newey et al. 2007). They are non-territorial, polygamous, show high fidelity to small home ranges and short natal dispersal ranges (<1km) (Newey et al. 2007; Harris and Yalden 2008). Arctic hares have been shown to journey long distances exceeding 100km in resource-poor environments (Lai et al. 2021). The furthest recorded journey for mountain hare was 200km in

Finland, though distances of 0-4km were more typical, following game stocking (Angerbjörn and Flux 1995).

As prey species, mountain hares have adaptations for predator detection and avoidance: eyes either side of the skull, large ears with good hearing, an ability to hide extremely well in vegetation and strong legs for fast fleeing (Chapman and Flux 1995; Macdonald 2001). They are nocturnal, hiding from predators by day, feeding and socialising mainly during the night (Barret-Hamilton 1910; Flux 1990). Despite such defences, mountain hares comprise an important part of predator diets: Golden eagle (*Aquila chrysaetos*), buzzard (*Buteo buteo*), fox (*Vulpes vulpes*), stoat (*Mustela erminea*), weasel (*Mustela nivalis*) (Flux 1990). Apart from potential competition with *L. europaeus*, mountain hares do not compete for resource with any other species: neither deer, sheep, rabbits nor grouse (Newey et al. 2007).

In many geographies mountain hares are hunted by humans. Published studies show hunting bag records going back more than 150 years: Scotland since 1900 (Aebischer 2019); Ireland since 1846 (Reid et al. 2007) Sweden since 1960 (Thulin 2003). Mountain hares in Scotland were traditionally shot for sport on grouse moor estates. Gamebag counts served as indices of population cycles. No records were kept of mountain hare gamebags in England (Aebischer et al. 2011; Bedson *In litt.*).

Because of their wide distribution across Eurasia, mountain hares have been categorised by IUCN as "Least Concern" (Smith and Johnston 2019) though populations are fragmented. There are distinct clades of mountain hares, formed by ancient reticulated expansions and retractions across Europe, following the progressions of glacial ice extents. Migrations and consequent isolation of some populations have resulted in the evolution of fifteen morphologically distinct relict subspecies, in different geographical areas and various elevations including: *L. t. timidus* (Sweden); *L. t. varronis* at 3,700m a.s.l. (Alps); *L.t. scoticus* (Scotland); *L.t. hibernicus* at sea level (Ireland) (Thulin 2003); with further sub-species in Russia, China and Japan (Angerbjörn and Flux 1995; Hughes et al. 2006).

Mountain hare populations are often stable, though may cycle over 4 to 10 years, influenced by gastro-intestinal parasites reducing fecundity and general health or with populations affected by weather patterns (Newey et al. 2007). Extensive threats to mountain hares include competition and hybridisation with European brown hares (*L. europaeus*) (Thulin 2003); severe weather or long-term oscillations hampering immediate or long-term vegetation productivity, causing food shortages and starvation (Angerbjörn and Hernquist 1984; Reid et al. 2021); climate change driving range shifts (Leach et al. 2015); and population collapses through virulent diseases, and where transmission may be assisted by high densities (Newey et al. 2007; Buehler et al. 2020). Predation upon mountain hares may interact with, rather than be additive to, other natural causes of their mortality and population dynamics (Chapman and Flux 1995; Newey et al 2007).

There exists a thorough body of knowledge of mountain hare zoology and ecology, notably: Barrett-Hamilton (1910); Flux (1970); Angerbjörn and Flux (1995); Harris and Yalden (2008). Most perspectives on mountain hare population dynamics come from the early days of modern conservation science examining broad ecological drivers (e.g. Hewson 1965; Hewson 1990). The more recent population studies are different; they tend to compare time series abundance estimates with effects of land use, rather than wider ecological drivers of populations (Watson and Wilson 2018; Aebischer 2019; Hesford et al. 2019). As suggested by Newey et al. (2007), there is no demographic study in the manner of Krebs et al. (2001) which comprehensively describes the population dynamics of the Yukon snowshoe hare, a key component of North American boreal forests. The Yukon Kluane study describes snowshoe hare demographics, age and sex structures, immigration, emigration, survival rates, the interaction effects of both predation and food supply, all influencing abundance cycles.

1.1.2 Mountain hares of the British Isles - Scotland

Barrett-Hamilton (1910), Thulin (2003) and Hamill et al. (2006) postulated that during the Pleistocene, mountain hares reached Scotland from northern Scandinavia. Eventually the ice receded; the Scottish population were isolated from continental Europe. It appears there was a severe reduction to the population in Scotland ~500 generations ago (we may speculate ~ AD 500), though the cause is unknown (Hamill et al. 2006). Indeed this ancient provenance and population bottleneck appears to have resulted in *L. t. scoticus* having the lowest genetic diversity of all mountain hare species across Europe (Hamill et al. 2006).

In the legacies of natural history writings, the mountain hares of the British Isles are deemed to have endured upon the coldest most inhospitable upland landscapes, receiving tacit human admiration (Ewart Evans 1972). The earliest mention of mountain hares may be from the twelfth century, the Sagas describing Harold of Norway visiting the Orkneys and hunting hares; the first zoological description may be from White in 1769 (Barrett-Hamilton 1910). From Victorian times, mountain hares became an important aspect of Scottish sport shooting heritage (Barrett-Hamilton 1910).

Since the mid-1800's, possibly much earlier, landowners commenced burning heather for grouse rearing (Bonn et al. 2009). This created an ideal habitat upon which mountain hares thrive, feeding on young pioneer heather shoots and hiding in taller undergrowth (Stoddart and Hewson 1984). Consequently numbers in Scotland increased dramatically (Hamill et al. 2006). The species now ranges across approximately 50% of the entire 79,000km^2 of Scotland (Hesford et al. 2020). It was frequently noted that mountain hare numbers on heather grouse moors exceeded 200km^{-2}, being some of the very highest densities in Europe (Angerbjörn and Flux 1995; Harris and Yalden 2008). Elsewhere in Scotland upon bog habitats or where vegetation overlaid nutrient poor rocks, densities were much lower ~ 3km^{-2} (Watson and Hewson 1973; Newey et al. 2007).

In more recent times there was a perception that mountain hares hosted ticks carrying louping ill virus, harmful to grouse (Harrison et al. 2010). With that came extensive culling. Forestry protection was also a motivation to shoot mountain hares (Patton et al. 2010). Some areas with high populations experienced large losses that never recovered (Patton et al. 2010; Watson and Wilson 2018).

From 1992 the mountain hare was assigned to Annex V of the EC Habitats Directive as a species "of community interest whose taking in the wild and exploitation may be subject to management measures" and requiring formal reporting to the EU (JNCC 2019). From the early 2000's, innovations for monitoring mountain hares were continually introduced, yet no formal census method was adopted (Newey et al. 2018; Werritty et al. 2019). Meanwhile the overall population estimate for Scotland reduced from 350,000 (JNCC 2007) to 135,000 mountain hares and with conservation status categorised as "unfavourable" (Mathews et al. 2018; JNCC 2019). With increasing conservation and public concerns about the effects of culling, legal protections were introduced in Scotland (Scottish

Parliament 2019). New monitoring schemes were incepted, involving wildlife agencies, landowners and the general public, co-ordinated by Scottish Natural Heritage and with Game and Wildlife Conservation Trust (Chapman 2020). Mountain hares have became a subject of tourism, a symbol of both wildlife persecution and conservation, and are used by stakeholders to justify complex and contrary political agendas (OneKind 2017; GWCT 2019).

1.1.3 Ireland

In Ireland, the subspecies *L. t. hibernicus* has remained since the Pleistocene era (Reid 2018). It has a different genetic background to *L. t. scoticus*, appearing to have reached Ireland via France and Cornwall (Hamill et al. 2006; Hughes et al. 2006) and with its own unique mtDNA haplotypes (Hughes et al. 2006). *L. t. hibernicus* has different morphology to other *L. timidus* subspecies, notably pelage which stays brown throughout the year, and is much larger in size (Reid 2018). The population is estimated to cover a range of 60% of the ~70,000 km^2 of Ireland with low densities of 3 hares km^{-2} and overall abundance of ~223,000 individuals (McGowan et al. 2019).

The population has suffered an 80% decline as a result of changes to climate oscillations and agricultural intensification (Reid et al. 2021) and is affected by hunting and coursing (Reid 2018). Since the 1970's, there has also been an increasing threat to the security of *L. t. hibernicus* arising from an introduced and expanding population of *L. europaeus* (Caravaggi et al. 2014). Professional widespread population monitoring of *L. t. hibernicus* for the Northern Ireland Environment Agency commenced in 2002 (Reid and Montgomery 2010) and continued with the National Parks and Wildlife Service (McGowan et al. 2019).

1.1.4 England

The mountain hare may have first existed in England during the Wolstonian glaciation (11,000 BP), a member of a range of steppe fauna including wolf (*Canis lupus*), reindeer (*Rangifer tarandus*), woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), Arctic fox (*Vulpes lagopus*), beaver (*Castor fiber*), bear (*Ursus arctus*) and bison (*Bison priscus*) (Yalden 1999). Barrett-Hamilton (1910) intriguingly refers to a species *L.variablis anglicus*, as "distinctly more primitive than the more northern such as *L. t. scoticus* ...(though) in the direct ancestral line of *L. hibernicus*...the better plan would be to treat is as a species sub-species". This definition did not endure throughout the subsequent literature. In the latter Pleistocene period, mountain hares were important prey for human hunters. With the final retreat of the glaciers, the mountain hares of England died out 6000 BP (Yalden 1999).

The mountain hare was then absent from English ecosystems during the bronze ages, Roman times, the Middle Ages, the later eras of the great Kings and Queens. It is missing from most of English natural history, rural land culture, the collective lexicon and literature.

In Victorian times far sighted landowners facilitated the translocation of mountain hares from Scotland to the uplands of Lancashire, Yorkshire and Derbyshire (Barrett-Hamilton 2010; Coward 1910; Stubbs 1929; Hewson 1956). At Upperwood House, the incumbent farmer described how his forefathers brought mountain hares in crates on the train, from Perthshire to Oldham (Bedson personal comms). These nineteenth century aspirations were to add a touch of Scottish sporting wildlife to the English grouse moors. The translocations to Lancashire and Yorkshire endured. Yet just further south of the Peak District, mountain hares Staffordshire were shot out (Barret-Hamilton 1910) and some groups nearby also seemed to just disappear (Hewson 1956; Yalden 1999). Other mountain hare translocations in Snowdonia, Brecons, Lake District and Cheviots persisted yet only to the 1970s (Mallon 2001).

The mountain hares were seen to occupy similar habitats as in Scotland: bogs, upland heather moors, a clear association with grouse moors. Amidst rugged areas of the Peak District, numerous hares would be seen amongst cliffs and rock fields. The population never migrated such as north beyond Rishworth, indicating that towns, road systems and the lack of contiguous heather moorland were barriers, confining the population. (Mallon 2001).

For a reference of size and scale Mathews et al. (2018) provide a "top-down" estimate of 2,500 animals upon 250km^2 of uplands. Numbers have seemed stable though with some substantial declines during severe winters as 1946-47, 1962-63 and 1986 (Mallon et al. 2003). There was some perception of range overlap with *L. europaeus* (Yalden 1971); yet scant evidence of interspecies competition. Genetic structure and hybridisation have not been known. Other listed threats included wildfires and roadkill (Mallon 2001; Mallon et al. 2003).

1.1.5 Peak District mountain hare conservation monitoring

Being the misplaced Arctic white animal upon the cultured hillsides of England, mountain hares attracted interest from the natural historians of the day. Field based population studies and estimates were provided by Hewson (1956), Yalden (1971, 1984), Mallon (2001), Mallon et al. (2003), the latter derived from the PhD thesis of Wheeler (2002). The local Sorby Natural History Society provided annual count estimates (Clinging 2003). There was insufficient monitoring to discern any population cyclicity.

Yet in some circles there was a perspective that because mountain hares in the Peak District were reintroduced i.e. not native, they did not merit study nor conservation. Whatever the hares' provenance, the importance and utility of wild mammal herbivores to assist biological sustainability of ecosystems are self-evident (Krebs 2001). Such holds true as this herbivore is quasi-native: a naturally consistent component of peatland ecosystems, neither competing for, nor harming, the wider natural resource base.

What is then the bio-economic value of the Peak District mountain hares? Referencing findings from this study, the population ranges over ~360km^2 with abundance of ~3,500 animals. This is approximately ten tons of biomass, which self-renews every 3 to 4 years, provides sustenance to other animals, and recycles nutrients for soils. If society wished to provide such quantity of game biomass on the moors for purposes of maintaining ecosystem functionality, herbivores and predator-prey food webs, the comparable annual cost might be ~£60,000 (Dorset Meat Company 2022: market retail value £17/hare as of 04/04/22), plus welfare and veterinary expenses. Hence the ecological and economic value of these mountain hares is considerable. Mountain hares provide additional societal, cultural, tourism, scientific and educational benefits.

Notwithstanding, there has been very little formal monitoring. This is remarkable as the recommendation from the Joint Nature Conservation Committee (UK BAP 2008) was: *"Actions as identified by experts...5: Continue to monitor the mountain hare population in northern England"*.

Scottish and Irish wildlife agencies monitor their mountain hares. The English wildlife agencies have not. Descriptions from Natural England regarding Sites of Special Scientific Interest (SSSI's), provide records of flora and fauna present. Yet of 246 SSSI's which comprise the mountain hare range, only two SSSI's possess any records at all of this species (Natural England 2020). There is no other professional monitoring scheme or capability in England.

1.1.6 The importance of European brown hares

The European brown hare (L. europaeus) must be mentioned: it is congeneric with mountain hares. This hare has similar phenology and is slight larger. However it does not turn white in winter. It is associated with pastoral and agricultural landscapes and is a grassland specialist and does not eat heather. (Harris and Yalden 2008) In habitats where the two species meet, brown hares have often outcompeted or hybridised with mountain hares. Brown hares represent one of the leading threats to mountain hare persistence (Thulin 2003). This species also receives much attention in the studies you are about to read.

1.2 Thesis Aims

The main aims of this PhD thesis were to measure fundamental population attributes of the isolated group of mountain hares within their bounded upland natural environment of the Peak District, England. This was achieved by taking field observations and collecting genetic material, consulting natural history sources and gathering citizen science records, assembling geographic information sources and environmental maps. These were combined and analysed to quantitatively describe the distribution, abundance and genetic structure of the population. Findings can be used to inform conservation assessments and to model extinction risk.

1.2.1 Objectives and focus areas

Chapter 2	Describe the distribution extent and ecological niche requirements for the mountain hare population and within that same extent for brown hares
Chapter 3	Develop and compare census methods to determine which are practical and provide statistically reliable estimates
Chapter 4	Estimate the population size, measure annual changes, stratify by habitat
Chapter 5	Determine genetic diversity and population structure. Identify level of hybridisation with brown hares
Chapter 6	Future monitoring and conservation imperatives

1.3 Thesis structure

Chapter 2

Splitting hares: Current and future ecological niches predicted as distinctly different for two congeneric lagomorphs

The objective was to identify the ecological niche and the geographic range of mountain hares now and in the future and comparing to brown hares, their major competitor. This would predict the climate, topography, habitat and land uses which attract, influence or deter mountain hares, and also predict the same for brown hares. The study drew upon 14,000 citizen science records of mountain and brown hare observations, combined these with ecological data, and used predictive algorithms and models to describe the current and future ecological niches of both species.

Chapter 3

Estimating density of mountain hares using distance sampling: a comparison of daylight visual surveys, night-time thermal imaging and camera traps

This study contributed to the ongoing development of census methods for mountain hares. The wildlife science community has held ongoing doubts regarding the credibility of daytime surveys of mountain hares. This elusive nocturnal creature lies up by day, hiding sometimes even until the observer literally steps upon them, making surveys difficult. This challenge is especially compounded by the rugged characteristics of Peak District habitats which are wild, experience bad winter weather and are difficult for human surveyors to access. The intention was to innovatively compare three survey methods of monitoring mountain hares. Each were tested and then assessed in terms of their practicality and their statistical reliability and plausibility.

Chapter 4

Highest densities of mountain hares (*Lepus timidus*) associated with ecologically restored bog but not grouse moorland management

The objective was to provide an abundance estimate and foundation for long term monitoring. In simple terms this would report the number of mountain hares which conservationists reference when assessing the abundance, safety or otherwise of this mammal population. Over five years spring-season daytime distance sampling surveys were conducted. These achieved ~2,000 observations, enabling thorough robust analyses and estimation of densities. During surveys there were obvious differences of density by habitats and land uses. Accordingly these were assigned to descriptive categories. The population estimates were then stratified by year and by habitat class, shedding light upon population dynamics and anthropogenic influences.

Chapter 5

Genetic structure of English hare species

This study investigated the genetic diversity of mountain hares and brown hares living in close proximity. Of all hare species across Europe, those considered as having the lowest genetic diversity were the mountain hares in Scotland. The mountain hares in the Peak District were their progeny. Therefore it was important to investigate founder effects, bottlenecks, population cyclicity as affecting genetic diversity. The local road and reservoir systems might also provide barriers to gene flow. Hybridisation with European brown hares was also a risk. To investigate these matters, genetic material was collected from 253 roadkill and field carcass flesh samples. In the laboratory, 16 microsatellites were used, to genotype individuals. Analysis provided an assessment of the genetic structure for both mountain and brown hares, possible hybridisation and determined whether the mountain hare groups showed any genetic population structure.

Chapter 6

Future monitoring and conservation imperatives

Recommendations are provided for ongoing monitoring of Peak District mountain hares. Some ideas are suggested for conservation interventions.

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CHAPTER 2 SPLITTING HARES: CURRENT AND FUTURE ECOLOGICAL NICHES PREDICTED AS DISTINCTLY DIFFERENT FOR TWO CONGENERIC LAGOMORPHS

Image: Hypothetical meeting of European brown hare and mountain hare.
Two hare photos were kindly merged by S. Koppelaar. The brown hare was photographed on heather moorland at Park Hall, Hayfield, Derbyshire, England, UK. Date: 17th June 2020. I do not recall whence came my accompanying mountain hare photograph.

Chapter 2

Splitting hares: Current and future ecological niches predicted as distinctly different for two congeneric lagomorphs

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Publication Reference

This chapter is published at:

Bedson, C.P.E., Devenish, C., Symeonakis, E., Mallon, D. Reid, N., Harris, W.E. & Preziosi, R. 2021b. Splitting hares: Current and future ecological niches predicted as distinctly different for two congeneric lagomorphs, Acta Oecologica, 111 https://doi.org/10.1016/j.actao.2021.103742.

Acta Oecologica 111 (2021) 103742

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Splitting hares: Current and future ecological niches predicted as distinctly different for two congeneric lagomorphs

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ARTICLE INFO

Keywords:
Climate change
Diet
Ecological niche model
Interspecies competition
Lepus europaeus
Lepus timidus

ABSTRACT

The congeneric lagomorphs *Lepus timidus* and *L. europaeus* share allopatric distributions in many areas of Europe characterised by competitive exclusion and hybridisation. We investigated prospects for these species under climate change in northern England uplands. We created ensemble models predicting niche realisation for these species, influenced by abiotic and biotic factors, estimating niche overlap in geo-environmental space. The two species occupy distinctly different niches, influenced more by vegetation preferences than climatic differences. The current climate niche for *L. timidus* featured higher elevations with cooler temperatures and 168 km^2 range extent. Its current habitat niche scale was larger at 269 km^2, comprised entirely of upland dwarf shrubs: heather, cotton grass, moorland grasses. By contrast, the current climate niche predicted *L. europaeus* occupying lowland areas with a milder climate and range extent of 252 km^2. Its current habitat niche was also greater, 401 km^2, being mostly improved grassland. Competition was presently limited. The current niche predictions showed very little geographic overlap between the species. Niche overlap measured by Schoener Index was low: current climate niche 0.16; current habitat niche 0.07. The future climate niches for 2050 (IPCC RCP2.6), predicted *L. timidus* range contracting to 19 km^2, on hilltops and *L. europaeus* range expanding to 765 km^2. Consequently *L. timidus* range would be wholly within the *L. europaeus* range. In many contact zones throughout Europe, *L. europaeus* outcompetes *L. timidus*; however, in the Peak District their distributions are largely distinct. Future replacement of *L. timidus* by *L. europaeus* may be engendered by dietary convergence, should a warmer climate cause a transition of upland dwarf shrub vegetation to grasses.

1. Introduction

1.1. Lagomorph niches and conservation status

Ecological niche models often predict opposing patterns of distribution and survival for two European lagomorph species: the mountain hare (*Lepus timidus)* and the European brown hare (*Lepus europaeus)* (Acevedo et al., 2012; Bisi et al., 2015; Leach et al. 2015a, 2015b, 2016, 2017). Despite differences in physiological adaptations and requirements, they often share distributions and compete for resources (Thulin 2003; Jansson et al., 2007). As herbivores both species are important to ecosystems for recycling vegetation nutrients, and are prey for carnivores and raptors (Harris and Yalden 2008; Barbar and Lambertucci (2018).

With a circumpolar distribution, *L. timidus* is adapted for cold temperatures and snow in hilly or mountainous areas, and is a habitat generalist, living upon boreal forest, mires, heaths and moorlands (Angerbjörn and Flux, 1995; Harris and Yalden 2008). The IUCN Red List status is Least Concern and population status is stable for *L. timidus* (Smith and Johnston 2019). Some populations are vulnerable, being quasi-cyclic (Newey et al., 2007) or limited by parasites, predation or starvation (Smith and Johnston, 2019). Climate change scenarios suggest *L. timidus* can be affected by changes in long-term weather patterns (Reid et al., 2021) and will move to higher latitudes and elevations (Anderson et al., 2009; Hof et al., 2012; Leach et al., 2015b), its range in Europe reducing by 70% (Acevedo et al., 2012).

By contrast *L. europaeus*, occupies temperate climate zones across Europe, is a habitat specialist, inhabiting grassland and agricultural

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2.1 Abstract

The congeneric lagomorphs *Lepus timidus* and *L. europaeus* share allopatric distributions in many areas of Europe characterised by competitive exclusion and hybridisation. We investigated prospects for these species under climate change in northern England uplands. We created ensemble models predicting niche realisation for these species, influenced by abiotic and biotic factors, estimating niche overlap in geo-environmental space. The two species occupy distinctly different niches, influenced more by vegetation preferences than climatic differences. The current climate niche for *L. timidus* featured higher elevations with cooler temperatures and 168km^2 range extent. Its current habitat niche scale was larger at 269km^2 , comprised entirely of upland dwarf shrubs: heather, cotton grass, moorland grasses. By contrast, the current climate niche predicted *L. europaeus* occupying lowland areas with a milder climate and range extent of 252km^2. Its current habitat niche was also greater, 401km^2, being mostly improved grassland. Competition was presently limited. The current niche predictions showed very little geographic overlap between the species. Niche overlap measured by Schoener Index was low: current climate niche 0.16; current habitat niche 0.07. The future climate niches for 2050 (IPCC RCP2.6), predicted *L. timidus* range contracting to 19km^2, on hilltops and *L. europaeus* range expanding to 765km^2. Consequently *L. timidus* range would be wholly within the *L. europaeus* range. In many contact zones throughout Europe, *L. europaeus* outcompetes *L. timidus;* however, in the Peak District their distributions are largely distinct. Future replacement of *L. timidus* by *L. europaeus* may be engendered by dietary convergence, should a warmer climate cause a transition of upland dwarf shrub vegetation to grasses.

Keywords
Climate change; diet; ecological niche model; interspecies competition; Lepus europaeus; Lepus timidus

2.2 Introduction

2.2.1 Lagomorph niches and conservation status

Ecological niche models often predict opposing patterns of distribution and survival for two European lagomorph species: the mountain hare (*Lepus timidus)* and the European brown hare (*Lepus europaeus)* (Acevedo et al.; 2012; Bisi et al. 2015; Leach et al. 2015a; Leach et al. 2015b; Leach et al. 2016; Leach et al. 2017). Despite differences in physiological adaptations and requirements, they often share distributions and compete for resources (Thulin 2003; Jansson et al. 2007) . As herbivores both species are important to ecosystems for recycling vegetation nutrients, and are prey for carnivores and raptors (Harris and Yalden 2008; Barbar and Lambertucci (2018).

With a circumpolar distribution, *L. timidus* is adapted for cold temperatures and snow in hilly or mountainous areas, and is a habitat generalist, living upon boreal forest, mires, heaths and moorlands (Angerbjorn & Flux 1995; Harris and Yalden 2008). The IUCN Red List status is Least Concern and population status is stable for *L. timidus* (Smith & Johnston 2019). Some populations are vulnerable, being quasi-cyclic (Newey et al. 2007) or limited by parasites, predation or starvation (Smith & Johnson 2019). Climate change scenarios suggest *L. timidus* will move to higher latitudes and elevations (Anderson et al. 2009; Leach et al. 2015b), its range in Europe reducing by 70% (Acevedo et al. 2012).

By contrast *L. europaeus*, occupies temperate climate zones across Europe, is a habitat specialist, inhabiting grassland and agricultural environments, favouring cereal, root crops or grasses (Tapper & Yalden 2010). For *L. europaeus* the IUCN Red List status is Least Concern and population status is recorded as decreasing due to agricultural intensification (Hackländer and Schai-Braun 2019). Recently some populations have revived, enabled by agricultural improvements (Viviano et al. 2021). Forecasts for *L. europaeus* under climate change suggests little response (Bisi et al. 2015) or range expansion (Leach et al. 2015b; Caravaggi et al. 2017).

Together, these two species form a recognised model of interspecific competition: a mechanism which acts as a determinant of species distributions (Elton 1927). Competition frequently involves one species exploiting food or shelter resources, much more effectively than another. To survive, the less effective species must either move to a different habitat or adjust its diet away from the competitor (Krebs 2001). Historic studies have reported large areas of *L. timidus* range being superseded by *L. europaeus* as a result of competition for space and resources or interspecific hybridisation with introgression, e.g. populations in Sweden and Russia (Thulin 2003), and Ireland (Caravaggi et al. 2014; Caravaggi et al. 2017). Where different habitats overlap, *L. timidus* maintains high elevations and deep forests, feeding on woody browse and excludes *L. europaeus.* Alternatively *L. europaeus* maintains its dominance over optimum grassland habitats, preferring a diet of soft greens, and may displace *L.timidus* (Flux and Angermann 1990; Thulin 2003; Jansson and Pehrson 2007). However the two species may exist in sympatry, such as in Italy where they share a spatially overlapping elevation gradient, though occupying different habitats: *L. europaeus* from 500m to 1500m a.s.l. upon arable land or sparsely vegetated areas; *L. timidus* from 1300m to 3000m in areas of dwarf mountain pine (Bisi et al. 2013; Bisi et al. 2015; La Morgia & Venturino 2017; Naldi et al. 2020) or parapatry as in Sweden where heath hare (*L. t. sylvaticus*) ranges lie entirely within those of *L. europaeus* (Thulin et al. 2021).

The species *L. timidus* is native to Great Britain though died out in England around 6000 BP (Harris & Yalden 2009) though persisted in Scotland where it is now is associated with upland heather moorlands (Hewson 1984; 1989). Because of heavy culling on some moors (Watson & Wilson 2018) and a large decline in abundance, the conservation status of the UK *L. timidus* population was downgraded to ‘unfavourable-inadequate’ (JNCC 2019a).

In England *L. timidus* was reintroduced through translocations from Scotland by sporting landowners in the 1870s and now occupies some 250km^2 of Peak District uplands. Population density has been estimated at 10 hares km^{-2} (Mathews et al. 2018). It is isolated by 300km from its founder population. Surveys described *L. timidus* preferring habitats of heather, cotton grass (*Eriophorum* spp.), moorland grasses (*Deschampsia flexuosa, Nardus stricta, Festuca* spp.*, Juncus* spp.) and dwarf shrubs (*Empetrum nigrum, Vaccinium myrtillis*) (Mallon 2003).

By contrast *L. europaeus* is thought to have been introduced to Great Britain during the Bronze Age (Thulin 2003) and certainly by Roman times (Harris and Yalden 2008) and now occupies arable landscapes. Once widespread, numbers have decreased by 80% since 1880 as a result of game-shooting and intensive farming practices, the last conservation assessment recording the species as in decline (UK BAP 2007). There have been no recent assessments (JNCC 2019b). Around the Peak District extensive surveys of *L. europaeus* during 2011-12 (Bolton 2013) recorded density amongst agricultural landscapes at 1.7 hares km^{-2}, though not in upland habitats. In the surrounding vicinity of Cheshire, Lancashire and Derbyshire, this population may have facilitated inward and outward migration (Bolton 2013; Mathews et al. 2018).

Within the UK competition between these two species has received little attention. Hewson (1976a) reported in Scotland that *L. timidus* maintained dominance upon heather moorland when *L. europaeus* was present. Within the Peak District, Yalden (1971) recorded a range overlap between *L. timidus* and *L. europaeus* between elevations of 280 to 500m; a rough boundary between arable and moorland ecosystems. The Peak District presents an ideal model environment, to provide an important understanding of competitive dynamics between these two species (Thulin 2003; Smith and Johnston 2008).

2.2.2 Study objectives

Niche model theories describe the conditions within which species maintain populations at different locations (Franklin 2009; Peterson et al. 2011). Models suggest species exist in environments having combinations of abiotic factors, topography and climate, that enable physiological survival i.e. the fundamental niche (Guisan and Zimmerman 2000); also described as the potential niche (Sillero 2011); or the climate / geomorphological niche (Peterson et al. 2011) and it is often considered that species express such preferences over large scales (countries or continents). Species occurrence may then be facilitated, constrained or "filtered" by biotic factors: food and shelter resources, competitors, predators, parasites, human influences, this being the realised niche (Guisan and Zimmerman 2000; Sillero 2011); the occupied or biotically reduced niche in the terms of Peterson et al. (2011) and which may be conventionally regarded as habitats (Krebs 2001: 66). However filtering processes may not always act in such a formulaic sequential hierarchy (Guisan et al. 2017: 23) and ecological or stochastic processes may alter species distribution in unexpected ways. Statistical models reference occurrence records, combined with environmental variables, to explain how species occupy these niches (Guisan et al., 2017) and the extent to which similar species co-exist together (Broennimann et al., 2012). Such evaluations assess the sustainability of populations and prompt monitoring, legal protections, revision of land uses, identification of species invasions, reintroductions or translocations, or warnings of future threats (Franklin 2009).

The aims of this study were to:

1) Predict and compare the current climate niche and current habitat niche of both *L. timidus* and *L. europaeus* in northern England. We hypothesised that *L. timidus* would be associated with high elevations, a cold climate, upland heather moorland and bog vegetation and *L. europaeus* low elevations, warmer climate and grassland or woodland (Tapper & Yalden 2010);

2) Measure the extent of overlap between the two species in geographic and environmental space, to estimate the degree of competition. We did expect some competition, though were unsure how strong this might be;

3) Forecast the future climate niche for the year 2050. We anticipated that with warming climate, *L. timidus* would move to higher elevations, reducing its range. For *L. europaeus* we had no specific expectation.

2.3 Materials and methods

2.3.1 Study Area

The study area encompassed the Peak District National Park, Northern England (Figure 2.1). The landscape is dominated by peat uplands with vegetation of upland heath, dwarf shrubs including berries, bog grasses and mosses and grasslands. (Anderson & Shimwell 1981). Topography consists of plateau-like hills, ranging up to 631m (OS Explorer Map 1 (2015). The uplands are surrounded by improved grassland areas, agriculture and cities.

2.3.2 Species records

Observations of species came from citizen-science sources, provided by walkers, wildlife enthusiasts, natural historians, landowners and environmental experts, sent by paper, post, email or mobile phone apps to one of ten relevant regional or national biological recording centres (BRC's). The BRC's then provided to us records from 2001 to 2018 for *L. timidus* (8,666 records) and *L. europaeus* (5,994 records) (see Hare Data Sources). These records gave species locations from which to derive environmental data, define the study extent and provide sufficient sample and prevalence sizes for modelling (Guisan et al. 2017).

To prepare the data set we considered sources of bias including autocorrelation, pseudo-replication, duplication or observer effects (Guisan et al. 2017). Within the records we assumed correct identification of species, except discarding 5 *L. timidus* records found >10km from the study extent as mis-identifications. We kept observations recorded to the nearest 100m, excluding records accurate only to 1,000m. We used kernel density plots to assess occurrence patterns for 2001 to 2018. For *L. timidus* in particular, these showed strong annual fluctuations, with a marked nadir during 2013 (Figure S1), less so for *L. europaeus* (Figure S2). We regarded likely causes as differences of observer effort, though ecological factors were possible. Indeed fifty percent of *L. timidus* records were contributed by the late Professor Derek Yalden, until he passed away in 2013 (Table S1). To mitigate for observer effort, maintain relevance to contemporary environmental data, and alleviate possible effects of hare population dynamics (Newey et al. 2007), we then used records for the last ten years.

To reduce duplication or autocorrelation, we discarded records occurring within 100m of each other using function [ecospat.occ.desaggregation] in R package 'ecospat' (Di Cola et al. 2017). Thus the final data set consisted of 1,690 *L. timidus* and 265 *L. europaeus* records (Figure 2.1). Of these 4% *L. timidus* and 30% *L. europaeus* records were on or within 100m of roads and of which less than 8% of records were roadkill. We acknowledged that using observations from roads might provide bias. It is unclear whether roads serve as a deterrent (Buckland et al. 2015) or attractant (personal observations) to lagomorphs. With the vast majority of records being submitted by eminent natural historians (Table S1), we otherwise accepted the slight risk of species mis-identification, acknowledging this might lead to minor modelling errors (Clare et al. 2019).

We defined potential pseudo-absences as any locations without a record for the respective species at the scale of 1 hectare. We opted for ratios of 50/50 presence / absence, generating 1,690 (*L. timidus*) and 265 (*L. europaeus*) pseudo-absence records. This ensured prevalence was above minimum sample sizes and ratios affecting modelling errors (Jimenez-Valverde et al. 2009; Guisan et al. 2017) and ratios would not influence the accuracy measure kappa, with TSS and AUC unaffected (Allouche et al. 2006). We restricted placement of pseudo-absence locations as randomly within a shape determined by designating, overlapping and dissolving 2000m circles around each species presence point, using R package 'dismo' using functions [circles] and [randomPoints] (Van Der Wal et al. 2009; Hijmans et al. 2017). Thus analysis utilised a randomly generated 1-ha scale grid with presence and absence points and environmental data per 1-ha.

We calculated a minimum convex polygon (MCP) of 639km^2 based upon *L. timidus* BRC records and only employed *L. europaeus* records which occurred within this MCP. To account for environmental influences at MCP edges, we added a 2km buffer, excluding water and urban features, to create a study extent of 805km^2. This extent therefore encompassed the northern Peak District uplands which was the known range of *L. timidus*. By contrast *L. europaeus* could disperse in and out of the study area from surrounding populations. We assumed both hare species were at equilibrium with environmental conditions. Hares exhibit short natal dispersal ranges and fidelity to small home ranges

(Harris & Yalden 2009; Tapper & Yalden 2010). We assumed hare records were representative of home ranges and habitat utilisation.

2.3.3 Environmental parameters

We assessed environmental factors hypothesised to influence occurrence of *L. timidus* and *L. europaeus*. Predictor variables were prepared within ArcMap 10.6.1 (ESRI, USA) and R (R Core Team 2011) referencing Bivand et al. 2013; Wegmann et al. 2016; Guisan et al. 2017.

Current climate niche predictors were based upon climate and topography. Climate predictors were the WorldClim set of metrics (Fick & Hijmans 2017): temperature, rainfall and radiation. These were downloaded at 1km scale, resampled using bilinear interpolation with the ArcGIS (ESRI, USA) resampling tool, providing smoothed 1-ha size values. Topography predictors were derived from OS 50m digital terrain model (Digimap 2019), used to calculate elevation, slope and aspect values. In addition the uplands contained micro-topographical features: extensive networks of peat gullies, anthropogenically caused by acid rain erosion (Bonn et al. 2009). These were used by *L. timidus* for shelter and movement. Gullies information was sourced as OS Vector data (Digimap 2019) with a 50m buffer applied.

Current habitat niche predictors consisted of vegetation providing food and shelter resources, roads indicating human activity, and the presence of the competitor species. Vegetation productivity indices were derived from Landsat 8 scenes (Path203/Row023, 4th May 2016), downloaded using the EarthExplorer tool of the United States Geological Survey (USGS; www.earthexplorer.usgs.gov), and resampled to 1-ha. Bands were subject to signal enhancement, to represent Normalised Difference Vegetation Index (NDVI), Normalised Difference Water Index (NDWI), Simple Ratio (SR) and Soil Adjusted Vegetation Index (SAVI). Bands were analysed in R with at-sensor reflectance and tasselled cap transformation, representing vegetation brightness, greenness and wetness (Wegmann et al. 2016; Guisan et al. 2017). To assess the importance of habitat and vegetation types, we also created a detailed bespoke landcover map, combining the UK landcover map (Rowland et al., 2017), with data from aerial images (Digimap 2019). From the UK landcover map (Rowland et al., 2017) we included polygons for pertinent lowland categories: arable, broadleaved or coniferous woodland, improved grassland (managed or unmanaged pasture comprising *Lolium* spp and clover (*Trifolium repens),* used for sheep farming), inland rock, neutral grassland, suburban, urban, or water. However those UK landcover map (Rowland et al. 2017) types which represented upland areas (64% of the study extent) appeared homogeneous e.g. bog. Such areas consist of ecotones of young and mature heather (*Calluna vulgaris*), cotton grass (*Eriophorum* spp.), moorland grasses (*Nardus stricta, Deschampsia flexuosa, Festuca* spp.*, Molinia caerulea* etc*)*, and berries (*Empetrum nigrum, Vaccinium* spp.), pertaining to *L. timidus* food and shelter (Hewson 1962, 1989). Therefore we assembled new map data to represent these vegetation categories by supervised classification of aerial images (Wegmann et al. 2016) taking 10,527 samples, supported by 440 ground-referenced photographs, using random forest classification to create an upland vegetation raster, with 82% accuracy (Table S2; Figure S3). Each hectare was classified to its largest single dominant vegetation type, though other types might have been present. The upland vegetation raster and lowland polygons were then combined to one single map. Individual landcover classes were used as binary categorical predictors. Road information was sourced as OS Open Roads data (Digimap 2019) with a 50m buffer applied. Maps of historical *L. timidus* and *L. europaeus* records suggested a small range overlap, therefore we included the presence of each species as a predictor to the other.

Future climate niches were projected using the IPCC Fifth Assessment Report Coupled Model Intercomparison Project Phase 5 (Taylor et al. 2009) future climatic data for the Representative Concentration Pathway (RCP) 2.6 for 2050 (averaged across 2041–2060) downloaded from WorldClim at 1km^2 grid cell resolution and resampled with bilinear interpolation to 1-ha scale. RCP 2.6 indicates a mean average global temperature increase of 2°C by 2050. Variables were averaged across five Global Circulation Models (GCMs), CNRM-CM5, GFDL-CM3, GISSE2-R, Had-GEM-ES and MIROC-ESM-CHEM. The RCP 2.6 climate scenario is considered the mildest and least likely of global warming scenarios. Attempts to model with higher RCPs, predicted near binary absence (*L. timidus*) and presence (*L. europaeus*) which was less informative. These future climate niche projections also included the same topographical predictor variables and values as for the current climate niche i.e. elevation, slope and aspect derived from OS 50m digital terrain model and gullies information from OS Vector data (Digimap 2019). To be consistent with the current climate niche, the future climate niche did not include any vegetation information, which was of course unknown.

2.3.4 Ecological Niche Modelling

Niche modelling analysis followed Guisan et al. (2017) using 'biomod2' (Thuiller et al. 2014), 'ecospat' (Di Cola 2017) and 'ade4' (Dray and Dufour 2007) packages in R. Predictors were normally distributed, though some were skewed, and were evaluated for collinearity with Pearson correlation coefficients using function [layerStats] from R Package 'raster' (Hijmans 2019). Strongly correlated predictors having Pearson coefficient $r > 0.75$ were removed (Guisan et al. 2017). Where choices arose, we retained those relevant to lagomorph ecology (Table 1) (Harris and Yalden 2008). For climate niche models we retained eight abiotic variables: BIO 6 minimum temperature of coldest month, BIO 7 temperature annual range, BIO 8 mean temperature of wettest quarter, BIO 9 mean temperature of driest quarter, BIO 12 annual precipitation, BIO 15 precipitation seasonality, aspect, gullies and slope (Table 2.1, Figure S4). For the habitat niche models we retained the following biotic variables: NDVI, brightness, wetness, all landcover types, roads and the presence of respective lagomorph species (Table 2.1, Figure S5).

Niche models used presences and pseudo-absences for each species and relevant predictor layers (Table 2.1). Predictive models were assembled in 'biomod2' (Thuiller et al. 2014) which hosts a series of process steps within the function [BIOMOD_ModelingOptions] to enable use of algorithms. For these we employed three with standard settings: General Linear Model (quadratic models, no interaction terms, testing on AIC); Random Forest (500 trees, 5 nodes); MAXENT (Phillips et al. 2006) (200 iterations with linear or quadratic features). Nine runs were conducted with cross-validation, 70/30 training/test data; performance monitored with kappa, TSS (Allouche et al. 2006) and AUC scores (Fielding and Bell 1997). Because each algorithm may perform differently with different environmental predictors, making evaluation and comparison difficult, we created ensemble models retaining all information from the candidate algorithms following Thuiller et al. (2009) and

Guisan et al. (2017), using function [BIOMOD_EnsembleModeling] within 'biomod2'. We chose between committee and weighted mean averaged models considering test scores for kappa, TSS and AUC. Predictor variables were ranked on average importance values for the GLM. The influence of each predictor was portrayed with evaluation strip charts (Elith et al. 2005). For each ensemble model we used optimised TSS value to determine probability threshold, predicting climate and habitat niches (Franklin 2009) using function [find.optim.stat] within 'biomod2' (Guisan et al. 17: 259). Using function [extract] in 'raster' we then measured the size of predicted niches for each species. We calculated min, max and mean abiotic values and vegetation productivity values for each species. For each landcover class we measured how much the models predicted as occupied. The future climate niche model applied the ensemble model values derived from the current climate model, to predict future climate values, forecasting for the year 2050 and quantifying range change (Fick and Hijmans 2017; Guisan et al. 2017). Some future climate variables had ranges outside those used to calibrate the current climate models. Therefore for the future climate niche models, we recorded how many variables were invoked to form predictions, thereby indicating where predictions might be uncertain, determined with the function argument [build.clamping.mask] in 'biomod2'.

Geographic overlaps were calculated from prediction maps. Elevation overlaps were assessed with Welch’s t-test for difference. Environmental niche overlap assessment followed Broennimann et al., (2012) predicting niche occupancy in environmental space, thereby removing geographic bias. This method was designed to detect niche overlaps in current environments. We assessed both the climate and habitat niches. Multivariate analysis of these factors applied principal components analysis to species presence points only, determining two leading components within 'ecospat' using function [ecospat.sample.envar] (Di Cola 2017) and function [dudi.pca] in R package 'ade4' (Dray and Dufour 2007). Overlap of niches were tested for equivalency and similarity using Schoener and Hellinger indices (Broennimann et al. 2012) using functions including [ecospat.niche.similarity.test] in 'ecospat' (Di Cola 2017).

2.4 Results

For both lagomorphs in all niches, ensemble modelling achieved high test scores and credible predictions of probability of occurrence (Franklin 2009; Guisan et al. 2017) (Table S3). Evaluations of maximised TSS scores provided thresholds for current climate, current habitat and future climate niches (Table 2.2) predicting distinctly different species niches (Figure 2.2).

2.4.1 Lepus timidus predicted niches

The current climate niche was predicted at 168km^2 comprising the highest elevations in the centre of the study extent (Figure 2.2). Referring to GLM models, the strongest abiotic predictors associated *L. timidus* presence with a narrow temperature range (BIO 7), the wettest quarter (BIO 8), the coldest temperature of the coldest month (BIO 6), less precipitation (BIO 12) and with no apparent association for topography (Table 2.3, Table 2.4, Figure S6).

In the current habitat niche, the predictors influencing *L. timidus* presence were mid-ranges of vegetation productivity: brightness and NDVI (Table 2.3, Table 2.5, Figure S6). Broadleaved and coniferous woodland and improved grassland suggested slight negative associations. Neither roads, nor the presence of *L. europaeus* were important predictors.

The current habitat niche was predicted as actually being 60% larger than the current climate niche, 269km^2 (Table 2.6, Figure 2.2). More than half of the landcover occupied by *L. timidus* was young or mature heather; moorland grasses or cotton grass made up the remainder. The current habitat niche model predicted 80% utilisation of available heather landcover (Table 2.6).

The future climate niche predicted for *L. timidus* a range reduction of 88% to 19km^2, remaining only on high elevation areas (Figure 2.2). The future probability of occurrence threshold was very low (Table 2.2). Suitable areas were mostly predicted in those locations where the model referenced at least seven abiotic variables, having ranges used to calibrate current climate niche models (Figure 2.2; Figure S7).

2.4.2 Lepus europaeus predicted niches

The current climate niche predicted a wide lowland area of 252km^2 encircling the uplands (Figure 2.2). Referring to GLM models, the main abiotic predictors for L. europaeus were less precipitation (BIO 12), a colder mean temperature of the wettest quarter (BIO 8) and warmer temperatures of the driest quarter (BIO 9), (Table 2.3, Table 2.4, Figure S6).

The current habitat niche was determined by vegetation productivity measures wetness and NDVI (Table 2.3, Table 2.5, Figure S6). The only important landcover predictors reported a disinclination towards cotton grass and a slight preference for improved grassland. There was a slight association with the presence of *L. timidus*. Roads provided a slight association, which we attribute to sample bias.

The current habitat niche was 401km^2, again larger than the current climate niche by 59% (Table 2.6, Figure 2.2). Of this, improved grassland and moorland grasses accounted for more than 70%, woodlands at least 14% and heather 10% including slightly on to the hills. Utilisation of available improved grassland was 100%.

The future climate niche predicted expansion by *L. europaeus* across the whole study extent to 765km^2, more than 3 times its current climate niche, and including all hill tops (Figure 2.2). The predicted future probability of occurrence threshold was low (Table 2.2). Suitable areas were predicted by five or more abiotic variables (Figure S7).

2.4.3 Niche overlap

Summed kernel density plots of all years' records for *L. timidus* and *L. europaeus* showed significant weak negative correlation (Pearson $r_{\text{timidus europaeus}}$ t = -55.6, df = 81002, correlation = -0.19, *P*-value<0.001) (Figure 2.3). Comparing current climate niches, there was an overlap of just 0.2km^2 between the species. For current habitat niches, there was overlap by 38.4km^2; 14% of *L. timidus* range and 9% of *L. europaeus* range (Figure 2.2). The future climate niche space predicted *L. timidus* range wholly within and comprising 3% of *L. europaeus* range (Figure 2.2).

The elevation ranges (Figure 2.4) in the current climate niche predicted *L. timidus* occurring at mean elevation 491m, moving in future up to 573m. For *L. europaeus* current climate niche mean elevation was 298m, moving in future to 369m (Figure 2.4). Assessment with Welch's t-test of mean elevation ranges between species showed these as significantly different (Table 2.7). Note these forecasts are based on relationships with climate and topographical variables, without reference to vegetation.

Based on occurrence points, *L. timidus* was present at temperatures ~1 degree colder than *L. europaeus*, with 241mm more annual precipitation (Table 2.4). Principal components analyses of abiotic variables on combined species occurrence points showed climatic variables more influential than topography; and of biotic variables, vegetation productivity indices were most important (Table 2.8). Kernel density plots of principal components axes showed the two species occupying separate niches (Figure 2.5). Overlap indices showed the niches as very different: current climate niche Schoener D = 0.16, Hellinger I = 0.31; current habitat niche Schoener D = 0.07, Hellinger I = 0.20. Both metrics are probability scales from 0 (no overlap) to 1 (complete overlaps).

2.5 Discussion

2.5.1 Two separate species, two separate niches

This study predicted two congeneric lagomorph species occupying distinctly different ecological niches in close geographic proximity with virtually no overlap. For both, their current climate niches predicted by temperature, precipitation and topography, were actually much smaller than their habitat niches predicted by vegetation productivity and composition. We found *L. timidus* occupied high elevation areas characterised by colder temperatures and higher precipitation levels. The landcover for *L. timidus* predominantly consisted of upland dwarf shrub vegetation: heather, cotton grass and moorland grasses. By contrast *L. europaeus* occupied lower elevation areas, just 1° Celsius warmer, with less precipitation. Its preferred landcover was improved grassland. Woodland and heather areas were also important. Whilst the margins of difference for preferred climate variables were small, they predicted strikingly separate niches across the landscape. Referencing climate values for RCP 2.6 for 2050, the *L. timidus* future climate niche was predicted to shrink to small patches at high elevations.

The *L. europaeus* future climate niche was predicted to expand to higher elevations, encompassing the uplands, completely covering the range of *L timidus*. Interspecies competition in terms of overlaps of geographic and environmental niche ranges was presently very low and yet inferred to increase in future.

2.5.2 Reasons for niche preferences

Environmental forces are often complex and difficult to categorise or explain (Sillero 2011). There are subtle reasons for niche differences between these two lagomorphs. Our study predicted both species actually occupied much larger habitat niches than climate niches. This is a different outcome to the perhaps conventional expectation that the habitat, i.e. realised niche, may be a limited version or subset of the climate, i.e. fundamental niche (Guisan and Zimmerman 2000; Sillero 2011). This finding reflects the view that ecological forces may indeed act stochastically (Guisan et al. 2017: 23). Both species were in effect tolerating wider climatic ranges than suggested by the current climate niche models. Across the entire study extent the climate variables reported small variations which were not of critical physiological importance to lagomorphs, yet could still indicate strong preferences, e.g. the widest temperature variation BIO 9 (mean temperature, driest quarter) ranged from 5.1ºC to 13.8ºC, the narrowest BIO 6 (min temperature coldest month) ranged from -2.2ºC to -0.8ºC; BIO 12 (annual precipitation) ranged 689-1,666 mm. The small climatic variations showed distinct steep local changes, resembling the hilly topography. Consequently, these values were sufficiently different to predict two separate climate niches for the two species. By contrast the biotic vegetation productivity variables (NDVI, tasselled cap brightness and tasselled cap wetness) showed midrange values covering a much wider geographical extent, with less severe graduations, thereby predicting much larger habitat niches.

Considering abiotic and biotic factors, it therefore appears the two species occupied separate niches because vegetation productivity, composition and associated dietary preferences, were more important than climate influences. Of note, the lagomorphs' different biotic niches were predicted by alternate aspects of vegetation productivity. Brightness (i.e. less exposed soil) and NDVI (i.e. actively photosynthesising plant growth) were most important for *L. timidus,* whereas, for *L. europaeus*, it was wetness (i.e. drier soil and vegetation moisture content). This then provided contrasting differences to the consequent proportion of vegetation types in the respective habitat niches of each species.

For *L. timidus,* the majority of its habitat niche was heather, with other upland bog vegetation also important (cotton grass and moorland grasses). This was consistent with reported dietary and shelter preferences for *L. timidus* in the UK (Hewson 1962, 1976b, 1989). In the Peak District, much heather resource exists because of grouse moor management (Anderson and Shimwell 1981). Other large areas of uplands are subject to blanket bog restoration: gully blocking to retain water and planting of upland dwarf shrubs (Bonn et al. 2009). These human interventions provide the vegetation that support the presence of *L. timidus*.

The habitat niche for *L. europaeus* was different: mostly improved grassland areas, with moorland grass, woodland and some heather also being important. This reflected the reported preferences of *L. europaeus,* favouring mixed agrarian landscapes: crops, cereals or grasses (Harris & Yalden 2009; Tapper & Yalden 2015).

Differences in niche preferences, and by implication diet, may be explained by vegetation qualities and productivity: energy content, moisture, digestibility of secondary compounds, terpenes, phenolic resins, and selected in an order of preference by lagomorphs (Hulbert et al. 2001; Rödel et al. 2004). The preference of *L. timidus* is grasses: *Deschampsia flexuosa, D. caespitosa, Nardus stricta, Festuca, Agrostis spp*. especially for females in summer (Harris and Yalden 2008). However, when winter grass nutritional quality is poor, *L. timidus* switches to a 90% heather diet, less digestible but tolerable. (Hewson 1962; Hulbert et al. 2001; Harris & Yalden 2008). Between the two species, *L. timidus* may be better able to detoxify phenolics occurring in shrubs and trees (Iason & Palo 1991). By contrast *L. europaeus* favours grassland resources throughout the year until there is no other option. It depends on weeds in agricultural lands (Reichlin et al. 2006). Thus, whilst *L. europaeus* may venture to utilise upland grasses, when these fall senescent in winter, instead of switching to heather in the manner of *L. timidus,* (Hulbert et al. 2001), *L. europaeus* chooses improved grasslands at low elevations. Absent competition, *L. europaeus* can broaden its dietary niche to selectively include shrubs (Green et al. 2013), possibly as a last resort (Rödel et al. 2004; Harris & Yalden 2008). Other studies suggest *L. europaeus* adapts its diet when food availability is limited (Puig et al. 2017). Yet, there is ample supply of lowland improved grassland in the Peak District, providing a distinct niche for *L. europaeus*.

2.5.3 Level of interspecies competition

We inferred that both abiotic and biotic factors combined to determine distinct species ranges, with very small overlaps between the two. For *L. timidus*, a boreal species adapted for harsh winter climates, it was anticipated that its climate niche would occur on hilltops with the coldest wet conditions. The seasonally white pelage of *L. timidus* has high densities of air-filled hairs providing insulation that allows it to utilise colder areas during winter (Zimova et al. 2016). The heavily furred hind feet of *L. timidus* are helpful for digging through snow to reach heather (Jansson and Pehrson 2007; Harris & Yalden 2008). Yet, although *L. europaeus* does not share these adaptations, physiologically it can survive very cold habitats at high elevations (>2000m a.s.l.) during winter (Green et al. 2013; Puig et al. 2017). In snowscapes, *L. europaeus* restricts its diet to taller vegetation that remains visible (Green et al. 2013); but in the Peak District, only heather and berry shrubs of low height are available. So whilst *L. europaeus* could theoretically endure the cold climate of the high elevations of the Peak District, it is less well suited than *L. timidus* and may avoid the energy costs of searching for less preferable forage in poor weather or under snow, by remaining at lower, warmer elevations. Indeed where both species share territory, *L. timidus* copes more effectively with cold snow conditions (Jansson and Pehrson 2007). There may also be competitive exclusion by *L. timidus*, though the mechanism is unclear (Reid and Montgomery 2007).

Grasslands were outside the habitat niche of *L. timidus,* consistent with reports of it typically occupying heather moorland, tundra or forest (Angerbjörn and Flux 1995). Surprisingly our niche models also predicted that in woodlands, *L. timidus* were absent, and yet *L. europaeus* were present. This is different to other localities in Europe, where *L. timidus* often utilises woodlands, feeding on

Salix, *Sorbus, Betula, Juniperus, Populus* and *Vaccinium spp.* (Hewson 1962; Angerbjörn & Flux 1995; Jansson and Pehrson 2007; Rehnus et al. 2013). Although this situation was recorded differently in Scotland whereby amongst mixed habitats, *L. timidus* was specifically shown to prefer heather moorland over newly planted Scots pine (*Pinus sylvestris*) woodland (Rao et al. 2003). Separate records across Europe describe *L. europaeus* pushing *L. timidus* out of forests (Flux and Angermann 1990); *L. europaeus* present in forests where clear-cuts promoted grass growth (Jansson and Pehrson 2007) or, otherwise, where *L. timidus* was absent (Rödel et al. 2004). Therefore, we are uncertain whether *L. timidus* avoids Peak District woodlands as its own preference or whether *L. europaeus* excludes them. This intriguing interspecies dynamic invites further study.

Competition occurs where dietary preferences converge. In these circumstances, *L. europaeus* often dominates, though this may depend upon local species densities (Acevedo et al. 2012). In Sweden, Jansson and Pehrson (2007) described how *L. europaeus* displaced *L. timidus* facilitated by warmer winters which increased grass availability in forests. In Ireland, the introduced *L. europaeus* outcompetes the native *L. timidus hibernicus* subspecies, which feeds mainly on grasses (Caravaggi et al. 2014; Caravaggi et al. 2017). By comparison, in the Peak District, the separate improved grassland which abuts the distinctly different heather moorland and the alternate dietary preferences allow the two lagomorph species to thrive in close proximity, seemingly without competition. These findings are consistent with those of Hewson (1976a) who reported that *L. europaeus* only invaded heather ranges when *L. timidus* numbers were very low. Flux and Angermann (1990) also describe separate dietary niches for both these hare species.

2.5.4 Future niches under climate change

The future climate niche scenarios predicted that, by 2050, *L. timidus* would occupy a reduced geographic range of smaller patch sizes at higher elevations, consistent with studies elsewhere (Anderson et al. 2009; Leach et al. 2016; Rehnus et al. 2018). The persistence of *L. timidus* may depend on available vegetation under warmer climates. Policies and investments support both grouse moor management and blanket bog restoration, providing heather resource. However, heather requires drier soil structures. Climate forecasts for England are for wetter winters and driers summers. Notwithstanding human intervention, there is much uncertainty regarding future vegetation composition (Bonn et al. 2009). Otherwise, to survive, *L. timidus* must adapt its diet (Harris & Yalden 2009). There are scant opportunities for *L. timidus* to disperse elsewhere. Peripheral areas comprise only small patches of heather moorland and are several kilometres away. There are large areas of intervening agriculture and roads: a difficult migration for a species whose natal dispersal range is less than 1km (Angerbjorn & Flux 1995). Notwithstanding these challenges, the warming climate also reduces snow cover, thereby increasing the vulnerability of *L. timidus* to predators, because of the camouflage mismatch arising from its white winter pelage (Zimova et al., 2020). The increasing number of wildfires inevitably also threatens hares on the uplands (Albertson et al. 2010).

By contrast, we predict by 2050 the widespread expansion of *L. europaeus* to higher elevations. Being descended from central European and Asian species, *L. europaeus* may be physiologically better able to thrive in warmer temperatures (Caravaggi et al. 2017). However, our habitat niche model and dietary evidence suggests *L. europaeus* relies on grasses. Its spread to hilltops would require upland dwarf shrub vegetation succumbing to warmer climate, the failure of human upland management interventions and a transition to grassland communities. Regardless, the dietary preference of *L. europaeus* allows it to migrate to prolific lowland agricultural landscapes of northern England.

The relationship between these species depends on whether vegetation availability and dietary requirements converge. Should the two species' climatic niches merge as predicted and the upland vegetation changes, this is likely to precipitate competition or hybridisation (Thulin 2003). This might occur remarkably swiftly (Caravaggi et al. 2017). We recommend ongoing monitoring of the respective niches and competitive dynamics of both lagomorph species.

Acknowledgements

This research was funded by the People's Trust for Endangered Species, the Hare Preservation Trust, the British Mountaineering Council, Queen's University Belfast, Penny Anderson Associates and South-West Action for Hares. We thank N. Sillero and W. Kasworm for niche modelling advice. We dedicate this research to the memory of Derek Yalden.

Hare Data Sources

Brown and mountain hare records were kindly provided by British Trust for Ornithology, Cheshire Record LRC, Derbyshire Mammal Group, Derbyshire Wildlife Trust, Moors for the Future, Liverpool Museum, National Biodiversity Atlas, Sheffield Biological Records Centre, Sorby Natural History Society and West Yorkshire Ecology.

Data availability

Species records remain copyright with the Biological Record Centres listed under Hare Data Sources .
WorldClim data is open access and available from htttps://www.worldclim.org
Both Ordnance Survey data and aerial images may be sourced from Edina, National Data Centre, University of Edinburgh, UK.
Ordnance Survey map and topography data are available from https://www.ordnancesurvey.co.uk.
Aerial images are supplied by Getmapping plc, Fleet, Hampshire UK

Author contributions

Carlos Bedson: Conceptualisation, data curation, formal analysis, writing-Original draft preparation. writing - Reviewing and Editing**. Christian Devenish:** formal analysis, validation. **Elias Symeonakis:** Software, Validation. **David Mallon:** validation. **Neil Reid**: Conceptualisation,. **W. Edwin Harris:** Conceptualisation. **Richard Preziosi:** Supervision. All authors were involved with Writing - Reviewing and Editing.

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Tables

Table 2.1 The models and variables used to predict hare ecological niches

<table>
<tr><th>Species</th><th><i>Lepus timidus</i></th><th><i>Lepus europaeus</i></th></tr>
<tr><td>Species Occurrence Data</td><td>BRC data
1690 presences
1690 pseudo-absences</td><td>BRC data
265 presences
265 pseudo-absences</td></tr>
<tr><td></td><td colspan="2">Current climate niche</td></tr>
<tr><td></td><td colspan="2">BIO.6 Min temp of coldest month
BIO.7 Temp annual range
BIO.8 Mean temp of wettest quarter
BIO.9 Mean temp of driest quarter
BIO.12 Annual precipitation
BIO.15 Precipitation seasonality
Aspect
Gullies
Slope</td></tr>
<tr><td></td><td colspan="2">Current habitat niche</td></tr>
<tr><td></td><td colspan="2">NDVI
Brightness
Wetness
Arable
Berries
Broadleaved woodland
Coniferous woodland
Cotton Grass
Young heather
Mature heather
Improved grassland
Moorland grasses
Roads
<i>L. timidus</i> or <i>L. europaeus</i></td></tr>
<tr><td></td><td colspan="2">Future climate niche</td></tr>
<tr><td></td><td colspan="2">BIO.6 Min temp of coldest month
BIO.7 Temp annual range
BIO.8 Mean temp of wettest quarter
BIO.9 Mean temp of driest quarter
BIO.12 Annual precipitation
BIO.15 Precipitation seasonality
Aspect
Gullies
Slope</td></tr>
</table>

Table 2.2 TSS and threshold scores for the models when projected using weighted mean ensemble modelling

Model	Max TSS	Threshold
L. timidus current climate niche	0.66	0.57
L. timidus current habitat niche	0.46	0.49
L. timidus future climate niche	0.09	0.07
L. europaeus current climate niche	0.73	0.54
L. europaeus current habitat niche	0.44	0.37
L. europaeus future climate niche	0.04	0.23

Table 2.3 Variable importance

Calculated with 3 permutations in biomod2, reporting by algorithm (GLM, Generalised linear model; RF, Random Forest and MAXENT). Variable importance is predicted by shuffling a single variable, then computing simple Pearson's correlation between reference predictions and the 'shuffled' one. The highest values show the more influence the variable has on the model, normalised to 100% i.e. 1.0 is most, 0.0 is no influence. Method does not account for interactions. (From package 'biomod2', Thuiller et al., 2013). Each model is ranked by GLM score.

L. timidus current climate niche

VARIABLE	GLM	RF	MAXENT
BIO.7	0.47	0.20	0.31
BIO.8	0.23	0.13	0.17
BIO.6	0.18	0.05	0.06
BIO.12	0.08	0.09	0.05
BIO.15	0.04	0.21	0.07
ASPECT	0.00	0.01	0.00
SLOPE	0.00	0.05	0.02
BIO.9	0.00	0.26	0.32
GULLIES	0.00	0.00	0.00

L. europaeus current climate niche

VARIABLE	GLM	RF	MAXENT
BIO.12	0.54	0.13	0.21
BIO.8	0.20	0.11	0.10
BIO.9	0.16	0.20	0.27
BIO.15	0.06	0.20	0.12
BIO.7	0.02	0.11	0.14
GULLIES	0.01	0.00	0.02
BIO.6	0.00	0.08	0.06
ASPECT	0.00	0.05	0.02
SLOPE	0.00	0.12	0.07

L. timidus current habitat niche

VARIABLE	GLM	RF	MAXENT
BRIGHTNESS	0.52	0.36	0.29
NDVI	0.32	0.29	0.12
BROADLEAF	0.04	0.02	0.01
IMPROVED.GRASS	0.04	0.08	0.08
WETNESS	0.04	0.11	0.08
CONIFEROUS	0.02	0.04	0.01
ROADS	0.01	0.01	0.01
L.europaeus	0.01	0.00	0.04
MOOR.GRASSES	0.00	0.02	0.10
MATURE.HEATHER	0.00	0.04	0.11
BERRIES	0.00	0.00	0.00
ARABLE	0.00	0.00	0.00
COTTON.GRASS	0.00	0.01	0.07
YOUNG.HEATHER	0.00	0.03	0.08

L. europaeus current habitat niche

VARIABLE	GLM	RF	MAXENT
WETNESS	0.47	0.28	0.17
COTTON.GRASS	0.19	0.03	0.06
NDVI	0.08	0.20	0.12
IMPROVED.GRASS	0.07	0.16	0.15
CONIFEROUS	0.06	0.03	0.06
ROADS	0.05	0.09	0.09
MATURE.HEATHER	0.03	0.02	0.05
BERRIES	0.03	0.01	0.00
L.timidus	0.02	0.01	0.05
BRIGHTNESS	0.00	0.13	0.07
ARABLE	0.00	0.00	0.00
BROADLEAF	0.00	0.00	0.03
YOUNG.HEATHER	0.00	0.01	0.07
MOOR.GRASSES	0.00	0.02	0.07

Table 2.4 Mean abiotic variable values for each hare species, at their respective locations. Temperatures are oC, precipitation mm

	L. timidus			*L. europaeus*		
	Min	Mean	Max	Min	Mean	Max
BIO.6 min temp, coldest month	-2.20	-1.83	-0.92	-2.13	-1.47	-0.88
BIO.7 temp annual range	17.20	17.91	19.47	17.60	18.55	19.64
BIO.8 mean temp wettest quarter	3.08	3.55	4.25	3.20	3.95	5.95
BIO.9 mean temp driest quarter	9.17	11.53	13.06	10.42	12.26	13.21
BIO.12 annual precipitation	997.20	1395.40	1664.4	926.90	1154.00	1595.46
BIO.15 precipitation seasonality	17.83	21.17	22.78	16.60	19.63	22.12
Slope	0.14	6.79	30.78	0.22	8.25	23.47
Aspect °		229			221	
Species locations at gullies		43%			34%	

Table 2.5 Ranges of vegetation productivity at the two hare species' locations

	L. timidus			*L. europaeus*		
	Min	Mean	Max	Min	Mean	Max
Brightness	0.83	0.95	1.47	0.85	1.01	1.2
Wetness	0.08	0.26	0.43	0.01	0.20	0.36
NDVI	-0.07	0.00	0.05	-0.08	-0.03	0.04

Table 2.6 Geographic occupation of current climate and habitat niches by L. timidus and L. europaeus for each landcover type.

		L. timidus				*L. europaeus*			
Landcover	Total Available	Climate niche	Habitat niche			Climate niche	Habitat niche		
	km^2	km^2	km^2	% of total available	% of climate niche	km^2	km^2	% of total available	% of climate niche
Arable	3.0	0.0	0.0	0%	-	0.3	2.3	78%	900%
Berries	7.4	1.0	0.1	1%	8%	3.2	0.8	11%	25%
Broadleaf	47.0	0.0	0.2	0%	1500%	26.3	30.0	64%	114%
Coniferous	33.6	1.2	0.2	1%	16%	18.2	27.0	80%	148%
Cotton grass	81.7	32.2	33.2	41%	103%	10.3	0.1	0%	1%
Improved grassland	205.9	0.2	0.0	0%	0%	97.2	205.8	100%	212%
Mature heather	143.5	58.3	115.8	81%	199%	25.2	10.7	7%	43%
Moorland grasses	201.2	41.1	54.5	27%	133%	51.9	94.0	47%	181%
Young heather	82.2	34.2	65.1	79%	190%	20.2	30.8	37%	152%
Total	805.5	168.1	268.9	33%	160%	252.8	401.5	50%	159%

Table 2.7 Welch's t-test comparisons of predicted mean elevations (m) of hare species for current and future climate niches

Comparison	t	df	*P*-value
L. timidus current vs *L. timidus* future	-56.81	2356	<.05
L. timidus current vs *L. europaeus* current	-313.7	38985	<.05
L. europaeus current vs *L. europaeus* future	-130.3	63858	<.05
L. timidus future vs *L. europaeus* future	-143.7	2180	<.05

Table 2.8 Percent contribution of each variable to principle components 1 and 2 used in the niche overlap models.

Values in bold as contributors

	Climate niche	
Variable	PCA 1	PCA 2
BIO.6	**11.8**	**21.6**
BIO.7	**15.2**	**11.2**
BIO.8	**15.4**	5.0
BIO.9	**13.7**	0.1
BIO.12	**24.1**	0.1
BIO.15	**18.3**	4.6
ASPECT	0.0	**19.2**
GULLIES	1.3	1.3
SLOPE	0.3	**37.0**

	Habitat niche	
Variable	PCA 1	PCA 2
NDVI	**27.2**	6.6
BRIGHTNESS	1.9	**37.5**
WETNESS	**27.1**	1.0
ARABLE	0.1	0.0
BERRIES	0.0	0.0
BROADLEAF	0.0	1.9
CONIFEROUS	0.1	3.2
COTTON.GRASS	2.5	1.7
YOUNG.HEATHER	1.9	1.1
MATURE.HEATHER	4.3	**18.8**
IMPROVED.GRASS	**28.1**	0.0
MOOR.GRASSES	1.9	**28.1**
ROADS	4.8	0.1

Figures

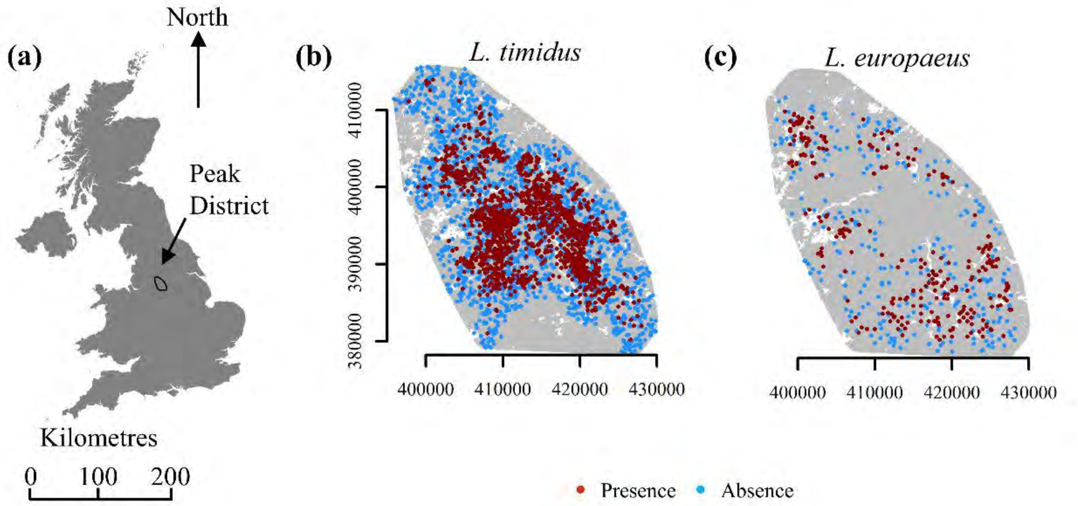
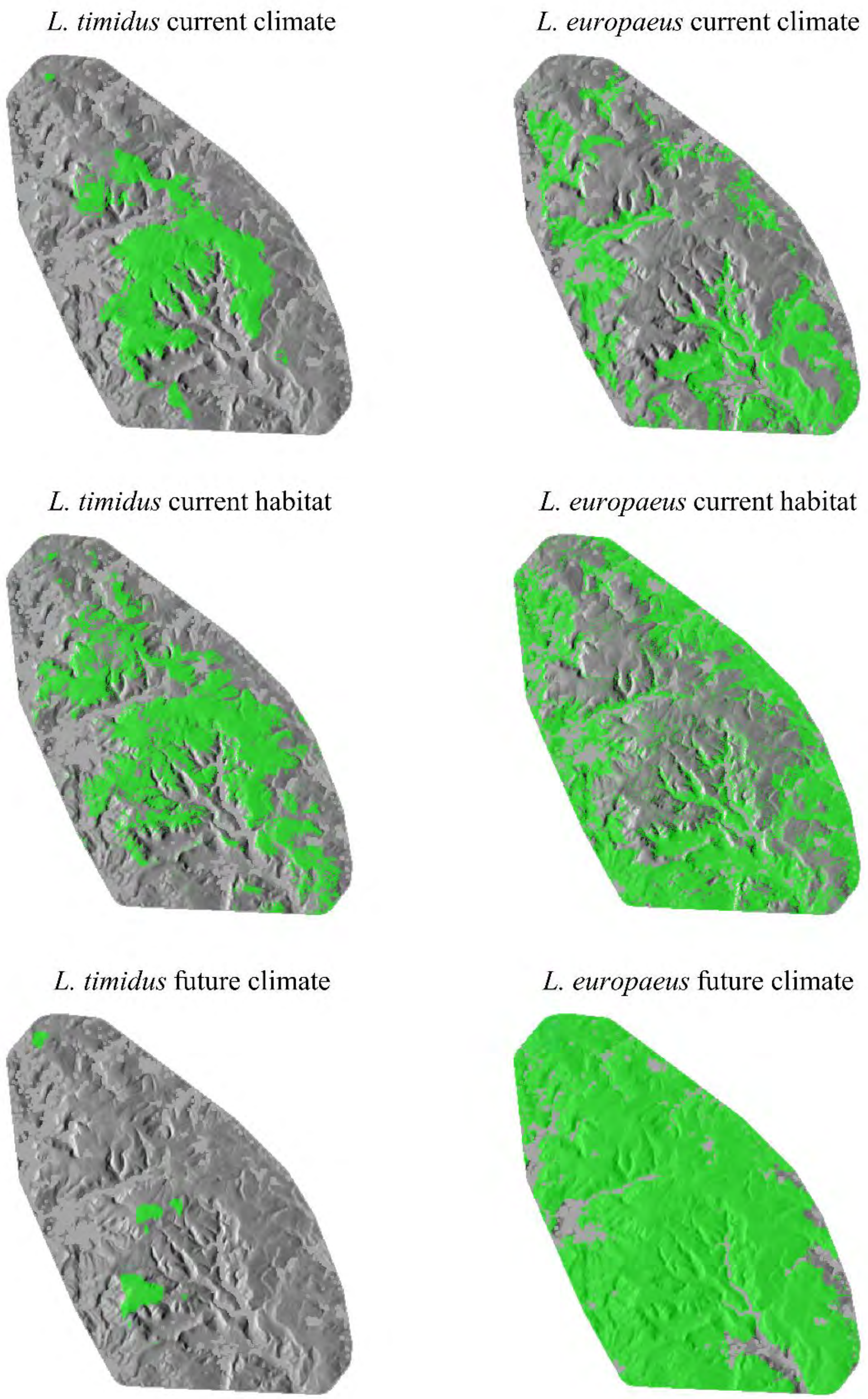


Figure 2.1 Maps showing hare observation locations.

(a) Great Britain, with Peak District; (b) Presence / pseudo absence data for *L. timidus;* (c) Presence / pseudo absence data for *L. europaeus*. Grey shape is study extent within Peak District National Park, UK, Latitude 53.3342° N, Longitude 1.7837° W. Map axes (b) and (c) represent Ordnance Survey information taken from British National Grid 100km tiles SK and SE with ticks at 10km intervals.



L. timidus current climate

L. europaeus current climate

L. timidus current habitat

L. europaeus current habitat

L. timidus future climate

L. europaeus future climate

Figure 2.2 Threshold maps showing current climate (year 2020) niche and current habitat niche, and future climate (year 2050) niche for L. timidus and L. europaeus.

Background hill shade based on elevation data. Green overlain shapes are predicted niches.

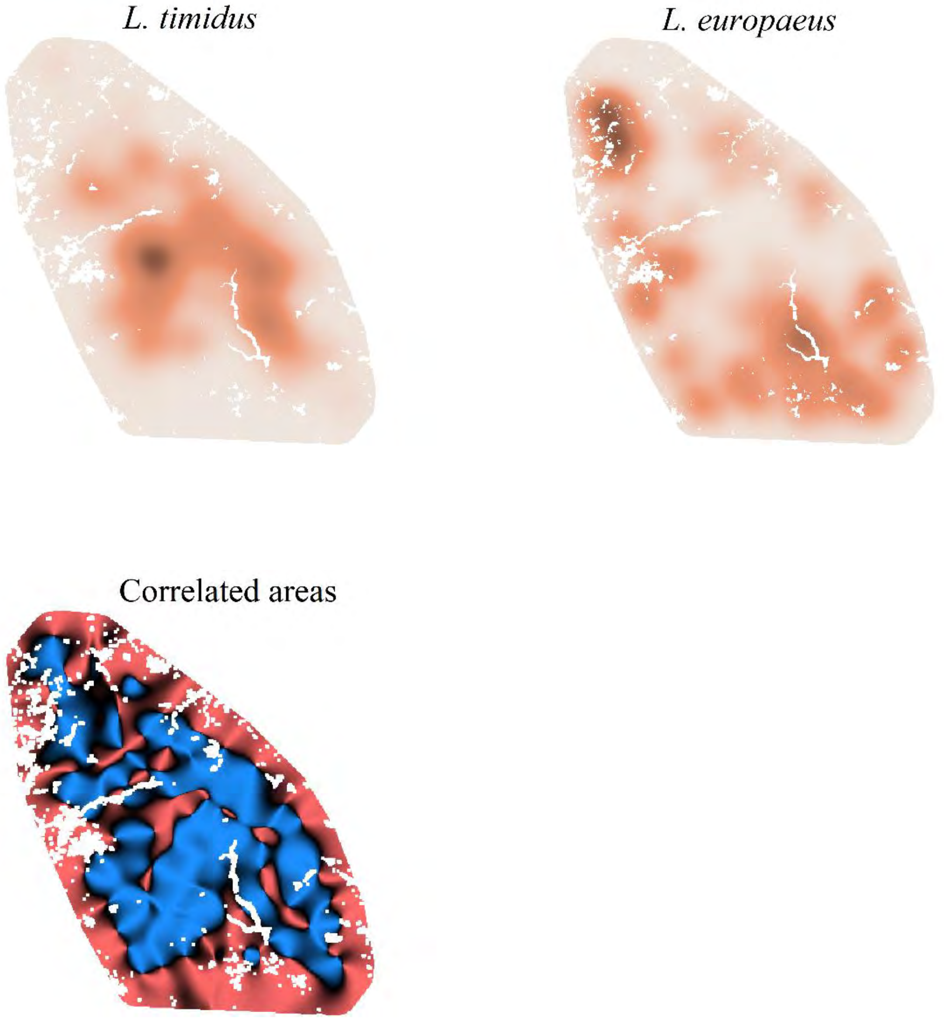


Figure 2.3 Kernel density plots of summed (2000 to 2018) records for L.timidus and L. europaeus.

Darker areas indicating higher density. Correlated areas chart: blue = L timidus; red = L. europaeus; correlated areas ("contact zones") indicated by shading increasing to black

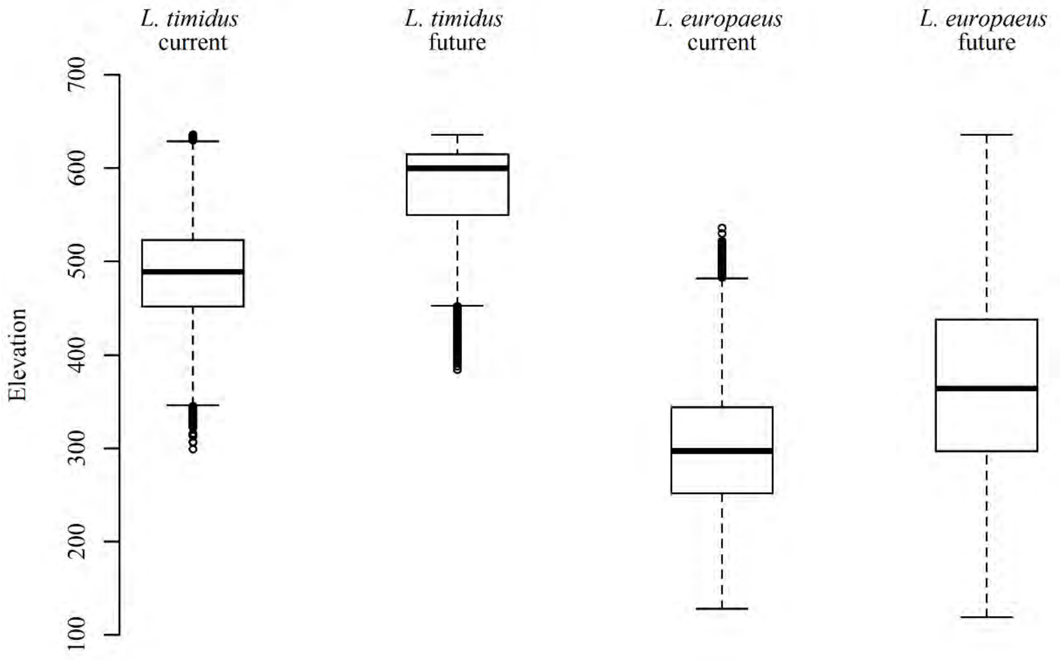
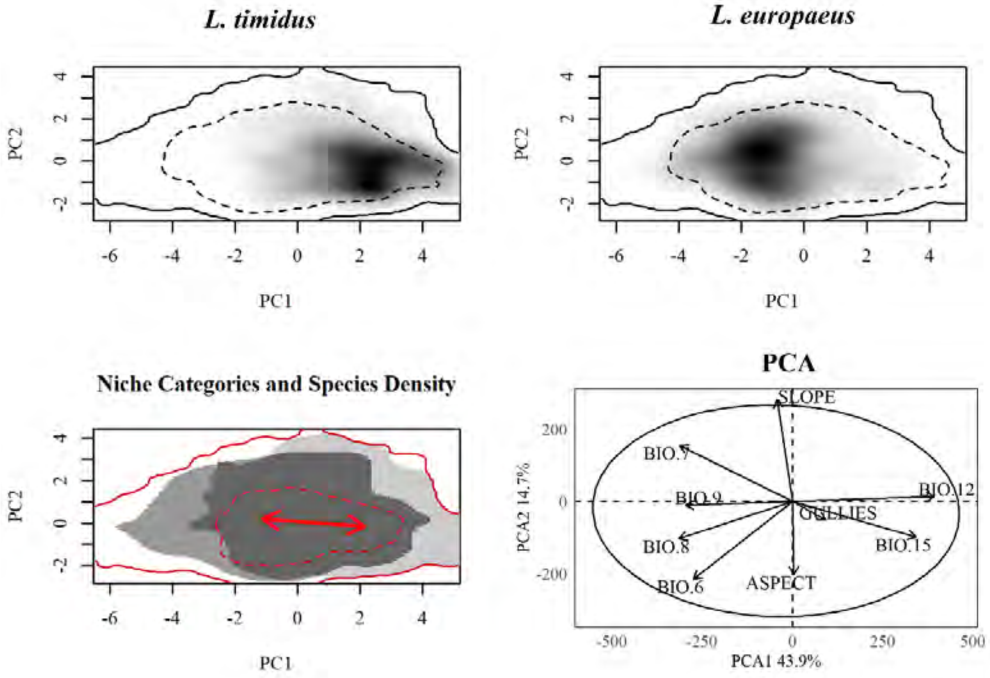
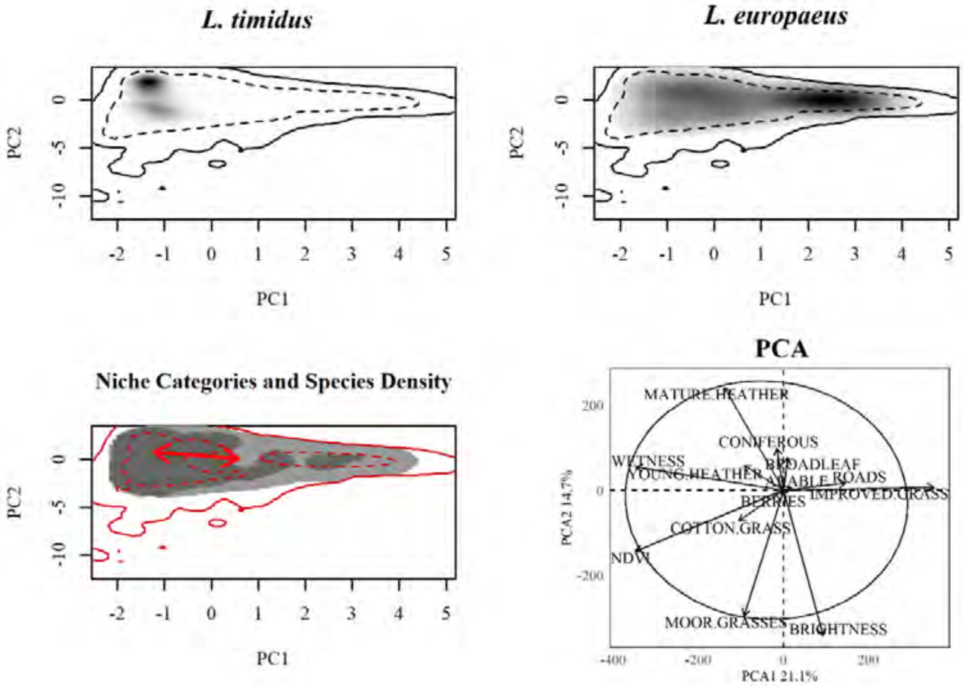


Figure 2.4 Boxplots showing predicted elevation ranges for L. timidus and L. europaeus.

Based on current and future climate niche threshold maps



(a) Current climate niche



(b)Current habitat niche

Figure 2.5 Niche overlap density and PCA plots

(a) Current climate (b) Current habitat. Density plots show ranges for L. timidus and L. europaeus, based on the first two principal components. The solid and dotted red line show 100% and 50% available environmental space. Bottom left charts: Light grey area indicates the native niche for L. timidus only, dark grey area (centre) common (stable, shared) niche between L. timidus and L. europaeus; and medium grey area native niche for L. europaeus only. The red arrow indicates the difference in the centroid of the niche, mapping between species. The PCA charts bottom right portray the niche variables plotted on the first two axes.

Supplementary information

Tables

Table S1 Number of BRC records for *L. timidus* and *L. europaeus*, Peak District and environs 2000 to 2018. Abbreviations: BTO British Trust for Ornithology; CLRC Cheshire Local Record Centre; DMG Derbyshire Mammal Group; DWT Derbyshire Wildlife Trust; GM LRC Greater Manchester Local Record Centre; MFTF Moors for the Future; NBNA National Biodiversity Network Atlas; SBRC Sheffield Biological Record Centre; SNHS Sorby Natural History Society; WYE West Yorkshire Ecology; DY Derek Yalden; DW Derek Whiteley; DM Dave Mallon.

L. timidus, number of BRC records, 2000 to 2018

	Source											Percent Records From		
Year	BTO	CLRC	DMG	DWT	GM LRC	MFTF	NBNA	SBRC	SNHS	WYE	Total	DY	DW	DM
2000			358	5	5		3	127	322	1	821	19%	6%	2%
2001		1	314	1			22	1	153		492	16%	33%	13%
2002		27	58	7			4	15	67		178	65%	5%	
2003		83	113	1	2		1	4	163		367	78%	2%	5%
2004		32	93	1			2	6	162	3	299	54%	3%	
2005		51	133	1				8	156	1	350	60%	1%	12%
2006		44	109	4			1	9	132		299	56%	5%	2%
2007		46	94				4	5	152		301	59%		23%
2008		69	104		3		6	5	142		329	65%	14%	10%
2009		52	115		2		6	12	155		342	53%	11%	15%
2010			168	1	2	2	11	40	170		394	27%	28%	10%
2011			40		20	1	10	19	124	7	221	43%	34%	
2012		4	68	2	8		34	28	92	13	249	50%	20%	
2013		1	44		2		19	14	42	4	126		52%	
2014	20	12	175	1	6		56	38	322	3	633		34%	1%
2015	27	2	388		7	160	210	7	234		1035		38%	
2016	20	2	235	253	27	302	220	4	10		1073		1%	
2017	17		7	139	16	234	118	19			550		2%	
2018	25	1		166		106	260	49			607		35%	

L. europaeus, number of BRC records, 2000 to 2018

	Source											Percent Records From		
Year	BTO	CLRC	DMG	DWT	GM LRC	MFTF	NBNA	SBRC	SNHS	WYE	Total	DY	DW	DM
2000		2	266	132	6		3	8		4	421		1%	
2001			239	205	1			3		1	449	4%	4%	1%
2002		26	197	123	24		12	4			386	17%	6%	1%
2003		9	209	110	25		23	1			377	6%	11%	3%
2004		10	237	108	1			6			362	11%	13%	2%
2005		8	200	76	2					3	289	7%	4%	1%
2006		4	157	30				1		1	193	2%	1%	
2007		3	335	34				3		6	381	6%	4%	4%
2008		14	312	35	2			3		8	374	7%	3%	5%
2009		11	306	17	4		5	9		6	358	4%	10%	4%
2010		2	266	1	9		3	11		22	314	5%	2%	10%
2011		2	15		48		38	5		6	114			
2012			81		43		52	16		2	194	5%	7%	4%
2013			79	4	12		16	54			165	1%		
2014	94	1	66	2	13	6	38	43	17	6	286		5%	21%
2015	104	5	149	3	12	24	4	17	34	10	362		10%	6%
2016	79	1	144		9	105	1	19		7	365		7%	
2017	92	1	2	5	3	66		48	9	2	228			1%
2018	92			154	1	116		11		2	376			

Table S2 Supervised classification test scores for the five moorland vegetation types based on 714km^2 of mosaicked 25cm aerial images resampled to 5m pixel size.

	Berries	Cotton grass	Moorland grasses	Young heather	Mature heather
Sensitivity	0.63	0.91	0.81	0.64	0.90
Specificity	0.98	0.95	0.98	0.94	0.91

Table S3 Ensemble niche model test scores.

Model	Committee Averaging			Weighted Mean		
	KAPPA	TSS	AUC	KAPPA	TSS	AUC
L. timidus current climate	0.70	0.70	0.92	0.67	0.67	0.93
L. timidus current habitat	0.46	0.46	0.79	0.46	0.46	0.81
L. europaeus current climate	0.68	0.68	0.91	0.73	0.73	0.94
L. europaeus current habitat	0.39	0.39	0.77	0.44	0.44	0.81

Supplementary figures

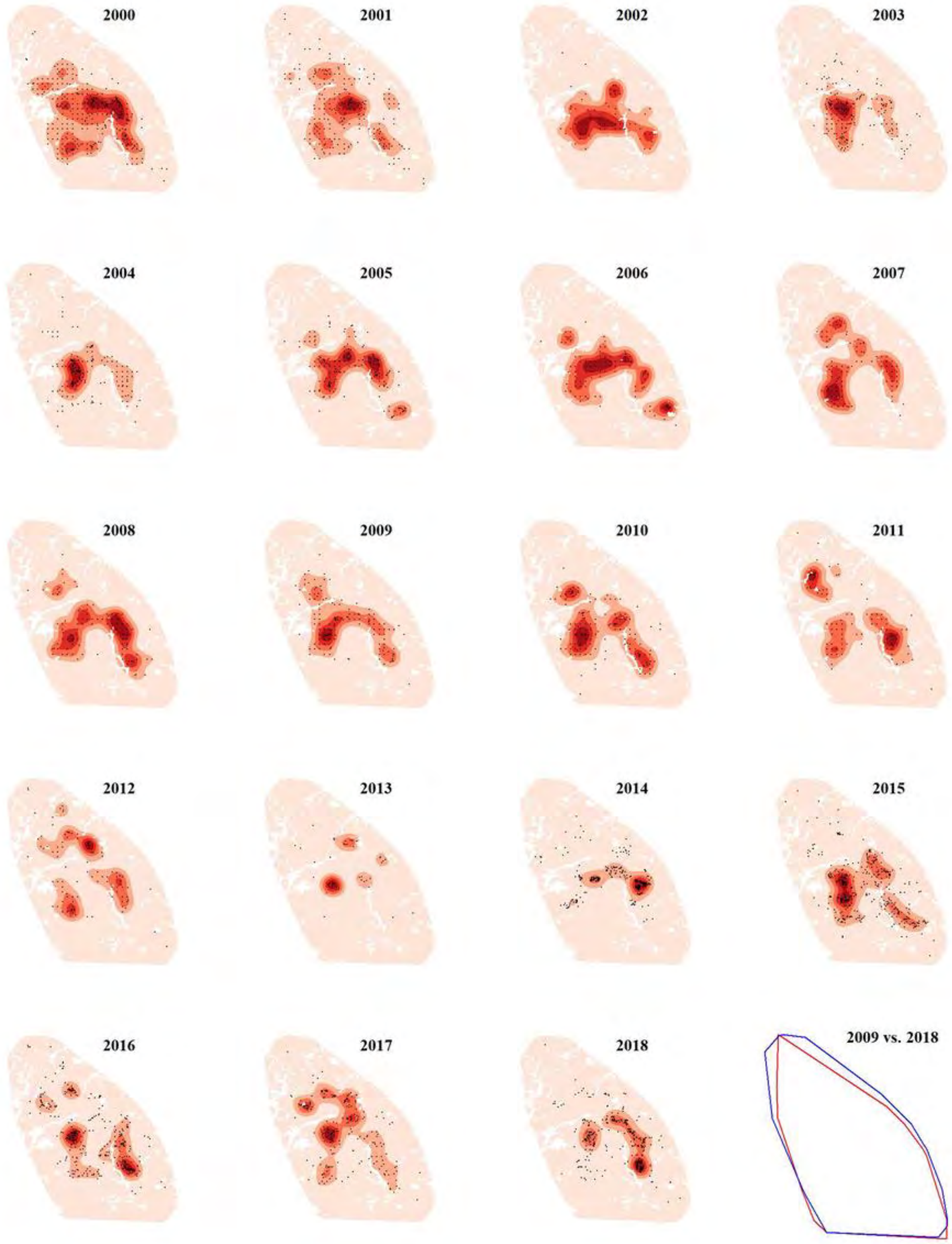


Figure S2.1 Kernel density plots of *L. timidus* 2000 to 2018, Peak District UK based on BRC data disaggregated to hectare scale, shown as black dots. Final plot shows minimum convex polygons for 2001 to 2009 (red) and 2010 to 2018 (blue).

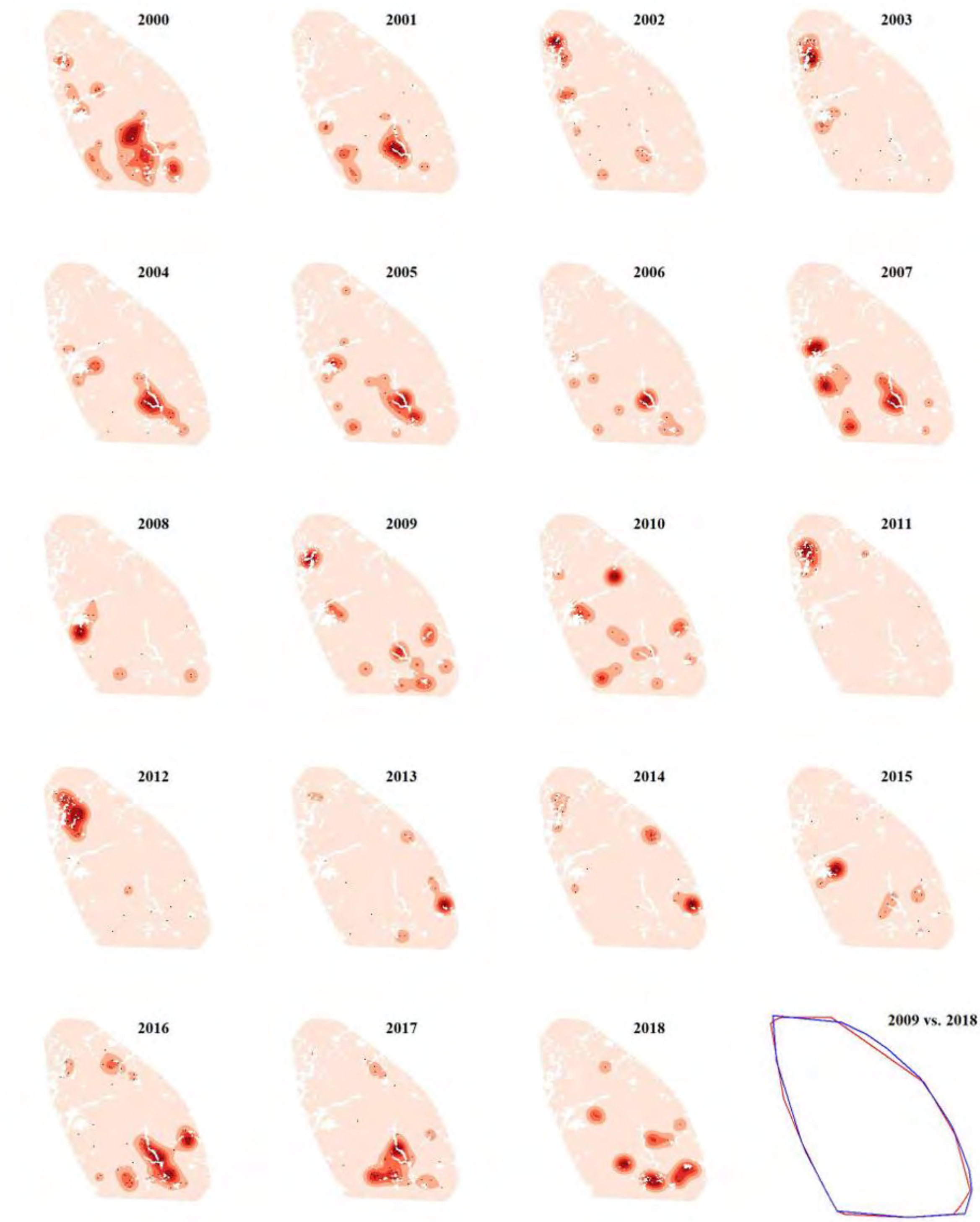
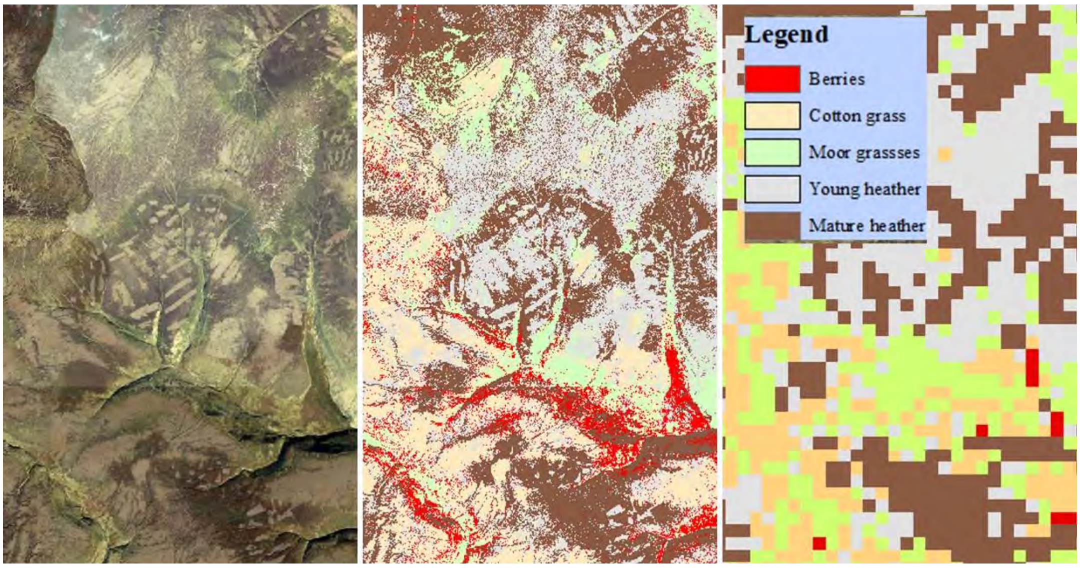


Figure S2.2 Kernel density plots of *L. europaeus* 2000 to 2018, Peak District UK based on BRC occurrence data disaggregated to hectare scale, shown as black dots. Final plot shows minimum convex polygons for 2001 to 2009 (red) and 2010 to 2018 (blue).



(b) **(c)**

Figure S2.3 Supervised classification sample images

(a) aerial photograph 5m pixels

(b) corresponding supervised classification 5m pixels

(c) supervised classification aggregated to 100m pixels

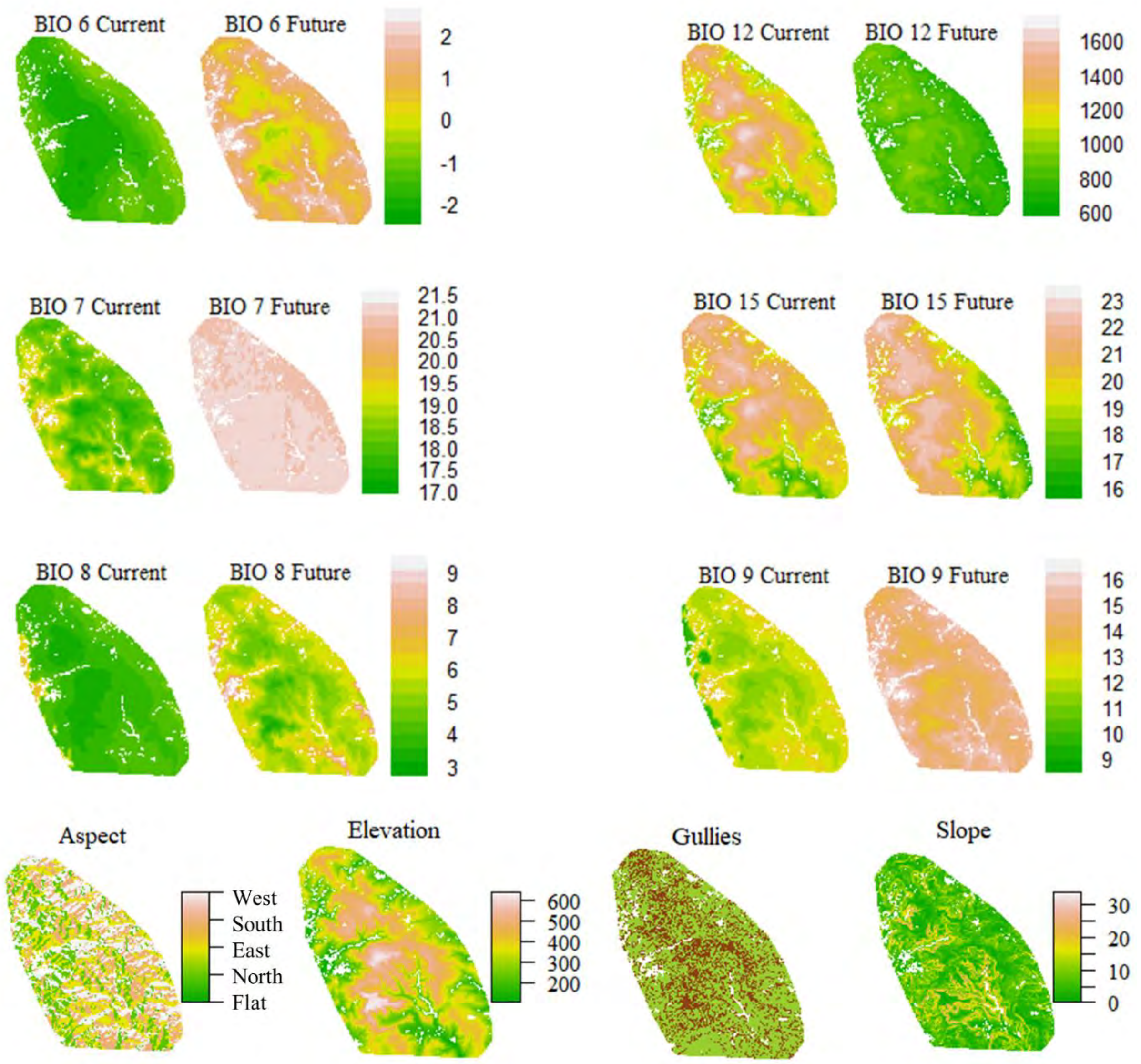


Figure S2.4 Climate niche model predictor layers showing current (year 2020) and future (year 2050) climatic variables and topography. Elevation is included for reference; it was not considered as a predictor. Gullies presence shown as brown pixels.

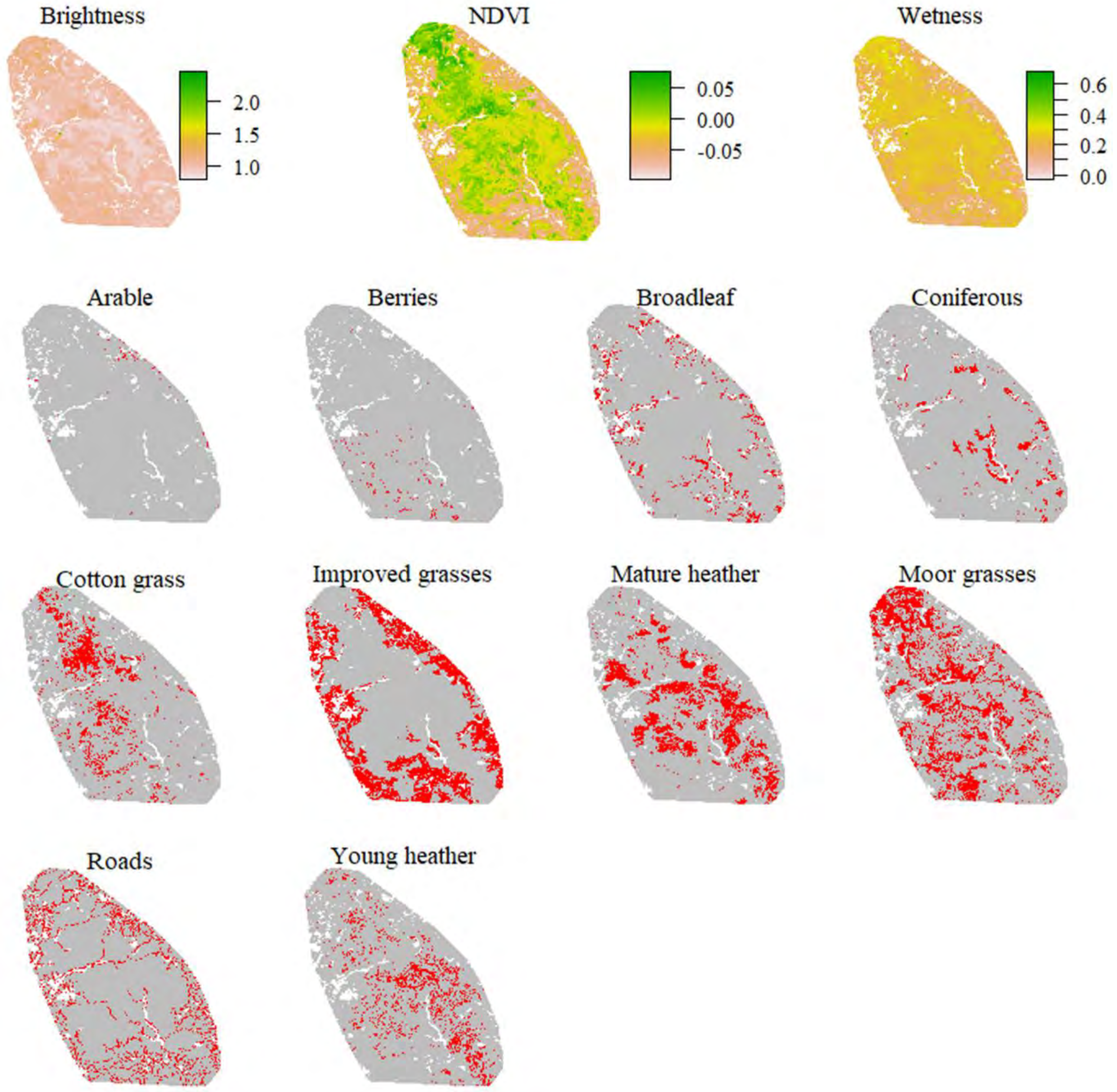
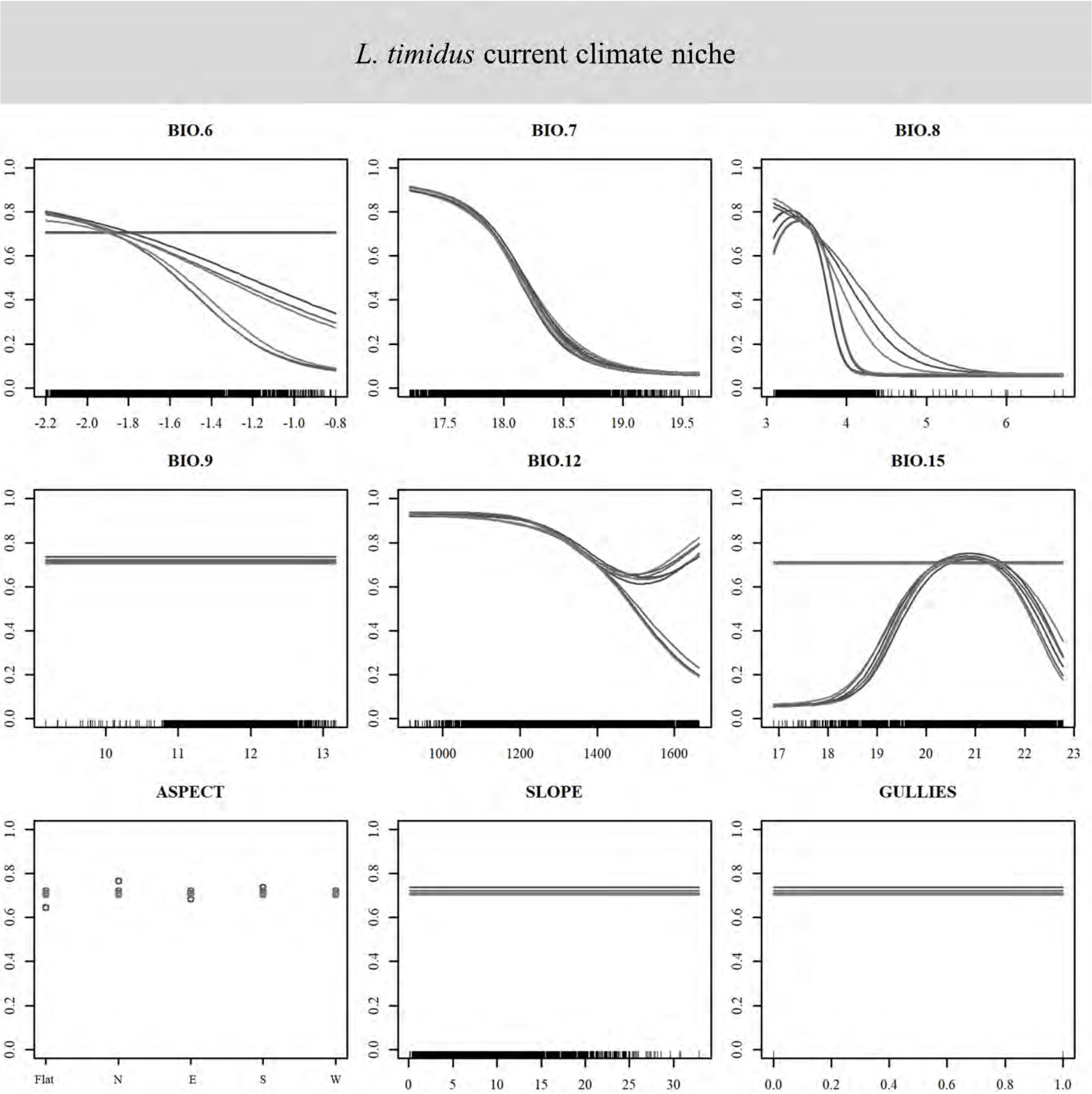
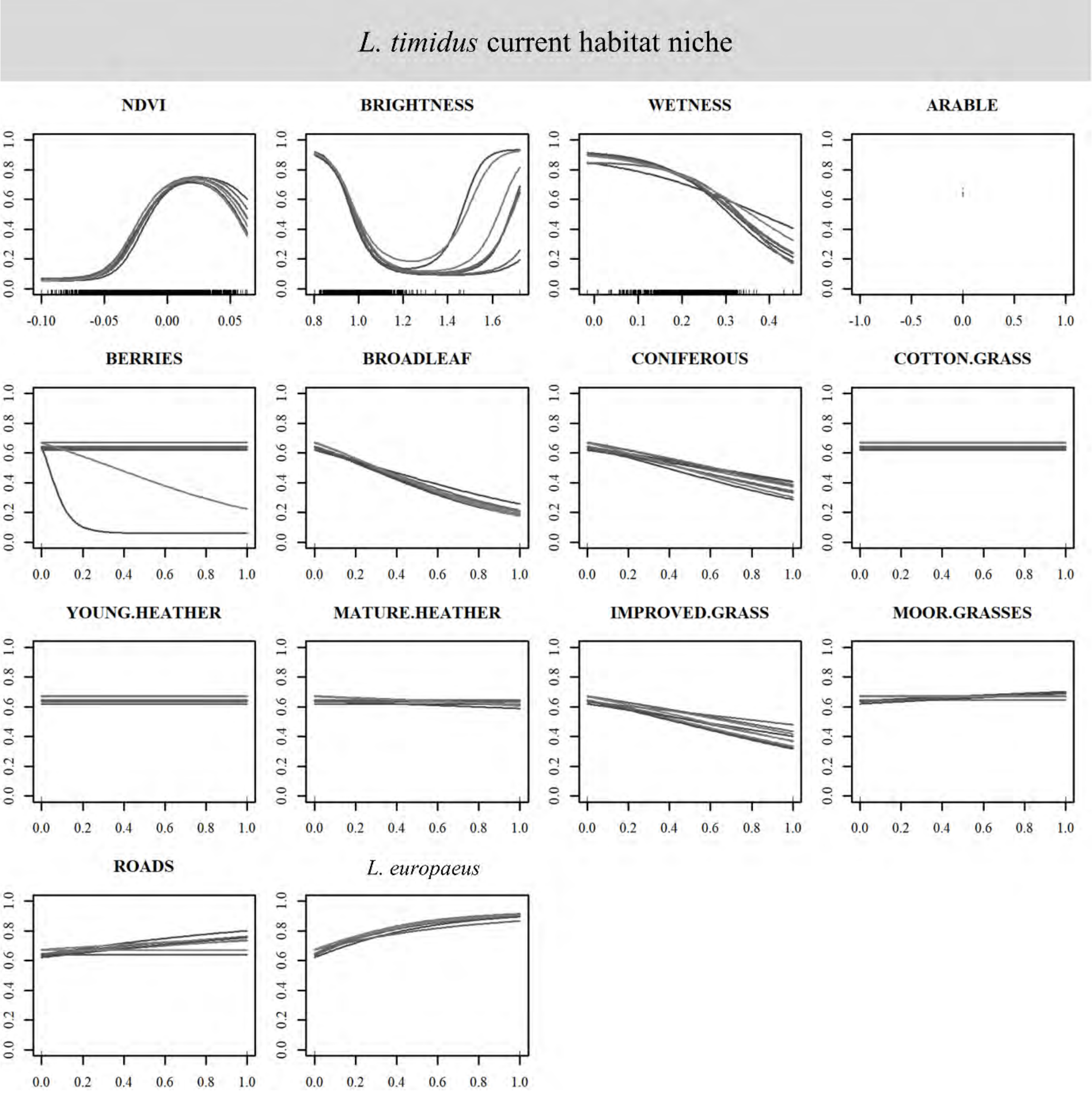
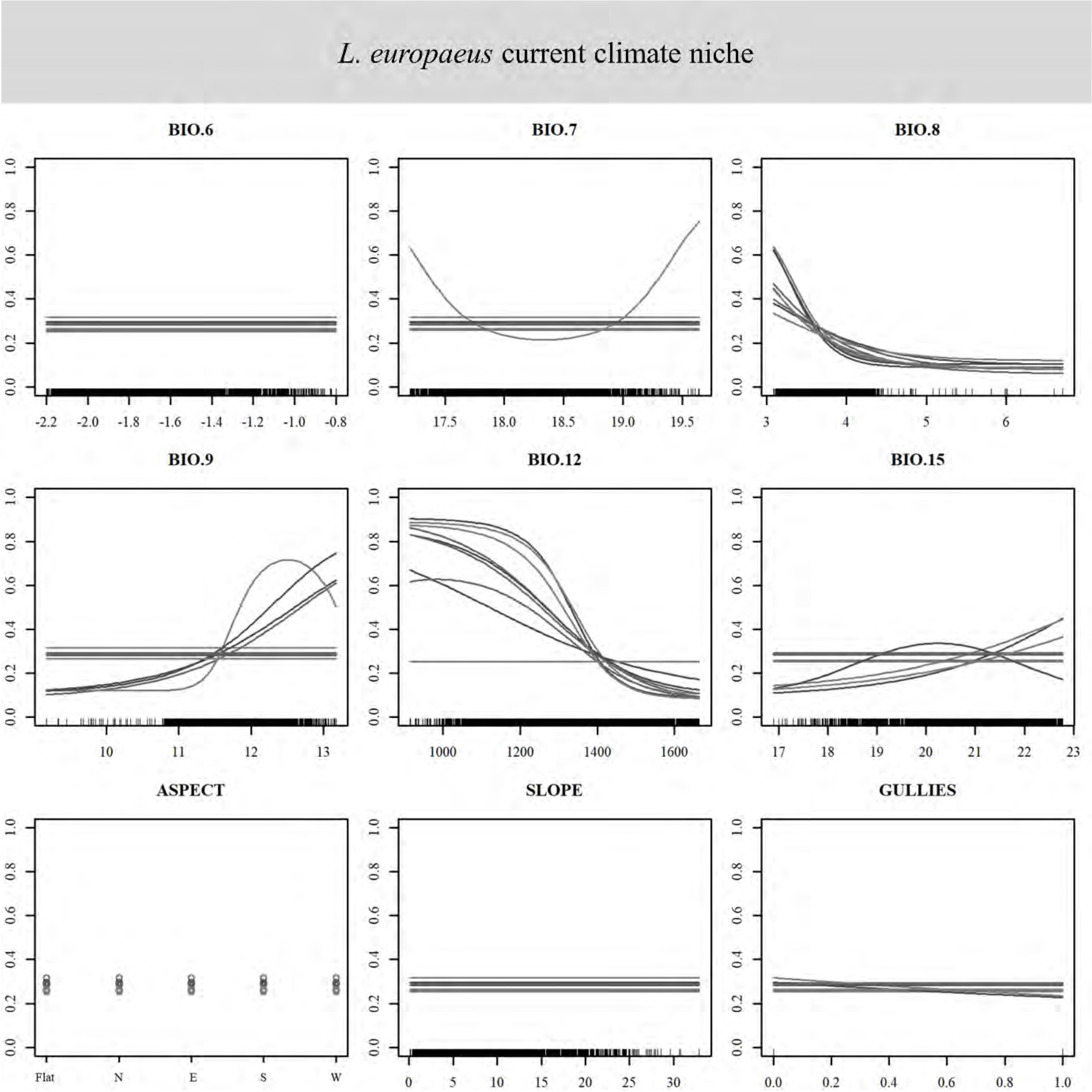


Figure S2.5 Habitat niche model predictor layers retained for niche modelling. Remote sensing derived vegetation productivity layers shown with graduated scales. Landcover predictors shown with red pixels indicating presence of feature


L. timidus current climate niche
BIO.6
BIO.7
BIO.8
BIO.9
BIO.12
BIO.15
ASPECT
SLOPE
GULLIES
0.0
0.2
0.4
0.6
0.8
1.0
-2.2
-2.0
-1.8
-1.6
-1.4
-1.2
-1.0
-0.8
17.5
18.0
18.5
19.0
19.5
3
4
5
6
10
11
12
13
1000
1200
1400
1600
17
18
19
20
21
22
23
Flat
N
E
S
W
0
5
10
15
20
25
30
0.0
0.2
0.4
0.6
0.8
1.0


L. timidus current habitat niche
NDVI
BRIGHTNESS
WETNESS
ARABLE
BERRIES
BROADLEAF
CONIFEROUS
COTTON.GRASS
YOUNG.HEATHER
MATURE.HEATHER
IMPROVED.GRASS
MOOR.GRASSES
ROADS
L. europaeus
0.0 0.2 0.4 0.6 0.8 1.0
-0.10 -0.05 0.00 0.05
0.8 1.0 1.2 1.4 1.6
0.0 0.1 0.2 0.3 0.4
-1.0 -0.5 0.0 0.5 1.0


L. europaeus current climate niche
BIO.6
BIO.7
BIO.8
BIO.9
BIO.12
BIO.15
ASPECT
SLOPE
GULLIES
0.0
0.2
0.4
0.6
0.8
1.0
-2.2
-2.0
-1.8
-1.6
-1.4
-1.2
-1.0
-0.8
17.5
18.0
18.5
19.0
19.5
3
4
5
6
10
11
12
13
1000
1200
1400
1600
17
18
19
20
21
22
23
Flat
N
E
S
W
0
5
10
15
20
25
30
0.0
0.2
0.4
0.6
0.8
1.0

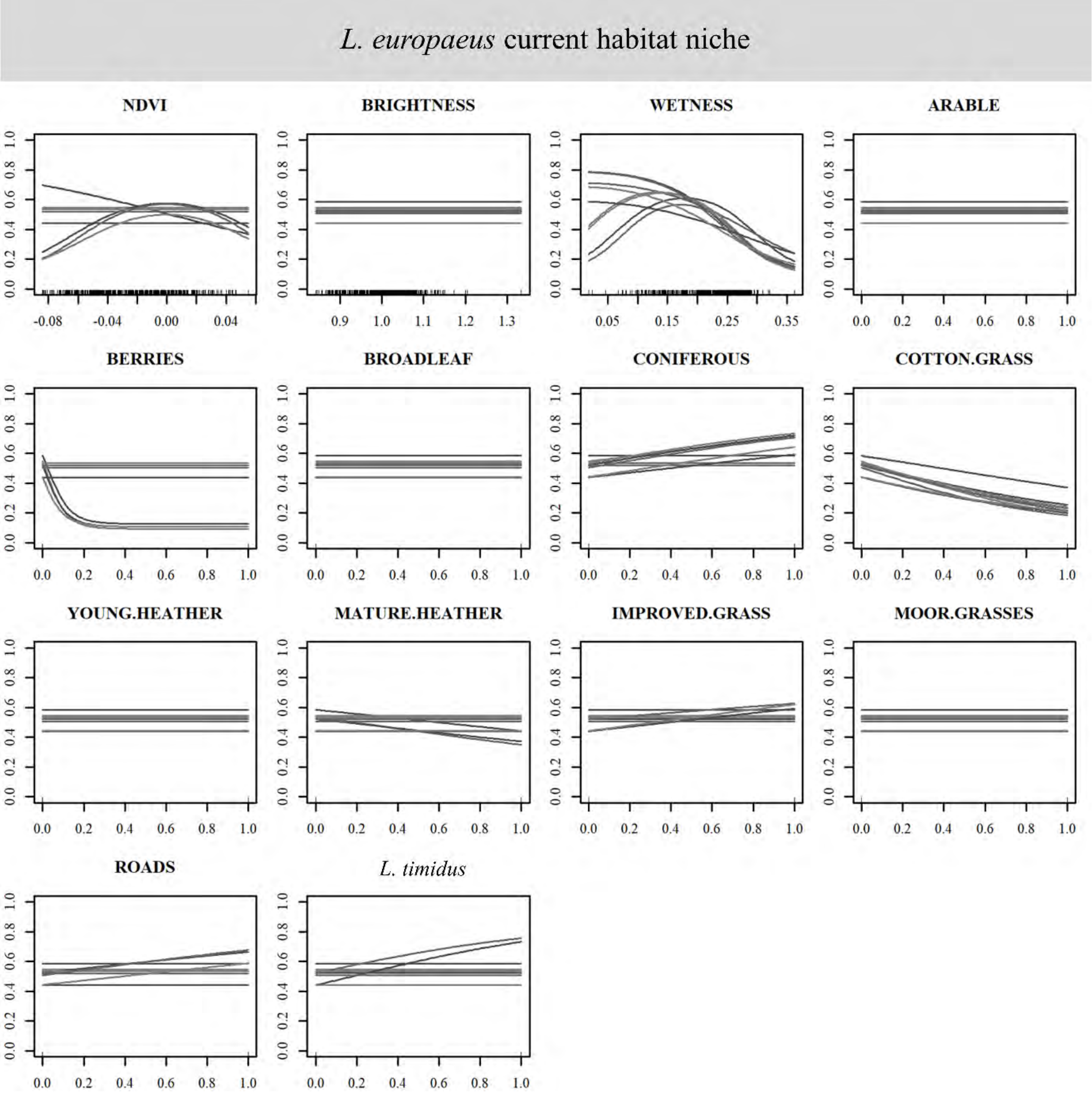


Figure S2.6 Evaluation strips of variable responses for each model. Curves are plotted with GLM algorithm and show the sensitivity of the model to each variable. The method does not account for interactions between variables. For each variable plot, the other remaining variables are set to mean.

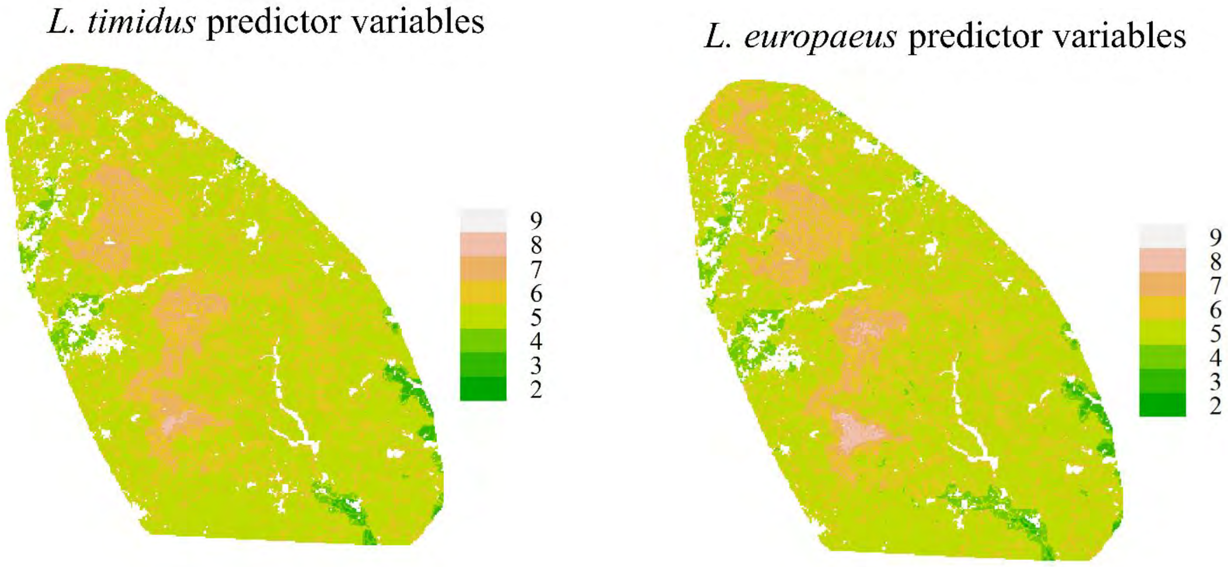


Figure S2.7 The number of predictor layers used for the future climate (year 2050) niche models. Scale shows number of layers used at each location, which is possible whenever value ranges are shared with original current climate (year 2020) predictors used to calibrate the models.

CHAPTER 3 ESTIMATING DENSITY OF MOUNTAIN HARES USING DISTANCE SAMPLING: A COMPARISON OF DAYLIGHT VISUAL SURVEYS, NIGHT-TIME THERMAL IMAGING AND CAMERA TRAPS

Image: Caught on camera: a damp dishevelled mountain hare which survived the fearsome freezing 2017-18 winter, notoriously referred to as the Beast from the East. Photo location was Bareholme Moss, just above Crowden Great Brook, Holme Moss, Derbyshire, England, UK. Date: 15th March 2018.

Chapter 3

Estimating density of mountain hares using distance sampling: a comparison of daylight visual surveys, night-time thermal imaging and camera traps

Authors

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Publication Reference

This chapter is published as:

Bedson, C.P.E., Thomas, L., Wheeler, P., Reid, N., Harris, W.E., Lloyd, H., Mallon, D. & Preziosi, R. 2021. Estimating density of mountain hares using distance sampling: a comparison of daylight visual surveys, night-time thermal imaging and camera traps. Wildlife Biology 2021: wlb.00802
doi: 10.2981/wlb.00802

Wildlife Biology 2021: wlb.00802
doi: 10.2981/wlb.00802

Subject Editor: Luca Corlatti. Editor-in-Chief: Ilse Storch. Accepted 27 April 2021

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Surveying cryptic, nocturnal animals is logistically challenging. Consequently, density estimates may be imprecise and uncertain. Survey innovations mitigate ecological and observational difficulties contributing to estimation variance. Thus, comparisons of survey techniques are critical to evaluate estimates of abundance. We simultaneously compared three methods for observing mountain hare *Lepus timidus* using Distance sampling to estimate abundance. Daylight visual surveys achieved 41 detections, estimating density at 14.3 hares km^{-2} (95%CI 6.3–32.5) resulting in the lowest estimate and widest confidence interval. Night-time thermal imaging achieved 206 detections, estimating density at 12.1 hares km^{-2} (95%CI 7.6–19.4). Thermal imaging captured more observations at furthest distances, and detected larger group sizes. Camera traps achieved 3705 night-time detections, estimating density at 22.6 hares km^{-2} (95%CI 17.1–29.9). Between the methods, detections were spatially correlated, although the estimates of density varied. Our results suggest that daylight visual surveys tended to underestimate density, failing to reflect nocturnal activity. Thermal imaging captured nocturnal activity, providing a higher detection rate, but required fine weather. Camera traps captured nocturnal activity, and operated 24/7 throughout harsh weather, but needed careful consideration of empirical assumptions. We discuss the merits and limitations of each method with respect to the estimation of population density in the field.

Keywords: camera traps, cryptic animals, distance sampling, population monitoring, survey methods, thermal imager, uplands

In a global era of biodiversity crisis, conservation monitoring which allows us to establish trends in wild animal abundance, is essential. The provision of reliable census estimates are considered vital to guide management interventions aimed at protecting vulnerable species (Krebs 1989). Effective surveys must be designed to reflect species distribution and life history traits which may affect animal detection. Studies must comprise sites which represent the range of habitats, climate and topography occupied by the target species and this will both inform and constrain survey methods (Sutherland 2006).

The mountain hare *Lepus timidus* is Britain's only native lagomorph and an icon for upland habitats and their conservation. Reliable estimates of mountain hare population density are important to inform conservation assessments and to evaluate the impact of anthropogenic disturbance on population numbers (e.g. impact of roadkill or control efforts on grouse moorland). Yet hares are mostly nocturnal mammals and can be difficult to detect (Newey et al. 2011, Petrovan et al. 2011). Despite having a white pelage in winter, hares are adept at hiding by day in rough vegetation: they lie motionless, flattening to 15 cm height, sometimes in shallow depressions, burrows or amongst rocks and even fleeing unseen. Hares emerge at night to feed (Hewson and Hinge 1990, Harris and Yalden 2008) and consequently daytime observation is characterised by low detection rates (Dingerkus and Montgomery 2002).

Surveying elusive or nocturnal animals is particularly challenging in environments such as upland terrains which often experience poor weather. Mountain hare habitats are also frequently rugose and difficult to access, creating safety issues for monitoring, especially at night. Mountain hares

---

3.1 Abstract

Surveying cryptic, nocturnal animals is logistically challenging. Consequently, density estimates may be imprecise and uncertain. Survey innovations mitigate ecological and observational difficulties contributing to estimation variance. Thus, comparisons of survey techniques are critical to evaluate estimates of abundance. We simultaneously compared three methods for observing mountain hare (*Lepus timidus*) using Distance sampling to estimate abundance. Daylight visual surveys achieved 41 detections, estimating density at 14.3 hares km^{-2} (95%CI 6.3–32.5) resulting in the lowest estimate and widest confidence interval. Night-time thermal imaging achieved 206 detections, estimating density at 12.1 hares km^{-2} (95%CI 7.6–19.4). Thermal imaging captured more observations at furthest distances, and detected larger group sizes. Camera traps achieved 3,705 night-time detections, estimating density at 22.6 hares km^{-2} (95%CI 17.1–29.9). Between the methods, detections were spatially correlated, although the estimates of density varied. Our results suggest that daylight visual surveys tended to underestimate density, failing to reflect nocturnal activity. Thermal imaging captured nocturnal activity, providing a higher detection rate, but required fine weather. Camera traps captured nocturnal activity, and operated 24/7 throughout harsh weather, but needed careful consideration of empirical assumptions. We discuss the merits and limitations of each method with respect to the estimation of population density in the field.

Key words

cryptic animals, uplands, survey methods, population monitoring, distance sampling, camera traps, thermal imager

3.2 Introduction

In a global era of biodiversity crisis, conservation monitoring which allows us to establish trends in wild animal abundance, is essential. The provision of reliable census estimates are considered vital to guide management interventions aimed at protecting vulnerable species (Krebs 1989). Effective surveys must be designed to reflect species distribution and life history traits which may affect animal detection. Studies must comprise sites which represent the range of habitats, climate and topography occupied by the target species and this will both inform and constrain survey methods (Sutherland 2006).

The mountain hare (*Lepus timidus*) is Britain's only native lagomorph and an icon for upland habitats and their conservation. Reliable estimates of mountain hare population density are important to inform conservation assessments and to evaluate the impact of anthropogenic disturbance on population numbers (e.g. impact of roadkill or control efforts on grouse moorland). Yet hares are mostly nocturnal mammals and can be difficult to detect (Newey et al. 2011; Petrovan et al. 2011). Despite having a white pelage in winter, hares are adept at hiding by day in rough vegetation: they lie motionless, flattening to 15 cm height, sometimes in shallow depressions, burrows or amongst rocks and even fleeing unseen. Hares emerge at night to feed (Hewson & Hinge 1990, Harris & Yalden 2008) and consequently daytime observation is characterised by low detection rates (Dingerkus & Montgomery 2002).

Surveying evasive and nocturnal animals is particularly challenging in environments such as upland terrains which often experience poor weather. Mountain hare habitats are also frequently rugose and difficult to access, creating safety issues for monitoring, especially at night. Mountain hares frequent low hills, gullies and deep vegetation, making detection difficult (Newey et al. 2018). Snow may hamper daytime observations of white camouflaged mountain hares. Effective monitoring therefore requires multiple observation points and benign weather.

Considering the suite of study methods available for wildlife monitoring, mark-recapture is regarded as the most reliable for hares (Boulanger & Krebs 1994). However, addressing welfare concerns surrounding the capture and handling of animals is resource intensive, particularly in rough terrain, making this method expensive and impractical. Faecal pellet counts can provide a useful index in areas of high hare density, assuming constant accumulation rates (Newey et al. 2003). Whilst it is also possible to obtain DNA from faecal pellets for genetic population monitoring with molecular mark-recapture, both plant material in the pellets and fast decay rates can reduce PCR effectiveness, requiring larger sample sizes and greater field and laboratory work and costs (DeMay et al. 2013).

Direct observation methods by day, such as line transect sampling, are commonly used yet are vulnerable to achieving fewer observations when such predominantly nocturnal animals remain undetected (Buckland et al. 2001). Areas of low density may result in low encounter rates and wide variance in estimates (Newey et al. 2018). Night-time spotlight surveys may miss animals as they rely on eyeshine reflections, and frequently sample along roads which animals may avoid and which locations represent only a small fraction of upland habitat (Reid et al. 2007; Reid & Montgomery 2010). Thermal imaging reduces false negatives by increasing target detections, contrasting body heat against a cold backdrop at night (Havens & Sharp 2016) but if the aim is to estimate density it also requires a means to determine distance to the object in darkness. Camera trapping provides a greater continuous survey effort including during night peak activity periods thus increasing total numbers of detections (Caravaggi et al. 2018), and with virtually no observer field presence to disturb animals (Sollman 2018).

In this study we compared three survey methods of mountain hares in upland habitat to estimate density and considered factors relating to spatial variation of hare detections: 1) daylight visual surveys, 2) night-time thermal imaging point transects and 3) fixed position camera traps. We analysed data from each method using comparable distance sampling models to estimate density and associated precision. For each method we recorded survey effort, observations, distances to target animals and group sizes as inputs to estimate density. As camera trap distance sampling methods are relatively recent, we also explored how different assumptions of space, time and animal behaviour affected density estimates. Since actual densities or population size were not known, we could not be certain which density estimate of the three methods might be closest to the truth. Nonetheless the overall precision of parameters and estimates could be compared. We compared variation of estimates among methods and survey sites, the effect of terrain type and how detection rates changed throughout the study period. We evaluate the merits and assumptions of each method relative to our findings, to inform study design decisions for conservation monitoring.

3.3 Methods and materials

3.3.1 Study site

Surveys took place at Holme Moss, a large hill, elevation 582m, situated in the north of England, UK (Fig. 3.1). Mountain hares were once native to England yet became extinct ~ 6,000 years ago (Yalden 1971). They were reintroduced to Holme Moss in the 1870s for sport shooting (Stubbs 1929; Yalden 1971). In this area historic records suggest the number of 1km squares occupied by mountain hares as ranging from 16 (Yalden 1971) up to 35 (Mallon et al. 2003). This group of hares is potentially partially isolated from other populations elsewhere in the area by reservoir systems and major road networks. Whilst sightings of mountain hares on Holme Moss have been particularly frequent in the past (Mallon et al. 2003), farmers and landowners report perceived declines across the site in the last decade. The local density on Holme Moss has never been formally quantified. Holme Moss comprises a flat plateau with peat gullies and steep sided valleys (Fig. 3.1) (Tallis 1987). The area consists of blanket bog vegetation dominated by heather (*Calluna vulgaris),* bilberry (*Vaccinium myrtillis*) and cotton grass (*Eriphorum* spp.). Over the last 200 years habitat conditions have declined as both acid rain caused peat layer reduction and intensive sheep grazing led to widespread vegetation loss (Anderson & Shimwell 1981). Most of the hill is managed by the RSPB Dove Stone reserve engaged in blanket bog restoration.

The study focused on the entire blanket bog plateau of Holme Moss, where elevation was above 335m i.e. the lower elevation range of mountain hare occurrence (Yalden 1971), and as limited by major roads to the north and east and different habitats to the south and west. This comprised 49km^2. Within this area we selected a smaller 5x5km central area for daylight visual surveys, thermal imager and camera trap surveys. This considered the area that could be covered on foot by two full time staff conducting field logistics: Holme Moss is largely pathless, often hazardous underfoot. Winter day lengths are short. The location of the 5x5km area was chosen to be central, equidistant from roads and habitat edges, avoiding edge areas frequented by the public, thereby reducing camera theft risk, though accepting this choice of centroid might cause bias. Within this area we then randomly selected (R-package 'sample') 5 x 1km squares as random cluster samples of points and transects, being representative of the flat blanket bog. The location of an additional sixth site was also randomly selected, yet at the request of wildlife agencies we altered its shape to comprise a narrow long strip to facilitate monitoring of an historic high density area (Mallon et al. 2003), accepting this might bias results. Contemporary density and distribution of hares was unknown. The 1km size of each study site enabled comprehensive continuous observation of terrain, detecting potential changes in hare occurrence over a few hundred metres. Hare home ranges can be small (0.1 to 0.8km^2), non-territorial, overlapping and hares sometimes group together (Hewson and Hinge 1990; Hulbert et al. 1996, Rao et al. 2003, Harrison 2011). The small 1km site scale facilitated efficient management of camera arrays and enabled observers to learn of local topography and hazards, prior to subsequent night surveys for thermal imaging. Within the six study sites, we chose transect and point layouts which would cover the same locations, to capture the same local variation. However some of the survey locations between methods differed slightly to account for the different observation ranges of equipment. Surveys occurred from November 2017 to May 2018 (Fig. S1). The period was characterised by exceptionally severe weather including seven heavy snowfalls (UK Met Office 2019).

3.3.2 Daylight visual surveys

Daylight visual surveys took place using line transects following Ordnance Survey (2015) Explorer Map 1 grid lines which bounded each survey site (Fig. 3.1). Transects were square circuits (Buckland et al. 2001: 237), intended to alleviate detection bias arising from a low winter sun position when walking different cardinal directions, wind or local topography effects, whilst enabling efficient use of survey time. Whilst surveys were conducted only during good visibility, poor weather and persistent snow cover limited the survey opportunities to only one visit per site transect. Observer routes were guided by a handheld GPS (Garmin GPSMAP64ST). A slow, measured walk was used (~ 1km per hour), with frequent scanning of the landscape using binoculars (Fig. 3.2). The location of each mountain hare was recorded, measuring radial distance from the observer with a laser range finder (Nikon ProStaff 7i) (maximum range 1,100m) and angle using a compass. These measurements allowed the calculation of the perpendicular distance of sightings from the line, and also enabled the location of each hare to be mapped. During surveys, mountain hares bore white pelage contrasting against the green and brown moorland. Hares were often lying-up and not detected until within 30m range (Fig. 3.2). Whilst some hares fled from the observer, this occurred within the range of vision, so distance and angles were measured to point of origin.

3.3.3 Night-time thermal imaging

We conducted nocturnal surveys at point transect locations using an Armasight Command 336 HD 30HZ 75 mm biocular (two view lenses) thermal camera (FLIR, USA), with a range of 2km, and a refresh rate 30Hz which enabled species identification of moving animals (Fig. 3.2). The camera was fitted with an Advanced Modular Range Finder 2200 (FLIR, USA) which operated in darkness. In trials, distances up to 1.8km could be measured. This assemblage was mounted on a tripod at each point location each spaced ~333 metres apart (about the diameter of a single hare home range) along the same 1km grid lines used during daylight visual surveys (Fig. 3.1). Thus, whilst a different survey method was used at a different time of day, survey sites were the same. Surveys did not occur at a location that had received a visit that day for other survey purposes, to ensure hares had not been disturbed. Points at sites 1 to 4 were visited 2 to 3 times over the winter; points at sites 5 and 6 were visited once only.

Surveys were conducted one hour after sunset with clear visibility though some surveys were curtailed by fog or high winds. Some surveys occurred on snow which assisted detection of hares. Walking by night from point to point took approximately 20 to 30 minutes. A red-light head-torch was used by observers to guide the way between points, minimising disturbance. Hares were seen twice only during transit. Once set up, the thermal imager assemblage was immobile; care was taken to situate it with the best field of view within 20m of the GPS point. Whilst setting up the thermal imager vantage point no hares were observed within 30m. Surveys at each point transect consisted of complete 360° field scans and typically took 10-20 minutes per point. Extensive practice with the thermal imager using the setting "white hot" ensured identification of hares which were easily distinguished from grouse (*Lagopus lagopus*) whose feathers blocked heat radiation except for beaks, and foxes (*Vulpes vulpes*) that were much larger (Fig. 3.2). It was assumed that all observed animals having the shape of lagomorph were mountain hares, not European brown hares (*L. europaeus*) and not rabbits (*Oryctolagus cuniculus*). For each detection, angle and distance measurements were recorded as during daylight surveys. Three sightings of leverets were excluded, to estimate adult densities only.

3.3.4 Camera trapping

We placed between 12 to 16 camera traps at each of the six survey sites (Fig. 3.1). Due to logistical constraints, camera traps were deployed at Site 1 before being moved sequentially to Site 6 (they could not be deployed simultaneously). Cameras were left *in situ* for two to five weeks at each site (Fig. S1), depending on weather conditions, camera performance and perceived risk of theft. Cameras were sited at the same locations as daylight visual surveys and thermal imaging surveys, along the Ordnance Survey map bounding grid lines of each site as well as several placed in the centre of each square for fuller coverage. Distances between cameras were thus 333m, again this being the assumed home range diameter of mountain hares. Cameras were 14MP NatureView No Glow (Bushnell, USA), set to high sensitivity. Pilot tests showed a large number of false detections would be elicited (wind blown vegetation). Capturing video might expend battery and memory capacity before revisits by staff and also make image review time excessive. Thus cameras were instead set to trigger at 1 second intervals with time-stamp recording. Camera functioning was evidenced by a 12 hourly “field scan” setting. Cameras were installed on posts at 40cm above ground level (Fig. 3.2) set facing north to avoid false triggers by sun movements. Bamboo canes were placed in a line at intervals of 2, 4, 6, 8 and 10m in front of each camera to measure the distance of each hare to the camera at 1 metre spacing (Fig. 3.2) (Hofmeester et al. 2016; Howe et al. 2017). Photos were managed with TIMELAPSE 2 (University of Calgary, Canada) software. Images were catalogued by location, date and time.

We reviewed the frequency of camera images of hares and considered one second as representing the survey snapshot period ("k") for point counts following advice from Howe et al. (2017) to use time periods < 3 seconds. For each positive detection we recorded each individual's radial distance to camera for distance sampling estimation. In a few cases with darkness or poor focus this was difficult to determine. Images showed some hares, having appeared in the camera zone, inspected the distance marker cane or the camera itself. We considered this attraction behaviour, known to contribute to sampling bias (Corlatti et al., 2019) and discounted those images.

Unlike daylight visual surveys and night-time thermal imaging where surveys were time limited, camera traps can make detections 24/7. No detections are likely to be made when an animal is resting and so survey effort during daylight is highly vulnerable to false negatives, potentially lowering average density estimates. We defined the hare activity cycle using a frequency histogram of detections against each hour of the 24-hour cycle, fitting a smoothed density function for each site according to standard methods (Ridout and Linkie 2009; Rowcliffe et al. 2014). Conservative approaches may consider analysis which refers to the peak diel periods when ~50% of activity occurs (Frey et al. 2017) or ≥55% activity (McGowan et al.2019). However our camera sites occurred over four months, winter solstice to spring equinox, when nights became shorter. Thus when assessing the activity frequency densities and potential correlations between sites with R-package 'overlap' (Meredith and Ridout 2020) we found different timings of bimodal activity patterns. For consistency we therefore defined the night-time period as sunset-to-sunrise at the mid-term date per site (HM Nautical Almanac Office 2019) thought to provide accurate levels of activity (Vazquez et al. 2019). This night-time period encompassed >95% of all camera trap detections.

3.3.5 Distance sampling

Data from each method were analysed using software Distance 7.2 (Thomas et al. 2010) including site, survey effort, number of detections, distance to each detection and cluster size (Buckland et al. 2001).

Daylight visual surveys were analysed using "line transect" protocols and thermal imaging as "points", each assuming 360° field-of-view. Camera trap surveys were also analysed as points; however survey effort had a restricted 42° field-of-view of each camera, thus distance analysis for camera trap data multiplied total effort "k" by 42/360 following Howe et al. (2017). Model fit was optimised in each case using truncation of the most distant detections and variable bin width as appropriate. Models assessed included uniform, half-normal and hazard-rate models; and model averaging was also considered. Models were evaluated by referring to Akaike Information Criterion (AIC), χ^2 goodness-of-fit test values, detection probability (P) values and coefficient of variation (P CV) using established methods (Buckland et al. 2001). As sequences of camera trap detections occurring over several seconds were not independent we calculated the overdispersion factor ($\hat{C}$) and used log likelihood ($\mathscr{L}$) to calculate QAIC, i.e. the two step model evaluation approach of Howe et al. (2018).

3.3.6 Statistical analysis

Descriptive statistics were tabulated for a suite of parameters capturing survey effort, numbers of detections, detection distances, and encounter rates for each survey method. Based on the surveys' efforts and results, we calculated and compared the level of effort to achieve a required precision of density estimate, using formulae from Buckland et al. (2001). Spatial autocorrelation of sightings (encounters) was examined with kernel density maps of detections using ArcGIS v10.6.1 (ESRI, California, USA) and tested using Moran's I Index for each survey method. Comparison of sighting densities between the three methods was assessed by Pearson correlation of the kernel density maps. ArcGIS was used to map topographical gullies plotted as shapefile vector data (Ordnance Survey 2018), converted into a raster of gully density using the line density and polygon to raster toolbox functions (100m cell size). The relationship between hare encounter rates and gully density was examined using linear regression for each survey method. Temporal trends in camera trap encounter rate were examined using a separate General Linear Mixed Model (GLMM) fitting “Site” as a Random Factor to account for multiple observations per site (multiple days recording) and the sequential deployment of cameras at different sites, and with “Days since start of survey” fitted as Fixed Effect. Daily detections followed a negative binomial distribution. Statistical analyses were conducted using R version 3.6.1 (R Core Team 2020) and R-package 'lme4' (Bates et al. 2015) for linear models following Crawley (2002).

3.4 Results

3.4.1 Daylight visual surveys

Over five days, the six sites were surveyed for a total of 26 hours (Table 3.1, Fig. S1). Daylight visual line transect surveys required 3-7 hours per transect which were 4-8km in length. Mean radial detection distance was 152m and the furthest was 532m. Thus, the survey rate was 0.98km^2 per hour (Table 3.1). In total, 41 mountain hare detections were recorded with 1 detection every 0.63hrs (~38mins). During daylight hours 95% of the detections were of solitary individuals, the remainder being pairs (Table 3.1). Owing to hiding and flushing behaviour of hares, 16 detections occurred within 30m of the observer. Thus to enable a choice of detection function models, we truncated data at 100m and assigned observations to bins at 5m, 10m, 20m and 100m (Table 3.2). Candidate models showed high χ^2 goodness-of-fit (GOF) values (>0.31) with similar detection probabilities. The half-normal model reported lowest AIC, P=0.28, (*cv*)=0.20 and was selected for density estimation. (Table 3.2, Fig. 3(a)). Following data truncation, encounter rate was 0.82/km, (*cv*)= 0.31 and observations were singles making 1.00 cluster size (Table 3.3). The contribution to variation of density estimate was encounter rate (72.5%) and detection probability (27.5%).

3.4.2 Thermal imaging

Over eleven nights, a total of 114 point transects located along the boundary of the six sites were surveyed for a total of 97 hours (Table 3.1, Fig. S1). Surveys needed 5-7 hours to cover up to 12 points per night. Mean detection distance was 264m and the furthest was 740m. Thus, the survey rate was 1.32km^2 per hour or 0.00587km^2 (i.e. 5,870m^2) per point (Table 3.1). In total, 206 mountain hare detections were made with 1 detection every 0.47 hrs (~28mins). During darkness 74% of detections were solitary individuals, the remainder groups of up to 8 hares (Table 3.1). For modelling, detections were truncated at 350m. All candidate detection functions achieved model fit (Table 2). The hazard-rate model had lowest AIC and highest χ^2 GOF=0.78 with P=0.34, (*cv*)=0.21 and was selected for density estimation (Fig. 3.3(b)). Following data truncation encounter rate was 1.33/k, (*cv*)=0.12 and estimated cluster size 1.31, (*cv*)=0.04 (Table 3.3). The contributors to variation of density estimate were encounter rate (24.5%), detection probability (73.9%), cluster size (1.6%).

3.4.3 Camera traps

Over four months, a total of 91 camera locations were installed throughout the six survey squares (total = 1,800 days i.e. 27,544 night hours) (Table 3.1, Fig.S1. In total, 107,000 images were captured, retrieving 5,112 images of mountain hares per 1 second snapshot window. The remaining images were false triggers: wind-blown vegetation or other animals e.g. foxes, stoats (*Mustela erminea*). Of these images 1,329 showed hares attracted to marker canes or the camera, so were excluded, leaving 3,783 separate detection events.

Of these, just 78 detections (2%) occurred by day; 3,705 detections (98%) during night-time, averaging 1 detection per 8.5 hours (Table 3.1). Night-time showed the largest activity peak after sunset, followed by moderate activity periods, and a distinct peak before dawn (Fig. 3.4). This pattern was similar at each site for the study duration: activity occurring over 17 night hours late November (Site 1), compressing into 13 night hours late March (Site 6). However the timing of night-time activity peaks differed between sites. The highest correlation was 86% between sites 1 and 5; the lowest correlation 51% between sites 3 and 6. Based on night-time detections, the mean detection distance was 2.4m and the furthest was 12m, and 95% of detections were within 5m of the camera (Table 3.1). Thus, the survey rate averaged 0.0003km^2 (i.e. 30.0 m^2) per camera (Table 3.1). Night-time detections for distance analysis modelling assessments were allocated to bins at 1m, 2m, 3-4m and 5m (Table 3.2). Having calculated QAIC and (C) for candidate models, the latter was lowest for the hazard-rate model at 1.8 and χ^2 GOF=0.18, thus was selected for reporting with P=0.17, (*cv*)=0.03 (Table 3.2 Fig. 3(c)). Camera trap encounter rate was 0.00030/k, (*cv*)=0.14(Table 3.3; Table S1).

Cluster size was 1.00, (*cv*=0.01). The contribution of variation to the density estimate was encounter rate (95.4%) and detection probability (4.5%).

3.4.4 Comparison of methods

Distance sampling models from daylight visual surveys estimated density at 14.3 hares km^{-2} (95%CI 6.3–32.5). Night-time thermal imaging from points estimated density at 12.1 hares km^{-2} (95%CI 7.6–19.4). Camera trapping estimated density was 22.6 hares km^{-2} (95%CI 17.1–29.9) (Table 3.3).

Extrapolated to the entire 49km^2 study site at Holme Moss, density estimates suggested a total population of 701 hares (95% CI 310–1,587) from daylight visual surveys, 593 hares (95% CI 372–951) from thermal imaging and 1,103 hares (95% CI 834–1,458) from camera traps (Table 3.3).

Assessing the density estimates and the effort required to achieve reliable precision i.e. 20% coefficient of variation, daylight visual surveys would require 109km of transects; thermal imagers would require 164 points; and camera traps would require 45 installations (Fig. 3.6). Comparing field effort daylight visual surveys surveying at 1.2km per hour would require 89 hours effort; thermal imager surveying 1.2 points per hour would need 140 hours effort. Camera traps needing 3 hours per installation (1h set up,1h revisit, 1h take down) would require 134 hours of field effort and if a manual image review process was used (e.g. Timelapse software with auto-completing data entry, estimating 15 seconds per image), a further 218 hours of desk time (Fig.3.5).

3.4.5 Spatial and temporal variation

Considering sighting locations per site (untruncated data), daylight visual surveys showed large differences of sightings (encounter rates) with site 3 lowest at 0.2km^{-1} and site 4 highest at 2.5km^{-1}, with a sparse distribution except for sites 2 and 4 (Fig. 3.6). Thermal imager observations occurred at a mean rate from 1.0 / point (site 5) to 3.9 / point (site 4) (Fig. 3.6) and appeared to show 2 clumped distributions around site 4 (Fig. 3.6). Of the thermal imager points, 99 achieved detections, 15 did not, indicating mostly widespread presence of hares across all sites. Camera trap observations occurred at a mean rate from 0.0002/k (site 3) to 0.0005/k (site 4), and showed the most intense occurrence around site 4 (Fig. 3.6). Of the 91 cameras, 77 achieved detections and 14 made no detection, indicating a widespread distribution though with some negative locations.

Hare detections were not spatially autocorrelated using any survey method (Moran's $I_{\text{daylight visual}} = -0.12$, $Z = 0.12$; Moran's $I_{\text{thermal imaging}} = 0.07$, $Z = 0.99$; Moran's $I_{\text{camera traps}} = -0.15$, $Z = -0.27$). Sighting density was strongly spatially correlated between the three methods (Pearson $r_{\text{daylight visual} \sim \text{thermal imager}} = 0.55$, $p<0.001$, $r_{\text{thermal imager} \sim \text{camera traps}} = 0.45$, $p<0.001$ and $r_{\text{camera traps} \sim \text{daylight visual}} = 0.52$, $p<0.001$ (Fig. 3.6 and Fig. S2). Site 4 was consistently estimated to have the highest sighting density regardless of the survey method (Fig. 3.6). Sites 1 and 2 also had substantial sighting densities.

Site encounter rates using daylight visual surveys and camera trap surveys were unaffected by gully density but encounter rates using night-time thermal imaging were significantly negatively associated with gully density ($F_{1,4} = 9.11$, $\beta \pm se = -0.833 \pm 0.0009$, $p = 0.039$, $r^2=0.69$). Site 4 which had the highest density estimate of mountain hares, had the lowest gully density of any site (Fig. 3.7).

Camera traps ran continuously (24/7) from November to March. Sequential deployment (accounted for imperfectly using the Random Factor of Site) reported encounter rates showing a near significant decline by 62% over the four months from 37.6 to 14.3 encounters per day (Fixed effects standardised $\beta = -0.009$, $z = -1.55$, $p = 0.12$; Random effects: Site Var = 0.10 Std. Dev = 0.324; Fig. 3.8).

3.5 Discussion

Our study compared three survey methods for mountain hares which provided very different kinds of observations and density estimates. Daylight visual surveys produced the fewest observations, seeing mainly single hares, and appearing to under record many hares hiding by day. The method did provide sufficient observations to enable monitoring of relative density but with very wide confidence intervals. By night the thermal imager frequently observed single or large groups of hares over the furthest distances and estimated density with narrower confidence intervals. However thermal imaging opportunities were limited by bad weather. Camera traps monitored constantly and achieved the largest number of detections reflecting night time activity of hares, capturing mostly single animals at very short observation distances. Camera trap density estimates were much larger than for daylight visual sampling and thermal imaging and were more reliable, but were susceptible to many assumptions. Notwithstanding differences in detection rates the locations of sightings from each method were highly spatially correlated.

3.5.1 Daylight visual surveys

Daylight visual surveys for mountain hares have been criticised when used in areas of low density or during the day when hares are inactive (Petrovan et al. 2011; Newey et al. 2018). Our expectation was Holme Moss would elicit frequent occurrences of hares (Mallon et al. 2003), yet we achieved very few observations. The small sample size we achieved was below the minimum required for distance sampling and contained some heaping of detection distances. The nature of hiding and flushing hares caused many detections to occur at short range. Thus, when selecting detection function models, we were obliged to use a smaller data set with few, wide bins. This selection may have also precipitated a narrow effective strip width and this may have contributed to the overall density estimate as being higher than for thermal imaging. This was surprising as one might expect thermal imaging to be observing more such nocturnal animals leading to a higher encounter rate and density estimate. Although detection probability variation was moderate, encounter rate variation was high. Consequently, the density estimate possessed wide confidence intervals and variation. To achieve reliable estimates, useful for ongoing monitoring, surveys should achieve 80 or more detections (Buckland et al. 2001). This suggests that studies similar to ours would benefit from replicate surveys to achieve a larger sample size to result in more accurate population density estimates, were this important for monitoring design goals. In retrospect for our own study we might have sacrificed some camera trap management time for more line transect surveys. Alternatively, daylight survey effectiveness might be improved by 3 or 4 observers walking abreast. Daylight visual surveys provided an advantage as transect routes forced the observer to traverse gullies, opening up fields of view and occasionally enabling sheltering hares to be seen.

3.5.2 Thermal imager

This study deployed an advanced thermal imager with mounted laser range finder for measuring distances to object in complete darkness and with point transect protocols. Whilst seemingly dangerous to walk across moorland by night, this could in fact be done as safely as by day, though slower. However, it was physically difficult to achieve 12 vantage points, spaced 333m apart, in a single night for a single observer. As the thermal imager was viewed through two lenses on its internal screen, it provided a 3D image and alleviated issues of eye strain. Cold temperatures below -5° C flattened batteries within 60 minutes. Sinking hill fog or increasing winds through some nights, cut surveys short. Thermal imaging enabled observations of hares across a broad landscape, where they exhibited feeding and social behaviour. The presence of the observer did not prompt evasive movement. The method worked well on snow. Encounter rates provided a sample size greater than the ~ 80 detections required according to distance analysis standard guidelines (Buckland et al. 2001). Distance histograms showed good model fit: a broad shoulder and gradually decreasing distance shape, providing lower variation of detection probability. The lack of detections within 30m might suggest evasive movement by hares, although this may be expected when carrying out distance sampling with point counts (Buckland et al. 2001). Rumpled terrain occasionally meant hares might be within viewing range but hidden in gullies. Future thermal imaging studies could by day prospect for a large set of unimpeded vantage points, from which to draw a random sample to visit by night. Our findings suggested high levels of precision could be achieved with a logistically manageable number of points, requiring ~15 nights, assuming favourable weather. Such a device is a considerable investment.

3.5.3 Camera traps

Camera traps provided a practical method of constant surveillance in all weathers including snow. Installation of cameras across moorland was slow: often one day for two people to move four cameras, two kilometres. The 2-3kg size of hares required maximum camera sensitivity, also capturing blowing vegetation and 'blank' images, requiring more filtering time. However, operating 24/7, cameras appeared to avoid false negative detections. Image times conveyed peak nocturnal activity periods, even during extremely cold nights. There were two night-time peak activity phases, consistent with records for Irish hare (*Lepus timidus hibernicus*) Caravaggi et al. (2018). The narrow field of view captured no more than 2 hares at a time, perhaps under recording larger groups, as observed by the thermal imager. Camera traps require financial outlay, bear theft risk and need considerable field effort. Image review time is substantial yet can be reduced using image recognition software (Schneider et al. 2020).

In our study, camera trap detections occurred at short ranges, so the detection probability histogram allocated 3,506 encounters to just four distance bins, producing low variation of detection probability (*cv*=0.03). Camera trap density estimates showed less variation than the thermal imager. Our findings suggested high levels of precision could be achieved with half the camera installations as we had used, with field time of ~20 days.

Monitoring surveys are expected to fulfil the principal assumptions of distance sampling. However, for the camera trap analysis we noted certain factors can have a large effect on density estimates (Fig. 3.9).

Firstly, most of our camera trap detections occurred at very short distances (≤5m) creating a fine scale sensitivity in the detection function histogram for our Distance analysis. The low detection probability estimate (0.17), implied to 5m, 83% of hare encounters were missed and reported a short effective strip radius (2.1m), implying a higher density estimate. This radius was smaller than recorded elsewhere e.g. Hofmeester et al. (2016) at 3.69m in dense understorey. This was surprising: when siting camera traps, we saw and avoided hare trails on snow and vegetation. However camera trap passive infra-red sensors can under-record at night, at different air temperatures, and micro-topography can affect detection rates (Hofmeester et al. 2018). It is possible detections may occur at further distances if surveying on flat arable-type land. Thus detection rates and measurement of lagomorphs in camera trap zones, merits further study within enclosure-based settings (Rowcliffe et al., 2008).

Secondly, snapshot window (k) definition greatly affected effort values and the number of defined detections. We opted for k=1 second, which provided both the highest number of absolute encounters and also the most conservative estimate of encounter rate. Other studies have used longer durations: k=2 seconds of Howe et al. (2017), k=13 seconds (Corlatti et al. 2019). Our alternative scenarios suggested a gradual increase of k value brought fewer encounters, though disproportionate to the larger decrease in k units, thereby increasing encounter rates and thus density estimates. This effect diminished with increasing values of k. Further assessments of this relationship may require consideration of animal movement duration relative to camera detections, possible behavioural biases; or when modelling, setting thresholds for the influence of different values of k.

Thirdly, encounter rate estimation may be impacted by the number of night hours, varying by time of year and latitude, or alternatively affected by choice of peak activity period (Frey et al. 2017; McGowan et al. 2019; Vazquez et al. 2019). Our activity frequency estimates showed different peak activity periods at different sites. This might have been caused by hares altering their feeding patterns because of changes to day length, or varying snow cover requiring longer foraging periods. Hence we chose sunset-to-sunrise for consistency between sites.

Fourthly, some images showed individual hares "dwelling" on the camera trap site. Even with videos, it is hard to define such behaviour as happenstance or genuinely biased. A rules set may assist for rejecting such images. For example, we discarded any image where the hare's nose was within ~5cm from the bamboo cane or camera. Attraction behaviour may be mitigated with marker canes used as reference photo, then removed, reprojecting their positions on ensuing computer images (Caravaggi et al. 2016), using video, or having two cameras facing each other.

3.5.4 Ecological inferences

Between the methods we found a strong correlation between sighting density, and the similarity of detection probabilities for each method lend credibility to reported densities. The spatial correlation suggests the methods detected similar patterns of animal distribution even though they exhibited different detection rates. Methodological constraints (e.g. timing delay due to inclement weather) may explain some variation in our findings: some sites were surveyed early or late in the winter, during which time hare behaviour and consequent detectability changes. By late March, daytime hare activity often changes from dormant isolation to social grouping and mating. The assessment with the camera traps, statistically mitigating for site differences, showed encounter rates largely decreasing throughout the survey season. This may be understandable: an exceptional season of high winds and deep snow falls may have caused winter mortality.

These findings represent important indicative baselines for local monitoring and may inform assessments of other groups of native or reintroduced mountain hares. Notwithstanding its remarkable 150 year tenure, the Holme Moss mountain hare densities may be considered low compared to many populations in Scotland which commonly reach 20 to 50 hares km^{-2} (Watson et al. 1973; Newey et al. 2018).

3.5.5 Conclusions

We report the practical survey effort, scale, encounter rates, density estimates and measures of precision which may be helpful for the planning of studies of elusive or nocturnal animals in difficult terrain. Daylight visual sampling is low cost, is logistically simple, can rapidly cover much ground, and can achieve precise density estimates, yet, transpiring by day, may fail to observe cryptic nocturnal animals, thereby reporting lower encounter rates and thus underestimating abundance. For somewhat more effort, a high power thermal imager achieves potentially more observations of nocturnal animals including at long distances and consequent higher density estimate precision. It is recommended when surveying accessible areas, with dependable fog and wind free weather. By contrast camera traps can provide constant monitoring and at night over long periods in all weathers.

They are thus useful for long term surveys, placed in locations which are difficult to access frequently or where it would be hazardous to venture in darkness. Camera traps can achieve large numbers of detections, including at night, recording the peak activity levels of nocturnal animals.
However between the methods, daylight visual sampling and thermal imager surveys both work well in applying the principles of distance sampling. Practically speaking, camera trap distance sampling operates effectively in achieving large data sets and can adopt distance sampling principles. However the consequent models need contemplation of additional assumptions and sensitivity modelling. Where there is insufficient empirical data, inferences may require subjective analytical decisions, potentially rendering camera trap distance sampling estimations less robust. Separately, another form of population monitoring, occupancy modelling using presence absence data from surveys, may be robustly accomplished when combining observations from several different survey methods (MacKenzie et al. 2005). Equipment costs are important, and subject to extensive fluctuation depending on market economics and purchasing power. Daylight visual sampling sampling requires the least outlay in terms of equipment costs. An array of camera traps may be purchased for intermediate costs; a high powered thermal imager may probably require much higher costs.

Acknowledgements

We thank RSPB Dove Stone and Upperwood Estate for fieldwork permissions and J. Mann of FLIR for advice on thermal imagers. We thank M. Kocsis, J. Minshull, K. Boyd, C. Rice, D. Hogg and A. Oliver for support with fieldwork and M. Jones, A. Reuleaux, A. Hashmi and two anonymous reviewers for comments which improved earlier drafts.

Funding

Research funding was kindly provided by the People's Trust for Endangered Species (PTES), the Hare Preservation Trust, the British Mountaineering Council, Queen's University Belfast (QUB), Penny Anderson Associates, South-West Action for Hares, and Manchester Metropolitan University (MMU).

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Tables

Table 3.1 Descriptive summary of sampling effort, detections and their distance from the observer and surveyed area (based on furthest detection distance) for daylight visual surveys, thermal imaging and camera trapping.

Samples and detections are total values before truncation. Per method "Summary" rows: Σ = column total; $\bar{x}$ = column mean. All camera trap values based on night-time (informed by Fig 4). Calculation of area surveyed at each site for cameras = (further detection distance per site)^2 x π x camera field of view restriction (42/360) x number of cameras per site. The survey rate (km^2 per hour) for camera traps is not calculated as they are considered to be in continual operation

Method (survey units)	**Samples**	**Hours effort**	**Detections**	**Mean Cluster Size**	**Mean Detection distance** (m)	**Furthest detection** (m)	**Detections per hour**	**Hours to 1st detection**	**Surveyed area** (km^2)	**Survey rate** (km^2 per hour)
Daylight visual surveys Sample units = Transect length km										
Site 1	4.62	3	8	1.00	149	305	2.67	0.38	3.11	1.04
Site 2	4.82	4	11	1.09	220	446	2.75	0.36	4.92	1.23
Site 3	4.71	4	1	1.00	192	192	0.25	4.00	1.93	0.48
Site 4	4.70	4	12	1.08	172	532	3.00	0.33	5.89	1.47
Site 5	4.89	4	5	1.00	87	362	1.25	0.80	3.95	0.99
Site 6	8.16	7	4	1.00	94	263	0.57	1.75	4.51	0.64
Summary	**Σ = 31.91**	**Σ= 26**	**Σ= 41**	**$\bar{x}$ = 1.03**	**$\bar{x}$ = 152**	**$\bar{x}$ = 350.0**	**$\bar{x}$ =1.75**	**$\bar{x}$ = 0.63**	**Σ = 24.31**	**$\bar{x}$ = 0.98**
Thermal imaging Sample units = points (number of replicates in brackets)										
Site 1	12 (20)	16	26	1.34	185	508	1.63	0.62	16.21	1.01
Site 2	12 (22)	22	38	1.31	256	612	1.73	0.58	25.88	1.18
Site 3	12 (27)	19	30	1.43	218	500	1.58	0.63	21.20	1.12
Site 4	12 (22)	20	87	1.44	270	682	4.35	0.23	32.14	1.61
Site 5	12 (12)	10	12	1.08	436	740	1.20	0.83	20.64	2.06
Site 6	11 (11)	10	13	1.38	220	528	1.30	0.77	9.63	0.96
Summary	**Σ = 71 (114)**	**Σ = 97**	**Σ = 206**	**$\bar{x}$ = 1.33**	**$\bar{x}$ = 264**	**$\bar{x}$ = 595.0**	**$\bar{x}$ = 1.96**	**$\bar{x}$ = 0.47**	**Σ = 125.71**	**$\bar{x}$ = 1.32**
Camera traps Sample units = number of cameras (total camera nights in brackets) [hours per night in square brackets]										
Site 1	16 (287) [17]	4,879	768	1.00	2.33	9	0.15	6.35	0.000475	-
Site 2	16 (376) [17]	6,392	550	1.00	2.60	10	0.08	11.62	0.000586	-
Site 3	12 (148) [16]	2,368	213	1.00	1.92	6	0.09	11.12	0.000158	-
Site 4	16 (331) [15]	4,965	1,128	1.00	2.91	12	0.23	4.40	0.000844	-
Site 5	16 (386) [14]	5,404	479	1.00	2.60	8	0.09	11.42	0.000375	-
Site 6	15 (272) [13]	3,536	573	1.00	2.41	9	0.16	6.17	0.000445	-
Summary	**Σ=91 (1,800) [varying]**	**Σ = 27,544**	**Σ = 3,705**	**$\bar{x}$ = 1.00**	**$\bar{x}$ = 2.46**	**$\bar{x}$ = 9**	**$\bar{x}$ = 0.13**	**$\bar{x}$ = 8.51**	**Σ = 0.002884**	**-**

Table 3.2 Summary of models and parameters.

Showing number of parameters (# para), AIC, Delta AIC, χ^2 values, degrees of freedom (df), and χ^2 goodness of fit (GOF), detection probability (P) and co-efficient of variation values (P CV). For camera traps, log likelihood (log 𝓛), overdispersion factor (Ĉ) and QAIC are shown for assessments of over-dispersed data (Howe et al. 2018). For each survey method, data selections and number of observations (n obs) are listed. Models selected for subsequent estimations are marked with asterisk *.

Reviewers please note "track changes" is **not** on for this table. The contents have changed entirely for Daylight visual surveys and Camera traps. Thermal imager data as previous version.

	Model (key)	# para	AIC	Delta AIC	χ^2	df	χ^2 GOF	P	P CV			
	Daylight visual surveys	*Data truncation at 100m, 5m bin width, n obs = 26*										
	Uniform + cos	2	74.3	2.3	0.7	1	0.40	0.31	0.36			
	Uniform + polynomial	1	72.3	0.3	0.6	2	0.73	0.30	0.18			
*	Half-normal + cosine	1	72.0	0.0	0.4	2	0.82	0.28	0.20			
	Half-normal + Hermite	1	72.0	0.0	0.4	2	0.82	0.28	0.20			
	Hazard-rate	2	74.6	2.6	1.0	1	0.31	0.33	0.15			
	Thermal Imager	*Data truncation at 350m, n obs = 152*										
	Uniform + cosine	2	1753.6	0.9	11.2	15	0.73	0.29	0.13			
	Uniform + polynomial	3	1755.9	3.3	11.2	14	0.66	0.31	0.12			
	Half-normal + cosine	3	1753.9	1.3	9.7	14	0.77	0.32	0.29			
	Half-normal + Hermite	1	1757.7	5.0	17.6	16	0.34	0.38	0.09			
*	Hazard-rate	2	1752.6	0.0	10.5	15	0.78	0.34	0.21			
	Camera traps	*Data truncation at 5m, bins at 1m, 2m, 3-4m, 5m; n obs = 3,506*										
										log 𝓛	Ĉ	QAIC
	Uniform + cosine	1	9371.4	875.2	876.4	2	0.00	0.30	0.01	-4684.6	438.2	12.9
	Uniform + cosine	2	8607.4	111.2	109.3	1	0.00	0.18	0.02	-4301.7	109.3	14.0
	Uniform + polynomial	1	10010.5	1514.3	1598.5	2	0.00	0.38	0.01	-5004.2	799.3	13.6
	Uniform + polynomial	2	9359.1	862.9	863.2	1	0.00	0.30	0.02	-4677.5	863.2	14.8
	Half-normal + cosine	1	8709.6	213.4	255.9	2	0.00	0.17	0.02	-4353.8	128.0	36.3
	Half-normal + cosine	2	8562.5	66.3	68.7	1	0.00	0.12	0.03	-4279.2	68.7	37.7
	Half-normal + Hermite	1	8709.6	213.4	255.9	2	0.00	0.17	0.02	-4353.8	128.0	36.3
	Half-normal + Hermite	2	8710.4	214.2	254.2	1	0.00	0.17	0.05	-4353.2	254.2	38.3
*	Hazard-rate + simple	2	8496.2	0.0	1.8	1	0.18	0.17	0.03	-4246.1	1.8	4721.9
	Hazard-rate + simple	3	8498.2	2.0	1.7	0	0.00	0.17	0.03	-4246.1	-	-

Table 3.3 Estimates of detection probability, density and abundance obtained from distance sampling analyses for all three survey methods.

Value = point estimate; CV = coefficient of variation; LCL & UCL 95% lower and upper confidence limits. Encounter rate: Daylight visual n/km = encounters per km; Thermal imager: n/k = encounters per point; Camera traps n/k = encounters per second. Abundance estimate derived from density value projected to the 49km^2 of Holme Moss.

Method	**Value**	**CV**	**LCL**	**UCL**
Detection probability				
Daylight visual surveys	0.28	0.20	0.19	0.42
Thermal imager	0.34	0.21	0.23	0.50
Camera traps	0.17	0.03	0.16	0.18
Encounter rate				
Daylight visual surveys (n / km)	0.82	0.31	0.36	1.81
Thermal imager (n k)	1.33	0.12	1.05	1.68
Camera traps (n/k)	0.00030	0.14	0.00023	0.00039
Cluster size				
Daylight visual surveys	1.00			
Thermal imager	1.31	0.04	1.20	1.44
Camera traps	1.00	0.01	1.00	1.00
Effective strip or radius width (m)				
Daylight visual surveys	28.3	0.19	18.9	42.2
Thermal imager	202.5	0.10	165.3	248.2
Camera traps	2.1	0.01	2.00	2.13
Density (hares km^{-2})				
Daylight visual surveys	14.3	0.37	6.3	32.5
Thermal imager	12.1	0.24	7.6	19.4
Camera traps	22.6	0.14	17.1	29.9
Abundance				
Daylight visual surveys	701	0.37	310	1,587
Thermal imager	593	0.24	372	951
Camera traps	1,103	0.14	834	1,458

Figures

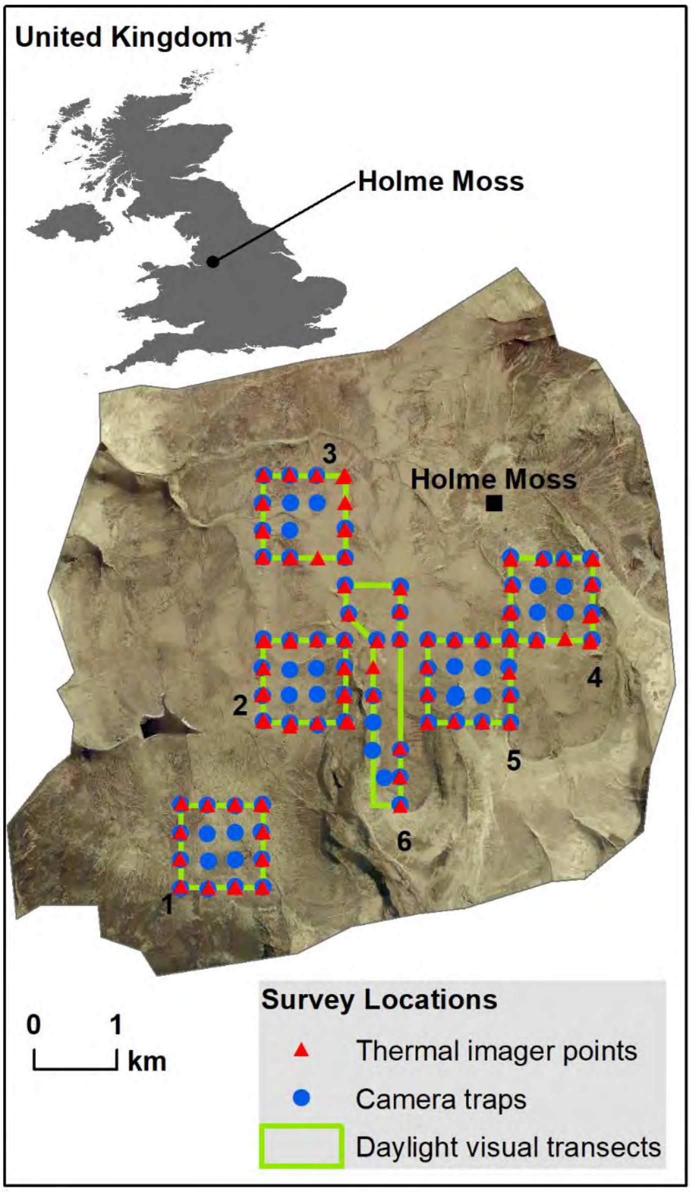

Figure 3.1 Location of Holme Moss study site, north west England, Great Britain.

Aerial photo origin is OS SE 401398 and shows extent of Holme Moss massif, above 335m elevation, bounded to north and east by major roads. The hill summit is indicated by the black square. Survey locations are shown, with site numbers. Sites 1 to 5 are 1km squares. Site 6 is the narrow polygon running north to south between sites 2 and 5. Daylight visual transects were the perimeter of 1km square, except site 6 being a near trapezoid shape. Thermal imager points were 333m apart as were camera traps, though with some minor deviations for topography, standing water or perceived theft risk. Note: one thermal imager point was used in Site 4 and repeated ~30m away in Site 5; 87 of 91 camera site locations are shown as 4 pairs of camera trap sites overlap; 2 were moved ~30m mid-term because of rising standing water; 2 were moved ~30m avoiding perceived theft risk. Three cameras were stolen from site 3 and one from site 6; their points are not shown, no data was recorded at those locations. Aerial photograph: Digimap sourced June 2019 from Digimap Ordnance Survey Collection: Getmapping aerial imagery.

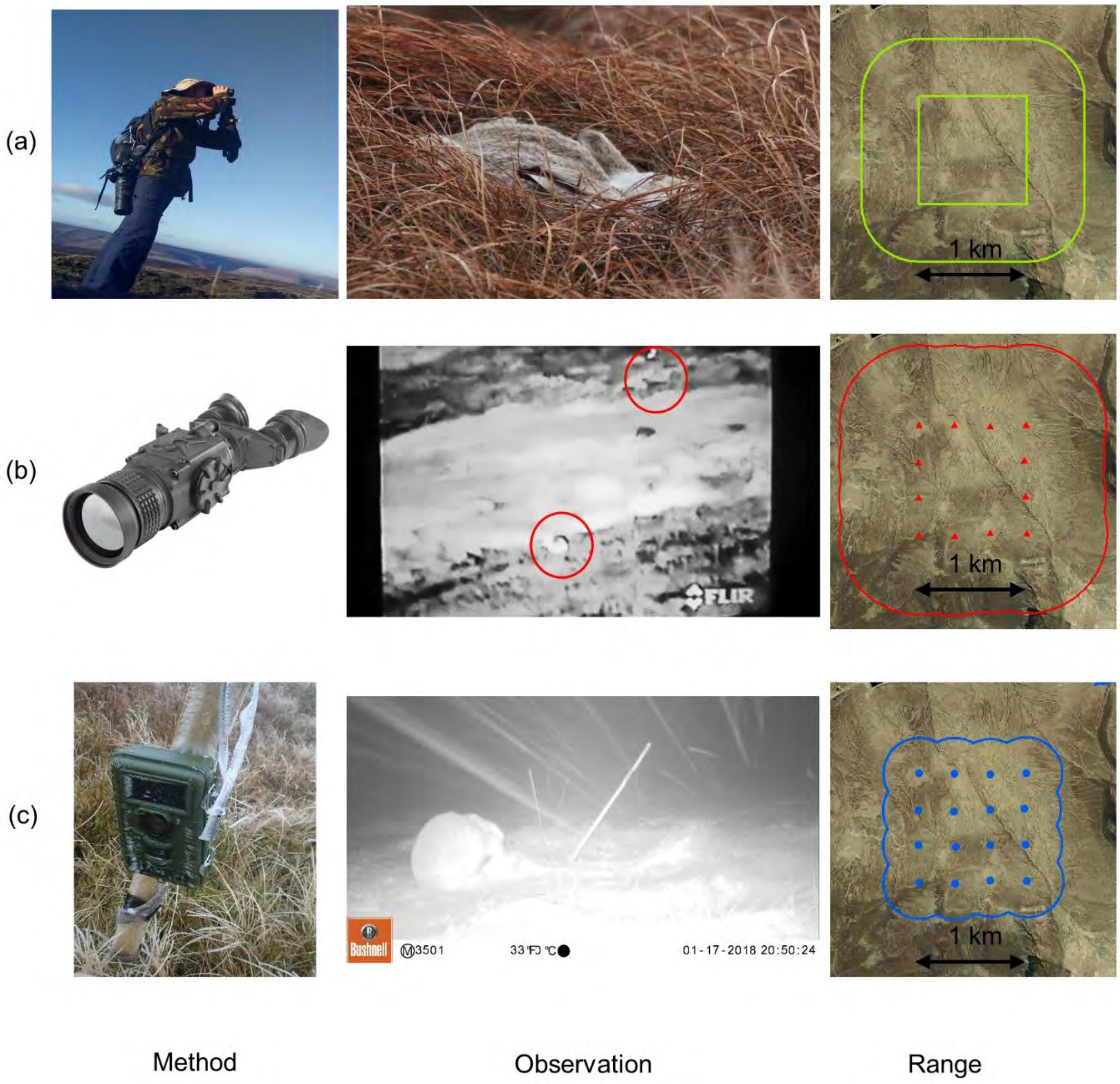

Figure 3.2 Photographs showing the three different methods.

a) Daylight visual surveys b) Thermal imager c) Camera trap. Left column shows the observation equipment. Central column shows each method's typical sighting of a mountain hare. Right hand column displays example survey location at site 1 for each method, duly surrounded by a buffer: measured to the furthest visual point (532m) for daylight visual surveys; (740m) thermal imager; for camera traps, buffer is portrayed to 333m of each camera, the assumed home range of local mountain hares.

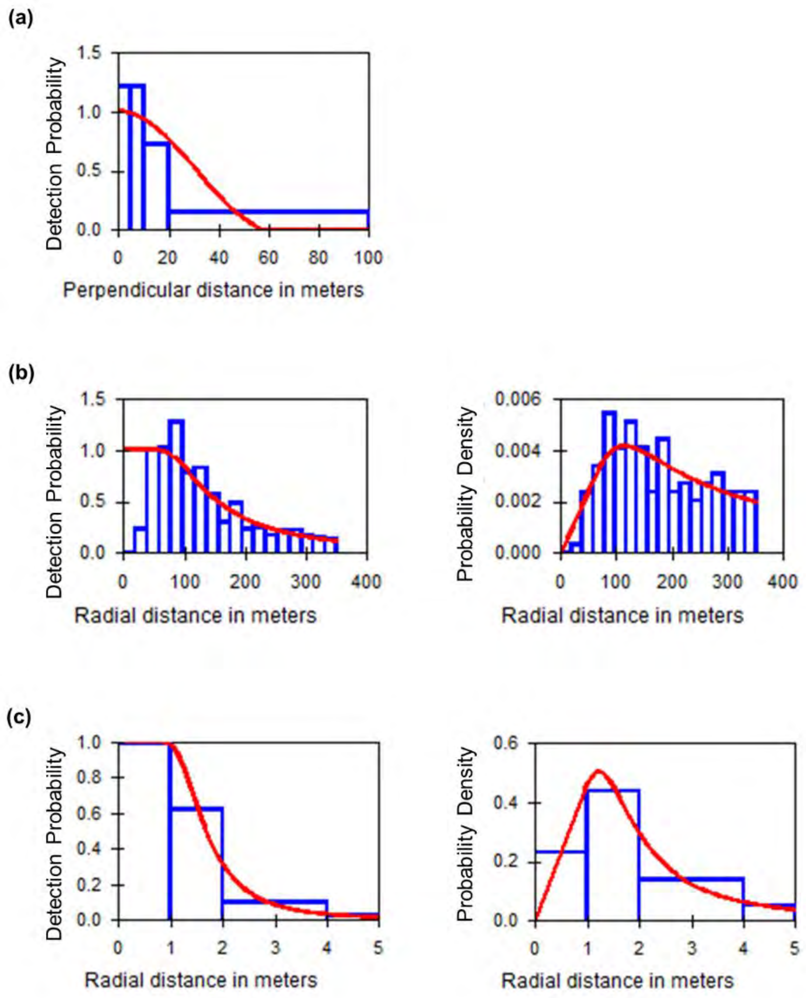

Figure 3.3 Distance sampling detection probability and probability density function histograms

(a) daylight visual surveys (uniform model with cosine adjustment and data allocated to bins at 5m,10m, 20m and to 100m), **(b)** nocturnal thermal imaging (hazard-rate model with simple polynomial adjustment and data truncated at 350m) . **(c)** camera traps (hazard-rate model with simple polynomial adjustment and data allocated to bins at 1m, 2m, 4m and to 5m.

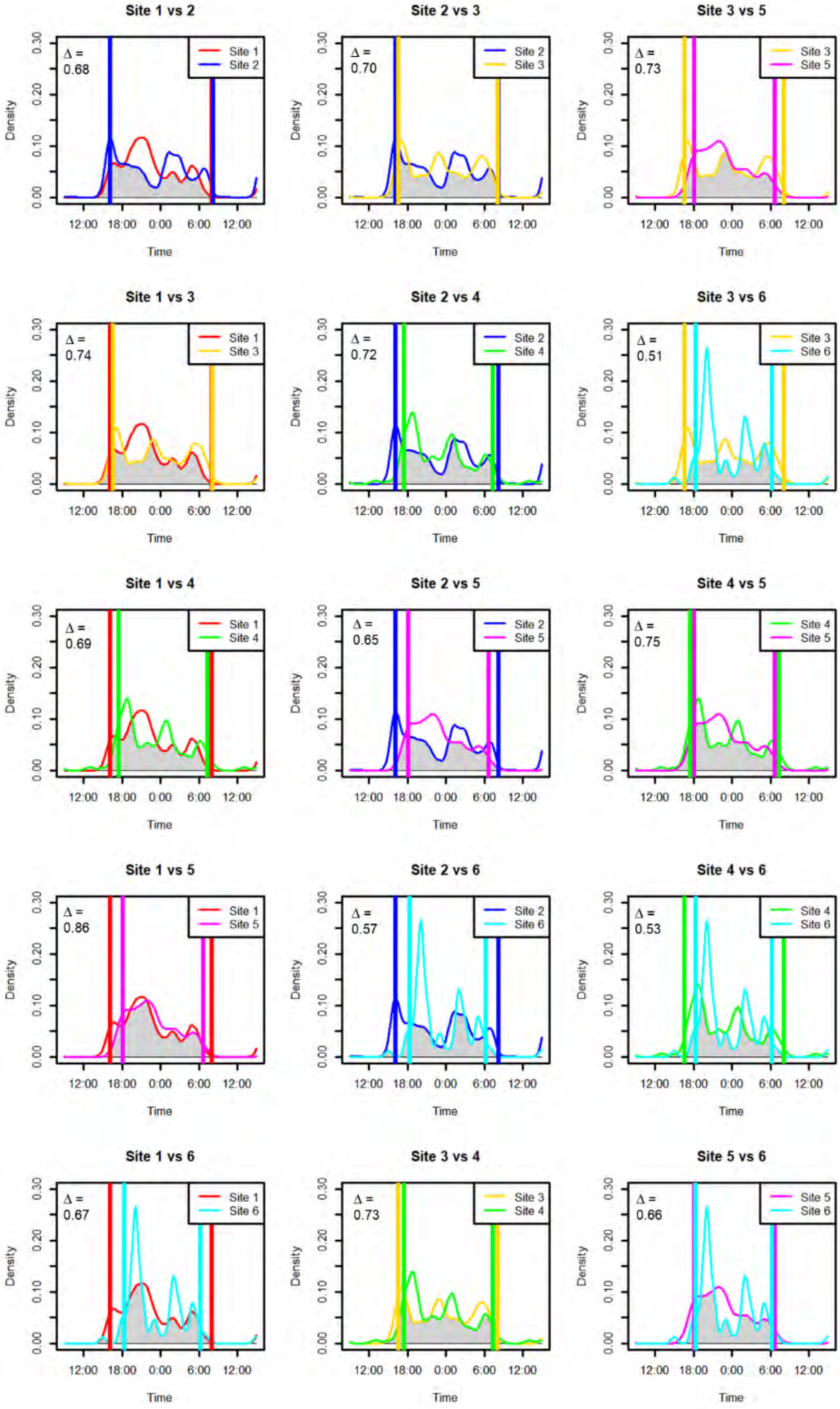

Figure 3.4 Diel activity at sites showing von Mises kernel densities and pairwise overlaps with other sites.

The x-axis shows time of day. The y-axis is the frequency estimate of detections. The overlap of densities, common to each pair of sites, is the shaded grey area below both curves. Overlap coefficient values between compared densities is top left. The mean overlap of all pairwise combinations was 68%; all exceeded 50%. Vertical lines indicate sunrise and sunset times for each site pair; night-time hours reducing with spring onset. Dates of operation: Site 1: 24/11/17-18/12/17 (17 night hours); Site 2: 11/12/17-11/1/18 (17 night hours); Site 3: 9/1/18-25/1/18 (16 night hours); Site 4: 25/1/18-9/3/18 (15 night hours); Site 5: 16/2/18-30/3/18 (14 night hours); Site 6: 9/3/18-30/3/18 (13 night hours). Images produced with R-package 'overlap' (Meredith and Ridout 2020) based on Ridout and Linkie (2009).

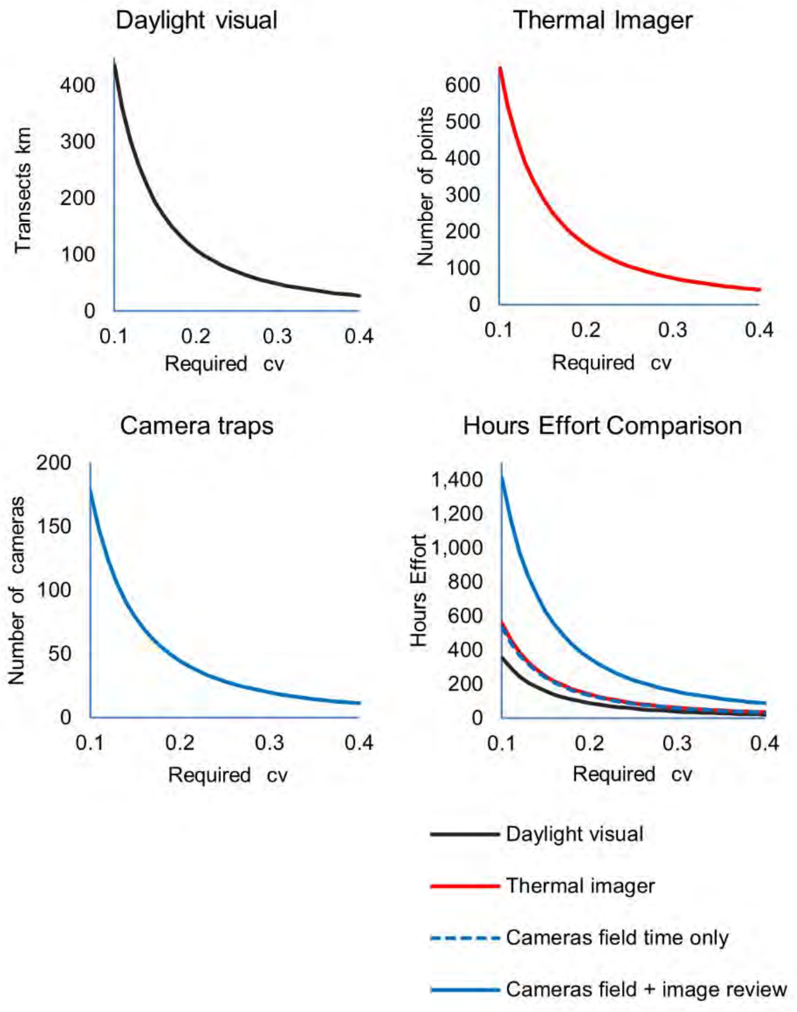

Figure 3.5 Effort required to achieve a target precision of density estimate, as measured by coefficient of variation

Input to the hours effort comparison is based on table 1 and assumes for daylight visual surveys 1.2km / hour walked; for thermal imagers 1.2 point / hour surveyed. Camera traps assumes cameras are in situ for average 21 days. "Camera field time only" based on 3 hours per camera being one installation visit, one maintenance visit, one retrieval visit. "Image review" time assumes 1,176 images per camera achieved with 15 seconds review time per image = additional 4.9 hours per camera.

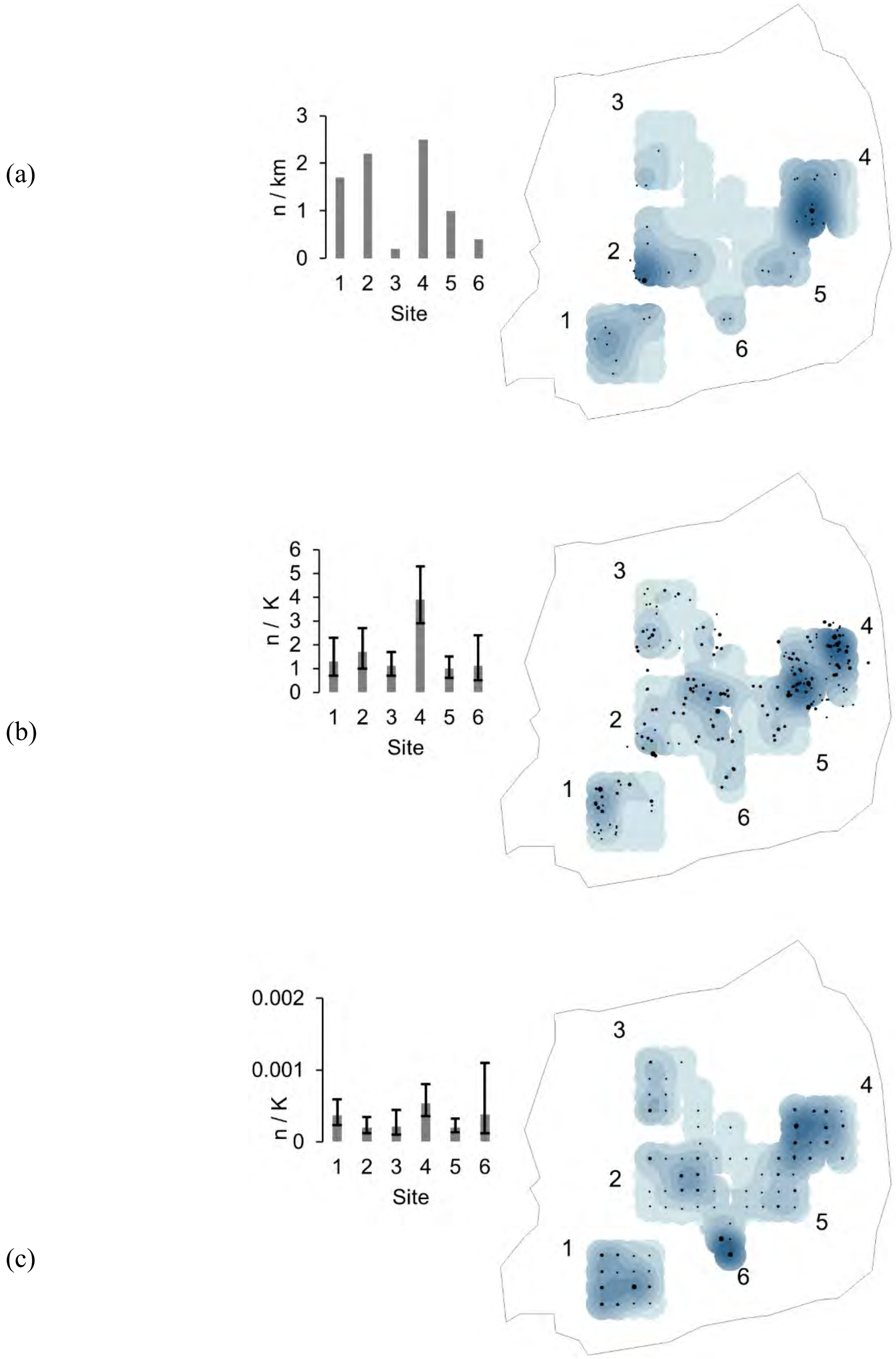

Figure 3.6 Sightings per method per site

(a) daylight visual surveys, (b) thermal imager and (c) camera traps. Column charts show encounter rate value estimates based on all sightings, with 95% confidence intervals for thermal imager and camera traps. Kernel density maps show spatial variation of hare sightings, with site numbers. Black dots indicate sightings, increasing in size to show clusters for daylight visual and thermal imager,(normalised for replicates) and camera traps (normalised for nights in operations). Background shading increases to dark based on sighting intensity. Kernel density boundaries are based on 333m buffer of camera locations, hence some daylight visual sampling and thermal imager encounters fall outside this area.

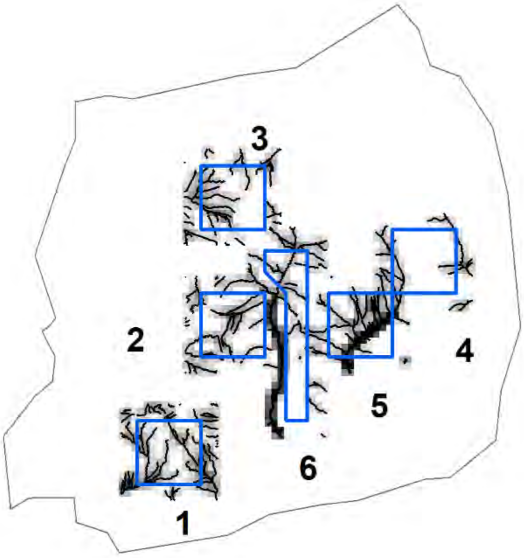

Figure 3.7 Map of gullies (lines) with gully density (cells) across the six study sites at Holme Moss.

Numbers denote each study site

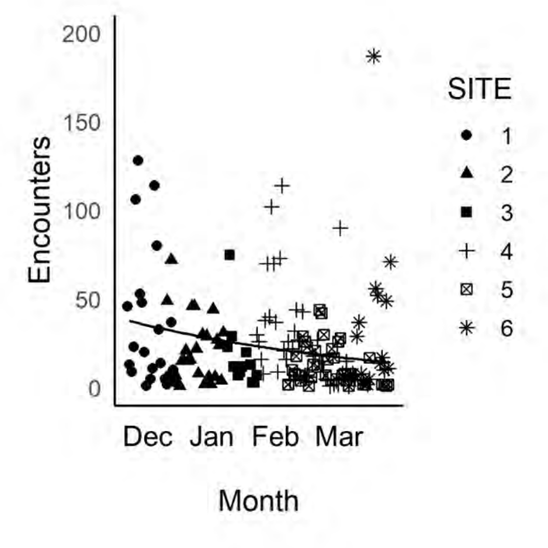

Figure 3.8 The regressed number of encounters per camera

The line is seen to decrease over the study period, end Nov 2017 to March 2018, taking into account "Site" as a random effect. Number of encounters per camera (point shapes); line is regression.

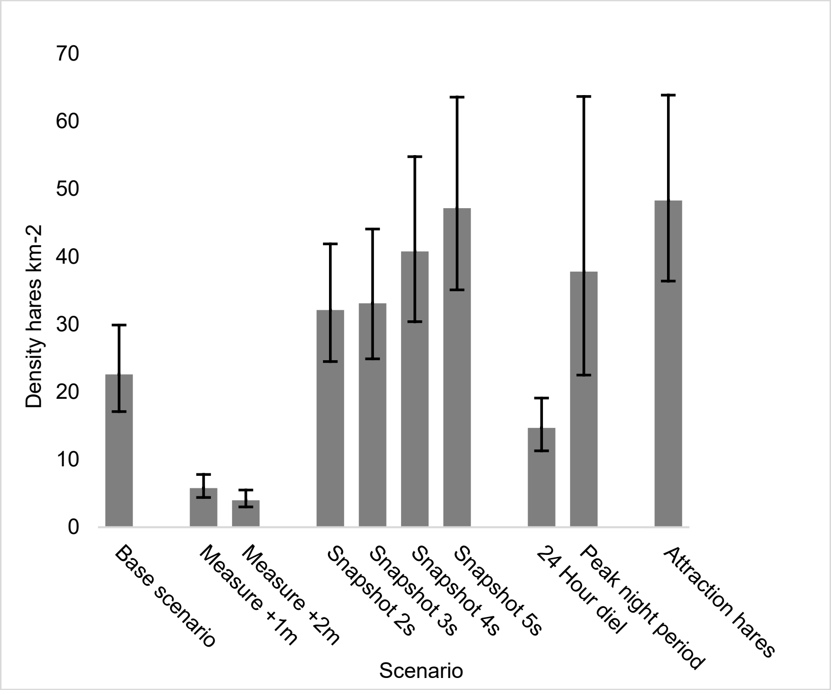

Figure 3.9 Analysis of alternate scenarios providing camera trap density estimates.

The x-axis shows different data treatments or assumptions. The y-axis shows consequent density of hares km^{-2}. Columns are density values with 95% confidence interval error bars. To maintain consistency amidst the comparisons, all scenarios used the same data filter with detection distances binned at 1m 2m 4m and to 5m with the Hazard-rate model with simple polynomial, which in all cases achieved lowest AIC scores of candidate models.

"Base scenario " was the scenario eventually chosen for our camera trap estimate for comparison with daylight visual sampling and thermal imager. This assumes correct measurements (metres) of distance to hare; k snapshot window = 1 second; diel period is sunset-to-sunrise (Fig 4); and hare images showing attraction behaviour are discounted.

The alternate scenarios each use the same assumptions and change one factor as follows:

"Measure +1m, +2m" highlights the effect of increasing the measured distance to camera of all hare detections by 1 metre or 2 metres which would lead to an increase in detection probability and lower density estimate. This is an exaggerated scenario, yet serves to demonstrate the sensitivity.

"Snapshot 2s 3s 4s or 5s" shows the effect of increasing snapshot window k, which reduces effort to a much greater degree than encounters, thus increasing density.

"24 hour diel" uses full 24 hour period, correspondingly greater effort, very few additional detections.

"Peak night period" uses a 55% peak night activity period per site (McGowan et al. 2019) with consequently reduced effort.

"Attraction hares" includes a further 1,318 images (after truncation) when dwelling behaviour observed.

Supplementary information

Table S1 Distance sampling records and parameter estimates for camera traps based on scenarios listed in Fig 5. Value = point estimate; CV = coefficient of variation; χ^2 GOF = χ^2 goodness of fit value; Effort = k seconds, n = encounters; n/k = encounter rate; P = detection probability; E (s) = estimated cluster size; D = density . All estimates use models with data allocated to bins at 1m 2m 4m and to 5m, fitting with Hazard-rate model, simple polynomial, 2 parameters. Base scenario is as used throughout the methods comparison: Night-time = sunset-to-sunrise; Measurements are assumed correct; k = 1 second; no attraction behaviour

Scenario	χ^2 GOF	Effort	Encounters	n/k	n/k CV	P	P CV	E (s)	E (s) CV	D	D (CV)
Base scenario	0.18	11,568,480	3,506	0.00030	0.14	0.17	0.03	1.00	0.01	22.6	0.14
Measure +1m	0.00	11,568,480	3,323	0.00028	0.14	0.62	0.03	1.00	0.01	5.8	0.14
Measure +2m	0.00	11,568,480	2,943	0.00025	0.15	0.80	0.03	1.00	0.01	4.0	0.15
Snapshot 2s	0.34	5,784,240	2,420	0.00041	0.13	0.16	0.04	1.00	0.01	32.1	0.13
Snapshot 3s	0.41	3,856,160	1,640	0.00042	0.14	0.16	0.05	1.00	0.01	33.1	0.14
Snapshot 4s	0.40	2,892,120	1,518	0.00052	0.14	0.16	0.05	1.00	0.01	40.8	0.14
Snapshot 5s	0.51	2,313,696	1,397	0.00060	0.14	0.16	0.05	1.00	0.01	47.2	0.14
24 Hour diel	0.00	18,144,000	3,581	0.00019	0.13	0.17	0.03	1.00	0.01	14.7	0.13
Peak night period	0.00	3,772,020	2,023	0.00053	0.26	0.18	0.04	1.00	0.01	37.8	0.26
Attraction hares	0.01	11,568,480	4,824	0.00041	0.13	0.11	0.03	1.00	0.01	48.3	0.14

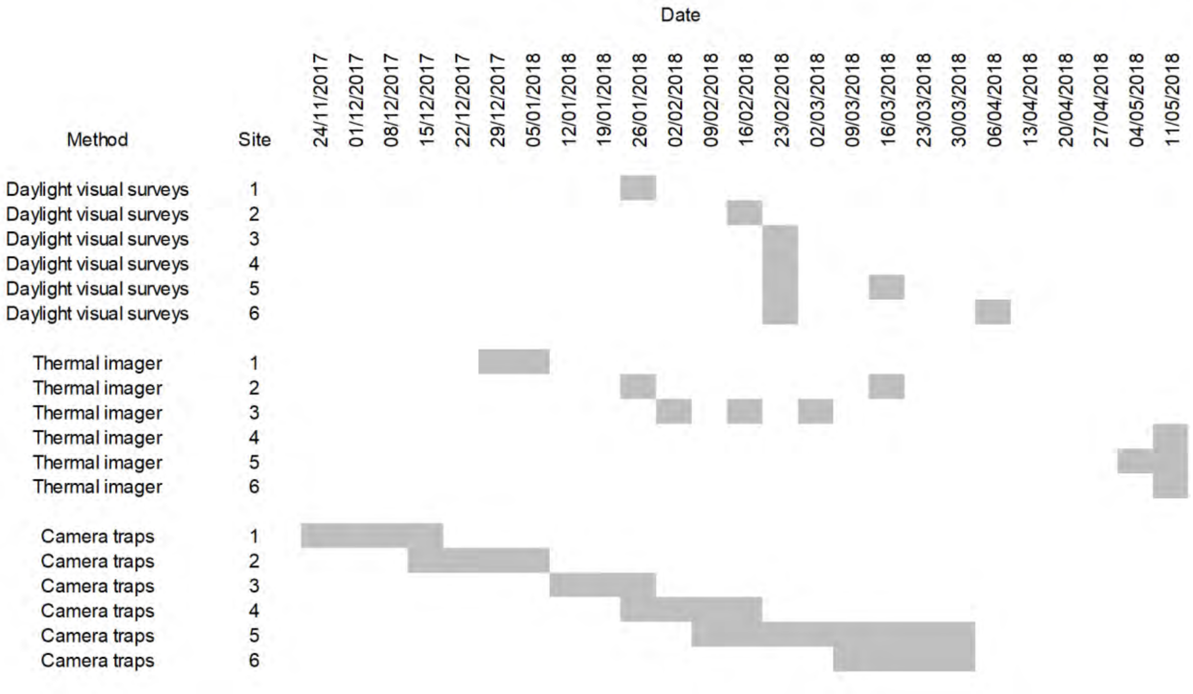

Fig. S1 Timeline listing survey methods by site by week. Daylight visual surveys and thermal imager surveys occasionally curtailed by fog, high wind or sudden snow, causing an irregular schedule

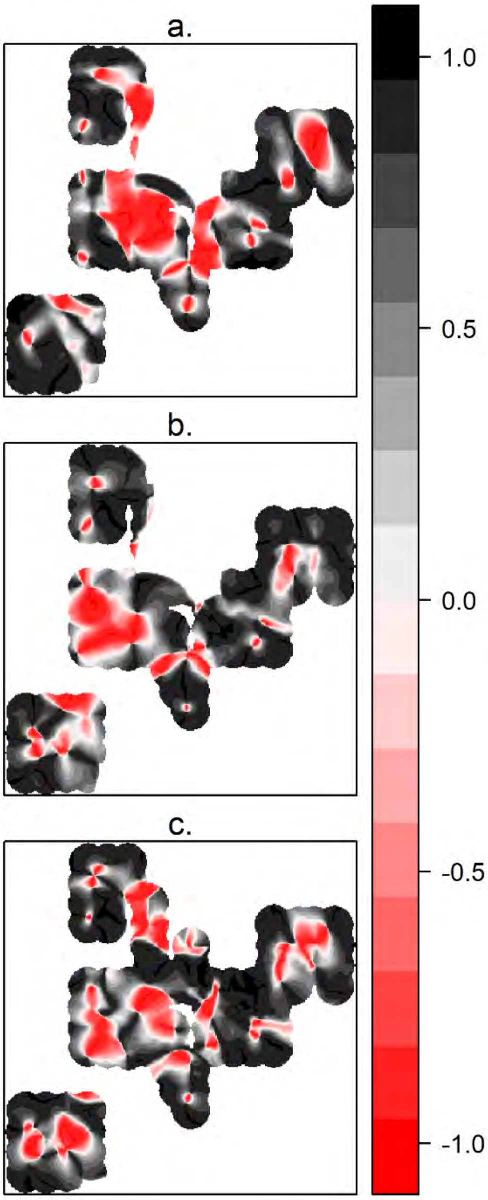

Fig. S2 Correlation plots comparing kernel density estimates of survey methods. **(a)** Daylight visual surveys vs Thermal imager; **(b)** Thermal imager vs Cameras; **(c)** Daylight visual surveys vs Cameras. Scale bar: black = positively correlated; red = negatively correlated.

CHAPTER 4 HIGH DENSITIES OF MOUNTAIN HARES (LEPUS TIMIDUS) ASSOCIATED WITH ECOLOGICALLY RESTORED BOG BUT NOT GROUSE MOORLAND MANAGEMENT

Image: Four mountain hares forage upon the lush vegetation of the restored blanket bog of Shelf Moor, Bleaklow, Derbyshire, England, UK. Date: 28th March 2017

Chapter 4

High densities of mountain hares (Lepus timidus) associated with ecologically restored bog but not grouse moorland management

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Publication Reference

This chapter has been further developed from the version below and is now published as:

Bedson, C.P.E., Wheeler, P.M., Reid, N., Harris, W.E., Mallon, D., Caporn, S. & Preziosi. 2022. Highest densities of mountain hare (Lepus timidus) associated with ecologically restored bog but not grouse moorland management. Ecology and Evolution 12(4): 8744 doi: 10.1002/ece8744

4.1 Abstract

On peatland ecosystems, historically degraded, internationally important, blanket bogs have benefited from restoration efforts over seventeen years. Meanwhile grouse moor land management has increased in intensity. During 2017-21, we surveyed mountain hares (*Lepus timidus scoticus*) within the Peak District, England, covering 830km, comparing densities on different moorland habitats. We recorded highest hare densities upon restored bog at 32.6 hares km^{-2} (95%CI: 25.2–42.1) substantially higher than on degraded unrestored bog 24.4 hares km^{-2} (95%CI: 20.6–28.9). Density on managed grouse moor bog was 12.2 hares km^{-2} (95%CI: 9.4–15.8) with statistically significant annual fluctuations and on managed grouse moor heather density was 10.0 hares km $^{-2}$ (95% CI: 6.1 to 16.5). Acid grassland used for sheep rearing reported density at 11.8 hares km^{-2} (95%CI: 7.3–19.2). Unmanaged dwarf shrub heath reported lowest density 4.8 hares km^{-2} (95%CI: 2.6-8.8). Thus, densities on bog habitats were significantly higher than all other habitat classes. Overall annual density for 2017 was 15.5 hares km^{-2} (95%CI: 10.1–23.8); increasing significantly by 60% in 2018, declining annually by ~14% 2018-2020 and remaining flat in 2021. Total park abundance was previously estimated in 2002 at 3,361 hares (95% CI: 2,431-4,612). Our 2019 park wide survey estimated abundance at 3,562 hares (95% CI: 2,291-5,624). Results suggest this mountain hare population is stable, with some interannual fluctuations, confounded by factors such as extreme weather and human causes. The population has thrived on blanket bog habitats, supported by restoration efforts. Contrary to historic studies, grouse moors produced intermediate volatile densities, suggestive of poor habitat quality or possible culling. The high variation of densities between habitats may increase local extinction risks and should be considered in management.

Keywords

Habitat degradation, landscape restoration, mire, blanket bog, grouse moor, mountain hare, monitoring, distance sampling

4.2 Introduction

Across the world many important ecosystems are suffering anthropogenic damage. Among these are peatlands, wetland ecosystems where decomposing vegetation has taken thousands of years to accumulate as peat layers. These are often vulnerable to human activities (e.g. cutting, grazing, burning, indirect erosion) and sensitive; their replacement may require millennia (Yu et al. 2010; Page and Baird 2016).Amongst upland regions they are known as moorlands and comprise mires, heathlands and acid grasslands, and are considered unique environments found in temperate and high altitude zones (Thompson et al. 1995; Tallis 1998; Holden et al. 2007).

Mires are high elevation landscapes which experience cold-wet climates, providing conditions for peat layer development. In the northern hemisphere they store 50% of total global soil carbon storage (Evans et al 2006), providing conservation value, hosting sensitive plants and animals. Many mires are degraded (Urak et al. 2017). Across Europe substantial investments (~ € 167m) have been invested in restoration (Andersen et al. 2017).

The UK's upland mires comprise 22,000km^2 and represent 13% of the world's total resource (Tallis 1998). These habitats lack high species diversity, yet contain bog communities of distinctive flora and fauna, classed as important under the EC Habitats Directive 92/43/EEC (Holden et al 2007). Bird assemblages comprise high proportions of migratory boreal, arctic and temperate species, which have legal protections: EC Birds Directive 79/409/EEC (Thompson et al. 1995). Many mires have been designated Special Areas of Conservation (SAC) (Bonn et al., 2009).

The South Pennine Moors lies towards the southern edge of UK mire distribution (Bonn et al., 2009) and received SAC designation in 2005 for its unique upland plant community and its population of breeding waders (Natural England 1993, 1994, 1999, 2005). These areas feature 25km^2 of the most degraded mires in Europe, suffering damage by air pollution from the industrial cities of Sheffield and Manchester (Tallis 1997; 1998; Andersen et al. 2017) which destroyed vegetation, leaving bare peat and extensive gully erosion (Alderson et al., 2019).

The UK uplands are reputed to contain a substantial portion of the world's heather moorland, with the majority in Scotland (Holden et al. 2007). The South Pennine Moors SAC also contain extensive heather moorland on which are 350km^2 of grouse moor estates which frequently practice rotational heather burning (muirburn), creating an ecosystem supporting red grouse (*Lagopus lagopus*) for shooting (Sotherton 2009; Phillips 2012).

Neighbouring these areas are large expanses of acid grasslands predominantly used for sheep raising. Indeed between 1930 and 1980, free roaming sheep numbers trebled (Anderson and Yalden 1981; Fuller and Gough 1999). Farmers burned and fertilised much of the heather moorlands, and with sheep overgrazing, 55km^2 of *Calluna* was replaced by *Deschampsia, Nardus, Molinia* and rushes i.e. transformed to acid grassland. (Anderson & Yalden 1981; Thompson et al., 1995).

Together these three mechanisms (i.e. air pollution erosion, muirburn, sheep overgrazing) caused extensive landscape degradation and precipitated much loss of diversity of flora and fauna (Anderson & Shimwell 1981; Thompson et al. 1995; Tallis 1998; Welch 1998; Fuller and Gough 1999; Ross et al. 2003; Tucker 2003; Sim et al., 2005; Pearce-Higgins et al. 2006; Yallop 2006; Wheeler 2008; Yalden 2009). The South Pennine Moors SAC was categorised as 99% “Unfavourable-recovering” or “Unfavourable-no change” (Natural England 2019).

From 2003 a well funded (~ **€** 35m) program commenced restoring the South Pennine Moors SAC (Alderson et al., 2019; Bedson *in litt.*). Conservation measures included fencing out grazing animals, reduced burning and trampling, removal of species e.g. *Molinia*. Hydrology was re-established with gully blocking. Bare peat was restored with netting, fertilisers, liming, mulches and reseeding with grasses, rushes, mosses, dwarf shrubs, heather and *Sphagnum* (Buckler et al., 2013; Alderson et al., 2019). Many bare peat areas recovered their vegetation (Alderson et al., 2019). Little was known about wildlife effects (Shepherd et al., 2013; Andersen et al. 2017).

One mammal species is restricted to UK uplands: the mountain hare (*Lepus timidus scoticus*), an important herbivore and prey for foxes (*Vulpes vulpes*), stoats (*Mustela erminea*) and raptors (Yalden 2009). Elsewhere across Europe and Asia, mountain hares occupies high latitudes and elevations inhabiting tundra, taiga, boreal forests, bogs and grasslands, at low population densities (1-6 individuals km^{-2}) (Angerbjorn and Flux 1995); ~3 individuals km^{-2} in the Alps (Rehnus and Bollmann 2016). Some of the highest densities of mountain hares (50-200 individuals km^{-2}) are recorded on grouse moors in Scotland. Muirburn provides early stage heather favoured by hares (Flux 1962; Hewson 1976; Savory 1986; Hewson 1989). Predator control to protect grouse was purported to support hares (Stoddart and Hewson 1984; Patton et al., 2010). Many grouse moor estates shoot hares for sport (Patton et al. 2010; Hesford et al. 2020). More recently culls were organised to substantially reduce hare numbers, on the grounds hares transmitted ticks carrying louping ill virus to grouse (Patton et al, 2010; Watson & Wilson 2018); although evidence of mountain hares being a principal vector for this disease transmission was ambiguous (Harrison et al. 2010). Reductions of hare numbers by up to 99% occurred on some moors (Watson & Wilson 2018). Annual offtake until 2016 averaged 39,000 hares (95% CI: 16,000-70,000) (Aebischer 2019). The recent assessment under Article 17 1992 EC Habitats and Species Directive, described UK mountain hare status as “deteriorating” and “unfavourable-inadequate” (JNCC 2019). Populations cycle by 80%, confounding trend evaluation (Newey et al, 2007). Yet numbers were considered to have genuinely declined from 350,000 (95% CI: 93,000-709,000) (JNCC 2007) to 132,000 individuals (95% CI: 79,000-516,000) (JNCC 2019). Mountain hares were vulnerable to reductions of dwarf shrub heath habitat (JNCC 2007). The presence of mountain hares was regarded as a useful habitat indicator (JNCC 2008).

In England mountain hares died out around 6000 BP and were reintroduced to areas of the South Pennines Moors lying within the present day Peak District National Park, by sporting landowners in the 1870s (Harris and Yalden 2008). From the 1970s basic studies described a small, stable population of ~1,000 individuals (Yalden 1971, Yalden 1984, Mallon 2001). The last field study estimated ~10,000 individuals, inconsistent with previous research (Mallon et al. 2003). The most recent consensus estimate was 2,500 individuals (Mathews et al. 2019). Over the past ten years there were widespread anecdotal reports of persecution (shooting and trapping) related to grouse moor estates in the Peak District. Although no monitoring data were available, there were concerns expressed about mountain hare population status. Mountain hares were associated with mixed *Calluna* / *Eriophorum* areas or *Calluna* areas on grouse moors (Yalden 1971; Mallon et al. 2003). There were concerns about the persistence of these habitats (JNCC 2007).

The aim of this research was to estimate mountain hare densities upon different upland habitats, over time and in different areas. We considered landcover types and land uses. We surveyed mountain hares and over five years recorded population fluctuations by habitat class and by year. In one year we surveyed the whole park to report abundance. This research was intended to accomplish investigations recommended by the UK Biodiversity Action Plan (JNCC 2008) and to inform future conservation status assessments.

4.3 Materials and methods

4.3.1 Study site

Field work was conducted in the uplands of the Peak District National Park, UK (Fig 4.1). These ~600km^2 of uplands are underlain by acidic gritstone and shale rocks forming hills up to ~630 m. The annual average temperature is 10.3 °C and precipitation 1,025 mm, creating a wet substrate on hill tops (UK Met Office 2020). The hills are covered with peat, commonly 2 metres deep (Anderson and Shimwell 1981), on which are wet upland blanket bog, wet and dry upland dwarf shrub heaths, acid grasslands, marsh grassland and in valleys old sessile oak woods (Natural England 1993; 1994; 1999; JNCC 2016). Surrounding areas consist of improved grasslands, woodlands, arable land, reservoirs and towns (Anderson & Shimwell 1981).

The upland habitats are deemed internationally important, despite having low species diversity. Prevalent species include heather *Calluna vulgaris*, cotton grasses *Eriophorum* spp., and grasses

(*Nardus stricta*, *Deschampsia flexuosa*, *Festuca ovina* etc) (Natural England 2019). The study site lies within the South Pennine Moors (SAC) and comprises three Sites of Special Scientific Interest (SSSI) whose proportions having unfavourable-recovering condition are: Dark Peak (87%), Eastern Peak District Moors (68%), South Pennine Moors (95%) (Natural England 2019).

To determine the study extent, we retrieved Biological Record Centre (BRC) mountain hare observations (Acknowledgments) for ten years to 2018, deduplicating to 100m between observations, eliciting 1,690 records. From these we created a large minimum convex polygon 610km^2 which we considered the mountain hare range (Fig 4.1).

4.3.2 Habitat classes

We developed a habitat classification map by layering several different data sources and mapping with a 1-ha scale cell grid in ArcGIS (ESRI USA) (Fig 4.2). We started with relevant landcover categories (Jackson et al. 2000) and the UK landcover map of Rowland et al. (2015) considering acid grassland, heather and bog areas, the main landcover types pertaining to mountain hare occurrence. Acid grassland we considered to be a single habitat and land use class. To identify grouse moor areas, we followed the method outlined in Watson and Wilson (2018) and examined aerial photos: any 1-ha cell showing a burn or mowed patch was designated as grouse moor and demarcated as "grouse moor bog" or "grouse moor heather" depending which underlying landcover category (Rowland et al. 2015) was present. Any remaining heather areas not grouse moor were classed as "Unmanaged dwarf shrub heath". The conservation partnership "Moors for the Future" (Acknowledgements) provided us with shapefiles that designated the bog areas where they had conducted recovery work to 2016: these were considered "restored bog". Remaining bog areas were considered "unrestored bog".

Thus the final map consisted of six mutually exclusive classes consisting of landcover and land use treatments. Fig 4.3 displays aerial photographs showing the habitat classes. Table 4.1 lists vegetation communities.

“Acid grassland” was at 300-550m elevation including steep slopes and was a broad habitat type of calcifugous swards dominated by grasses (*Festuca ovina*, *Nardus stricta*), sedges, herbs on lime-deficient soils, pH <5.5 (Jackson et al. 2000; Rowland et al., 2015). In winter (i.e. mountain hare survey season) grasses and bracken (*Pteridium*) were senescent; *Calluna, Juncus* and *Molinia* reach 120cm height (Stace 2010). These areas were used for sheep rearing and otherwise unutilised.

The bog areas comprised ombotrophic wetlands supporting *Eriophorum* and *Sphagnum* spp. vegetation forming peat. (Rowland et al., 2015). The separate heather areas consisted of heather-dominated communities and some grasses *Festuca ovina* and shrubs *Vaccinium* spp. or gorse *Ulex* spp. (Elkington 2001; Rowland et al. 2015). Bog and heather areas were each subdivided as follows.

Grouse moor areas featured extensive muirburn and infrastructure associated with grouse management: shooting butts, grit trays, quad bike tracks, predator traps. "Grouse moor bog" at elevations 350-530m were wet heath and peaty areas with eroded gullies, *Calluna*, more *Eriophorum* spp. and mosses. "Grouse moor heather" at elevations 280-510m, were drier areas with shallow peat, few gullies and more extensive continuous fields of *Calluna* (Allen et al. 2016). In practice on the ground one could not always tell where "grouse moor bog" ended and "grouse moor heather" began. Yallop et al. (2006: 9) demonstrated this gradual transition from wet heath bog to muirburn, portraying the difficulty of drawing a line between the two. Hence we relied upon the underlying landcover definitions and raster files provided by Rowland et al. (2015). Muirburn comprised different succession stages: suppressed ("pioneer") heather on burned ground, vegetation height to 15cm; sub-dominant heather, age to 10+years, height ~15cm, coverage ~40%; dominant heather, age up to 25 years, height ~30-100cm coverage, 60+% (Bardgett et al 1998; Allen et al. 2016; Stace 2010; Whitehead et al. 2021). Also present were *Eriophorum*, *Sphagnum* and other mosses, cross-leaved heather *Erica tetralix*, bell heather *Erica cinerea*, bilberry *Vaccinium myrtillus* and crowberry *Empetrum nigrum* (Bardgett et al 1998; Whitehead et al. 2021). Peak District burned heather areas were previously recorded at typically 29% of potential burnable area with patch sizes 500-1000m^2 (Allen et al. 2016).

“Restored bog” were bog landcover areas (~20km^2) at elevations 480-630m which had historically deteriorated to the condition of complete bare peat. From 2007 restoration efforts included gully blocking, fertiliser, liming, laying of jute textiles, reseeding, planting, spreading heather brash, taking up to six years to achieve vegetation cover: *Calluna, Eriophorum and Sphagnum* spp. (Alderson et al., 2019). By 2016, this work achieved 75% vegetation cover (Alderson 2019); much was in lush, verdant condition with continual growth and development . *Calluna* height was up to ~100cm, winter grasses were senescent reaching heights ~30cm (Stace 2010). The extensive networks of eroded gullies were revegetated and the water table was high (Alderson 2019). There was no predator control practiced. Sheep were fenced out.

Remaining bog areas were classed as “Unrestored bog” at elevations 300-630m. Whilst these had not historically deteriorated to the point of comprising bare peat, they were nonetheless ecologically impoverished i.e. "unfavourable-recovering" condition (Natural England 2019). They consisted of extensive fields of *Eriophorum* spp. and grasses, winter height ~30cm, and some Calluna patches height ~ 100cm (Stace 2010). They also featured eroded gullies, without gully blocking as was the case for "restored bog", therefore drier with water run-off. No predator control was practiced and there were some sheep.

The remaining heather area not grouse moor was classified as “Unmanaged dwarf shrub heath” at elevations 250-520m including steep slopes and few gullies. This was upland heath comprising mosaics of 70% dense / 30% open heather, predominantly *Calluna* (Rowland et al. 2015) of height to 120cm (Bardgett 1998; Stace 2010). There was no predator control and few sheep.

Otherwise, all other landcover categories had no mountain hare records, and were excluded: improved grasslands; calcareous grasslands; woodlands; human infrastructure (Rowland et al., 2015).

4.3.3 Surveys

We wanted to identify how mountain hares preferred different habitats and how densities might change over time. When planning surveys, a random stratified approach is often used (Morrison et al. 2010), however this could miss groups of mountain hares that might prefer certain ranges (Flux 1962). Therefore instead we sought to cover large contiguous areas to ensure we did not overlook any concentrations of hares. We reflected that the typical mountain hare home range is ~ 0.3km^2 (Hewson and Hinge 1990; Rao et al. 2003). From pilot surveys we determined we could achieve mountain hare detections beyond 500m. We sought a survey plan ensuring continuous coverage probability >0.01 without gaps (Buckland et al. 2001), with sufficient scale to encompass large areas of all the habitat classes. This would allow us to identify density patterns over a few hundred metres. Hence we designed survey sites as 5x5km areas. For transect shape we covered selected 1km squares of the Ordnance Survey grid (OS Explorer Map 1 (2015). The perimeters of each square were surveyed as circuits, walking all four sides of the square as one continual transect. By covering all cardinal directions this balanced out any differences arising with slope, weather or lighting. Each transect was thus independent. Although there was overlap of transects at adjoining corners, we calculated that if, for example, the effective strip width measured 100 metres, the overlap would comprise just 2% of the survey area: insufficient to justify modifying estimates for increased coverage probability. Instead we maintained standard distance sampling assumptions, with the quantum of survey effort acting as denominator for encounter rate (Buckland et al 2001: 233-235; Buckland et al. 2004: 224; Buckland et al. 2015: 27).

We sought a high level of encounters i.e. sample size, to facilitate the estimation of a robust detection function i.e. less variation to help detect meaningful differences of density when stratifying by habitats or time. From BRC records we noted 37% of historic observations were on 23% of the study area: Bleaklow and Margery Hill, with 4km of non-surveyed land between them (Fig 4.1). Thus we configured the 5x5km areas atop these two hills, acknowledging that ensuring density estimates might be higher than elsewhere in the wider park. We surveyed alternate 1km^2 squares i.e. 13 squares on Bleaklow, 13 squares on Margery Hill. Surveys commenced for 2017, repeated in 2018, 2019, 2020 and 2021 with the same 26 squares being used in each year (Fig 4.1).

We added an additional 5x5km site on Holme Moss with a further set of 13 tessellated squares in 2018, repeated in 2019. During 2019 we extended surveys to achieve an estimate for the entire Peak District, with the support of 6 trained observers. Because the rest of the park was much larger, for logistical reasons we now configured remaining surveys of areas as 26 random 1km^2 squares, ("peripheral areas"), with 6 squares deliberately chosen as pairs, for efficiency (Fig 4.1).

Survey transects followed the 1km^2 square perimeters, guided by GPS. Occurring January through April, the survey schedule randomised squares the first year, maintaining schedule each year as logistics allowed. Each side of the square was surveyed once, looking either side of the transect, walking very slowly and taking 2-5 hours. Surveyors scanned ahead with binoculars every 200 m to locate hares or groups of hares in the undulating terrain. Only observations made while walking along the transect line were included in the analysis.

Mountain hare observations were recorded with distance sampling protocols (Buckland et al., 2001): date; time; grid reference; cluster size; distance to hare (laser range finder); angle (angle board), discounting potential double counts. Surveys were consistent with Newey et al. (2018), in clear weather with wind speed <20mph. Stronger winds did not influence hare detections (Flux 1962), but caused difficulties holding the laser range finder steady. No surveys took place with snow present.

4.3.4 Distance modelling

For Bleaklow and Margery Hill, mountain hare observations were attributed to the habitat class on which the animal was first seen, according to standard distance sampling methods (Buckland et al., 2015) (Fig 4.1), determined using the "extract" function in package Raster (Hijmans and van Etten

2012) within R (R Core Team 2011). Transect lengths by habitat class were also derived by "extract" function. Because we were not able to survey the other areas (Holme Moss / peripheral areas) every year, we excluded those from habitat analyses, retaining them for discrete "area only" estimations.

We analysed distance sampling data in software DISTANCE v.7.3 (Thomas et al., 2010), using combinations of different data filtering and model selections (Buckland et al. 2001). We assessed different truncation distances and bin widths. We investigated detection models with three key functions: uniform, half-normal, and hazard rate, with cosine or polynomial expansion terms (Buckland et al., 2001 47; Williams & Thomas 2001). We assessed the suitability of data selections and models by referring to histograms and quantile-quantile plots, χ^2 goodness of fit statistics, and the fit of the detection function close to the transect line g(0). We compared and sought models with fewer parameters, lower AIC values between models using the same data selection, higher χ^2 goodness of fit statistics and lower detection probability *cv* values (Buckland et al. 2001). The furthest observation distance was 780 metres; we endeavoured to retain as many observations as possible, truncating to 520 metres. Both the uniform and half-normal model struggled to achieve a suitable (i.e. >0.05) χ^2 goodness of fit statistic. Rather, the hazard-rate model was better, with its characteristic wide should and steep drop off of the detection function. With data truncated at 520 metres it provided a high χ^2 goodness of fit statistic (0.77) for the detection function, with P=0.18 and low detection probability cv=0.04 (Table 4.2, Fig 4.4).

We stratified the sampling data and reported in four ways:

1) by habitat class i.e. pooling all observations in each habitat class over the five years together;
2) by year i.e. pooling all observations in each year, without habitat information;
3) by habitat and by each year i.e. 6 habitats x 5 years = 30 strata
4) by area only and to enable the 2019 population estimate

This was accomplished by separate data loads and modelling runs within software Distance, using the same data, each time allocating transects and observations to different strata definitions (Thomas et al. 2010). In each case we used the same global detection function, for reasons as follows.

As our principle objective was to assess differences between habitats, we compared two approaches to stratification: 1) detection function using pooled "global" data; 2) detection function separately stratified. Using pooled habitat data and the global detection function, three parameters were used, AIC=22148.43, global P *cv*=0.04. Using the same pooled habitat data but with a stratified detection function, 16 parameters were used, AIC= 22110.73 (i.e. 0.17% lower), yet very high values for P *cv* on three of the six habitats: acid grassland=0.24; grouse moor heather=0.30; unmanaged dwarf shrub heath= 0.36. Also, in this case the detection function for unrestored bog was invalid: g(0)>1; and the sample size for unmanaged dwarf shrub heath was 37 observations, below that recommended by Buckland et al. (2001). Separate attempts to use strata as covariates also resulted in greater AIC values and were dismissed. Nonetheless we considered whether the habitat classes showed genuine differences for the detection process: i.e. were there differences in the detection function for areas of deep heather such as grouse moor heather or unmanaged dwarf shrub heath? To investigate this we obtained parameter estimates from the mean habitat classes (pooled all years) stratified by detection function. We then conducted linear regression, comparing sample sizes with estimated P, P *cv* and effective strip width (ESW). This suggested that it was larger sample sizes and not the habitat classes themselves that were significantly associated with higher P, lower P cv and longer effective strip widths (Figure A1). The maximum observed radial distances (metres) for each habitat class were each very far: acid grassland 747m; grouse moor bog 623m; grouse moor heather 565m; restored bog 780m; unrestored bog 732m; unmanaged dwarf shrub heath 566m, suggesting detections were possible at long ranges in any habitat. For all these reasons we did not believe a stratified detection function was more informative than a global detection function and so did not pursue that approach.

We also reflected that for the other stratification methods (2,3,4 listed above) we wanted to ensure comparisons were consistent i.e. without different tailored detection functions which might provide less reliable estimate, exceptions of small sample sizes or modelling difficulties. Therefore we opted for the parsimonious approach of a single global detection function for all stratification queries. We duly estimated with the global detection function, stratifying by encounter rates and cluster size per habitat class and or year (Buckland et al. 2001: 89-91). Estimates for the survey year 2019 also used data truncated at 520m and the hazard-rate model; inevitably its global detection function f(0) differed slightly from the smaller data set of Bleaklow and Margery Hill. We reported parameters and estimates with 95% confidence intervals.

Comparisons between strata used the t-statistic based on the Satterthwaite approximation, accounting for unequal sample sizes (Buckland et al., 2001: 84-86). This test takes into account the lack of independence of data arising from using a common detection function between strata. We evaluated significance with a Bonferonni corrected *P*-value and also calculated effect sizes.

Abundance for the Peak District was calculated for 2019 based on the additional survey effort. The 2019 surveys showed very strong density fall offs from centre to edge of the Park. Therefore to determine extent for calculating abundance we created an alpha hull shape measuring 325km^2, from BRC hare records. We discarded six outlying records to cover only the known range of hares. This alpha hull shape differed very slightly from survey areas so we merged them to total 358km^2, based on habitat classes. Abundance was calculated for each of Bleaklow and Margery Hill and Holme Moss and peripheral areas, multiplying density estimates by area km^2. Boundaries between survey areas were not truly distinct; and in practice may have comprised graduations of densities.

4.4 Results

4.4.1 Observations

In 2017 Bleaklow and Margery Hill surveys covered 120km of transects, recording 304 detections; 2018 covered 121km with 504 detections; 2019 covered 112km with 401 detections; 2020 covered 123km with 402 detections; 2021 covered 120km with 374 detections (Table 4.3; Fig 4.5). Encounter rate estimates varied from highest 7.4 mountain hares km^{-1} (2020 restored bog) to lowest 0.2 mountain hares km^{-1} on unmanaged dwarf shrub heath 2017 (Table A1, Fig 4.6). Cluster sizes were slightly above 1.0, most were single hares (Table A1, Fig 4.6). The surveys of 2018 on Holme Moss covered 60km with 89 observations and 2019 covered 57km with 50 observations. Peripheral areas in 2019 covered 112km with 101 observations (Table 4.3, Fig A2).

4.4.2 Density and abundance

On Bleaklow and Margery Hill, the highest five year mountain hare density estimate was on restored bog, 32.6 hares km^{-2} (95% CI: 25.2 to 42.1) (Table 4.3, Fig 4.7). The next highest density was estimated for unrestored bog 24.4 hares km^{-2} (95% CI: 20.6 to 28.9). For acid grassland, density was estimated 11.8 hares km^{-2} (95% CI: 7.3 to 19.2); grouse moor bog 12.2 hares km^{-2} (95% CI: 9.4 to 15.8); grouse moor heather at 10.0 hares km $^{-2}$ (95% CI: 6.1 to 16.5) unmanaged dwarf shrub heath 4.8 hares km $^{-2}$ (95% CI: 2.6 to 8.8).

Within habitats, of fifteen pairwise comparisons, there were significant differences between 10 pairs (Table 4.4). Restored bog density was significantly higher than all other classes except for unrestored bog. Restored bog hare density compared not quite significantly higher than unrestored bog, though registered a small-medium effect size (t(1.92)=99.03, *p*=0.057, r=0.19). Unrestored bog also showed significantly higher densities than the other classes. Acid grassland, grouse moor heather, grouse moor bog were similar. Grouse moor bog hare density was not significantly higher than grouse moor heather, and registered a small effect size (t(0.76)=47.19, *p*=0.449, r=0.11). Acid grassland and grouse moor bog were significantly higher than unmanaged dwarf shrub heath. Grouse moor heather was not quite significantly higher than unmanaged dwarf shrub heath, though registered a medium effect size (t(1.90)=43.10, *p*=0.064, r=0.28). When comparing habitats within each individual year, many of these differences were often apparent in individual years (Table A2).

Most assessments of density upon any given habitat type, showed no significant change from year to year, except on three occasions (Table 4.4). From 2017 to 2018, unrestored bog showed a significant increase of hare density from 18.6 hares km^{-2} (95% CI: 12.9 to 26.7) to 30.6 hares km^{-2} , ((t(2.64)=57.93, *p*=0.011, r =0.33)). From 2017 grouse moor bog reported hare density increasing significantly from 8.7 hares km^{-2} (95% CI: 4.5to 16.7) to 21.4 hares km^{-2} (95% CI: 16.3 to 28.0) , (t(3.29)=40.07,*p*=0.002, r=0.46). On grouse moor bog hare density from 2019 to 2020 decreased significantly from 18.4km^{-2} (95% CI: 11.1 to 30.2) to 5.4km^{-2} (95% CI: 3.1 to 9.4) , (t(2.88)=21.65, p=0.009, r=0.53) and this was the only significant decrease of any habitat type between years.

On Bleaklow and Margery Hill, annual density estimates showed a significant increase in hare density from 2017 to 2018 from 15.5 hares km-2 (95% CI: 10.1 to 23.8) to 24.8 hares km-2 (95% CI: 19.5 to 31.5) , (t(2.29)=57.56, p=0.025, r =0.29) (Table 4). Density then dropped ~ 14% from 2018 to 2019 and again by ~14% to 2020. From 2020 to 2021 density reported effectively no change (-0.01% difference) and in 2021 was 18.3 hares km-2 (95% CI: 12.5 to 26.7).

Of the 2019 survey areas, the highest density of hares was reported for Bleaklow with 27.2 hares km-2 (95% CI: 19.8 to 37.8), significantly higher than any other area (Table 4.4, Fig 4.8). Margery Hill density was also high at 18.6 hares km^{-2} (95% CI: 9.7 to 35.4). Holme Moss had low density of mountain hares 6.1 hares km^{-2} (95% CI: 3.4 to 10.9) and this was similar to the peripheral areas 6.1 hares km^{-2} (95% CI: 4.0 to 9.4) .

For 2019 abundance for the Peak District study area (alpha hull shape + surveyed areas) estimated 3,562 hares (95% CI 2,291-5,624) (Table 4.5; Figure 4.9). Bleaklow was 11% of area and accounted for 31% of hares ; Margery Hill was 11 % of area and 21% of hares; Holme Moss 11% area and 7% of hares; peripheral areas 66% area and 41%. of hares.

4.5 Discussion

This study presents important new findings demonstrating the consequences of human activity upon peatland ecosystems and wildlife assemblages. Hitherto most such studies have concentrated on levels of degradation and the potential effects of recovery interventions upon hydrology, water tables, soil quality, carbon and methane storage and vegetation (Holden et al. 2007; Bain et al. 2011; Page and Baird 2016; Alderson et al. 2019). There have been few studies showing how vertebrates, particularly mammals, are influenced by upland habitat quality or improvement (Andersen et al., 2017). Our research suggests that polluted impoverished landscapes i.e. degraded bogs, can be restored to health with positive benefits to fauna. This is encouraging, because many sensitive ecosystems are in such poor condition and restoration is expensive, taking decades to effect recovery (Anderson et al. 2017).

Our study provides density estimates for an isolated population of mountain hares occupying upland habitats. For the UK this represents the first such comparison based on surveys of live mountain hares (i.e. not game bags), using geo-spatial measurements of animal occurrence and comparing densities across the full range of habitat classes used by this species. Our findings complement other research in Europe that describe mountain hare habitat utilisation: preferences for thickets of *Salix*, *Betula* and *Picea* with dense understorey in Scandinavian woodland (Hiltunen 2004); preference for dwarf mountain-pine (*Pinus mungo*) regardless of patch size in the Alps (Bisi et al 2013); preference for moorland over woodland in Scotland (Rao et al. 2003). The mountain hare densities we recorded are higher than many in Europe and possibly the highest recorded on bog landscapes. Notable high densities elsewhere include populations on heather moorland in Scotland (~200km^{-2} , Newey et al. 2018) and on predator-free heather dominated islands off Sweden (~400km^{-2} , Angerbjorn and Flux 1995). Separately, snowshoe hare densities reach up to 300km-2 in boreal forests (Krebs et al. 2001). Notwithstanding high densities, under climate change the range of mountain hares is forecast to move northwards and to higher elevations (Leach et al. 2015; Bedson et al. 2021a) which may result in lower abundances.

4.5.1 Degraded habitats

We observed wide variation of densities: restored and unrestored bog areas exhibiting the highest; grouse moor bog, grouse moor heather and acid grassland intermediate densities; unmanaged dwarf shrub heath the lowest density. We found significant differences between habitat classes, implying genuine contrasts in quality, diversity and attractiveness to hares. We detected a significant increase in density 2017-18 followed by 2-3 years of decrease.

Restored bog areas contained eroded gullies used by mountain hares for shelter and movement pathways. Taking advantage of the intricate micro-topography, during bad weather, hares could simply move ~20m to new shelter amongst peat hags and gullies. These areas featured diverse vegetation: *Calluna* eaten by hares in both winter and summer; *Eriophorum* spp., grasses and sedges, comprising summer diet (Hewson 1989; Harris & Yalden 2008). Our findings contrasted with historic observations of heather absence (Anderson & Yalden 1981) and few hares (Yalden 1971), suggesting a positive impact of restoration on hare density. Restoration, lime and fertiliser applied to bare peat, potentially provided a lingering amount of phosphorous and nitrogen in the vegetation (Alderson et al., 2019), affording nutritional benefits to hares (Miller 1968; Watson et al., 1973; Hewson 1989). Such would contribute to animal health and higher numbers (Watson et al., 1973). However it is not clear whether food availability or nutritional quality limits hare populations (Keith 1983; Newey et al. 2010) so it is hard to make inferences that food is the main cause of differences of hare density between habitats. It is also conceivable the higher water table provides more water and moisture availability to mountain hares, particularly important during summer.

Unrestored bog areas showed consistently high mountain hare encounter rates and density estimates. Density on unrestored bogs was 31% lower than restored bogs, not statistically significantly different though with medium statistical effect size, implying restoration benefits might be in early stages. Unrestored bog areas were similar to restored bog with many eroded gullies. However unrestored bog areas featured extensive swathes of cotton grass with small pockets of heather; not the diverse micro-mosaic patchwork of assorted grasses, heather species and mosses seen on restored bog. Therefore peat fertilisation and diverse vegetation replanting on restored bog may have contributed to higher numbers of hares. The absolute extent of unrestored bog and its high densities made this the most important habitat for sustaining this hare population.

We did not find evidence that the presence of grouse moors was associated with high mountain hare density. Grouse moor bog showed significantly lower density than unrestored bog despite having similar vegetation and with gullies present as potential shelter. Hare density on grouse moor bog was slightly higher than grouse moor heather. Both reported densities similar to acid grassland, noted as ecologically impoverished (Anderson & Yalden 1981). Density on grouse moor bog was significantly higher than unmanaged dwarf shrub heath. However density on grouse moor heather was not significantly different to unmanaged dwarf shrub heath, although the effect size was near medium. The benefit to mountain hare density from muirburn did not appear as substantial as previously reported (Yalden 1971). We observed the lower slopes of grouse moor heather were often dry (Holden et al., 2015). Frequent extensive heather burning reduced vegetation diversity and cover (Bonn et al., 2009: 178). On some of these areas no hares were seen. On less frequently burned areas, groups of hares were occasionally observed feeding upon pioneer heather (Hewson 1961; 1989). The grouse moor bog included deeper mature heather, where some hares hid, though finding movement difficult (Stoddart and Hewson 1984; Hewson 1989). Indeed Yalden (1971) recorded fewer hares in areas of pure *Calluna*. We could not confirm predator control was beneficial. There were far more hares on bog areas without predator control. In all habitat classes we occasionally observed predated mountain hare carcasses.

We estimated lower mountain hare densities on grouse moors than historically reported in Scotland or the Peak District. In Scotland, high densities of mountain hares on grouse moors were first reported in three studies. Watson et al., (1973) produced raw count data estimating up to 300 hares km^{-2}. Stoddart and Hewson (1984) suggested an association of hares with grouse moors from game bags, estimating hares 42km^{-2}. Watson & Hewson (1973) reported count data, comparing density by habitat, with high densities in valleys 26.3 hares km^{-2}, on grouse moors 32.6 hares km^{-2} in the Cairngorms; lower at arctic-alpine areas 7.9 km^{-2}; suggesting grouse moor as optimum habitat . More recently studies in Scotland have shown the persistence of mountain hares in terms of occupied range and count indices as associated with moors managed for driven grouse shooting (Hesford et al. 2019; Hesford et al. 2020). Very high densities (18-249 hares km^{-2}) were recorded on grouse moors in north east Scotland

(Newey et al. 2018). In the Peak District Yalden (1971, 1984) and Wheeler (2002) found highest counts on heather moorland, followed by bog and acid grassland.

It was therefore unexpected to find lower mountain hare density on grouse moors in the Peak District. Possibly mountain hares had shifted habitat use to high elevations, making for higher densities on the biologically diverse bogs. On restored and unrestored bog, patches of heather resource were ample, dispersed amidst a variety of other vegetation species and easy for hares to move around. Grouse moor bog had similar vegetation species to unrestored bog; grouse moor heather was characterised by heather species. Yet on both grouse moor bog and heather, the *Calluna* existed in such large deep expanses that movement for hares could be difficult. It may be that intense muirburn resulted in inferior vegetation quality or diversity compared to Scotland. On grouse moor bog there was a significant increase of mountain hare density 2017-18 and significant decrease 2019-20. On grouse moor heather there were large reductions of mountain hares in 2018-20. These fluctuations contradicted the other habitat types, though heather was found in all of them. The forces which govern populations ought to have been similar: weather, availability of food resource within each habitat class, disease, parasites (Newey et al. 2007a); contributing to similar dynamics. We reflect that in Scotland, grouse moor estates have conducted lethal removal of mountain hares (Laurenson et al. 2003; Harrison et al. 2010; Patton et al. 2010; Watson & Wilson 2018). We then speculate whether the same occurred on grouse moors within the Peak District, causing lower and fluctuating mountain hare densities.

Mountain hare density on acid grassland showed high variation. Whilst containing much *Nardus* and *Molinia* disliked by mountain hares, some areas contained *Calluna* patches, enabling hares to feed, without trapping them within it. Unmanaged dwarf shrub heath areas mostly reported lowest hare densities. Its deep mature woody *Calluna* was frequently impenetrable. These findings are consistent with previous work Yalden (1971), Watson et al. (1973), Hewson (1989). Acid grassland and unmanaged dwarf shrub areas were mostly at extent edges, possibly experiencing human pressure from higher road densities, walking paths, sheep farms and settlements.

4.5.2 Survey efficacy

Use of daylight distance sampling for mountain hares has been criticised as hares are nocturnal and rest up, hiding by day, resulting in lower observed encounter rates (Newey et al. 2018). However our research achieved large sample sizes and encounter rates with narrow confidence intervals, a function of high densities on Bleaklow and Margery Hill, and demonstrating distance sampling by day can be effective. By contrast, in mountain hare surveys on the Scottish Lammermuir hills Pettigrew (2020) recommended 90 minute surveys by dawn light as hares are more active and visible at this time rather than by mid-day when dormant. However the suggestion lacked information regarding imperfect detection process or detection probability so is hard to compare; and those surveys occurred on small accessible areas ~26km^2 of relatively flat elevation 420- 520m. By contrast the Peak District required >120km of transects and featured steep hills elevation 630m with transect elevation changes >350m over 1km. These hills were often fog shrouded early morning, so dawn surveys were not possible. Consequently Peak District surveys took up the whole day (2- 4 hours per square, two squares in a day). Bedson et al. (2021b) compares nocturnal survey methods for mountain hares, showing day time surveys as effective.

We also consider possible differences of detection process between different habitat classes, particularly as mountain hares might hide beneath deep heather on muirburn. However our surveys went on straight line transects, following the Jenkins et al. (1963) method of flushing hares from cover. We consider that with the stratified detection function, the lower detection distance (P and ESW) estimated from grouse moor heather, arose from low sample sizes, not detectability, and that with an ongoing accumulation of detections, P and ESW would have increased considerably. The P and ESW values for grouse moor heather were similar to acid grassland, even though one might expect more visibility on the latter. On the whole, all habitat classes contained winter vegetation up to ~100cm height and with mountain hares flattening to ~15cm height, they can hide in any habitats.

When assembling these analyses, we also considered several alternative habitat class definitions e.g. merging restored and unrestored bog; grouse moor bog and grouse moor heather. Such alternatives did not change the substantive findings that bog habitats reported significantly higher density than managed grouse moor or acid grassland habitats. During surveys, when walking from one habitat to another, we typically observed an immediate abrupt change of encounter rates within <200m.

We acknowledge that mountain hares may move between habitat classes and we did not employ telemetry to measure this. Hewson (1961 and 1989) suggested hares would moving by dusk to feed on grouse moor pioneer heather patches. We rarely observed such movement. Both the high elevation restored and unrestored bog areas contained some heather resource, obviating the need for a nightly migration. We analysed habitat classes based on where each hare was first seen. Hare home ranges may be very small ~0.1km^2 (Hewson and Hinge 1990; Rao et al. 2003). Because our visual range exceeded 700m and our transects were effectively running at 1000m parallel range, we felt that coverage of home ranges was likely to be comprehensive, although we could not be certain of this. Our surveys occurred without snow lie present, which might otherwise prompt hares to seek for heather which might better protrude out of the snow.

Notwithstanding these challenges, our surveys achieved global detection probability of 18% of hares (i.e. nearly 1 in 5 hares) to a range of 520 metres. We duly consider distance sampling by day as effective across habitats. .

4.5.3 Conservation status

In the Peak District since 1971, there were four previous reports of mountain hare abundance suggesting a population of up to ~1,000 individuals (Mallon 2001). The distance sampling survey of winter 2001-2002 using different methods to this paper, estimated abundance at ~12,000 hares (CI: 7,000-20,000) (Mallon 2001; Wheeler 2002; Mallon et al., 2003). We retrieved that data and applied the same analyses as for 2017-20. This revised 2002 density estimate to 9.4 hares km^{-2} (95% CI 6.8 to

12.9); abundance for survey extent 3,361 (95% CI 2,431-4,612) individuals. However we recommend caution with 2002 values as its survey methodology was varied from of 2017-21: i.e. different transect shapes, different locations, no use of binoculars, no laser range finder for measuring distance to object, no GPS measurement of transect length, all observations recorded as singles i.e. no clusters.

Estimates for 2017 to 2021 reported high densities upon Bleaklow and Margery Hill. We acknowledge that using these two high density areas for 2019 surveys (i.e. as 40% of survey areas), may bias that estimate upwards. The Peak District mean abundance estimate for 2019 refers to densities from the wider survey and alpha hull shape, reporting as 3,562 (95% CI 2,291-5,624) individuals.

Therefore estimates for 2002 compared with 2019 appear similar: a stable population. The length of this study (2017-21) is too short to detect population cycles, which are subject to complex factors (Newey et al., 2007). Population dynamics for congeneric snowshoe hare (*Lepus americanus*) suggest annual fluctuations with observed increases by 25% or decreases by as much as 75%, linked to food supply and predation (Krebs et al. 2001). Cycle periodicity of mountain hares in Scotland has a range of 4-15 years, with amplitude of up to 90% (Newey et al. 2007b).

We cannot identify explicit causation for the population fluctuations we observed. Winter 2017-18 was exceptionally severe (UK Met Office 2020) possibly causing additional mortality. Summer 2018 was extremely hot, potentially contributing to difficult breeding conditions arising from dry vegetation and reduced water availability.

This Peak District mountain hare population assessment shows how their confinement to the uplands and sensitivity to different habitats makes them a useful mammal species for ecosystem monitoring. They provide an understanding of mammalian responses to climate change: a cold-niche specialist at the periphery of their climatic range (Harris & Yalden 2008). We suggest both degrading forces and restoration efforts impact upon hare density. There is substantial variation of density between habitat classes, predisposing the population to local extinction events (Patton et al. 2010). Management agendas should consider how future changes to habitat landcover and land use may affect this mountain hare population.

Acknowledgements

This research was funded by the People's Trust for Endangered Species, the Hare Preservation Trust, the British Mountaineering Council, Penny Anderson Associates, South-West Action for Hares, Queen's University Belfast and an MMU matched-funded PhD scholarship to CB. We thank RSPB Dove Stone, The National Trust, United Utilities and Upperwood Estates for access support. We thank Moors for the Future for shapefiles showing restored bog areas. We thank E. Rexstad of University of St. Andrews for R code enabling the t-test analyses. We thank J. Minshull, D. Hogg, K. Boyd, I. Commerford, C. Shaw, M. Moore and C. Thelier for fieldwork. Mountain hare BRC records kindly provided by British Trust for Ornithology, Cheshire Record LRC, Derbyshire Mammal Group, Derbyshire Wildlife Trust, Moors for the Future, Liverpool Museum, National Biodiversity Atlas, Sheffield Biological Records Centre, Sorby Natural History Society and West Yorkshire Ecology. We thank Simon Caporn and Anna Reuleaux who advised on earlier drafts of this paper.

Data Availability Statement

Data available upon reasonable request.

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Tables

Table 4.1 Habitat classes with NVC categories

Sources: (Jackson 2000; Elkington et al., 2001; Hall, Kirby & Whitbread 2004; Natural England 2014; Rowland et al., 2015; JNCC 2016).

Habitat class	**NVC category**
Restored bog	M1 and M2 *Sphagnum* bog-pools M3 and M20 *Eriophorum* bog pools M4 Carex rostrata – Sphagnum recurvum mire M5 Carex rostrata – Sphagnum squarrosum mire M6 *Carex – Sphagnum* mires M9 Carex rostrata – Calliergon cuspidatum/giganteum mire M15 Scirpus cespitosus – Erica tetralix wet heath M16 Erica tetralix – Sphagnum compactum wet heath M19 *Calluna – Eriophorum* blanket mires
Unrestored bog	As for Restored bog
Grouse moor bog	As for Restored bog
Grouse moor heather	H1 *Calluna – Festuca* heath H8 *Calluna – Ulex* heath H9 *Calluna – Deschampsia* heath H10 *Calluna– Erica* heath H12 *Calluna – Vaccinium* heath H18 *Vaccinium – Deschampsia* heath M19 *Calluna – Eriophorum* blanket mires
Unmanaged dwarf shrub heath	H1 *Calluna – Festuca* heath H8 *Calluna – Ulex* heath H9 *Calluna – Deschampsia* heath H10 *Calluna– Erica* heath H12 *Calluna – Vaccinium* heath H18 *Vaccinium – Deschampsia* heaths
Acid grassland	U1 *Festuca ovina – Agrostis capillari - Rumex acetosella* grassland U2 *Deschampsia flexuosa* grassland U4 *Festuca ovina – Agrostis capillaris – Galium saxatile* grassland U5 *Nardus stricta – Galium saxatile* grassland U6 *Juncus squarrosus – Festuca ovina* grassland *W16 Quercus* spp. *– Betula* spp. *– Deschampsia flexuosa* woodland (for bracken)

Table 4.2 Range of candidate models based on all data for Bleaklow and Margery Hill pooled. (2017, 2018, 2019, 2020, 2021).

n = number of observations; Model (key) = Key function with series expansion; AIC = Akaike Information Criterion; ΔAIC = delta AIC value within comparable data selections; χ2 GOF (p)= chi-square goodness of fit *P*-value; P = detection probability function; P *cv* = detection probability coefficient of variation. We chose to use data truncated at 520m with the hazard-rate model and polynomial, for all analyses.

Data selection	**n**	**Model (key)**	**# para**	**AIC**	**ΔAIC**	**χ2 GOF (p)**	**P**	**P *cv***
Truncate at 520m	1985	Uniform + cosine	3	22353.25	204.82	0.00	0.30	0.01
		Uniform + poly	3	22672.06	523.63	0.00	0.40	0.01
		Half-normal + cosine	3	22260.09	111.66	0.00	0.25	0.02
		Half-normal + Hermite	1	22619.32	470.89	0.00	0.35	0.01
		Hazard rate + cosine	3	22152.52	4.09	0.61	0.19	0.04
		Hazard rate + poly	3	22148.43	0.00	0.77	0.18	0.04
Truncate at 500m	1980	Uniform + cosine	3	22234.13	185.62	0.00	0.30	0.01
		Uniform + poly	3	22533.32	484.81	0.00	0.40	0.01
		Half-normal + cosine	3	22153.85	105.34	0.00	0.26	0.02
		Half-normal + Hermite	1	22503.44	454.93	0.00	0.36	0.01
		Hazard rate + cosine	3	22050.69	2.18	0.62	0.19	0.04
		Hazard rate + poly	3	22048.51	0.00	0.70	0.19	0.04
Truncate at 480m	1970	Uniform + cosine	3	22025.26	165.86	0.00	0.30	0.01
		Uniform + poly	0	0.00	0.00	0.00	0.00	0.00
		Half-normal + cosine	3	21952.22	92.82	0.00	0.26	0.02
		Half-normal + Hermite	1	22278.42	419.02	0.00	0.36	0.01
		Hazard rate + cosine	3	21863.44	4.04	0.19	0.20	0.04
		Hazard rate + poly	3	21859.40	0.00	0.37	0.20	0.04

Table 4.3 Stratified distance sampling survey parameter estimates.

Data selection based on 520m truncation with hazard rate model. n = encounters; L = line length km; K = number of transects; E(s) = mean cluster size; $\hat{D}$ = density estimate km^{-2}; *cv* = parameter coefficient of variation. $\hat{D}$ is calculated with probability density function f(0) and f(0) *cv*.(Buckland et al., 2001: 84,85). "Habitats" data source is Bleaklow and Margery Hill only with probability density function f(0) = 0.010467 and f(0) *cv* = 0.0407 and represents 2017 to 2021 totalled effort and encounters, mean cluster size and density estimate values. “Years” data source: Pooled by year (not by habitat) for Bleaklow and Margery Hill only with same probability density function. Survey areas 2019 is modelled with all data for all areas for all areas (2,225 observations) with probability density function f(0) = 0.011522 f(0) *cv* = 0.0407 . However the table just reports estimates for the surveyed areas for 2019 only.

	n	n *cv*	L	K	E (s)	E (s) *cv*	$\hat{D}$	$\hat{D}$ *cv*
Habitats								
Acid grassland	75	0.23	42.3	36	1.28	0.05	11.8	0.24
Grouse moor bog	285	0.12	133.9	85	1.09	0.01	12.2	0.13
Grouse moor heather	79	0.23	48.6	23	1.18	0.03	10.0	0.24
Restored bog	544	0.12	97.8	54	1.12	0.01	32.6	0.12
Unrestored bog	965	0.07	232.6	117	1.12	0.01	24.4	0.08
Unmanaged heath	37	0.30	45.3	47	1.12	0.04	4.8	0.30
Years								
2017	304	0.20	120.9	26	1.18	0.02	15.5	0.21
2018	504	0.10	121.6	26	1.14	0.01	24.7	0.11
2019	401	0.14	112.5	26	1.13	0.01	21.1	0.15
2020	402	0.25	123.1	26	1.05	0.01	17.9	0.26
2021	374	0.18	120.8	26	1.13	0.01	18.3	0.18
Survey areas 2019								
	n	n CV	L	K	E (s)	E (s) CV	$\hat{D}$	$\hat{D}$ CV
Bleaklow	246	0.14	56.7	13	1.09	0.01	27.2	0.15
Margery Hill	155	0.30	55.8	13	1.16	0.03	18.6	0.30
Holme Moss	50	0.26	57.5	13	1.22	0.03	6.1	0.27
Peripheral Squares	101	0.19	112.7	26	1.19	0.04	6.1	0.20

Table 4.4 Pairwise t-tests comparing strata

Based on values from Table 1. S1 = Stratum 1; S2 = Stratum 2. D̂ difference subtracts S2 D̂ from S1 D̂. A positive value indicates Stratum 1 is larger; a negative value means Stratum 2 is larger. SE is the standard error of D̂ difference. Values are assessed with Satterthwaite t test reporting t statistic and degrees of freedom. Asterisk * and bold lines indicate *P*-value significant and using Bonferonni within-cohort correction. Effect size calculated with Cohen's *d* and considered as r=.10 (small); r=0.30(medium); r=0.50(large) (Field et al. 2012). Abbreviations: AG = Acid grassland; GMB = grouse moor bog; GMH = grouse moor heather; RB = Restored bog; UB = Unrestored bog; UDSH = Unmanaged dwarf shrub heath.

S1	S2	D̂ Difference	SE Diff	t stat	df t stat	p value	Significant	Bonferonni-corrected significant	Effect size
Habitats									
Acid grassland	Grouse moor bog	-0.26	3.2	0.08	66.04	0.934			0.01
Acid grassland	Grouse moor heather	1.84	3.6	0.50	64.44	0.615			0.06
Acid grassland	**Restored bog**	**-20.73**	**4.9**	**4.26**	**105.67**	**0.000**	*	**	**0.38**
Acid grassland	**Unrestored bog**	**-12.44**	**3.3**	**3.75**	**86.17**	**0.000**	*	**	**0.37**
Acid grassland	**Unmanaged heath**	**7.09**	**3.2**	**2.23**	**61.53**	**0.029**	*		**0.27**
Grouse moor bog	Grouse moor heather	2.10	2.8	0.76	47.19	0.449			0.11
Grouse moor bog	**Restored bog**	**-20.46**	**4.2**	**4.83**	**85.35**	**0.000**	*	**	**0.46**
Grouse moor bog	**Unrestored bog**	**-12.18**	**2.3**	**5.28**	**313.71**	**0.000**	*	**	**0.29**
Grouse moor bog	**Unmanaged heath**	**7.35**	**2.1**	**3.53**	**139.46**	**0.001**	*	**	**0.29**
Grouse moor heather	**Restored bog**	**-22.57**	**4.6**	**4.89**	**90.60**	**0.000**	*	**	**0.46**
Grouse moor heather	**Unrestored bog**	**-14.28**	**2.9**	**4.86**	**66.43**	**0.000**	*	**	**0.51**
Grouse moor heather	Unmanaged heath	5.25	2.8	1.90	43.10	0.064			0.28
Restored bog	Unrestored bog	8.29	4.3	1.92	99.03	0.057			0.19
Restored bog	**Unmanaged heath**	**27.82**	**4.2**	**6.55**	**82.52**	**0.000**	*	**	**0.58**
Unrestored bog	**Unmanaged heath**	**19.53**	**2.3**	**8.40**	**222.27**	**0.000**	*	**	**0.49**
Comparison of Habitats Year to Year									
AG17	AG18	2.1	13.1	0.15	14.11	0.877			0.04
AG18	AG19	0.6	10.7	0.05	12.96	0.957			0.01
AG19	AG20	5.6	8.2	0.67	9.30	0.510			0.21
AG20	AG21	-1.2	6.8	0.18	12.43	0.859			0.05
GMB17	**GMB18**	**-12.7**	**3.8**	**3.29**	**40.07**	**0.002**	*	**	**0.46**
GMB18	GMB19	3.0	5.0	0.60	31.19	0.549			0.11
GMB19	**GMB20**	**12.9**	**4.6**	**2.88**	**21.65**	**0.009**	*	**	**0.53**
GMB20	GMB21	-2.3	2.1	1.09	35.64	0.283			0.18
GMH17	GMH18	-13.6	5.9	2.31	5.59	0.063			0.70
GMH18	GMH19	13.3	10.3	1.29	6.54	0.239			0.45

GMH19	GMH20	3.3	9.1	0.35	4.58	0.738			0.16
GMH20	GMH21	-2.8	4.4	0.62	7.28	0.554			0.22
RB17	RB18	0.4	11.1	0.03	17.95	0.975			0.01
RB18	RB19	0.4	8.0	0.05	22.45	0.964			0.01
RB19	RB20	-13.5	13.8	0.97	14.28	0.344			0.25
RB20	RB21	7.8	15.1	0.51	17.82	0.612			0.12
UB17	**UB18**	**-11.9**	**4.5**	**2.64**	**57.93**	**0.011**	*	**	**0.33**
UB18	UB19	4.2	4.9	0.86	55.74	0.393			0.11
UB19	UB20	4.2	65.0	0.65	43.63	0.518			0.10
UB20	UB21	-2.4	6.3	0.38	41.99	0.705			0.06
UH17	UH18	-9.8	7.1	1.38	10.37	0.195			0.39
UH18	UH19	5.6	8.1	0.69	15.80	0.498			0.17
UH19	UH20	-0.5	4.9	0.10	15.09	0.919			0.03
UH20	UH21	3.8	3.4	1.12	14.58	0.279			0.28

S1	S2	$\hat{D}$ Difference	SE Diff	t stat	df t stat	p value	Significant	Bonferonni-corrected significant	Effect size
Years	**(Bleaklow and Margery Hill combined)**								
2017	**2018**	**-9.21**	**4.0**	**2.29**	**57.56**	**0.025**	*		**0.29**
2018	2019	3.65	3.9	0.94	61.36	0.350			0.12
2019	2020	3.13	5.4	0.58	47.34	0.563			0.08
2020	2021	0.36	5.6	0.06	49.37	0.948			0.01
Survey areas 2019									
Bleaklow	**Margery Hill**	**8.68**	**6.8**	**1.27**	**23.31**	**0.214**			**0.25**
Bleaklow	**Holme Moss**	**21.13**	**4.2**	**5.03**	**18.78**	**0.000**	*	**	**0.76**
Bleaklow	**Peripheral Squares**	**21.10**	**4.1**	**5.20**	**16.90**	**0.000**	*	**	**0.78**
Margery Hill	Holme Moss	12.45	5.8	2.13	14.76	0.050			0.48
Margery Hill	**Peripheral Squares**	**12.42**	**5.7**	**2.16**	**13.89**	**0.049**	*		**0.50**
Holme Moss	Peripheral Squares	-0.03	2.0	0.01	27.84	0.987			0.00

Table 4.5 Abundance of mountain hares for Peak District for year 2019

Based on density estimates derived from pooled observations for each of the four denoted surveyed areas. Calculation of km^2 for each surveyed areas is based on relevant habitat classes only i.e. acid grassland; grouse moor bog; grouse moor heather; restored bog; unrestored bog; unmanaged dwarf shrub heath. Thus non-relevant types e.g. woodland are excluded. Density estimate is shown with 95% confidence limits; abundance also with 95% confidence limits.

	Bleaklow	Margery Hill	Holme Moss	Peripheral areas	
Density km^{-2}	27.4	18.6	6.1	6.2	
Density LCL	19.9	9.7	3.4	4.1	
Density UCL	37.8	35.5	10.9	9.4	
					Total
Area km^2	40.4	40.4	40.4	236.3	357.5
Abundance	1,107	750	247	1,458	3,562
Abundance LCL	802	393	139	957	2,291
Abundance UCL	1,528	1,433	442	2,221	5,624

Figures

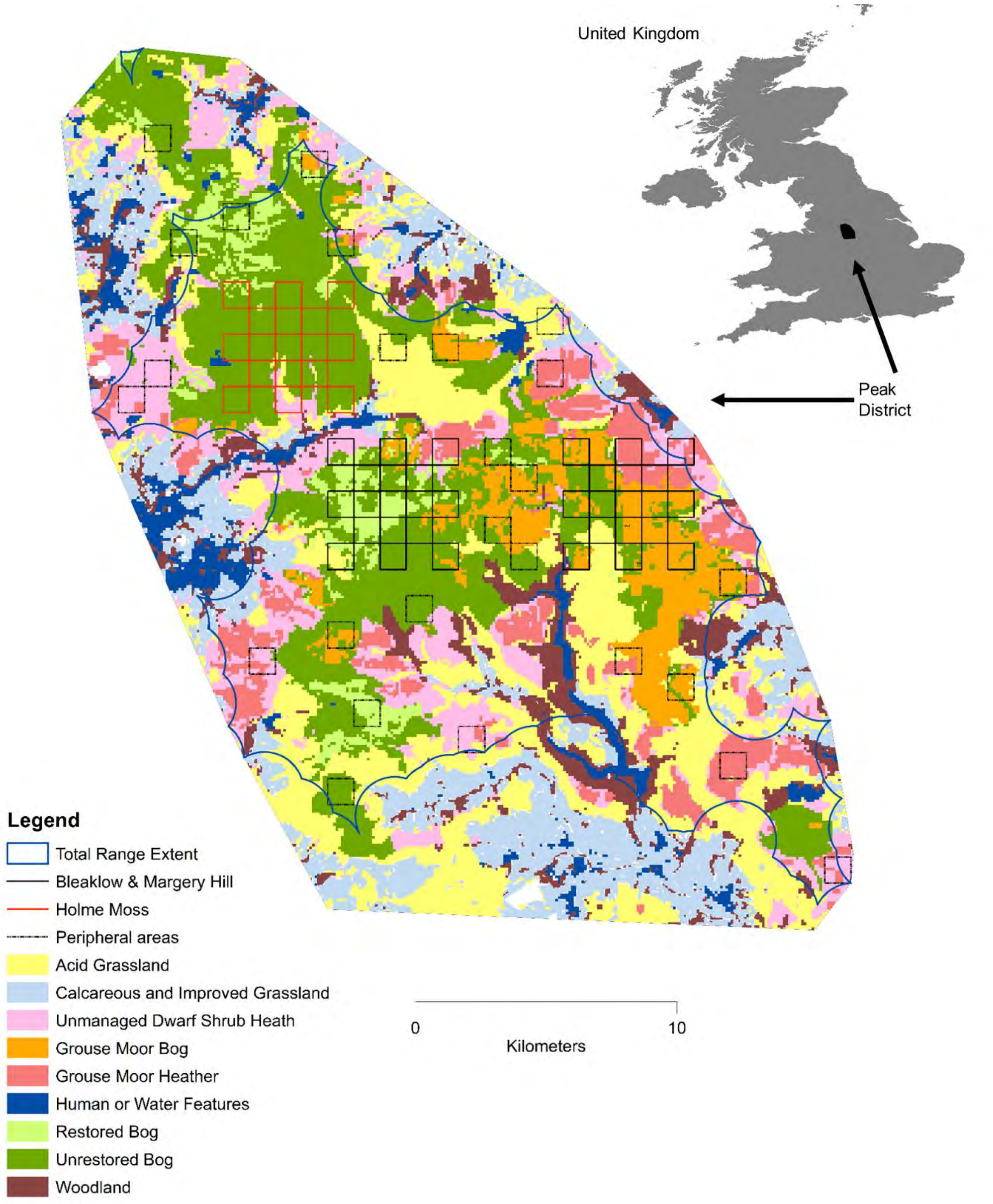

Figure 4.1 Map of study area.

The locations of ten years of BRC mountain hare records informed the minimum convex polygon, being the outer shape. The extent of hares for abundance projection was the alpha hull shape, shown by the blue line and also the survey areas. The survey transects are shown for Bleaklow and Margery Hill (black squares); Holme Moss (red squares); peripheral areas (dotted squares). Legend shows habitat classes. Inset map shows location of Peak District in the United Kingdom. Peak District map origin is British National Grid Reference SK Easting 390000 Northing 370000.

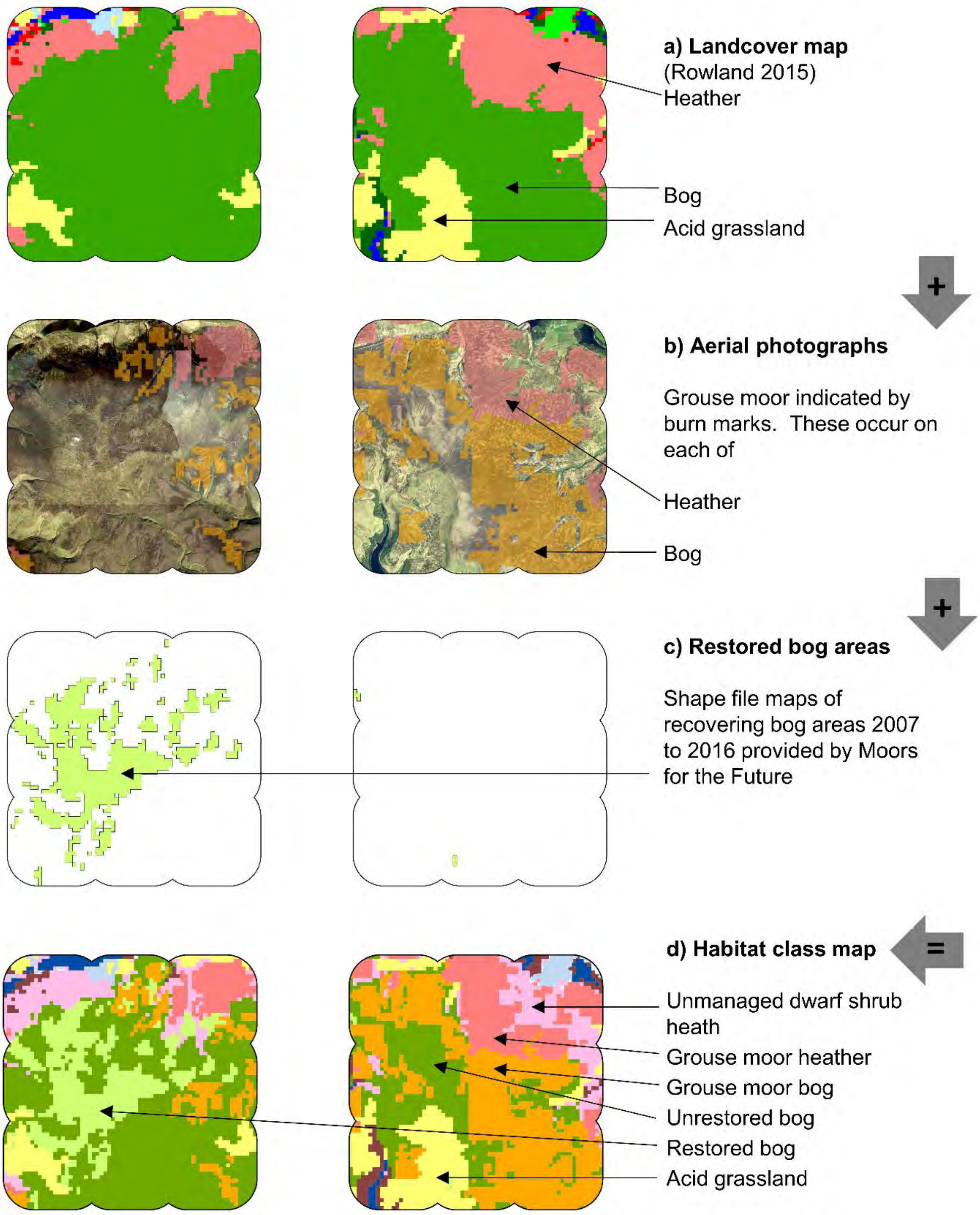

Figure 4.2 Step by step construction of habitat class map

For surveyed extent (5x5km with 800m buffer) with 1-ha pixel, for each of Bleaklow (left) and Margery Hill (right) (British National Grid origin SK Easting 408000 Northing 394000). Map a) shows landcover classification system of Rowland (2015) which is used as starting point. Map b) Aerial photographs (5 metre pixels) are assessed and any with burn mark within any hectare denoted as either grouse moor bog or grouse heather, referencing the underlying landcover determined by Rowland (2015). Map c) Shape files provided by Moors for the Future, showing recovering bog areas which received treatment up to 2016. Map d) The final map with all habitat classes pertinent to mountain hares. Any heather without burn mark is therefore regarded as unmanaged dwarf shrub heath.

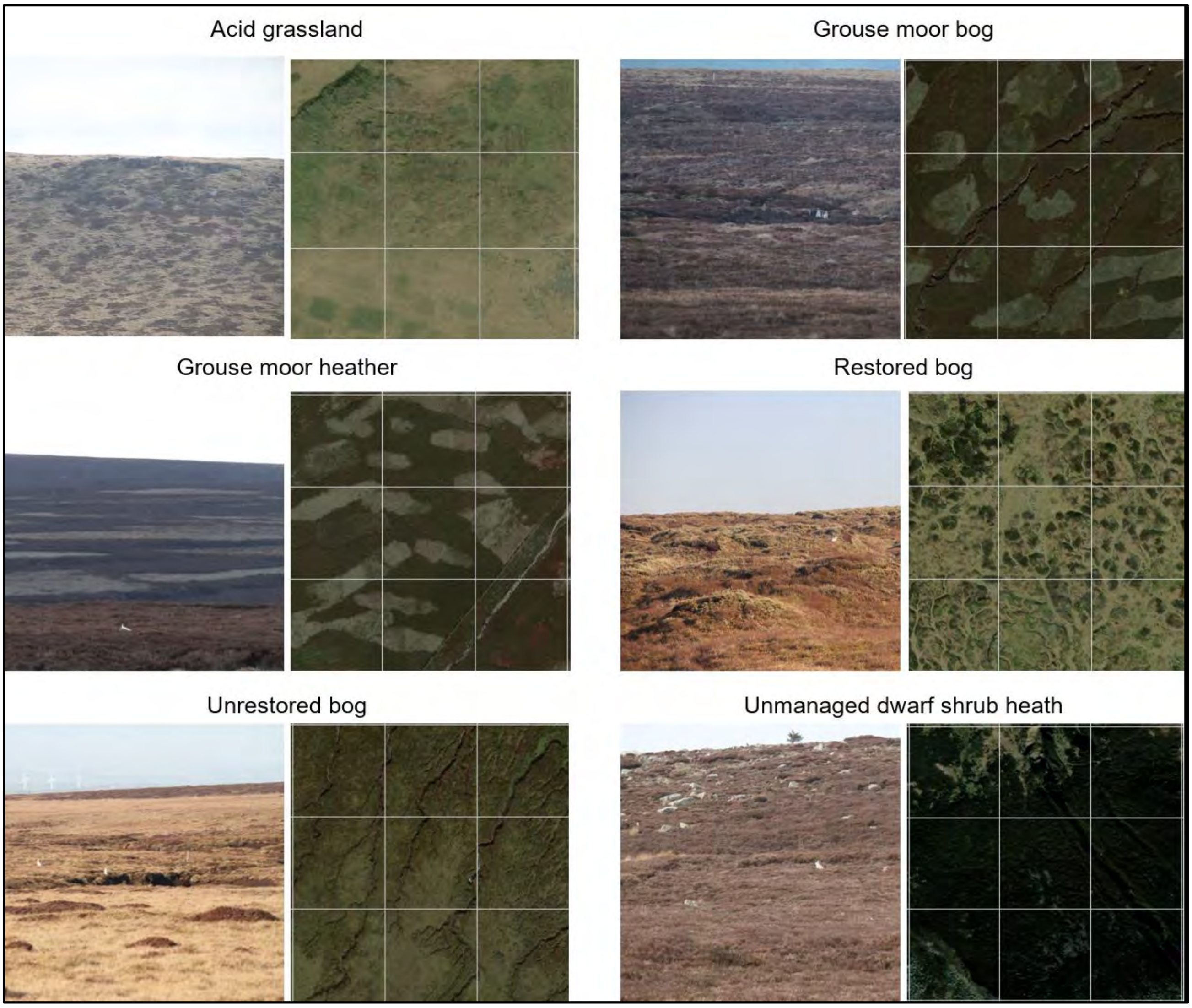

Figure 4.3 Photographs of each of the habitat classes

For each habitat class the left photos is taken from the ground. The right side photos are aerial images at 300metres by 300metres with a 100m fishnet grid overlain, for scale therefore aerial photo scale as appears on page 1:4000 25mm=100m. Source: ArcGIS ESRI "WorldImagery" downloaded 3 August 2021. Colours are natural, not enhanced.

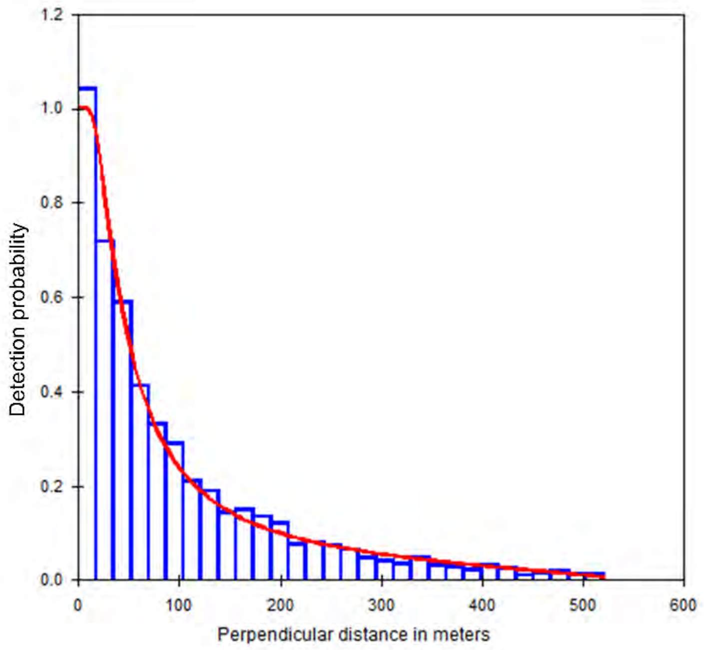

Figure 4.4 Histogram for all distance sampling data from 2017 to 2021

Fitted with the hazard rate model. Data includes Bleaklow & Margery Hill, Holme Moss and Peripheral areas. Data is truncated at 520m and has 2,225 observations.

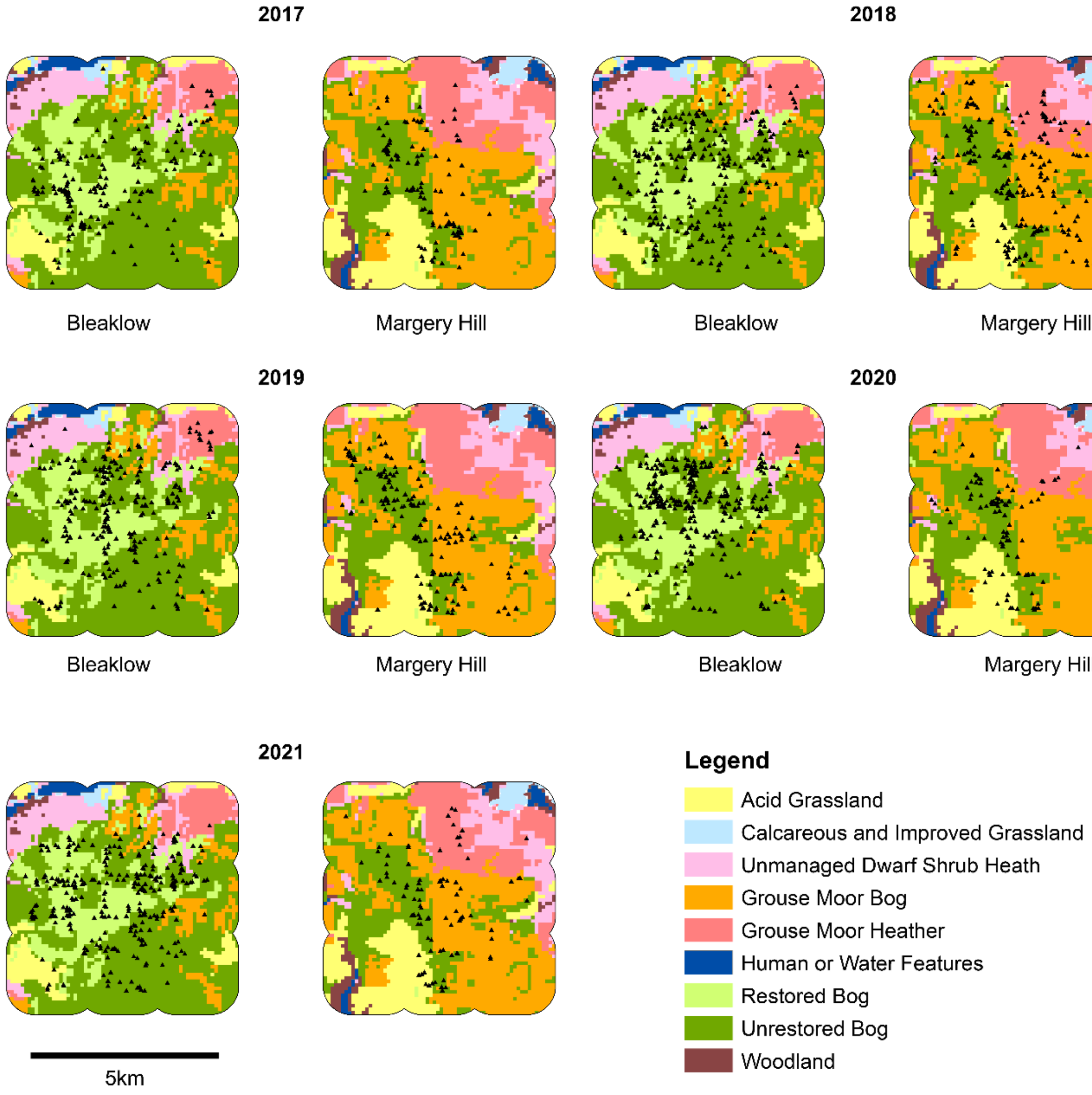

Figure 4.5 Distance sampling observations for Bleaklow and Margery Hill

The two survey sites with 800m buffer, for years 2017 to 2021. Habitat classes as legend. Bleaklow map origin is British National Grid Reference SK Easting 308000 Northing 394000. Margery Hill survey site is duly positioned 4km to east. Black triangles indicate all observed mountain hares (untruncated data).

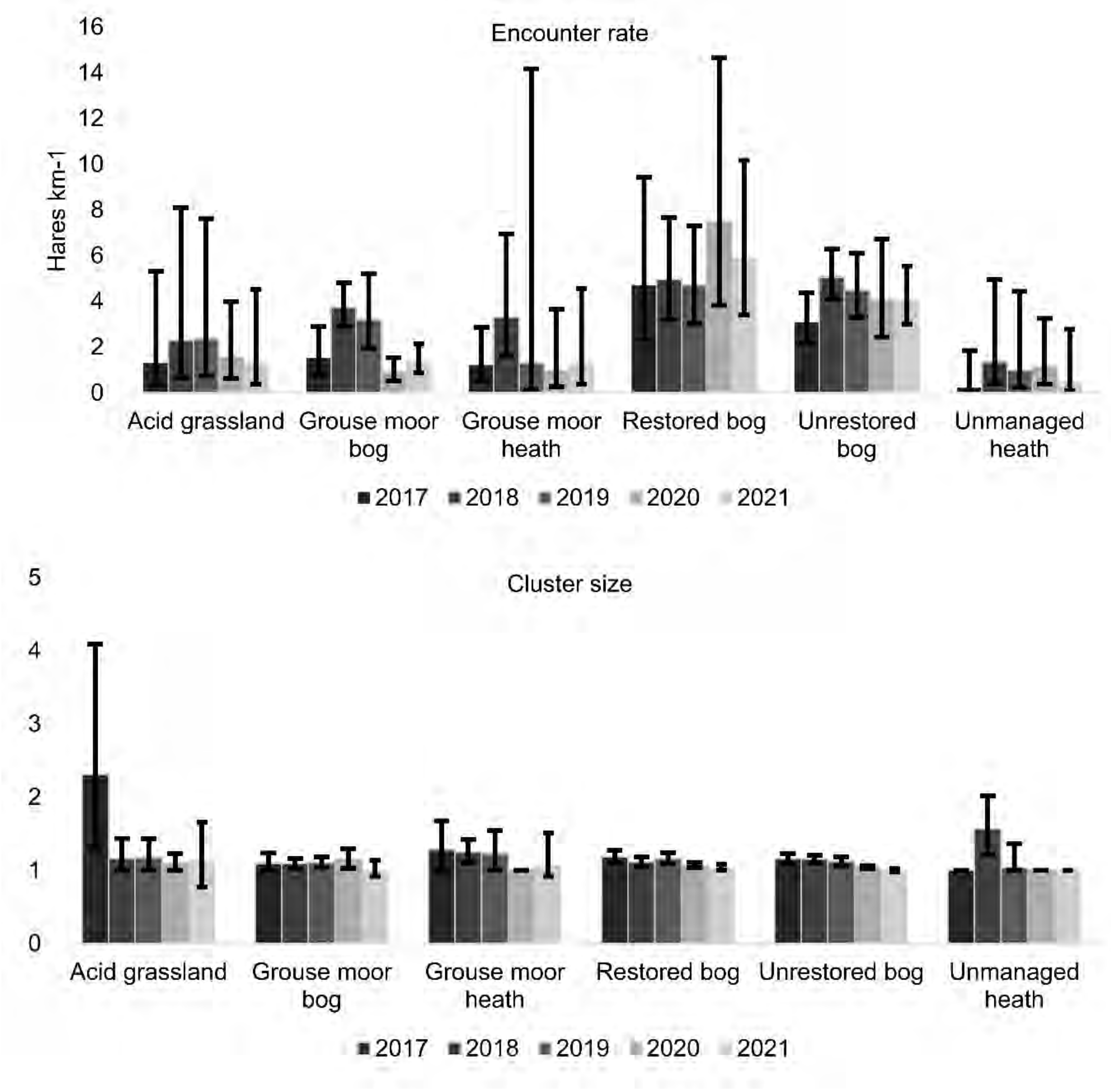

Figure 4.6 Encounter rate and cluster size estimates

For each habitat class and year based on Bleaklow and Margery Hill data. In total the number of hares recorded was 385 in 2017; 622 in 2018; 517 in 2019; 434 in 2020; 458 in 2021 .

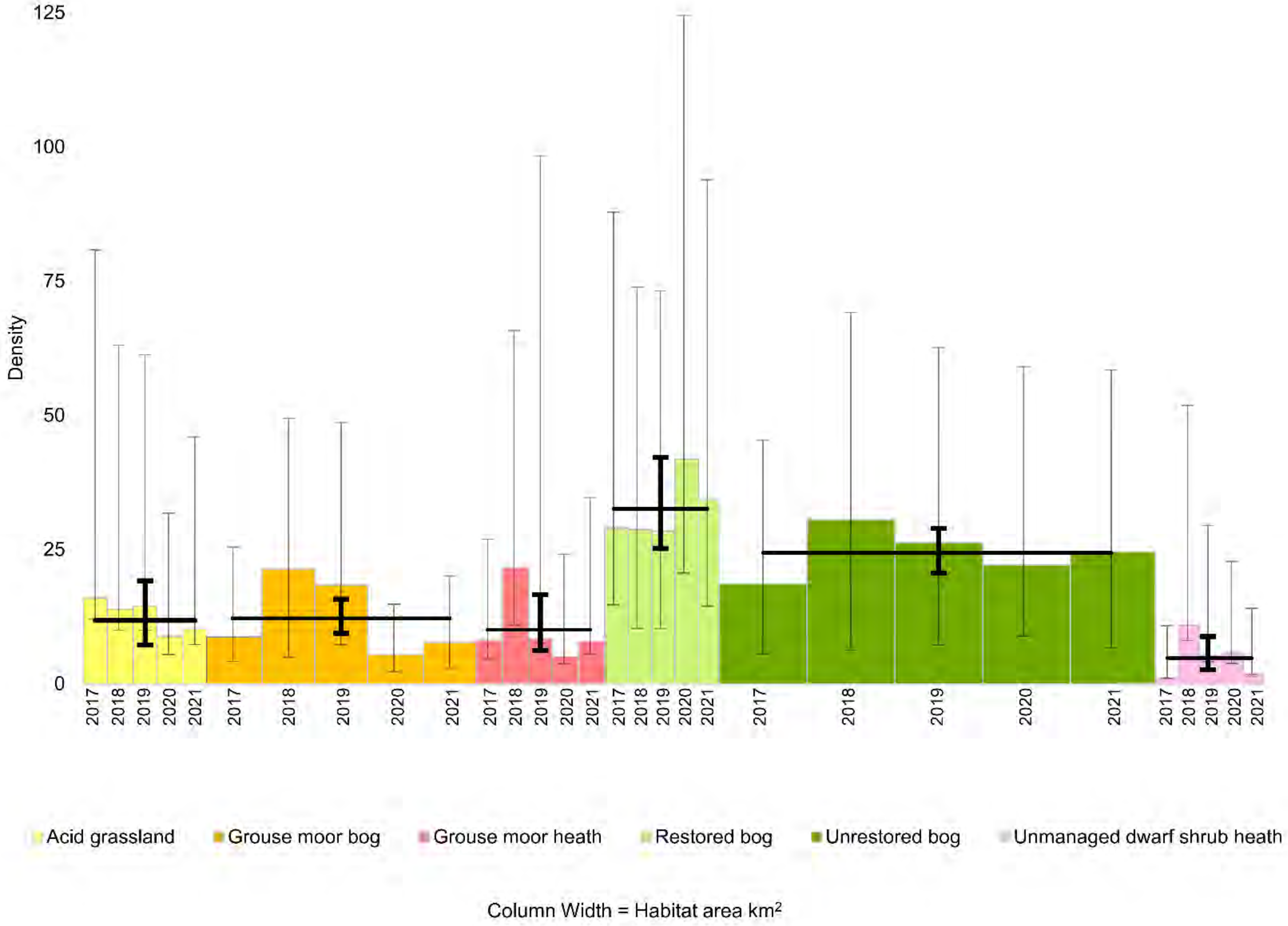

Figure 4.7 Estimates of abundance of mountain hares by habitat class, each year, as reported by distance sampling analysis for Bleaklow and Margery Hill only

The x-axis column widths represent habitat area in km^2 which were: acid grassland 8.5; grouse moor bog 18.4; grouse moor heather 18.7; restored bog 7.9; unrestored bog 29.8; unmanaged dwarf shrub heath 7.4. Column height is density (D) value. Column error bars indicate lower and upper 95% confidence limits on density estimate. The size of shaded column area therefore represents the abundance of hares on each habitat type each year based on point density values. Black horizontal bars indicate mean density value for each habitat over the 4 years, with black vertical error bars showing 95% confidence limits (following Clymo 2014: 230).

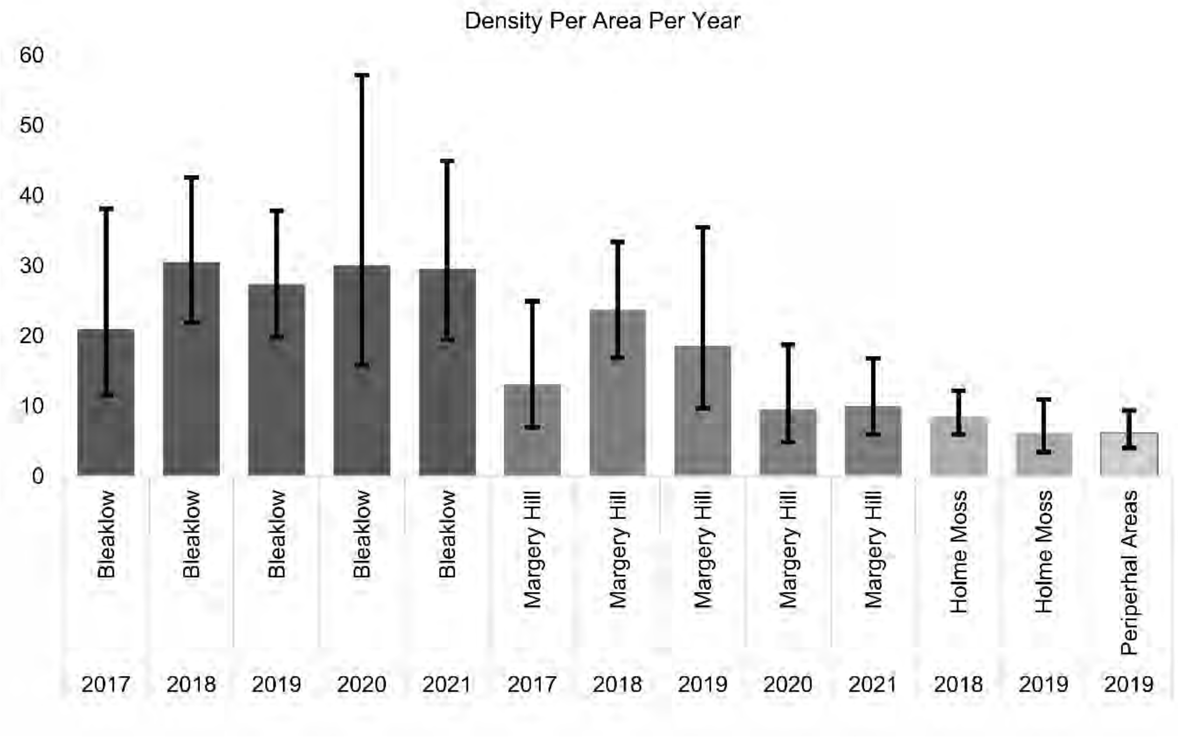

Figure 4.8 Estimates of total mountain hare density per year per survey area

Based on pooled observations each year. Error bars indicate 95% lower and upper confidence limits. Upon Bleaklow and Margery Hill there was a 56% increase in density from 2017 to 2018. This was followed by a decrease 2018-19 by 13%; 2019-20 by 14%. Density upon Bleaklow and Margery Hill was significantly higher than Holme Moss when it was surveyed in 2018 and 2019 and also significantly higher than peripheral areas in 2019.

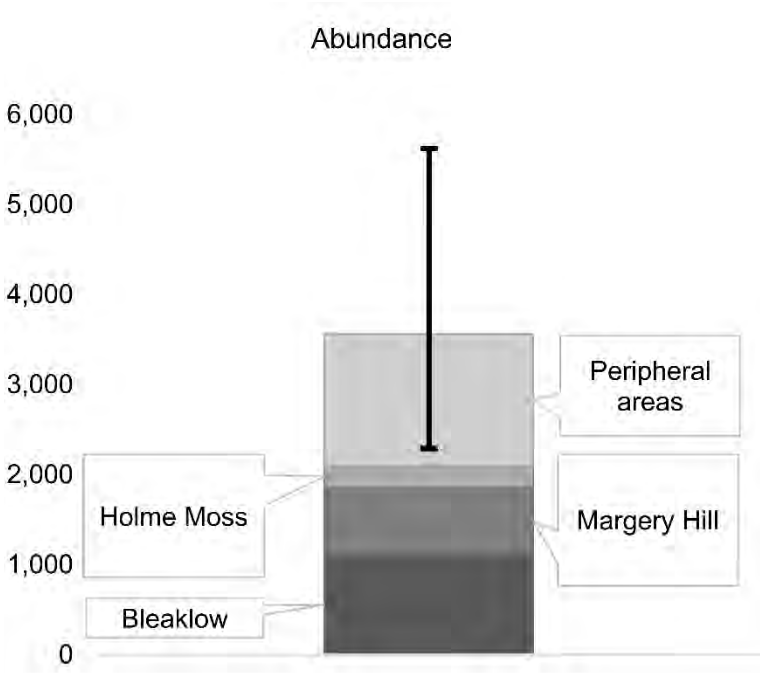

Figure 4.9 Abundance estimate for Peak District for year 2019

Based on density estimates derived from pooled observations for the four different survey areas indicated by call outs. Error bars indicated 95% lower and upper confidence limits for total abundance. Source data from Table 3.

Appendices

Table A1 Stratified distance sampling survey parameter estimates for habitat classes each year for Bleaklow and Margery Hill. n = encounters; L = line length km; K = number of transects; E(s) = mean cluster size; $\hat{D}$ = density estimate km^{-2}; *cv* = parameter coefficient of variation. $\hat{D}$ is calculated with probability density function f(0) = 0.010467 and f(0) *cv* = 0.0407 (Buckland et al., 2001: 84,85). AG = Acid grassland; GMB = Grouse moor bog; GMH = Grouse moor heather; RB = Restored bog; UB = Unrestored bog; UH = Unmanaged dwarf shrub heath and each year shown as suffix e.g. AG17 is acid grassland in 2017 survey.

	n	n *cv*	L	K	E (s)	E (s) *cv*	$\hat{D}$	$\hat{D}$ *cv*
AG17	11	0.61	8.3	7	2.31	0.25	16.0	0.67
GMB17	41	0.31	27.0	17	1.10	0.05	8.7	0.31
GMH17	12	0.31	9.8	5	1.28	0.12	8.2	0.34
RB17	93	0.32	19.8	11	1.19	0.03	29.3	0.32
UB17	145	0.17	47.1	24	1.16	0.02	18.7	0.17
UH17	2	1.12	8.7	9	1.00	0.00	1.2	1.12
AG18	20	0.55	8.7	7	1.16	0.10	14.0	0.56
GMB18	102	0.12	27.2	18	1.09	0.03	21.4	0.13
GMH18	32	0.23	9.6	4	1.25	0.06	21.8	0.24
RB18	99	0.20	19.9	12	1.11	0.02	28.9	0.20
UB18	239	0.10	47.1	23	1.15	0.02	30.5	0.11
UH18	12	0.62	8.9	10	1.56	0.11	11.0	0.63
AG19	19	0.50	8.0	7	1.17	0.09	14.5	0.51
GMB19	80	0.23	25.1	17	1.10	0.03	18.3	0.24
GMH19	12	1.04	9.1	5	1.23	0.10	8.5	1.04
RB19	86	0.19	18.3	10	1.16	0.03	28.5	0.20
UB19	196	0.14	43.6	23	1.12	0.02	26.3	0.15
UH19	8	0.73	8.1	9	1.04	0.11	5.4	0.74
AG20	14	0.39	8.9	7	1.09	0.06	9.0	0.40
GMB20	25	0.25	27.6	17	1.15	0.05	5.5	0.26
GMH20	10	0.42	10.0	4	1.00	0.00	5.2	0.42
RB20	150	0.30	20.0	11	1.07	0.01	42.0	0.31
UB20	193	0.24	47.5	23	1.04	0.01	22.1	0.25
UH20	10	0.48	8.9	9	1.00	0.00	5.9	0.48
AG21	11	0.56	8.4	8	1.49	0.12	10.2	0.57
GMB21	37	0.20	26.9	16	1.08	0.05	7.8	0.22
GMH21	13	0.46	9.8	5	1.15	0.14	8.0	0.49
RB21	116	0.24	19.7	10	1.11	0.03	34.2	0.25
UB21	192	0.14	47.1	24	1.15	0.02	24.5	0.15
UH21	5	0.91	10.5	10	0.82	0.18	2.0	0.93

Table A2

Pairwise t-tests comparing habitat class strata each year based on values from TableA1 for Bleaklow and Margery Hill. S1 = Stratum 1; S2 = Stratum 2. $\hat{\hat{D}}$ difference subtracts S2 $\hat{\hat{D}}$ from S1 $\hat{\hat{D}}$. A positive value indicates Stratum 1 is larger; a negative value means Stratum 2 is larger. SE is the standard error of $\hat{\hat{D}}$ difference. Values are assessed with Satterthwaite t test reporting t statistic and degrees of freedom. Asterisk * and bold lines indicate *P*-value significant and also when applying Bonferonni within-cohort correction. AG = Acid grassland; GMB = Grouse moor bog; GMH = Grouse moor heather; RB = Restored bog; UB = Unrestored bog; UH = Unmanaged dwarf shrub heath and each year shown as suffix e.g. AG17 is acid grassland in 2017 survey.

Comparison between habitats within each year

S1	S2	$\hat{\hat{D}}$ Difference	SE Diff	t stat	df t stat	p value	Significant	Bonferonni-corrected significant	Effect size
AG17	GMB17	7.3	10.9	0.66	9.23	0.521			0.21
AG17	GMH17	7.8	10.9	0.72	9.17	0.492			0.23
AG17	RB17	-13.2	14.1	0.93	17.59	0.360			0.22
AG17	UB17	-2.7	11.0	0.24	9.72	0.810			0.08
AG17	UH17	14.8	10.7	1.39	8.37	0.200			0.43
GMB17	GMH17	0.5	3.9	0.14	16.60	0.891			0.03
GMB17	RB17	-20.5	9.8	2.09	12.31	0.058			0.51
GMB17	**UB17**	**-9.9**	**4.2**	**2.34**	**43.72**	**0.023**	*		**0.33**
GMB17	**UH17**	**7.5**	**3.1**	**2.44**	**23.74**	**0.022**	*		**0.45**
GMH17	RB17	-21.0	9.8	2.14	12.17	0.053			0.52
GMH17	**UB17**	**-10.5**	**4.2**	**2.48**	**22.51**	**0.021**	*		**0.46**
GMH17	UH17	7.0	3.1	2.28	8.00	0.052			0.63
RB17	UB17	10.6	9.9	1.06	13.11	0.307			0.28
RB17	**UH17**	**28.0**	**9.5**	**2.94**	**10.92**	**0.013**	*		**0.66**
UB17	**UH17**	**17.5**	**3.5**	**4.98**	**32.92**	**0.000**	*	**	**0.66**
AG18	GMB18	-7.4	8.2	0.90	8.18	0.393			0.30
AG18	GMH18	-7.9	9.4	0.83	9.99	0.422			0.25
AG18	RB18	-14.9	9.7	1.53	13.63	0.148			0.38
AG18	UB18	-16.6	8.4	1.97	9.00	0.080			0.55
AG18	UH18	2.9	10.4	0.28	14.60	0.782			0.07
GMB18	GMH18	-0.4	5.8	0.07	5.87	0.940			0.03
GMB18	RB18	-7.5	7.5	1.17	17.67	0.256			0.27
GMB18	**UB18**	**-9.1**	**4.1**	**2.22**	**55.33**	**0.030**	*		**0.29**
GMB18	UH18	10.4	7.4	1.39	12.86	0.186			0.36
GMH18	RB18	-7.1	7.8	12.61	12.61	0.380			0.25
GMH18	UB18	-8.7	6.1	1.44	7.03	0.193			0.48
GMH18	UH18	10.8	8.7	1.24	12.73	0.235			0.33

RB18	UB18	-1.6	6.6	0.24	20.39	0.806			0.05
RB18	UH18	17.9	9.1	1.97	20.27	0.062			0.40
UB18	**UH18**	**19.5**	**7.6**	**2.56**	**14.43**	**0.022**	*		**0.56**
AG19	GMB19	-3.8	8.5	0.44	11.14	0.664			0.13
AG19	GMH19	6.1	11.5	0.52	9.00	0.613			0.17
AG19	RB19	-14.0	9.2	1.51	13.28	0.153			0.38
AG19	UB19	-11.8	8.3	1.42	10.31	0.184			0.40
AG19	UH19	9.2	8.4	1.09	10.09	0.300			0.32
GMB19	GMH19	9.9	9.8	1.00	6.17	0.354			0.37
GMB19	RB19	-10.2	7.0	1.46	21.70	0.158			0.30
GMB19	UB19	-8.0	5.7	1.41	40.21	0.166			0.22
GMB19	**UH19**	**13.0**	**5.8**	**2.22**	**24.00**	**0.036**	*		**0.41**
GMH19	RB19	-20.0	10.4	1.91	7.52	0.094			0.57
GMH19	UB19	-17.9	9.6	1.85	5.76	0.115			0.61
GMH19	UH19	3.1	9.7	0.32	5.77	0.760			0.13
RB19	UB19	2.2	6.6	0.32	20.71	0.746			0.07
RB19	**UH19**	**23.2**	**68.0**	**3.40**	**17.78**	**0.003**	*	**	**0.63**
UB19	**UH19**	**21.0**	**5.5**	**3.82**	**24.96**	**0.001**	*	**	**0.61**
AG20	GMB20	3.5	3.8	0.92	8.51	0.381			0.30
AG20	GMH20	3.7	4.2	0.89	9.39	0.393			0.28
AG20	**RB20**	**-33.0**	**13.1**	**2.51**	**11.96**	**0.027**	*		**0.59**
AG20	**UB20**	**-13.1**	**6.4**	**2.05**	**28.48**	**0.049**	*		**0.36**
AG20	UH20	3.1	4.5	0.68	13.00	0.507			0.19
GMB20	GMH20	0.2	2.6	0.08	5.88	0.930			0.03
GMB20	**RB20**	**-36.5**	**12.7**	**2.87**	**10.64**	**0.016**	*		**0.66**
GMB20	**UB20**	**-16.7**	**5.5**	**3.02**	**26.49**	**0.006**	*	**	**0.51**
GMB20	UH20	-0.4	3.1	0.13	12.28	0.894			0.04
GMH20	**RB20**	**-36.8**	**12.8**	**2.86**	**10.99**	**0.015**	*		**0.65**
GMH20	**UB20**	**-16.9**	**5.8**	**2.92**	**26.21**	**0.007**	*	**	**0.50**
GMH20	UH20	-0.6	3.6	0.18	10.59	0.860			0.06
RB20	UB20	19.9	13.7	1.45	14.25	0.168			0.36
RB20	**UH20**	**36.1**	**12.9**	**2.79**	**11.41**	**0.017**	*		**0.64**
UB20	**UH20**	**16.2**	**6.0**	**2.68**	**31.19**	**0.011**	*		**0.43**
AG21	GMB21	2.4	6.1	0.4000	8.94	0.690			0.13
AG21	GMH21	2.2	7.0	0.3100	12.19	0.756			0.09
AG21	**RB21**	**-24.0**	**10.2**	**2.3600**	**16.68**	**0.031**	*		**0.50**
AG21	UB21	-14.3	6.8	2.1006	14.13	0.054			0.49
AG21	UH21	8.2	6.2	1.3200	9.34	0.216			0.40
GMB21	GMH21	-0.2	4.2	0.0500	6.66	0.961			0.02
GMB21	**RB21**	**-26.4**	**8.5**	**3.1200**	**10.56**	**0.010**	*		**0.69**

GMB21	**UB21**	**-16.8**	**3.9**	**4.3400**	**38.25**	**0.000**	*****	******	**0.57**
GMB21	**UH21**	**5.7**	**2.5**	**2.2900**	**22.79**	**0.032**	*****		**0.43**
GMH21	**RB21**	**-26.2**	**9.1**	**2.8600**	**13.19**	**0.013**	*****		**0.62**
GMH21	**UB21**	**-16.6**	**5.2**	**3.1800**	**15.04**	**0.006**	*****	******	**0.63**
GMH21	UH21	5.9	4.3	1.3800	7.42	0.208			0.45
RB21	UB21	9.7	9.0	1.0770	13.62	0.300			0.28
RB21	**UH21**	**32.2**	**8.5**	**3.7700**	**10.81**	**0.003**	*****	******	**0.75**
UB21	**UH21**	**22.5**	**4.0**	**5.6100**	**37.44**	**0.000**	*****	******	**0.68**

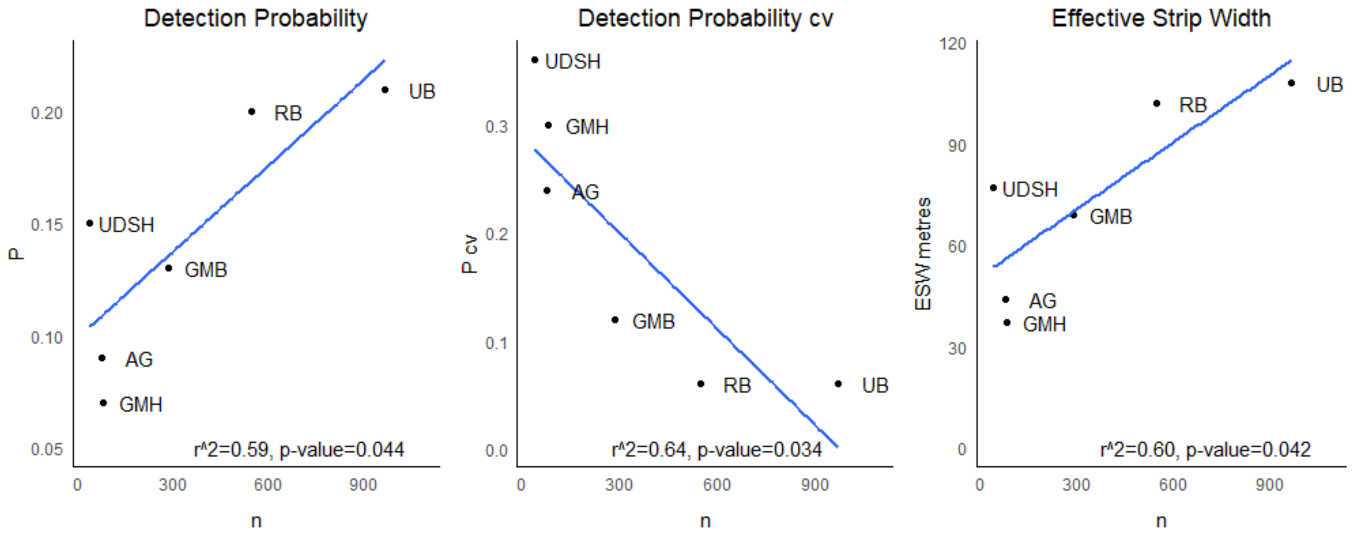

Figure A1 Regression charts comparing sample size (n) on x-axis, with distance parameter estimates on y-axis for each of detection probability (P); detection probability (P cv) and effective strip width (ESW) in metres. Linear regressions report: r^2 = adjusted R^2 value; and *P*-values. Data set is all observations from Bleaklow and Margery Hill for 2017 to 2021, pooled by habitat class. Distance sampling analysis truncated data at 520m and applied the hazard-rate model with the detection function stratified for each habitat class. Abbreviations: AG = Acid grassland; GMB = Grouse moor bog; GMH = Grouse moor heather; RB = Restored bog; UB = Unrestored bog; UH = Unmanaged dwarf shrub heath. Each chart shows that with increasing sample sizes, P increases, P *cv* decreases and ESW increases, suggesting these parameters are influenced by accumulating more observations.

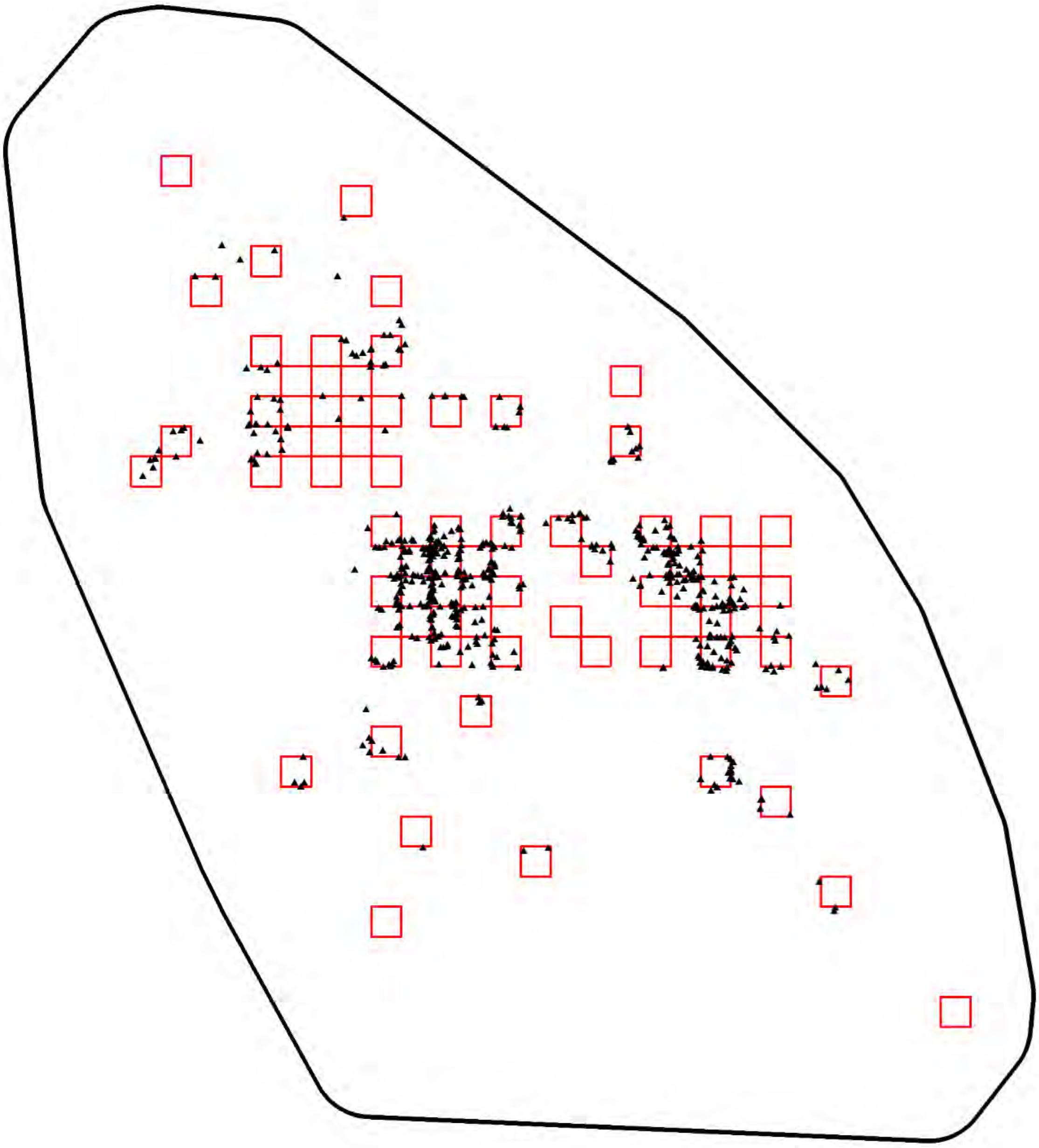

Figure A2 Distance sampling observations for entire Peak District survey for 2019. Map origin is British National Grid Reference SK Easting 390000 Northing 370000. Transects are red 1km squares. Black triangles indicate all observed mountain hares (untruncated data).

CHAPTER 5 GENETIC STRUCTURE OF ENGLISH HARE SPECIES

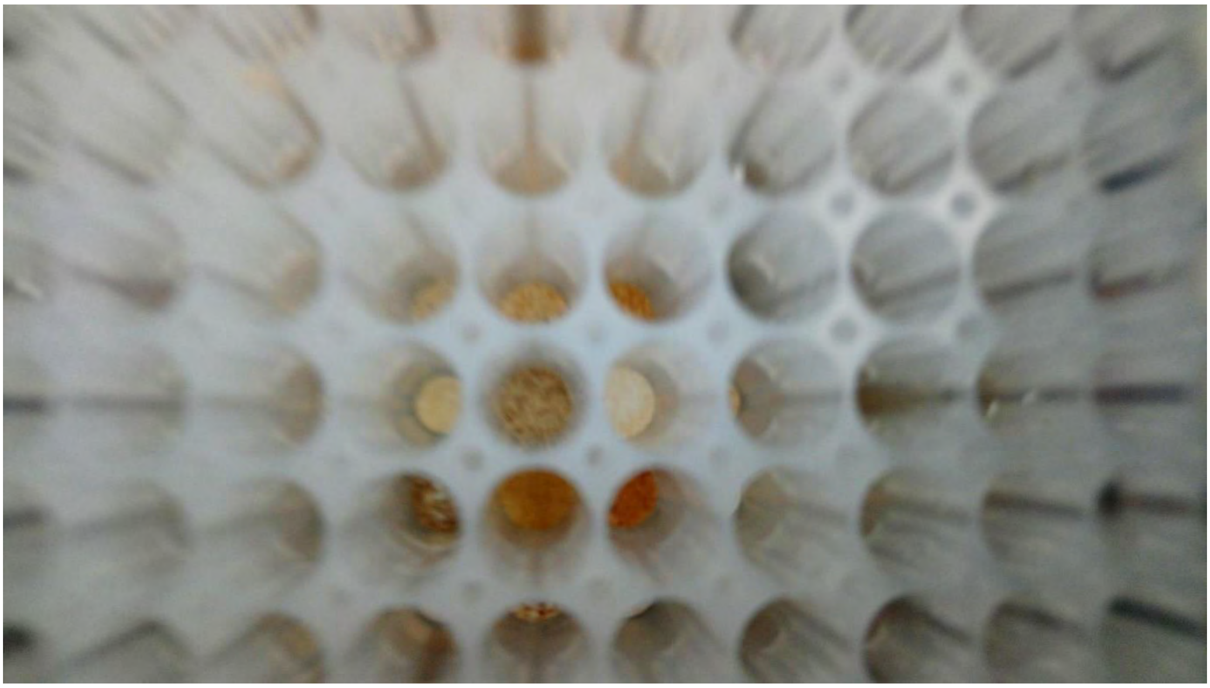

Image: DNA extraction plate showing 96 different mountain and brown hare samples.
MMU genetics laboratory, Manchester, England, UK. Date: 13th June 2019.

Chapter 5 Genetic structure of English hare species

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5.1 Abstract

The mountain hares (*Lepus timidus*) of Scotland have the lowest genetic diversity for this genus across Europe. From these, small founder groups, translocated to England 150 years ago, now thrive as a small population on confined hills. They are surrounded by sympatric European brown hares (*L. europaeus*) previously reported as having low genetic diversity. We investigated the genetic structure of both species. We obtained 253 flesh samples and, using microsatellites, estimated diversity, introgression, and gene flow. Genotyping success was poor: only 30% of allelic data retrievable; thus we could only assess 97 mountain hares and 18 brown hares with from 5 to 11 loci, identifying 36 individuals with 100% probability. Of the two hare species, allelic richness was higher in brown hares ($\bar{x}$= 2.97), mountain hares ($\bar{x}$= 2.37); more private alleles/individual (brown hare= 1.22; mountain hare= 0.49). Tests for Hardy Weinberg equilibrium (HWE) showed the genetic diversity of brown hares was lowest in Europe (He= 0.51; Ho= 0.47). Mountain hare genetic diversity (He= 0.42, Ho=

0.46) was also low, though higher than previously reported in Scotland. Admixture assessment suggested 8% of alleles were common to both species (K=2). We identified evidence of brown hare ancestry in at least 5 mountain hare individuals. Mountain hares were assessed as seven notional small groups, 5-25km apart. Allelic richness for these groups ranged from 1.83 to 2.11 and HWE tests (He range 0.36-0.61) and fixation indices (F_{IT}= 0.076; F_{ST}= -0.003; F_{IS}= -0.075) suggested no inbreeding. There was no genetic differentiation among groups except for one (Range of pairwise F_{ST} values= 0.025-0.129); and no evidence of isolation by distance (Mantel test z= 21.04, *P*-value= 0.217). Findings suggest continual gene flow between mountain hare groups. Because of the imperfect data we are cautious with interpretation of results. This research is continuing with CIBIO, Research Centre in Biodiversity and Genetic Resources, University of Porto, Portugal.

5.2 Introduction

5.2.1 Genetic diversity of hares

Genetic diversity is important to species survival (Allendorf et al. 2013; Mills 2013). Inbreeding depression results in lower heterozygosity. Because of the increased homozygosity levels, deleterious recessive alleles may be exposed and result in animals that are less able to adapt to or resist environmental stochasticity and populations can experience lower recruitment, deformities or higher rates of sickness (Frankham et al. 2013) such as dental malformations and ovarian tumours seen in hares of New Zealand (Suchentrunk et al. 2001).

5.2.2 Mountain hares

The genus *Lepus* originated 12 Myr ago (Alves et al. 2008). The divergence of mountain hare and European brown hare maternal lineages occurred 2-4 Myr (Thulin et al. 1997). Of the three Pleistocene arctic hare clades which include arctic hare (*L. arcticus*) and Alaskan hare (*L. othus*); the mountain hare has most genetic diversity (Waltari & Cook 2014).

During Pleistocene glacial periods, the mountain hare expanded from arctic areas across the central plains of Europe to the southern peninsulas of Europe. With the last northwards glacial retreat, the mountain hare followed the ice and withdrew from Europe, leaving relict populations in the Alps, Poland, Sweden, Finland and the British Isles (Thulin 2003). Smith et al. (2017) suggested at the end of the Pleistocene the mountain hare, with its generalist nature, tracked rapid habitat changes during the Holocene transition, did not suffer sudden demographic impacts and maintained genetic diversity; in contrast to reduced genetic diversity experienced by other Pleistocene mammals e.g. red squirrels (*Scirius vulgaris*).

Recently from ~ 1800 AD, substantial range reductions of mountain hare occurred in Russia, southern Sweden and Ireland. The principal cause was competitive exclusion or hybridisation with introduced European brown hare (Thulin 2003; Smith and Johnson 2008). Referring to south Sweden, Thulin (2003) wrote *"The game bags rapidly switch from mountain hares to brown hares until mountain hares vanish completely."*

Hamill et al. (2006) identified distinct differences of mountain hare genetic structure between subspecies across Europe. Diversity was highest in northern arctic-boreal latitudes. Diversity was high and similar between the populations of temperate regions (*L. t. timidus*) Fennoscandia and (*L. t. varronis*) Alpine (F_{ST} ~0.1) suggesting continual and relatively recent gene flow across the European plain; or a rapid expansion post glaciation and large population sizes. There was significantly higher diversity in Fennoscandia relative to Irish and Scottish subspecies which have a different subset of genetic variation. There was lower diversity within and high divergence between populations in Irish hares (*L. t. hibernicus*) Ireland and mountain hares (*L. t. scoticus*) Scotland, ($F_{ST}>0.4$). Either smaller population sizes contributed to genetic drift and isolation, or late glacial era colonisation occurred across a separate land bridge from France via Cornwall to Ireland. Heterozygosity excess suggested the current large population in Scotland (~135,000 individuals, JNCC 2019) was a recent (<~500 generations ago) expansion from much lower densities, facilitated by the development of grouse moors cultivating extensive heather (Hamill et al. 2006). However differences between Scotland and Ireland populations were greater than the average across Europe. Melo-Ferreira et al. (2005) hypothesised that introgression from the European brown hare might contribute to genetic diversity in mountain hare. Hamill et al. (2006) found very limited evidence for this.

The mountain hare (*Lepus timidus scoticus*) in Scotland has the lowest genetic diversity of all European hare populations and also when compared with snowshoe hares of North America (Table 5.1). One consequence may be that their progeny in the Peak District, England have similarly low diversity.

5.2.3 Brown hares

During the Pleistocene, the brown hare originated from the steppes of central Asia and expanded across southern Europe. Three clades emerged: Asia Minor; Balkans and Italy, yet none reached north of the Alps during the glacial periods. (Fickel et al., 2008). Once the glaciers receded ~ 10,000 bp, brown hares colonised northwards from the Italy clade, following human agricultural expansion and persisting throughout northern Europe (Thulin 2003; Fickel et al. 2008). Recently during the last two centuries, brown hares became an important game species, with unsustainable harvest rates (Angermann and Flux 1990); e.g. in Germany game bags dropped from 3 million to 0.5 million over ten years (Fickel 2005). Across Europe populations have reduced by as much as 80% because of agricultural intensification (Smith et al. 2005).

Brown hare populations can show much genetic variability with low levels of inbreeding e.g. in Germany (Ho = 0.51-0.65; F_{ST}= 0.31) (Fickel et al. 2005). In Italy Canu et al. (2013) recorded brown hare heterozygosity as high (He= 0.68), similar to other European populations: Sweden (He= 0.52–0.69); Bulgaria (He= 0.70) and Iberia (He= 0.56). Canu et al. (2013) suggested that extensive translocations between countries disrupted population structures or harmed the genetic integrity of local populations. Likewise Andersen et al. (2009) reported amongst groups in Denmark, high fixation indices arising from translocations (F_{ST}= 0.24; pairwise F_{ST}= 0.6-0.57).

Brown hares did not reach England prior to the formation of the English Channel (Yalden and Barrett 1999; Suchentrunk 2001). However fossil evidence suggests brown hares were present during the Neolithic period, presumably introduced by humans (Yalden & Barrett 1999). An alternative view is the Romans introduced them (Thulin 2003); with small numbers, low success rates and subsequent population bottlenecks (Suchentrunk 2001). Some considered brown hares on mainland Britain British Isles as a separate subspecies (*L. e. occidentalis* de Winton) (Corbet 1986). The only genetic study of brown hares in Britain, investigating allozyme and mtDNA, showed them to have lower diversity than those of Europe (Suchentrunk et al. 2001). Brown hares were absent from, yet released in to Scotland, during the 1880s (Long 2003). Their range now covers most of the country, apart from the north west Highlands (Matthews et al. 2018).

5.2.4 Hybridisation

Hybridisation may be a precursor to speciation or a threat to the genetic integrity of a species (Allendorf et al. 2001). Mountain and brown hares are distinct species, yet show morphological plasticity and occasional similarity i.e. their physical characteristics may vary and be similar between the two species. After translocation they may differentiate in body size within 100 years and pelage colour within 40 years (Flux and Angermann 1990; Thulin et al. 2006a; Giska et al. 2019). Crosses between the two species were presumed as unidirectional: mountain hare females producing viable offspring, then backcrossing to either parental species (Thulin et al., 1997). However in captivity, whilst mountain hare females mated spontaneously with brown hare males, the reverse did not occur (Thulin and Tegelstrom 2002). Hybridisation occurred from direction of brown hare to mountain hare in Russia (Thulin et al., 2006b) and the Alps (Suchentrunk et al., 2005).

There are extensive patterns of hybridisation across Europe. In Iberia the presence of mountain hare mtDNA within brown hare specimens (and congeneric *L. granatensis*), suggested ancient introgression and hybridisation. Following a history of allopatric distributions, climatic and glacial changes led to several oscillations of mountain hare ranges overlapping with other hare species, from the Alps to the Iberian Peninsula (Alves et al., 2003; Alves et al., 2008) with up to 93% of brown hare populations possessing mountain hare mtDNA (Melo-Ferreira et al., 2005).

In 1857 brown hares were introduced to Sweden for game hunting and replaced mountain hares in the southern half of the country (Thulin 2003). Thulin et al. (1997) assessed mtDNA in samples of both hare species in Scandinavia: in six out of 18 brown hare specimens, two different haplotypes of mountain hare origin were detected. Further investigation by Thulin et al., (2006a) in Sweden, assessing mtDNA at seven loci, showed distinct genetic differences between species (F_{ST}= 0.18-0.24; Rho_{ST}= 0.09-0.16; Nei's D= 0.05-0.68). Brown hares had been introduced 50-100 years previously, and mountain hare mtDNA was considered likely incorporated in to the brown hares. Brown hare genotypes with introgressed mountain hare mtDNA were similar to brown hares with species-specific mtDNA from the same regions. Yet Thulin and Tegelstrom (2002) reported 10% of 552 brown hare specimens having mtDNA from mountain hares, which then disappeared absent continuous interspecific gene flow.

Levanen et al. (2018) identified mountain hares comprised one Fennoscandian population, across Sweden and Finland. By contrast Swedish and Finnish brown hare populations were genetically separate and distinct. The Swedish brown hare gene pool appeared as an admixture of brown hares from different parts of continental Europe, with introgression from mountain hares. Yet Finnish brown hares reflected stepwise or gradual expansion pattern from the edge of their range, with introgression from mountain hares. Introgression was asymmetric: brown hares were backcrosses; mountain hares were purebred.

In east Denmark Fredsted et al., (2006) found mountain hare mtDNA haplotype in 6% of brown hare specimens, implying brown hares migrated or were translocated from Sweden. In Switzerland Suchentrunk et al. (2005) found ~14% of mountain hares were hybrids. Zachos et al., (2010) identified five out of 113 mountain hare specimens in Switzerland possessed introgressed brown hare mtDNA. In Ireland bilateral hybridisation was found in 33 Irish hare samples: five were from male brown hares mating with female Irish hares; one hybrid came from a female brown hare mating with a male Irish hare (Hughes 2009). Brown hares as a species are now regarded as a significant threat to the ecological security, i.e. the long term survival, of Irish hares (Caravaggi et al., 2014). Hybridisation clearly affects the persistence of both species, with mountain hares mostly losing out. Conversely doubts persist whether any genuinely pure brown hares remain in Europe (Thulin et al., 2006a).

5.2.5 Dispersal and population cyclicity

Dispersal mechanisms may serve to maintain higher levels of genetic diversity. However lagomorphs are non-migratory, with short natal dispersal ranges, once thought to engender genetic isolation by distance (Topchieva et al., 2013). Burton et al. (2002) assessed ~350 snowshoe hares throughout the boreal forest range from Alaska to Montana (70,000km2). Analysing seven loci, they found high levels of genetic variation (Mean alleles= 13.4; He= 0.67). Differentiation was low among Yukon and Alaska sites,(F_{ST}= 0.015); the Montana site was moderately differentiated (F_{ST}= 0.20). There were just five private alleles in Montana; eight other alleles were present in all areas except Montana. There was decreasing genetic similarity with increasing geographic distance. Dispersal of snowshoe hares was deemed widespread with a stepping-stone model of gene flow and no sex bias. Findings suggested genetic diversity was not reduced by the parasite vector that commonly reduces fecundity and induces population cyclicity (Flux and Angermann 1990).

Across southern Ireland, Irish hares showed weakly differentiated populations, suggesting 2 divergent demes (Hamill et al., 2007). Diversity was moderate (He= 0.54); 4-5 alleles per locus; private alleles were extremely rare. There were no significant differences between samples 10-30km apart; populations were patchy, not continuous (F_{ST}< -0.05). Assignment tests suggested males dispersed more than females, but no significant difference. Separately, an assessment of four sparsely populated groups of mountain hares in Karelia, reported lower heterozygosity (Ho= 0.43). Each group was distant by ~150km, with significant genetic differences (F_{ST}= 0.13) (Topchieva et al., 2013). In another study in Switzerland, Zachos et al. (2010) recorded over a large canton, Graubunden, ~ 7000km2, moderate genetic diversity of mountain hares (He= 0.54; Ho= 0.40)

5.2.6 Mountain hares and brown hares in England

The reintroductions of mountain hares to the Peak District during the 1870's were a remarkable success, yet their practices may have inadvertently constrained genetic structure. Six groups of ~20 to 50 mountain hares, conceivably local captures of related groups, were translocated from Perthshire, Scotland to locations at either extreme of the Peak District: westmost, Oldham, Lancashire; eastmost, Bolsterstone, Yorkshire (Mallon 2001). Typically six weeks after translocations, ~50% of animals succumb to predation, starvation, stress and death (Sokos et al. 2015). Surviving hares likely dispersed at short distances < 1km.

The present population comprises ~ 3,700 individuals ranging over ~360km^2 (Bedson et al. 2021a). Severe winters (1946-47), (1962-63) leading to reduced numbers (Mallon 2001) may have resulted in bottlenecks. As the population is small, population cyclicity, typically 90% amplitude every four to ten years (Newey et al. 2007), or limited dispersal opportunity, might affect genetic structure. Locally there are high concentrations of mountain hare groups on major large hills, separated by busy roads and reservoir systems and remaining areas very sparse of hares (Bedson et al. 2021a).

Surrounding the mountain hares, is an extensive meta-population of brown hares occupying grassy agricultural lowlands. The level of contact between these species appears low (Bedson et al. 2021b).

Hybridisation has been rarely observed in the past (Mallon 2001). Forecasts are for an increasing range overlap between the two species, so hybridisation opportunities may increase.

5.2.7 Study objectives

We hypothesised the genetic structure of the brown and mountain hare populations occupying the environs of the Peak District were very different. We speculated that allelic diversity of mountain hares might be maintained by admixture with brown hares. We speculated that the mountain hare population had low genetic diversity, with some evidence of localised population structure.

We used molecular genetics methods to investigate these matters. The aims were:

1. Measure allelic richness and genotype diversity for the two hares species.
2. Conduct admixture analysis to investigate potential hybridisation.
3. For the mountain hares, assess genotype diversity within groups and determine evidence of local population structures.

5.3 Methods

5.3.1 Study area and sample collection

The study area was the Peak District National Park in northern England, comprising ~360km^2 of upland heath and bog landscapes (Figure 5.1). Separate studies identified population concentrations upon three hills, separated by roads and reservoir systems. Brown hares occupied neighbouring agricultural and pastoral areas. The ranges of the two hare populations met at distinct boundaries, with little overlap (Bedson et al. 2021a).

From 2017 to 2020, we retrieved 253 genetic hare roadkill and field carcass samples and whenever possible took photographs of specimens. Time since death was usually within the previous six weeks, though some field carcasses were up to twelve months old. Species identification referenced morphological features (pelage, tail and ear tip colour, head shape, ear length) though this was not perfect when only body parts remained. We identified 210 mountain hares and 26 brown hares. There were 17 hare carcasses which were obliterated so that species was not identifiable. Flesh or ear samples were taken from carcasses and stored in Nucleic Acid Preservation buffer (Camacho-Sanchez et al. 2013). Sample locations were recorded by GPS (Figure 5.1b).

5.3.2 Genotyping

Samples were analysed in a laboratory specialising in DNA handling. Developing methods from Beugin et al. (2017) we created three multiplexes comprising 16 microsatellite primers identified from Rico et al. (1994); van Haeringen et al. (1996); Mougel et al. (1997); Surridge et al. (1997); Kryger et al. (2002); Rehnus and Bollman (2016). Multiplexes were designed using Multiplex Manager 1.2 (Holleley and Geerts 2009) to minimise difference in annealing temperatures, minimise total number of reactions and maximise spacing between primers in the same multiplex.

Thus we used three multiplexes with annealing temperatures as follows
Multiplex 1: SAT5, SOL28, SOL30, SOL33, SOL8 at 60C
Multiplex 2: OCELAMB, SAT08; SAT12; SAT13; SOL44 at 52C
Multiplex 3: LSA2; LSA3; LSA6; LSA8; OCELS1B; SOL3 at 52C

We formulated a library to enable identification of the biological samples and primers. Within multiplexes, each set of primers was index tagged with universal tail sequences derived from Blacket (2012) with amplicons having different tails at each end. Thus, as example, the primer pair for one marker had the following kind of structure: the lowercase portion was either the Blacket_D (forward) or the Blacket_C (reverse) universal tail, and the uppercase portion was the marker specific sequence.

Example:

Forward primer

5’-cggagagccgagaggtg-GGTACTCTATTAGGGAACCCG-3’

Reverse primer

5’-caggaccaggctaccgtg-GCTAGTTGCCATTAGCTCCC-3’

Individual DNA samples were amplified on a plate matrix using combinations of index tags sourced from Taberlet et al. (2018). The tag types were separated by degenerate nucleotides.

Example:

Index1_BLKTD = 5’-acacacac-NN-CGGAGAGCCGAGAGGTG

Index9_BLKTC - 5’-cgctctcg-NNN-CAGGACCAGGCTACCGTG

Sufficient primers of the above format were added to fill the plate matrix. The PCR in each well therefore contained 16 primers within (5* uSat specific forward, 5* uSat specific reverse, 1* universal row index, 1* universal column index). These were assembled so that the microsatellite specific primers would be exhausted in the first few (10 cycles), leaving enough universal primers to maintain amplification for the remaining 18-25 cycles. The resulting PCR products were prepared for Illumina sequencing using a TRU-Seq PCR free library prep kit, and ligating sequencing adapters.

The uSat specific forward and uSat specific reverse primer sequences were used as indexes for each marker, and using this method, 20 primers used to uniquely index (3*96) 288 PCR products. Plates were given an index using the TRU-Seq ligation method.

The structure of the final library was thus:

5’-
AATGATACGGCGACCACCGAGATCTACACTCTTTCCCTACACGACGCTCTTCCGATC*T-
acacacac-NN-CAGGACCAGGCTACCGTG-
GGTACTCTATTAGGGAACCCG…[region_of_interest]
….GGGAGCTAATGGCAACTAGC-CACCTCTCGGCTCTCCG-NNN-cgagagcg-
GTTCGTCTTCTGCCGTATGCTCTA-index-
CACTGACCTCAAGTCTGCACACGAGAAGGCTAG-3’

Total adapters/indexes account for 218bp, giving 382bp (assuming 2*300 cartridge) for the ‘region of interest’.

For all the samples, arranged in 3 plates, two stage Polymerase Chain Reaction (PCR) amplifications were conducted. The first PCR used 20-µl reactions, consisting of ~20ng of lyophilised DNA, 2.0 µL of each primer, 10.0 µL Qiagen Type-IT and 6.0 µL of molecular water. Samples were denatured at 94C for 5 minutes, followed by 35 cycles denaturing at 94C, annealing at 50 C or 52 C, elongation at 72C; and a final elongation step of C for 15 minutes. PCR products were assessed for quality control with Bioanalyser 2100 (Agilent, Waldbronn, Germany) and Qubit 2.0 Fluorometer (Life Technologies, Carlsbad USA). Library preparation followed Illumina (San Diego, USA) protocols. Sample cleaning was conducted with Agencourt AMPure Xp bead kit (Beckmann Coulter Life Sciences, Indianapolis, USA) . Second stage PCR was sequenced with an Illumina MiSeq thermal cycler. Two sample runs were undertaken. The first was a nano flow cell trial of 8 samples using a 4 nM library targeting 250 reads / marker and this generated 2,093 reads comprising 555MB data of which 94.7% passed QC and 89.4% passed Q30 QC. The main run used a high throughput flow cell with a 4 nM library also targeting 250 reads / marker. This generated 24,960 reads comprising 7.1GB of data, of which 95.01% passed QC and 74.38% passed Q30 QC.

5.3.3 Bioinformatics

Illumina sequencing generated FASTQ files which were used to develop genotypes following de Barba et al. (2017). Read quality was assessed with FastQC (Andrews 2010). Files were concatenated in Unix. Genotype identification was conducted by first applying Cutadapt (Martin 2011) to trim adapter sequences. MEGASAT (Zhan et al. 2015) was then used to identify and count reads of microsatellite sequences based on relative abundance within each read. Overall amplification success was determined as the proportion of PCR reads for each locus which could be attributed to each allele.

With 253 samples and 16 loci there were potentially 4,048 allele counts available for analysis. However on the first 2 PCR plates (themselves divided into 3 further multiplex plates), the column tags 5 and 8 inexplicably failed, resulting in 24 missing samples. Though this failure did not happen on the 3rd PCR plate. There were difficulties demultiplexing the FASTQ files using Cutadapt and MEGASAT . As consequence the final information output produced 32 samples with no data and a further 98 samples with data for only 1 to 4 loci. There were also 4 loci for which zero data was obtained, across all samples. Therefore of all samples, 71% of data was missing, leaving 18 brown hare, 97 mountain hare and 9 unidentified hare species samples with allele information for 5 loci or more (Table 5.2; Figure 5.1c). All subsequent analysis therefore used this set of 115 samples which had from 5 to 11 loci. (Therefore microsatellites not used were LSA2, LSA3, LSA8, SOL3, SOL44). The information for this final set of samples with loci, was then still missing 34% of data (assuming 11 loci max) (Figure 5.2). The allele data was then subject to limited manual pooling: those alleles 1 bp apart were moved to the next neighbouring bp length which had the most samples. Any locus with alleles > bp in excess of reported literature were excluded – e.g. large unexpected lengths ~300 bp or more. No further analysis was conducted on the 9 unidentified species of hare samples.

5.3.4 Data analysis

Analysis was conducted for the two separate hare species. Mountain hares were also analysed separately by assigning samples to seven groups, subjectively based on locations where more were collected and had progressed successfully through PCR, and choosing locations having a common topography (e.g. hill or valley), and separated from the next group by >4km. This allowed investigations of possible genetic or geographic population structure. (Figure 5.1d).

For the 115 samples, the proportion of available data for each loci, the presence of null alleles, possible linkage disequilibrium between all pairs of loci, rarefaction of loci and genotype accumulation curves, were calculated and plotted in 'poppr' (Kamvar et al. 2014). Evaluation of potential null alleles was within 'PopGenReport' using a maximum likelihood method (Adamack and Gruber 2014). Although 9 null alleles were potentially so identified (including when considering within mountain hare sub-groups), given the sparse data set and consulting advice from Allendorf et al. (2013) we did not discard any and retained all in further analysis. Relative allele frequencies were plotted, and private alleles identified using 'PopGenReport ' (Adamack and Gruber 2014). Allelic richness was determined using 'hierfstat' (Goudet 2005). Tests for deviation from Hardy-Weinberg equilibrium (HWE) were conducted with 'pegas' (Paradis 2010) by estimating observed and expected heterozygosity for each locus for each group and testing for significant departures from HWE with an exact test on Monte Carlo permutations of alleles .

For both hare species we tested for genetic structure by comparing the distribution and differentiation of alleles between groups using F-statistics. These measure the departure from HWE proportions of individuals or subpopulations relative to the base population. We calculated the Weir and Cockerham (1984) unbiased estimator FST with 'hierfstat' and Wright's F_{ST} was calculated within 'pegas' (Paradis 2010). Analysis of molecular variance (AMOVA) between groups was assessed with 'poppr' (Kamvar et al. 2014), assessing the two. We assessed isolation by distance for the mountain hare groups We calculated pairwise F_{ST} between the mountain hare groups, using 'heirfstat'. Geographic Euclidean distances between the centroids of each group were calculated using the Generate Near Table tool in ArcGIS (ESRI, USA). Mantel test of the pairwise genetic distances and geographic distances were conducted with package 'ape' (Paradis and Schliep 2019) and visually portrayed with 2 dimensional kernel density plot and regression line using 'MASS' (Venables and Ripley 2002).

We made evaluations of population structure using discriminant analysis of principal components in 'adgenet' (Jombart 2008; Jombart et al. 2010). This is a "model free" approach which can be useful in explaining and summarising how allelic data is structured amongst pre-defined groups. Discriminant analysis maximises separation between groups whilst minimising variation within groups, and may be more useful in displaying group differences.

To evaluate potential admixture we applied assignment tests to the two brown and mountain hare populations. We also applied assignment tests separately to the hypothesised mountain hare groups, to evaluate spatial genetic clustering. Tests used STRUCTURE v2.3.4 software which uses Bayesian analysis to group closely related individuals into clusters (Pritchard et al. 2000). We used the no admixture ancestry model with species or group identity as priors and assumed correlated alleles. This model is known to be particularly effective at identifying subtle population structures. Other parameter settings e.g. admixture model, no priors, were less informative. Assessments consisted of a burn-in period of 50,000 runs and 150,000 Markov Chain Monte Carlo (MCMC) repetitions. Cluster values for K were set from 1 to 9, using ten iterations. Subsequent selection of appropriate values for K used the method of Evanno et al. (2005) referring to the highest mean likelihood for K over the ten runs and also the lowest Δ K for each K, based on the second order rate of change of the likelihood function. These values were obtained from the Structure Harvester web portal (Earl and von Holdt 2012). From the species assignment tests, we categorised potential hybrid or intermediate genotype individuals following (Thulin 2006a). We again reviewed photographs for those samples, to confirm species morphology.

5.4 Results

5.4.1 Allele frequencies

For all samples among the 11 loci we identified a total of 110 alleles ($\bar{x}$= 10 per loci) ranging from 3 (SAT 12 and LSA6) to 25 (SOL28) (Table 5.3). The standardised index of association, assessing whether alleles were paired by loci, was very small and not significant (Figure 5.3) (Brown hares $\bar{r}$= -0.026, *P*-value= 0.99; mountain hares $\bar{r}$= -0.001 *P*-value= 0.35), indicating no linkage disequilibrium. Assessment of samples showed all to be individual multilocus genotypes (Table 5.3). Therefore neither loci nor samples required to be excluded from subsequent analysis.

Rarefaction curves suggested that for the majority of loci, greater than 100 samples would be needed to reach asymptote of expected number of alleles (Figure 5.4). Given the quantum of missing data (Figure 5.2) this was never achieved. Genotype accumulation suggested that 9 loci would enable identification of individuals with 100% accuracy (Figure 5.5). Therefore for the entire sample set it would be possible to identify 3 brown and 33 mountain hares with certainty.

Mean allelic richness was higher for brown hares (2.97) than for mountain hares (2.37) (Table 5.3a; Figures 5.6) & 5.7a). Of the mountain hare the groups with the highest allelic richness were Margery Hill (3.62) and Bleaklow (3.57) and the lowest was Derwent (3.27) (Table 5.3b, Figure 5.7b). Of private alleles, brown hares averaged 1.22 / sample and mountain hares 0.49 / sample. Given the substantial amount of missing data, reported private allele numbers were likely underrepresenting true values.

5.4.2 Hardy Weinberg Equilibrium

Brown hare expected heterozygosity was 0.51 and observed heterozygosity was 0.47 (Table 5.4a)). Mountain hare expected heterozygosity was 0.42 and observed heterozygosity was 0.46 (Table 5.4a)). For both hare species, the difference in expected vs observed heterozygosity was not significant at nearly all loci, except Brown hares completely homozygous for SAT12, and mountain hares with heterozygosity deficit at SOL28 and excess at SOL30 and SOL8 (Table 5.4a). Of the mountain hare groups the highest heterozygosity was at Bleaklow and the lowest at Derwent (Table 5.4b). All showed heterozygosity excess except for Woodhead (He= 0.39, Ho= 0.38) which was the only group with a loci showing significant departure from HWE.

5.4.3 Inbreeding coefficients

There was almost complete differentiation between the two the hare species at locus SAT12 and some differentiation at SOL30 5 (Table 5.5a). Yet for most other loci and overall the fixation indices for the two species were very low, showing very little distinction between the two species (F_{IT}= 0.074; F_{ST}= 0.055; F_{IS}= 0.031). Therefore we conclude there was not inbreeding within either population of the two species, relative to the combined lagomorph population.

For the mountain hare population as groups, at most loci the fixation indices were low i.e. below 0.20 except SOL 30 (F_{IT}= -0.238) and SAT5 (F_{IT}= 0.225) (Table 5.5b). The mean fixation indices were very low (F_{IT}= -0.076; F_{ST}= 0.003; F_{IS}= -0.075) (Table 5.5b) meaning the probability of any individual being inbred relative to its group or the total population, or any group compared to the population, was very low.

5.4.4 Population differentiation and structure

Pooling brown and mountain hares, Weir and Cockerham estimate of F_{ST} was 0.066 and F_{IS} -0.067. Nei's pairwise F_{ST} between the two species was 0.053. For the mountain hare groups the Weir and Cockerham estimate of F_{ST} was -0.001 and F_{IS} -0.09. These results also indicate very little inbreeding.

Comparing mountain hare groups, pairwise F_{ST} values were at lower ranges (<0.1) except for the comparisons of Woodhead/Saddleworth (Fst= 0.103)) and Bleaklow/Saddleworth (F_{ST}=0.129) (Table 5.6). Considering all pairings of groups, the Mantel test comparing genetic distance with geographic distance was not significant (z= 21.04; *P*-value= 0.217) The kernel density plot and linear regression line based on pairwise points also suggested there was no association (Figure 5.8). Amova tests showed that nearly all genetic variation was between individuals rather than within or between groups (Table 5.7).

The discriminant analysis for the two species showed strong distinction between the two species (Figure 5.9). Discriminant analysis for the mountain hare groups showed it was possible to identify a little variation between the groups, with Saddleworth appearing distinctive (Figure 5.10) .

Using the Evanno method for assessing STRUCTURE analyses of the comparison of brown hares and mountain hares, the lowest Δ K suggested K=2 as the most likely level of genetic clustering (Figure 5.11). This definition showed there was distinct and largely opposite clustering of alleles. The cluster comprising alleles for mountain hares was in 8% of the brown hares. There was 20% of the largest brown hare allele cluster in the mountain hares. The STRUCTURE barplot for K=2 showed 8 mountain hare individuals whose genotypes were at least an 80% match to that of brown hares.

Considering the assessment of mountain hare groups, the Evanno method showed K=2 as marginally more likely than no structure (Mean LnP(K): K1 = -1365.07; K2= -1373.07; K8= -1416.85) (Table 5.8, Figure 5.12). The ΔK values (second order rate of change of the likelihood function) for K=2 vs K=1 were extremely close (difference = 0.016). Values for both K=2 and K=8 were also close (difference= 0.274). Assuming structure were in fact present, K=8 was chosen as it provided a more informative level of clustering. Assessing the groups with K=8 suggested the inferred clusters for Saddleworth might be slightly different to the other groups.

Assuming that our morphological identification of hares was correct, we found 5 mountain hare individuals with >90% brown hare ancestry, 10 with intermediate ancestry. We found 1 potential brown hare with intermediate ancestry. Of these 16 individuals, 11 had been photographed during sample collection and whilst some individuals or carcass remnants had ambiguous morphology, there were at least two white mountain hares having high percentages of brown hare genotypes (Figure 5.13). Most of these putative hybrids and intermediates were located deep within the mountain hare distribution range (Figure 5.14; Bedson et al. 2021a).

5.5 Discussion

5.5.1 Low genetic diversity and hybridisation

This study showed obviously anticipated genotypic differences between brown hares and mountain hares species. Levels of allelic richness appeared lower than for those species elsewhere across Europe (Table 5.1). Genetic diversity appeared low for each species, which may be concerning. The diversity indices for brown hares suggest a deficiency of heterozygotes. The values (He=0.51, Ho= 0.47) appear as some of the lowest in Europe, close to values reported by Melo-Ferreira et al. (2014) at a site of 69 brown hare samples in Spain (He=0.55, Ho=0.47) (Table 5.1). It seems plausible that English brown hare diversity is therefore low. Suchentrunk et al. (2001) suggests: *"...genetic diversity could have been reduced in fragmented populations with long-term low densities in suboptimal habitats after woodland regeneration in the post-Roman period."*

However the mountain hare diversity indices reported for the Peak District are higher than recorded in Scotland (Hamill et al. 2006). There is no obvious reason for this higher estimate. One might speculate this occurred by chance or the mountain hares received alleles from brown hares. Heterozygosity levels suggest the mountain hares in the Peak District are the fifth least diverse of any in Europe.

It can be difficult to ascribe explicit or circumstantial causes of varying levels of heterozygosity in mammal species. Example comparisons of heterozygosity values do show differences, potentially influenced by population sizes, spatial scales or population histories. In Montana, a population of ~750 vagile grizzly bears (*Ursus arctos horribilis*) having large home ranges of ~600km2 among a continuous ecosystem of scale 31,000km^2 , connected to a wider population in Canada, were found to have high levels of heterozygosity (He=0.74) (Kendall et al. 2009). By contrast, the Ethiopian wolf (*Canis simensis*), population size ~500 individuals dispersed amongst six island populations showed low heterozygosity (He = 0.24) (Gotelli et al. 1994). The present day relatively populous cheetah (*Acinonyx* j*ubatus*) was recorded across southern and eastern Africa having low heterozygosity (Ho = 0.44) on account of an ancient (12,000 BP) population bottleneck (Driscoll et al. 2002). Stemming from a single colonisation 7.5000-11,000 BP, within seven separate regions of the UK, isolated populations of hazel dormice, having home ranges ~0.8ha, were found with moderate heterozygosity (He = 0.53-0.71). These comparisons imply the levels of heterozygosity for Peak District brown hares are moderate (He=0.51) and for mountain hares (He = 0.42) are low.

We appeared to identify putative hybrid hares. The location of some of these were high up on the hills (e.g. A57 Snake Summit) 2-4km away from the brown hare range. Hybridisation and replacement of mountain hares by brown hares is an important cause of species loss across Europe. We recommend further investigations of potential hybridisation at contact zones in England and throughout Scotland: especially because loss of heather moorland in Scotland (Robertson et al. 2001) may create an environment more conducive to brown hares (Bedson et al. 2021b)

5.5.2 Panmictic mountain hare populations

For the mountain hare groups, the fixation indices suggested a panmictic population. STRUCTURE analysis appeared to corroborate this finding. The mean log-likelihood probability for K=1 and K=2 were extremely close. Indeeed Evanno et al. (2015) comment that ΔK itself will not find the "best" K if K=1. Differences of allelic richness between groups also appeared rather marginal. There were slight differences of heterozygosity between locations, without obvious cause; migration between locations might have been uneven. As corroboration, the isolation by distance assessment showed two groupings, suggesting no impediment to gene flow and migration. However there was a very slight difference of inbreeding coefficient at Saddleworth (F_{ST} range 0.06-0.12); conceivable as that area has low density of hares, and is distant and impeded from the main population centre of Bleaklow and Margery Hill by a road and reservoir system (Bedson et al. 2021b). Whilst intriguing, these values are only slightly indicative of possible structure. As comparison, an assessment of 18 populations of *L. europaeus* across 9 European countries showed higher pairwise F_{ST} ranges from 0.02 to 0.29 (Means: Europe=0.11; Africa=0.10; Near East=0.07). As further comparison, an evaluation of 9 distinct populations of n= 99 invasive grey squirrels (*Scirius carolensis*) dispersed across Ireland showed statistically significant pairwise F_{ST} ranges 0.06-0.25 (Mean = 0.18) (McLaughlin et al. 2022). The overall picture for the Peak District may be a weak, i.e. diverse, genetic structure. This may be unsurprising, considering Burton et al. (2002) showed Yukon snowshoe hares as a panmictic population across a geography of several thousand square kilometres.

5.5.3 Further research

There are improvement opportunities arising from this study. First and foremost, because of the partial data set we suggest results are indicative, not definitive. That said, the Bayesian analytical principles which operate within STRUCTURE may mitigate some weaknesses of missing data. Using roadkill as samples, collection sites were geographically biased. Yet suitable field carcasses were few: we gathered 24 samples on Bleaklow, 11 on Margery Hill, 3 on Holme Moss, none from Kinder Scout, despite five searches. Hence the study depended on road casualties. When subsequently analysing data, the locations we chose as representing mountain hare groups were subjective, though with careful deliberation. Were we to achieve full data for all 253 samples, this would have provide a much clearer picture of gene flow and any landscape resistance effects. For hybrid evaluations, rather than using assignment tests, there are now SNP based diagnostic methods for identifying hybrids (Marques et al. 2017).

It is remarkable that apart from Suchentrunk et al. (2001) there have been no other genetics studies of brown hares in England, Wales or Scotland and we strongly recommend this be conducted. Given the low diversity of mountain hares in Scotland, that population merits further investigation of genetic structure and possible environmental or land use influences. Hamill et al. (2006) recommended assessing the sparse population of north west Scotland, to help inform reasons for the low diversity they recorded for the Cairngorms population. Mountain hares in the Southern Uplands are separated from others by ~50km and in decline (Hesford et al. 2020). There are some Scottish island populations.

One may speculate whether there may be genetic divergence of mountain hares in the Peak District as compares to Scotland. For example, those introduced from Norway to the Orkney's 1850's adopted a winter-grey pelage morph (Giska et al. 2019).

The samples from this genetics research have been provided to José Melo-Ferreira of the Genomics of Evolutionary Change research group, at CIBIO, Research Center in Biodiversity and Genetic Resources, InBIO Associate Laboratory, University of Porto (Associação BIOPOLIS) Portugal. Their aim is to study the dynamics of hybridisation in natural populations of mountain and brown hares, in particular in contact zones affected by climate change. Genetic data for mountain hares may also be combined with landscape information: topography such as deep valleys; human infrastructure of roads and reservoirs; fields of deep unmanaged heather; each of which may present barriers to population movement and gene flow. This may be combined with renewed STRUCTURE analysis. Findings may be influenced by the intensity of sampling of individuals and markers, to develop hypotheses of migration patterns e.g. hierarchical islands or contact zones (Evanno et al. 2005).

Acknowledgements

This research was funded by the People’s Trust for Endangered Species, the Hare Preservation Trust, the British Mountaineering Council, Penny Anderson Associates, South-West Action for Hares, Queen’s University Belfast. We thank RSPB Dove Stone, The National Trust, United Utilities and Upperwood Estates for access support. We thank J. Minshull, D. Hogg, I. Commerford, C. Shaw, L. Thomas, M. Moore and C. Thelier for fieldwork in collecting carcasses and samples. We thank Z. Kamvar for advice on Amova calculations when working with missing data.

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Tables

Table 5.1 Summary of comprehensive review of microsatellite genetic research for hare species across Europe and North America

Mountain hare (L. timidus), European brown hare (L. europaeus), broom hare (L. castrovieji), Iberian hare (L. granatensis) and snowshoe hare (L. americanus). Subpops = Sub-populations sampled; n = Samples; Loci = number of loci used; He/Ho=expected / observed heterozygosity. Fst = Mean deficiency of expected heterozygotes among sub-populations with respect to that expected for the total population; Fis = Mean deficiency of observed heterozygotes among individuals vs expected across sub-populations. Spaces = no data

Author	Year	Species	Location	Subpops	n	Loci	Total alleles	Mean alleles	Allelic richness	Private alleles	He	Ho	F_{IS}	F_{ST}
Andersson et al.	1999	L. timidus	Norway	1	18	5	26	5.2			0.54	0.42		
		L. europaeus	Sweden	1	19	5	33	5.4			0.70	0.56		
Burton et al.	2002	L. americanus	Yukon	12	317	11		12.1		8	0.64			0.015
			Alaska	1	27	11		8.7		8	0.68			0.012
			Montana	1	19	11		5.5		5	0.67			0.200
Fickel et al.	2005	L. europaeus	Germany	21	307	5		11.2		12	0.62	0.59	0.054	
Estonba et al.	2005	L. castroviejoi	Iberia	1	11	6		2.3			0.28	0.23		
		L. granatensis	Iberia	1	19	6		3.2			0.49	0.29		
		L. europaeus	Iberia	1	39	6		6.6			0.55	0.48		
		L. europaeus	Bulgaria	1	31	6		8.0			0.69	0.64		
Hamill et al.	2006	L. timidus timidus	Finland	5	91	7	42	6.8		22	0.67	0.63		0.06 - 0.10
		L. timidus timidus	Sweden	2	20	7		6.2			0.70	0.69		
		L. timidus timidus	Norway	1	7	7		5.1			0.71	0.71		
		L. timidus varronis	Italy	1	19	7	58	5.5		5	0.59	0.53		0.06 - 0.10
		L. timidus varronis	Switzerland	1	38	7		6.4			0.60	0.59		
		L. timidus scoticus	Scotland	5	95	7	31	3.1		3	0.32	0.30		0.40 - 0.50
														0.35
														0.20
		L. timidus hibernicus	Ireland	8	311	7	79	4.4		1	0.52	0.49		0.40 - 0.50
														0.10
														0.20
Thulin et al.	2006	L. timidus timidus	Sweden	Meta-pop	60	7		16.2			0.57	0.56		0.18-0.24
		L. europaeus	Sweden	Meta-pop	60	7		16.2			0.58	0.70		0.18-0.24
Hamill et al.	2007	L. timidus hibernicus	Ireland	1	53	7		4.9	4.3		0.51	0.49	0.04	
				1	10	7		4.3	-		0.53	0.47	0.13	
				1	48	7		4.7	4.3		0.54	0.50	0.09	
				1	50	7		5.3	4.6		0.58	0.54	0.08	
				1	20	7		3.9	3.8		0.47	0.43	0.07	
				1	25	7		4.1	4.1		0.53	0.53	-0.02	
				1	19	7		4.3	4.3		0.49	0.45	0.09	
				1	48	7		4.6	4.2		0.51	0.45	0.11	
				1	48	7		4.0	3.7		0.47	0.46	0.02	

Table 1.1, continued

Author	Year	Species	Location	# Subpops	Samples	# Loci	Total alleles	Mean alleles	Allelic richness	Private alleles	He	Ho	Fis	Fst
Schwartz et al.	2007	L. americanus	MT, ID, USA	2	40	9		3.4			0.57	0.51		
Slimen et al.	2008	L. europaeus	Europe	5	64	11	74	5.2	3.6		0.60	0.51	0.17	0.11
		L. europaeus	Near East	4	45	11	74	5.3	4.0		0.64	0.53	0.22	0.08
		L. capensis	Africa	9	178	11	85	5.7	4.3		0.67	0.58	0.19	0.11
Zachos et al.	2010	L. timidus varronis	Switzerland	1	128	13		6.67			0.54	0.40		
Modesto et al.	2011	L. europaeus	Italy	1	109	8		6.5		11	0.67	0.64	0.04	0.04
		L. europaeus	Italy	1		8		5.7		5	0.61	0.62	0.01	
Thulin et al.	2012	L. europaeus	Sweden	1	31	11		5.6	4.4	3	0.55	0.52		0.04 - 0.14
				1	53	11		7.4	5.6	6	0.68	0.68		0.02 - 0.11
				1	33	11		7.1	5.5	6	0.65	0.63		0.08 - 0.11
				2	204	11		6.5	4.4	5	0.54	0.52		0.08 - 0.14
Antoniou et al.	2013	L. europaeus	Balkans	5	268	10	168	16.8			0.75	0.48	0.354	
Canu et al.	2013	L. europaeus	Italy	13	249	8		12.5			0.68	0.65		0.02
Topchieva et al.	2013	L. timidus	Karelia	4	49			5.6			0.67	0.37		0.13
Cheng et al.	2014	L. americanus	Boreal North America	27	442	8		7.0	5.3		0.72	0.64		> 0.2
			Pacific NW America	9	251	8		7.0	4.7		0.65	0.62		> 0.2
			US Rockies	3	160	8		6.6	3.9		0.55	0.53		> 0.2
Melo-Ferreira et al.	2014	L. granatensis	Spain	2	194	6		5.1	4.4		0.38	0.28		0.36
		L. europaeus	Spain	1	69	6		7.0	6.3		0.55	0.47		
		L. europaeus	Alps	1	40	6		7.8	7.7		0.55	0.49		
		L. timidus	Spain	1	39	6		7.8	7.7		0.54	0.46		
Djan et al.	2015	L. europaeus	NE Serbia	1	123	6		13.3		9.3	0.80	0.53	0.30	0.16
		L. europaeus	NW Serbia	1	34	6		5.5		0.2	0.60	0.47	0.20	
Mengoni et al.	2015	L. corsicanus	Italy	Meta-pop	149	13		6.6			0.43	0.29	0.31	
		L. europaeus	Italy	Meta-pop	146	13		11			0.68	0.58	0.58	
		L. timidus	Italy	Meta-pop	72	13		9			0.67	0.48	0.48	0.06
		L. capensis med.	Sardinia	Meta-pop	91	13		8			0.59	0.53	0.53	
Rehnus et al.	2016	L. timidus	Switzerland	1	78	10		5			0.50	0.51		
Vernesi et al.	2016	L. timidus	Italy	3	55	7		4.26	3.46		0.45	0.42	0.09	
		L. europaeus	Italy	5	110	9		6.08	5.56		0.62	0.65	0.05	
Beugin et al.	2017	L. timidus	French Alps	Meta-pop	141	12		6.1			0.47	0.38	0.20	
		L. europaeus	French Alps	Meta-pop	532	12		10.5			0.62	0.56	0.11	
Cheng et al.	2017	L. americanus	MT, USA	5	61	8		11.9				0.71		
Schenker et al.	2019	L. timidus varronis	Switzerland	Meta-pop	96	7		4.4			0.43	0.39		

Table 5.2 Cumulative frequency count showing how many hare samples had data for how many loci.

For all subsequent analysis, tables and figures, we used samples with least 5 loci: 18 brown hares and 97 mountain hares. We did not use the unidentified hare species in any analysis.

# loci with data	Brown hare	Mountain hare	Unidentified hare species	Total
0	0	30	2	32
1 or more	26	180	15	221
2 or more	25	157	13	195
3 or more	24	137	10	171
4 or more	22	121	10	153
5 or more	18	97	9	124
6 or more	13	80	7	100
7 or more	11	63	6	80
8 or more	8	44	6	58
9 or more	3	32	5	40
10 or more	1	19	3	23
11 or more	0	7	0	7
12 or more	0	0	0	0
13 or more	0	0	0	0
14 or more	0	0	0	0
15 or more	0	0	0	0
16	0	0	0	0

Table 5.3 Population allele summary.

Number of multi-locus genotypes reported by poppr (Kamvar et al. 2014). Number of alleles per locus reported by 'adgenet' (Jombart 2008). Rarefied allelic richness reported by 'hierfstat' (Goudet 2005). All samples are separate multi-locus genotypes.

a) Both hare species

	Both hare species	Brown hares	Mountain hares
n Samples	114	18	96
n Multi-locus genotypes	114	18	96

	n alleles per locus	Rarefied Allelic Richness	
SAT12	3	1.69	1.00
LSA6	3	1.00	1.10
SAT13	12	4.00	2.37
SAT8	5	1.18	1.21
SOL28	25	5.38	4.69
OCELAMB	6	2.21	1.96
SOL30	15	2.98	3.28
SAT5	11	3.07	2.40
SOL8	14	4.04	3.34
OCELS1B	8	4.74	2.53
SOL33	8	2.41	2.20
Mean	10	2.97	2.37
Std Error	1.94	0.43	0.33
Low		1.00	1.00
High		5.38	4.69

b) Mountain hare groups

	Rarefied Allelic Richness						
	Snake	Bleaklow	Holme Moss	Saddleworth	Woodhead	Margery Hill	Derwent
n Samples	45	4	14	8	8	9	8
n Multi-locus genotypes	45	4	14	8	8	9	8
SAT12	1.13	1.00	1.00	1.29	1.33	1.00	1.33
LSA6	1.11	1.00	1.00	1.29	1.00	1.00	1.00
SAT13	1.92	NA	1.67	2.84	1.00	1.80	2.08
SAT8	1.10	1.50	1.15	1.00	1.57	1.00	1.00
SOL28	3.39	3.57	3.35	3.60	3.57	3.62	3.27
OCELAMB	1.70	2.33	1.88	1.67	1.50	2.08	1.29
SOL30	2.48	2.33	2.59	2.41	2.83	2.98	2.86
SAT5	2.11	2.00	1.96	1.00	1.40	2.23	1.83
SOL8	2.69	3.00	2.63	3.18	2.86	2.56	2.18
OCELS1B	2.16	2.00	2.60	2.00	1.97	3.00	2.00
SOL33	2.04	2.00	1.25	1.80	2.20	2.00	1.33
Mean	1.98	2.07	1.92	2.01	1.93	2.11	1.83
Std Error	0.21	0.22	0.23	0.26	0.25	0.26	0.22
Low	1.10	1.00	1.00	1.00	1.00	1.00	1.00
High	3.39	3.57	3.35	3.60	3.57	3.62	3.27

Table 5.4 HWE tests from 'Pegas' (Paradis 2010) based on Nei (1987).

He/Ho = expected/observed heterozygosity. * = significant on Monte Carlo test, 999 permutations (Guo and Thompson 1992).

a) Both hare species

	Brown hares		Mountain hares	
	He (Hs)	Ho (Hi)	He (Hs)	Ho (Hi)
SAT12	**0.233**	**0.000 ***	0.000	0.000
LSA6	0.000	0.000	0.035	0.035
SAT13	0.686	0.667	0.428	0.479
SAT8	0.059	0.059	0.069	0.070
SOL28	0.943	0.917	**0.889**	**0.831 ***
OCELAMB	0.418	0.500	0.358	0.328
SOL30	0.567	0.429	**0.690**	**0.869 ***
SAT5	0.597	0.600	0.489	0.593
SOL8	0.806	0.846	**0.728**	**0.866 ***
OCELS1B	0.843	0.833	0.556	0.563
SOL33	0.500	0.333	0.393	0.458
Mean	0.514	0.471	0.421	0.463

b) Mountain hare groups

	Snake		Bleaklow		Holme Moss		Saddleworth	
	He	Ho	He	Ho	He	Ho	He	Ho
SAT12	0.07	0.07	0.00	0.00	0.00	0.00	0.14	0.14
LSA6	0.05	0.05	0.00	0.00	0.00	0.00	0.14	0.14
SAT13	0.41	0.48	1.14	NA	0.30	0.33	0.73	1.00
SAT8	0.05	0.05	0.25	0.25	0.08	0.08	0.00	0.00
SOL28	0.88	0.84	0.93	1.00	0.86	0.89	0.83	0.67
OCELAMB	0.35	0.24	0.57	0.67	0.42	0.30	0.31	0.33
SOL30	0.67	0.90	0.57	0.67	0.66	0.88	0.63	1.00
SAT5	0.53	0.65	0.57	1.00	0.46	0.57	0.00	0.00
SOL8	0.73	0.82	0.71	1.00	0.70	0.78	0.85	1.00
OCELS1B	0.54	0.53	0.57	1.00	0.63	0.33	0.40	0.50
SOL33	0.47	0.58	0.43	0.50	0.12	0.13	0.36	0.40
Mean	0.43	0.47	0.52	0.61	0.38	0.39	0.40	0.47
Mean diff		-0.04		-0.09		0.00		-0.07

	Woodhead		Margery Hill		Derwent	
	He	Ho	He	Ho	He	Ho
SAT12	0.16	0.17	0.00	0.00	0.16	0.17
LSA6	0.00	0.00	0.00	0.00	0.00	0.00
SAT13	0.00	0.00	0.36	0.40	0.49	0.43
SAT8	0.27	0.29	0.00	0.00	0.00	0.00
SOL28	0.87	**0.50** *	0.92	0.86	0.83	0.80
OCELAMB	0.23	0.25	0.51	0.67	0.14	0.14
SOL30	0.75	0.80	0.74	0.80	0.73	1.00
SAT5	0.19	0.20	0.57	0.80	0.45	0.60
SOL8	0.76	1.00	0.71	1.00	0.60	0.71
OCELS1B	0.53	0.50	0.66	1.00	0.43	0.50
SOL33	0.51	0.60	0.44	0.50	0.16	0.17
Mean	0.39	0.38	0.45	0.55	0.36	0.41
Mean diff		0.01		-0.10		-0.05

Table 5.5 Wright's inbreeding coefficient values per locus, for hare species

Reported by 'pegas' (Paradis 2010) using Weir and Cockerham (1984) for each allele averaged per locus over different alleles Fit = Mean deficiency of observed heterozygotes among individuals with respect to that expected for the total population; Fst = Mean deficiency of expected heterozygotes among sub-populations with respect to that expected for the total population; Fis = Mean deficiency of observed heterozygotes among individuals with respect to expected across sub-populations.

a) Hare species (comparing brown hares with mountain hares)

	Fit	Fst	Fis
SAT12	1.000	0.187	1.000
LSA6	-0.014	-0.010	-0.004
SAT13	-0.047	0.043	-0.094
SAT8	-0.025	-0.011	-0.014
SOL28	0.095	0.033	0.064
OCELAMB	0.018	-0.017	0.035
SOL30	0.073	0.234	-0.210
SAT5	-0.154	0.025	-0.183
SOL8	-0.171	-0.002	-0.168
OCELS1B	0.078	0.068	0.010
SOL33	-0.037	0.058	-0.100
Mean	0.074	0.055	0.031

b) Within mountain hare groups

	Fit	Fst	Fis
SAT12	-0.022	-0.010	-0.012
LSA6	-0.013	-0.018	0.005
SAT13	-0.115	0.000	-0.114
SAT8	-0.011	0.023	-0.035
SOL28	0.065	-0.015	0.079
OCELAMB	0.082	-0.034	0.112
SOL30	-0.238	0.036	-0.284
SAT5	-0.225	0.020	-0.250
SOL8	-0.187	0.004	-0.192
OCELS1B	-0.011	-0.042	0.029
SOL33	-0.160	0.005	-0.166
Mean	-0.076	-0.003	-0.075

Table 5.6 Pairwise FST(below diagonal) and Euclidian distances (km) values between mountain hare groups.

Euclidian distances were calculated within ArcGIS (ESRI USA), measuring between centroids of group sample locations. Genetic distances were calculated in 'pegas' (Paradis 2010) based on the formula of Weir and Cockerham (1984).

	Geographic Euclidean distance km						
Genetic distance	Snake	Holme Moss	Derwent	Woodhead	Saddleworth	Bleaklow	Margery Hill
Snake		10.7	14.4	11.2	13.7	5.2	14.7
Holme Moss	0.025		19.2	7.2	4.4	5.7	15.5
Derwent	0.038	0.047		13.3	23.6	15.1	6.5
Woodhead	0.041	0.046	0.081		11.4	7.0	8.5
Saddleworth	0.067	0.074	0.061	0.103		9.3	19.8
Bleaklow	0.046	0.056	0.085	0.080	0.129		13.1
Margery Hill	0.039	0.050	0.050	0.081	0.080	0.082	

Table 5.7 Analysis of molecular variance (AMOVA) results for mountain hares performed for all groups.

Amova was calculated within 'poppr' using 50% cut-off for missing loci, following advice from Z. Kamvar (https://groups.google.com/g/poppr).

	df	Sum of squares	Mean squares	Sigma	% of variation
Between groups	6	34.6	5.7	0.0	-0.6%
Between samples within groups	65	424.1	6.0	0.1	1.2%
Within individuals	72	459.1	6.3	6.4	99.5%
Total	143	917.9	6.4	6.4	100.0%

	Phi
Phi-samples-total	0.005
Phi-samples-Pop	0.011
Phi-Pop-total	-0.006

Table 5.8 Evanno table showing assessment of K=1-9 values.

K= clusters; Mean LnP(K) = mean log-likelihood of K; StDev = standard deviation; Ln'(K) = mean difference between successive likelihood values of K; |Ln''(K)|= absolute value of difference between successive values of K; ΔK = mean of absolute values of L''K averaged over runs, divided by standard deviation of L(K)

Output derived from Structure Harvester (Dent and Von Holdt 2012).

K	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	ΔK
1	-1365.075	0.936	-	-	-
2	-1373.075	12.183	-8.000	0.200	0.016
3	-1380.875	9.722	-7.800	13.725	1.412
4	-1402.400	12.765	-21.525	14.200	1.112
5	-1409.725	12.643	-7.325	26.175	2.070
6	-1443.225	5.158	-33.500	59.875	11.607
7	-1416.850	4.078	26.375	60.050	14.725
8	-1450.525	28.414	-33.675	7.800	0.275
9	-1492.000	52.947	-41.475	-	-

Figures

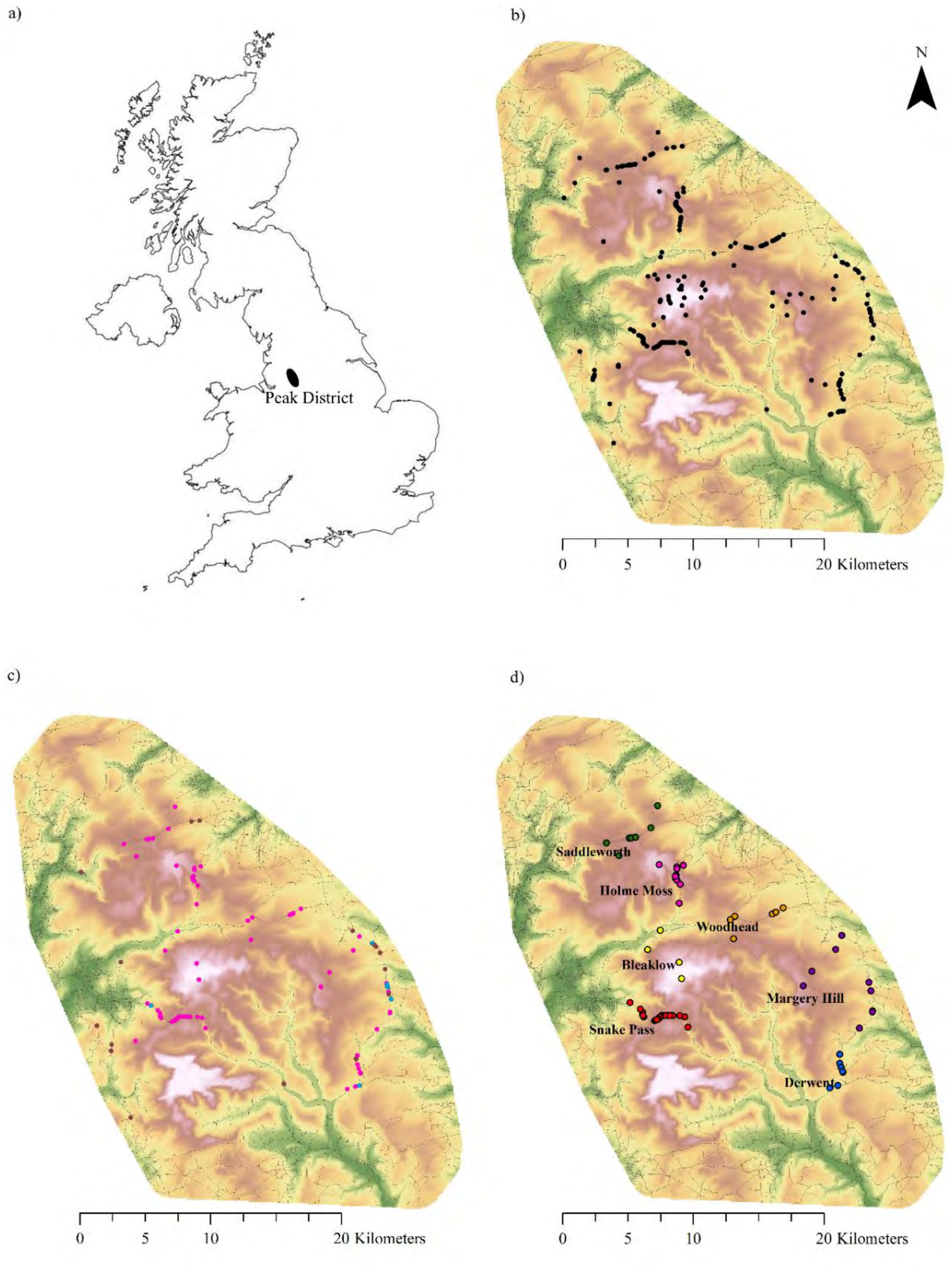
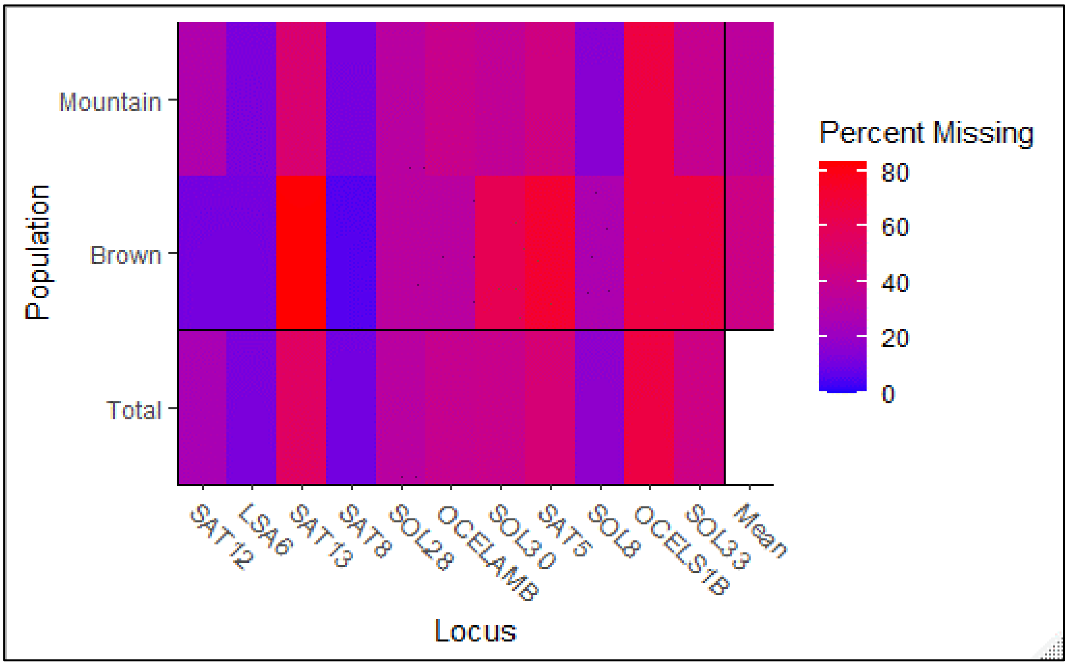


Figure 5.1 Maps showing Peak District with genetic sampling locations.

a) United Kingdom; b) c) and d) are Peak District colour relief maps, graduating from green at low elevations to white at high elevations, with roads in dark grey. b) All 254 sample locations c) Genotyped hare samples: pink = 97 mountain samples; brown = 18 brown hare samples; black = hare species unidentified d) Genotyped 97 mountain hare samples, coloured by group location, the name of each group placed at its centroid.



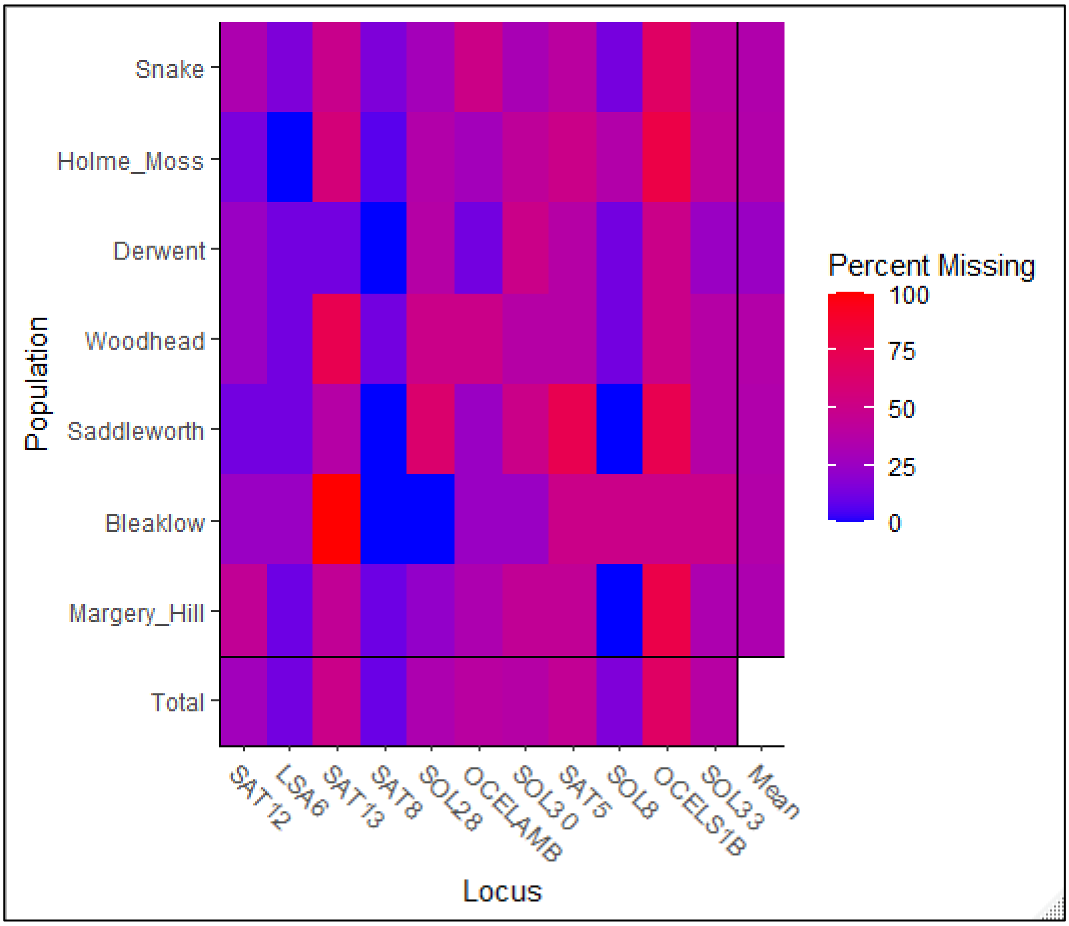


Figure 5.2 Missing data for the 115 hares samples, per loci

Calculated in 'poppr' (Kamvar et al. 2014). The upper box is for the two species; the lower box is the mountain hare groups.

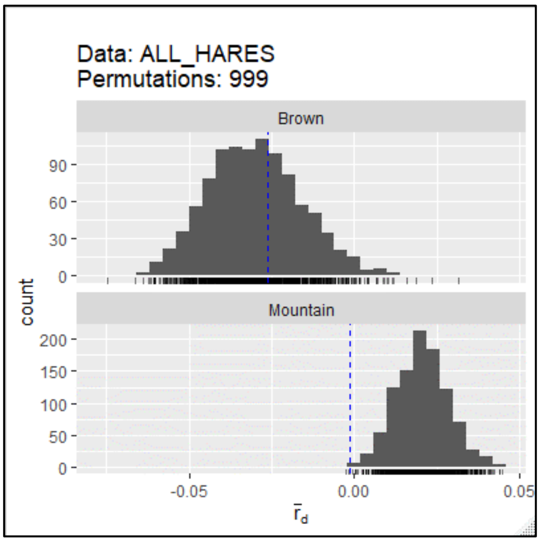


Figure 5.3 Linkage disequilibrium for the two hares species.

The histograms show permuted r linkage values (association of alleles between pairs of loci) following (Agapow and Burt 2001). The blue line indicates standardised r.

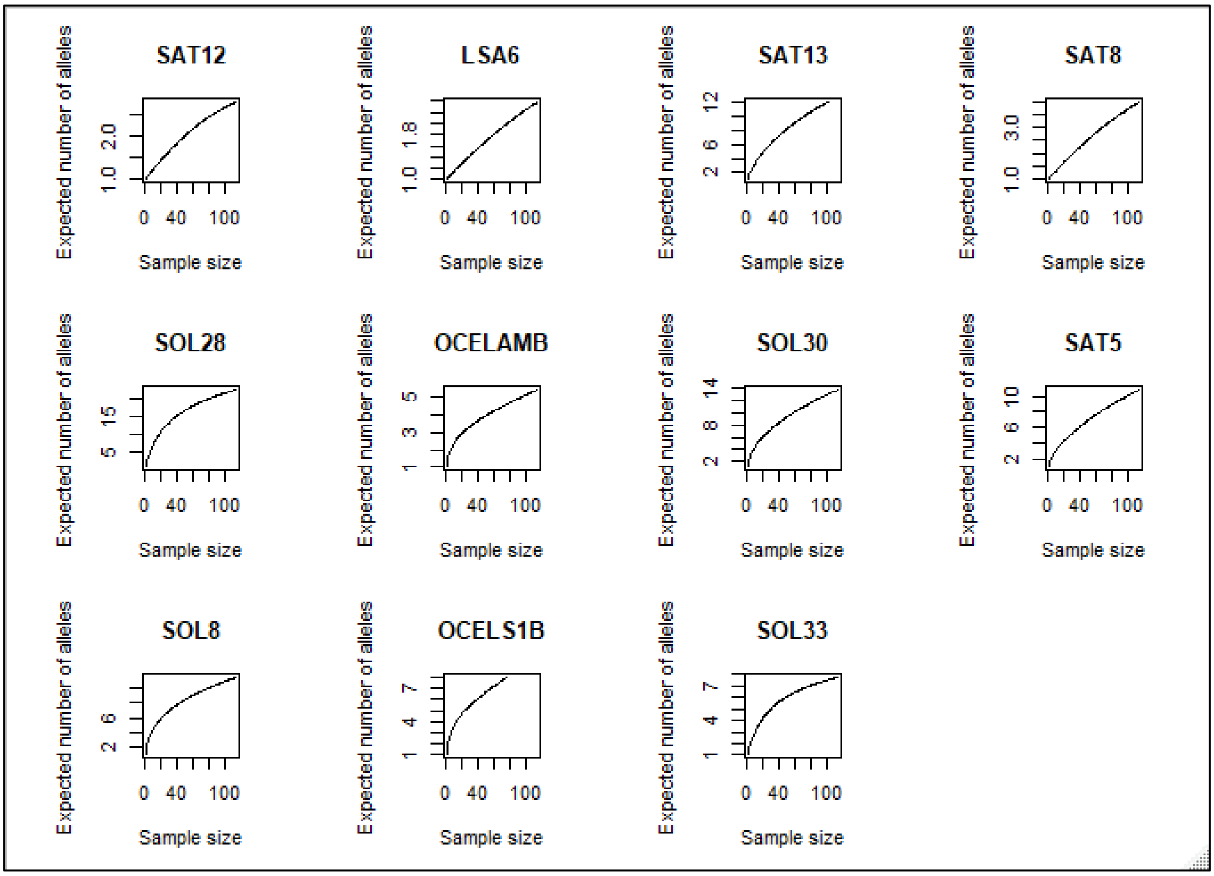


Figure 5.4 Rarefaction plots for each loci for all of both mountain and brown hares samples

Assessed within 'poppr' (Kamvar 2014) .   Rarefaction curves compute the number of alleles with respect to sample size using Hurlbert's (1971) method.

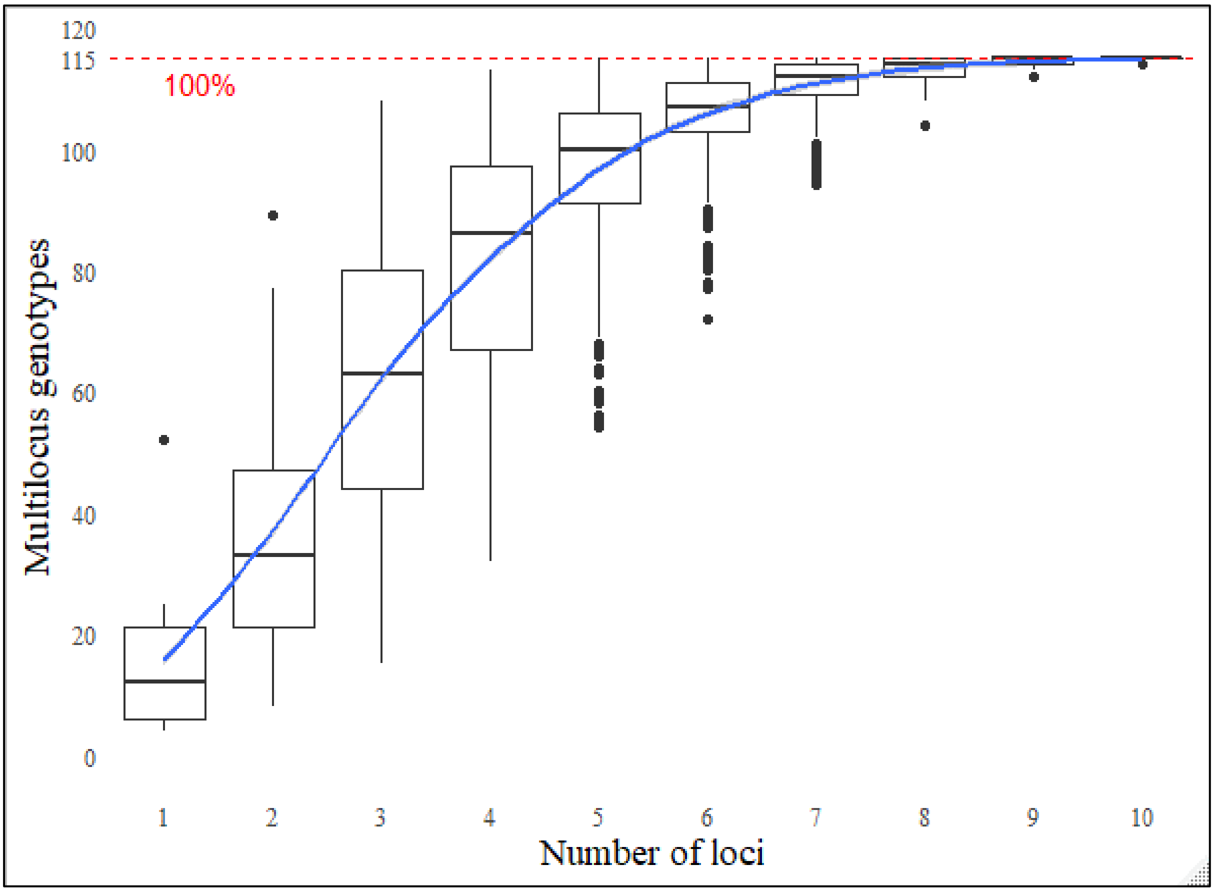


Figure 5.5 Genotype accumulation curve based on all hare samples

As reported from poppr (Kamvar 2014). Loci are randomly sampled without replacement, calculating the number of multilocus genotypes that are observed.

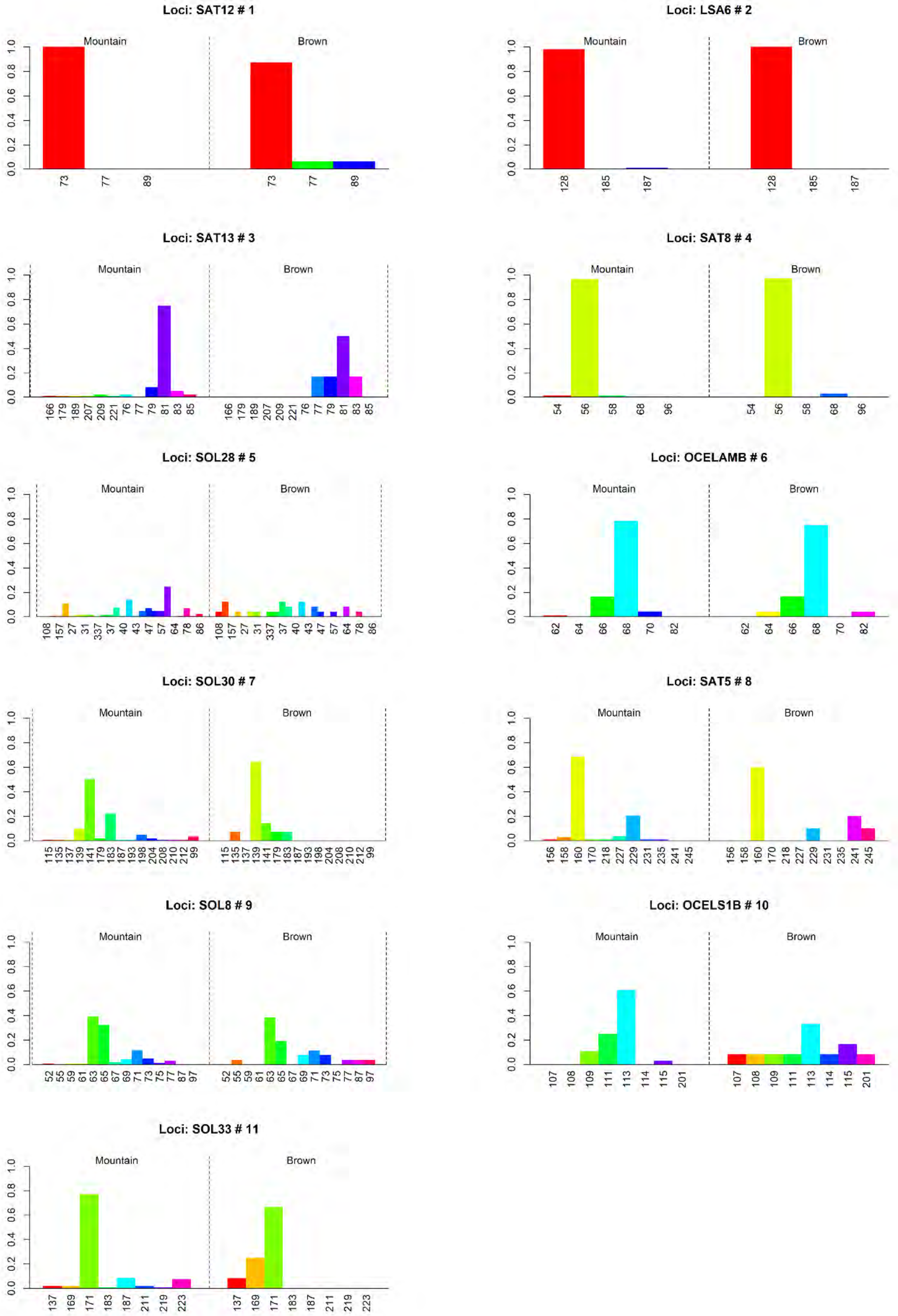


Figure 5.6 Histograms showing allele frequencies, within each of the two hare species for each locus.

Plot produced by PopGenReport (Adamack and Gruber 2014). SAT12 is suggestive of null alleles, there were 16 samples for brown hare with 3 different homozygotes and 69 samples for mountain hare all with the same homozygote. This chart is not reproduced for mountain hare groups.

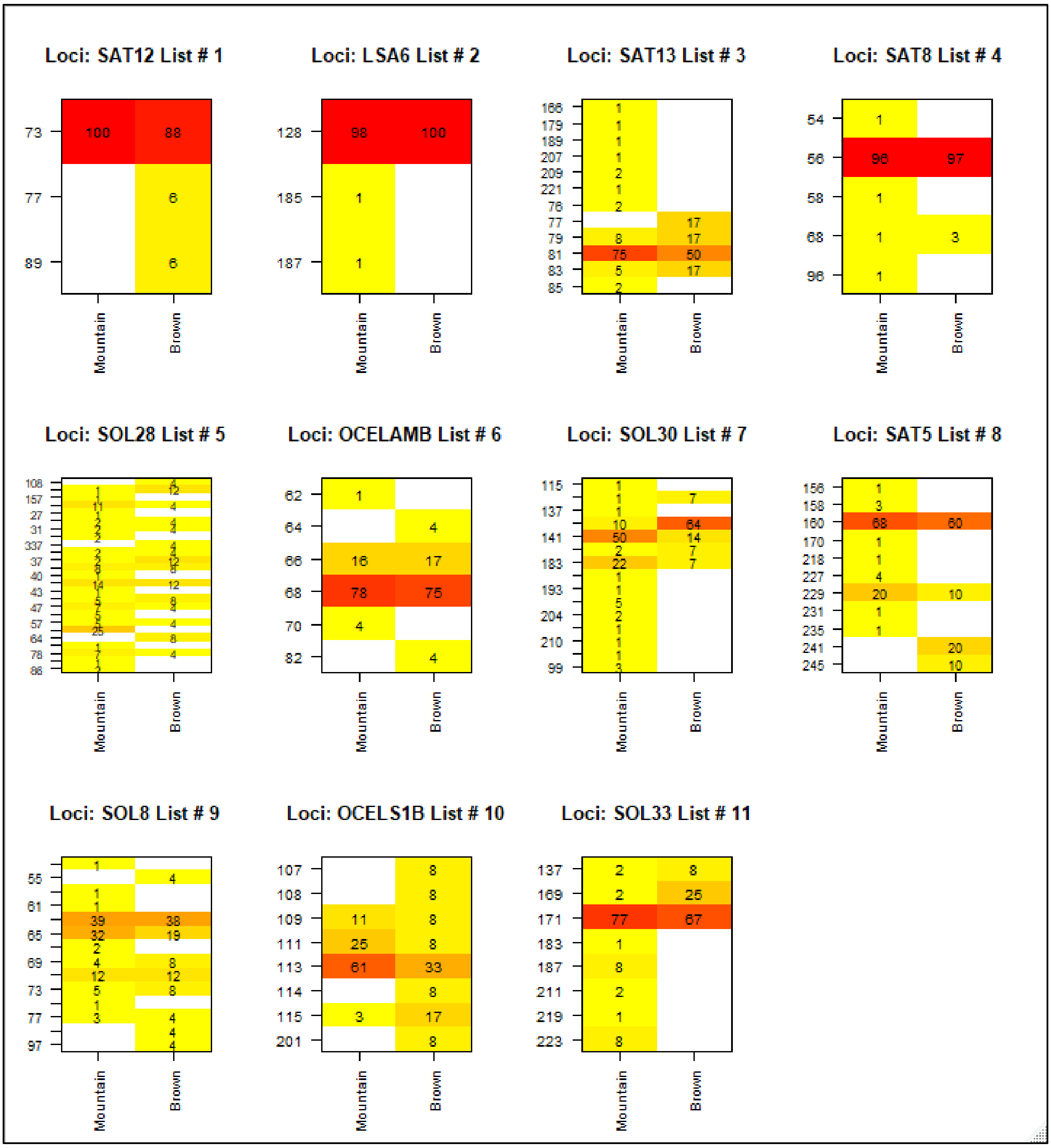
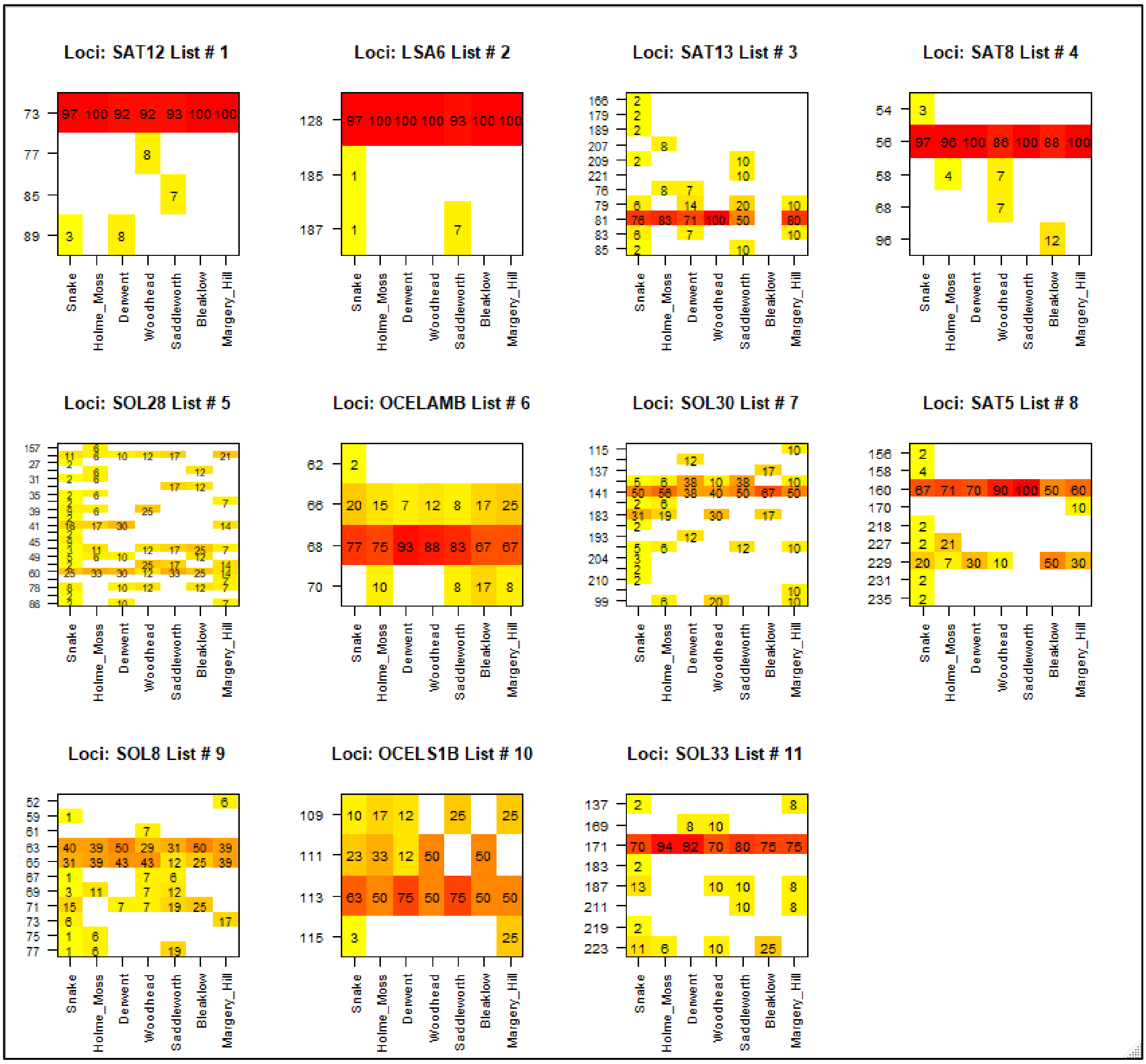


Figure 5.7 Heatmap showing relative allele frequencies

a) within each of the hare species for each locus.

Plot produced by PopGenReport (Adamack and Gruber 2014). The data is therefore the same as for the previous figure, but as relative frequencies. Note the chart shows % values, so small sample sizes are not necessarily apparent.


Loci: SAT12 List # 1

Loci: LSA6 List # 2

Loci: SAT13 List # 3

Loci: SAT8 List # 4

Loci: SOL28 List # 5

Loci: OCELAMB List # 6

Loci: SOL30 List # 7

Loci: SAT5 List # 8

Loci: SOL8 List # 9

Loci: OCELS1B List # 10

Loci: SOL33 List # 11

b) Within each of the mountain hare groups for each locus.

Plot produced by PopGenReport (Adamack and Gruber 2014). Note the chart shows % values, so small sample sizes are not necessarily apparent.

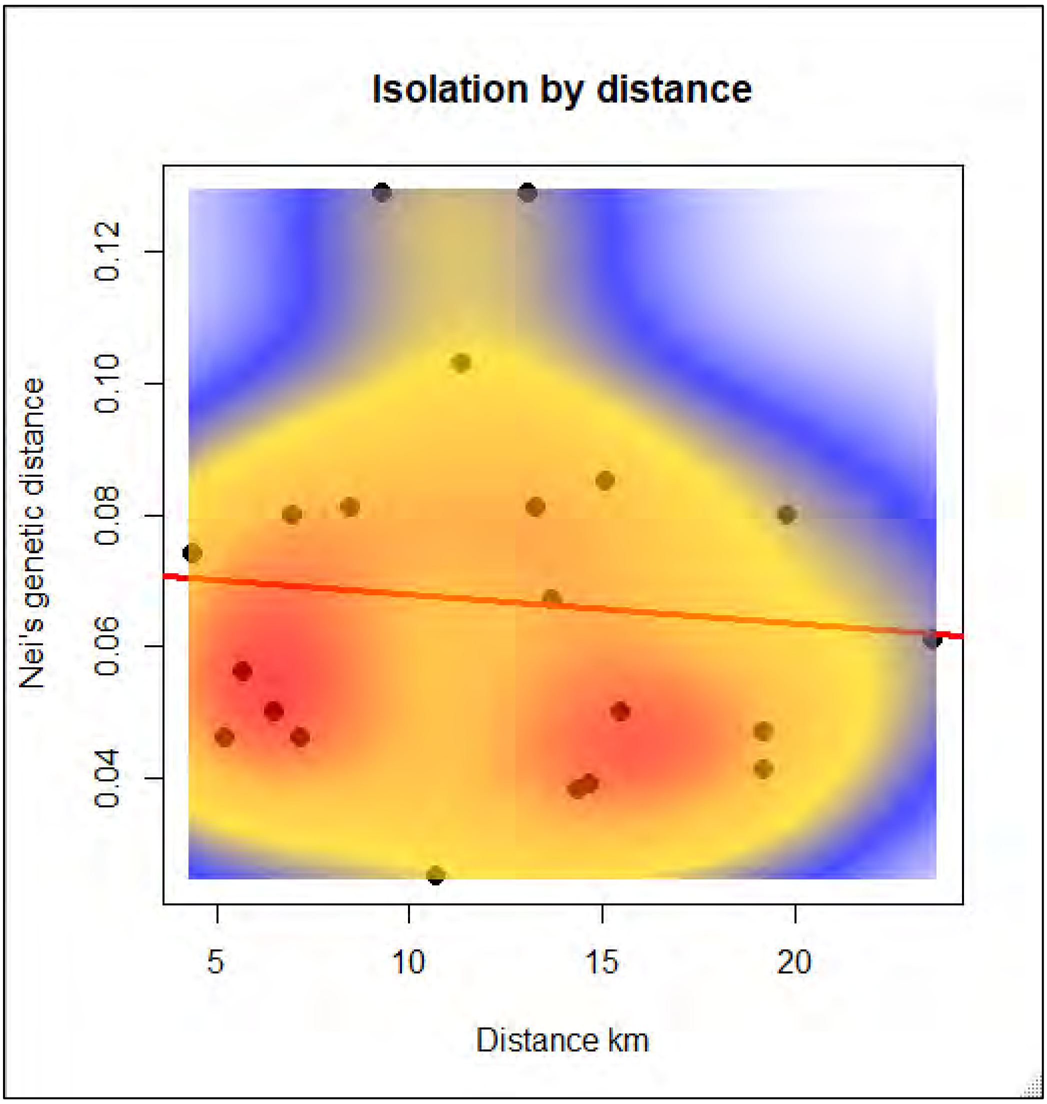


Figure 5.8 Isolation by distance plot, for each mountain hare group

Pairwise comparison of Euclidean geographic distance (x-axis) with genetic distance (y-axis). Background colours represent 2d kernel density, assessed against the points (blue low density; red high density). The red line indicates the linear regression of the points.

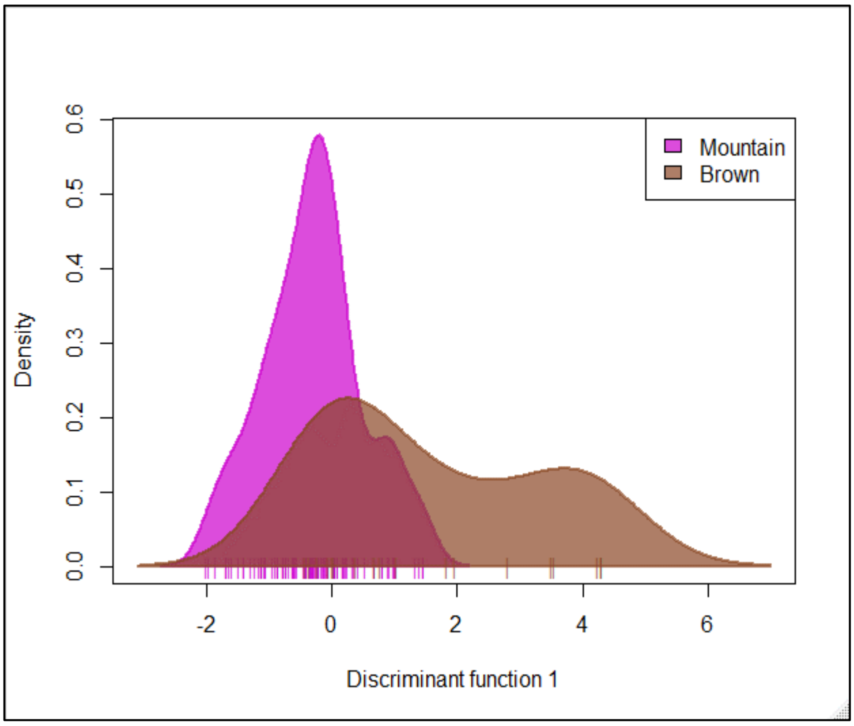


Figure 5.9 Scatter plot of discriminant principal components analysis for the two hare species groups.

Number of principal components = 20 Number of discriminants = 50. There are K= 2 clusters, so only one single discriminant function is retained. Plot produced by 'adegenet' (Jombart 2008) following methods later described in Jombart et al. (2010).

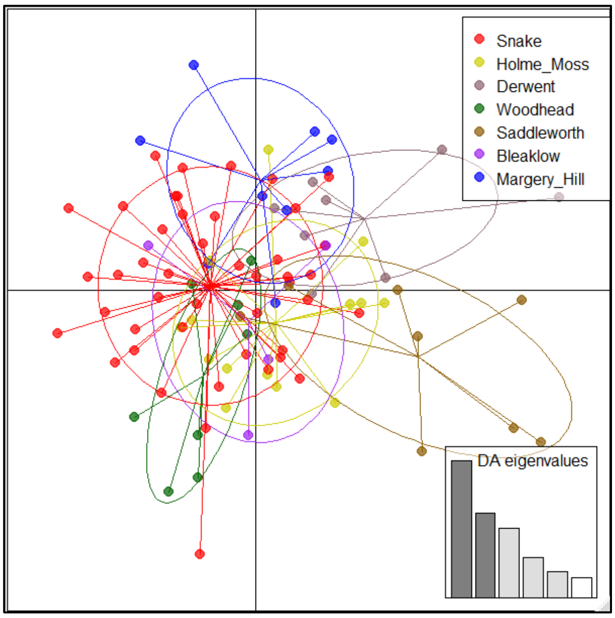
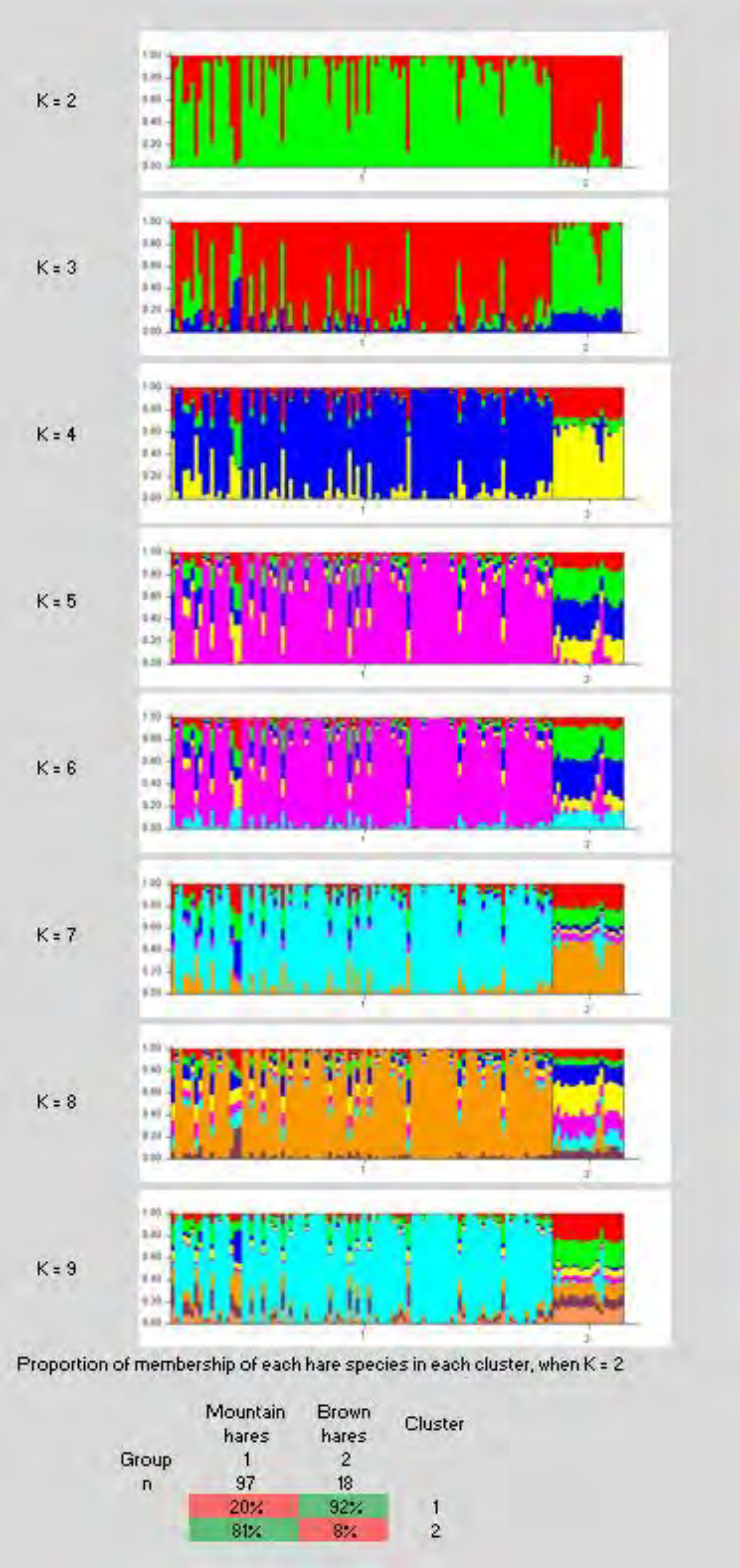


Figure 5.10 Scatter plot of discriminant principal components analysis for the mountain hare groups.

Number of principal components = 20 Number of discriminants = 5. Eigenvalues of the analysis are inset. Plot produced by 'adegenet' (Jombart 2008) following methods later described in Jombart et al. (2010).

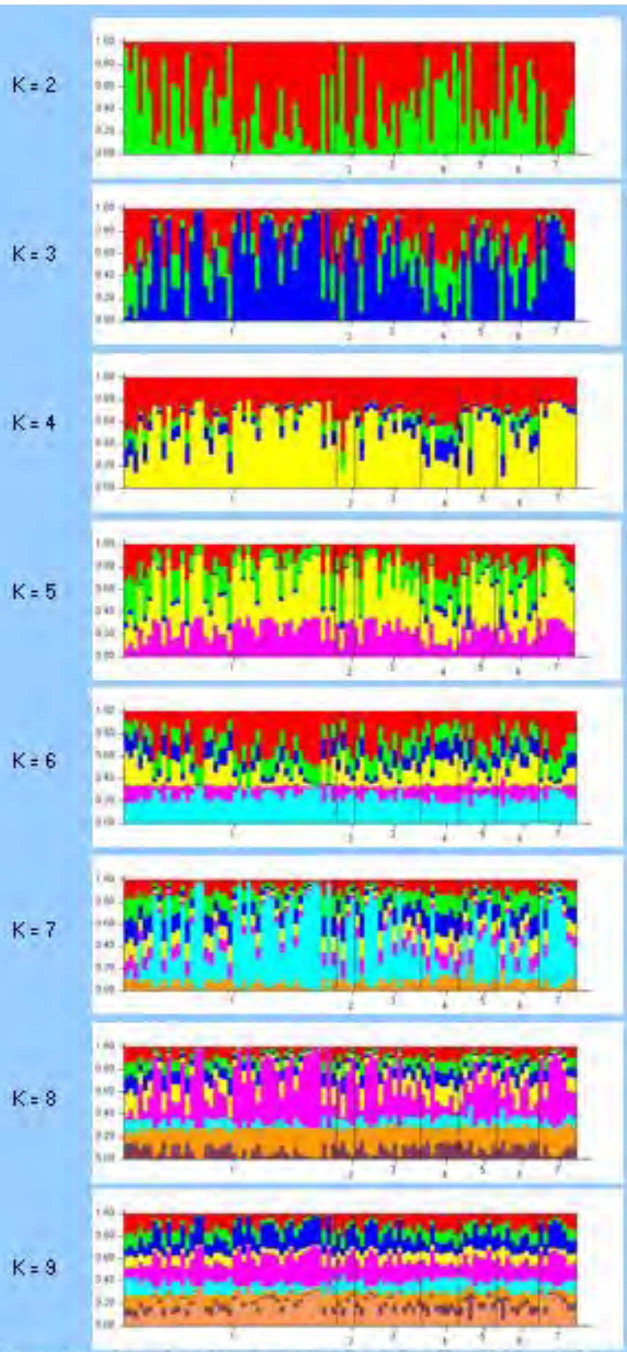


Proportion of membership of each hare species in each cluster, when K = 2

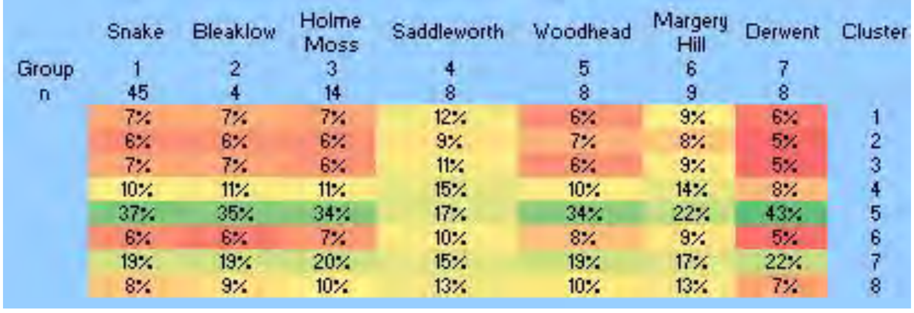
	Mountain hares	Brown hares	Cluster
Group	1	2	
n	97	18	
	20%	92%	1
	81%	8%	2

Figure 5.11 Barplots for the two hare species showing the proportion of each individual sample assigned to each cluster.

Plots originated from STRUCTURE 2.3.4 software (Pritchard et al 2000). Parameters were no admixture, groups as priors, correlated alleles. Group 1 is mountain hares; group 2 is brown hares. The heatmap table shows the proportion of each hare group's alleles that fall within each of the K clusters with n as sample size.



Proportion of membership of each mountain hare group in each cluster, when K = 8



	Snake	Bleaklow	Holme Moss	Saddleworth	Woodhead	Margery Hill	Derwent	Cluster
Group	1	2	3	4	5	6	7	
n	45	4	14	8	8	9	8	
	7%	7%	7%	12%	6%	9%	6%	1
	6%	6%	6%	9%	7%	8%	5%	2
	7%	7%	6%	11%	6%	9%	5%	3
	10%	11%	11%	15%	10%	14%	8%	4
	37%	35%	34%	17%	34%	22%	43%	5
	6%	6%	7%	10%	8%	9%	5%	6
	19%	19%	20%	15%	19%	17%	22%	7
	8%	9%	10%	13%	10%	13%	7%	8

Figure 5.12 Barplots for mountain hare groups showing the proportion of each individual sample assigned to each cluster.

Plots originated from STRUCTURE 2.3.4 software (Pritchard et al 2000). Parameters were no admixture, groups as priors, correlated alleles. Groups as: 1 Snake Pass, 2 Bleaklow, 3 Holme Moss, 4, Saddleworth, 5 Woodhead, 6 Margery Hill, 7 Derwent. The heatmap table shows the proportion of each hare group's alleles that fall within each of the K clusters with n as sample size.

Sample ID	19233
Assumed species	Mountain
Brown hare genotype	99% (8 loci) = hybrid
Collection date	9/3/2020
Location	Strines Road (Margery Hill)

Sample ID	18060
Assumed species	Mountain
Brown hare genotype	94% (5 loci) = hybrid
Collection date	15/5/2018
Location	Snake Pass

Sample ID	19207
Assumed species	Mountain
Brown hare genotype	94% (5 loci) = hybrid
Collection date	7/7/2019
Location	Snake Pass

Sample ID	20305
Assumed species	Mountain
Brown hare genotype	83% (5 loci) = intermediate
Collection date	31/3/2020
Location	Snake Pass

Sample ID	19135
Assumed species	Mountain
Brown hare genotype	80% (10 loci) = intermediate
Collection date	26/2/2019
Location	Snake Pass

Sample ID	19118
Assumed species	Mountain
Brown hare genotype	61% (5 loci) = intermediate
Collection date	15/2/19
Location	Margery Hill

Sample ID	20325
Assumed species	Mountain
Brown hare genotype	60% (7 loci) = intermediate
Collection date	22/4/2020
Location	Snake Pass

Sample ID	19172
Assumed species	Mountain
Brown hare genotype	58% (5 loci) = intermediate
Collection date	15/4/19
Location	Saddleworth

Sample ID	20309
Assumed species	Mountain
Brown hare genotype	53% (10 loci) = intermediate
Collection date	6/4/2020
Location	Strines Road (Margery Hill)

Sample ID	20326
Assumed species	Mountain
Brown hare genotype	50% (9 loci) = intermediate
Collection date	22/4/2020
Location	Snake Pass

Sample ID	19239
Assumed species	Brown
Brown hare genotype	45% (7 loci) = intermediate
Collection date	19/3/2020
Location	Strines Road (Derwent)

Figure 5.13 Photographs of hare individuals with potential hybrid or intermediate genotypes

Tables show: sample IDs; Assumed species = as identified by morphological characteristics; Brown hare genotype = % of brown hare genetic cluster within the individual, determined by STRUCTURE 2.3.4 (Pritchard et al. 2000) and number of loci with data for the sample; Collection date and Location are listed. Specimens from Snake Pass were 5km from nearest brown hare distribution range (Bedson et al. 2021). Margery Hill field specimen was at Pike Lowe ~1km from brown hare range. Strines Road is the contact zone mountain and brown hare ranges. Saddleworth specimen was on hill top ~2km from brown hare range.

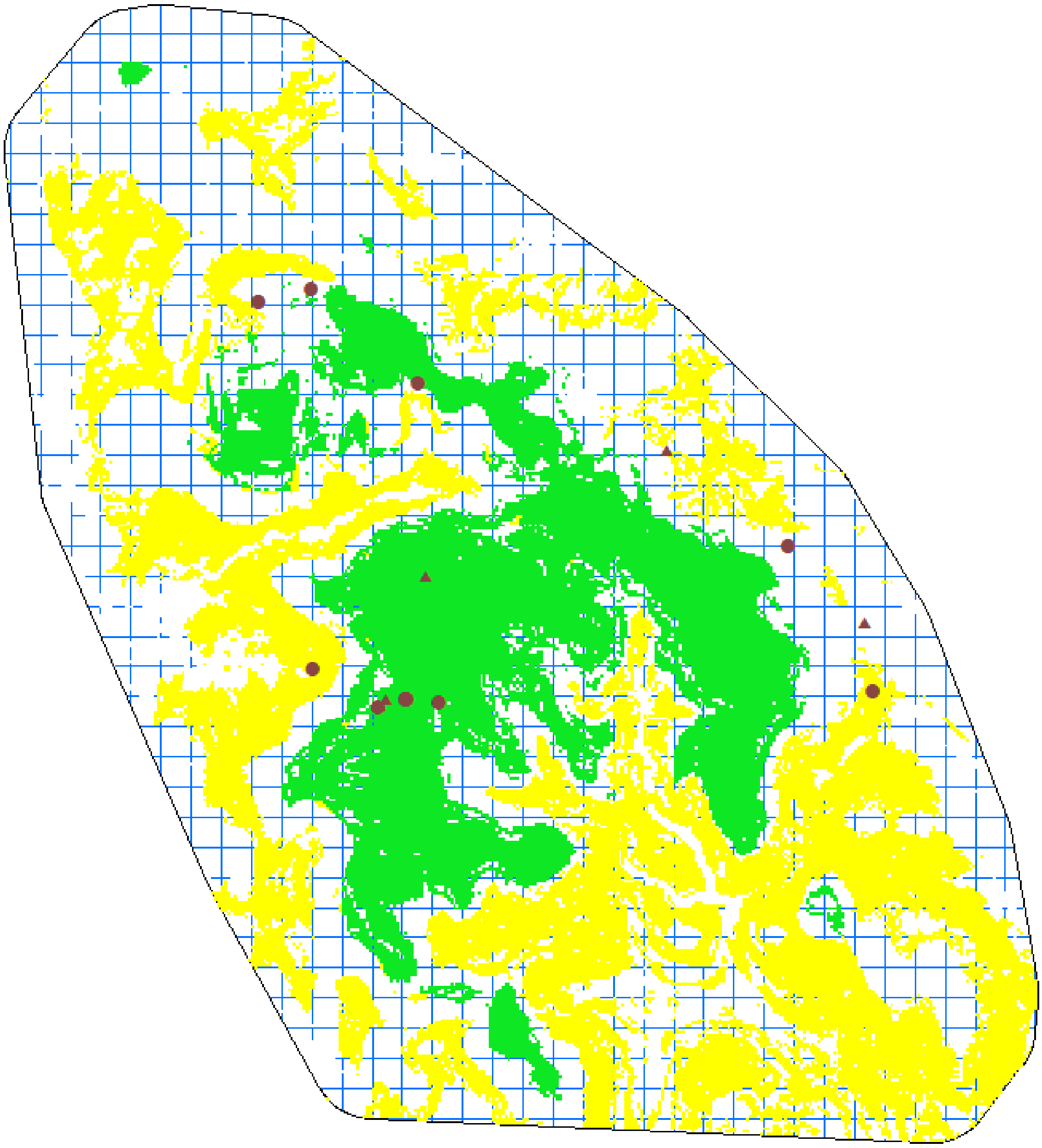


Figure 5.14 Map showing locations of putative hybrid hares

Brown triangles = mountain hares with >90% brown genotype. Brown circles = mountain hares with 50-90% brown hare genotype. Map shading derived from Bedson et al. 2021a (Ecological niche model) and shows green = mountain hare fundamental niche extent, yellow = brown hare fundamental niche extent. Fishnet is 1km gridlines for measurement purposes.

CHAPTER 6 FUTURE MONITORING AND CONSERVATION IMPERATIVES

Image: Just a few weeks old, a young mountain hare leveret gently forages, unaware it is sought as dinner by crows and ravens. Shining Clough Moss, Bleaklow, Derbyshire, England, UK. Date: 30th August 2020.

6.1 Abstract

The aim of this PhD thesis was to measure population attributes of the isolated group of mountain hares within their bounded upland natural environment of the Peak District, England. Findings can be used to inform conservation assessments and to model extinction risk. Here are presented suggestions for future monitoring, research and possible conservation interventions.

6.2 Future population monitoring

6.2.1 Continuing monitoring

There is a clear need to measure abundance periodically to ensure mountain hare populations persist amidst all threats. Annual monitoring is more likely to detect sudden increases and declines. Mountain hare populations can cycle and crash, causing any surviving groups to be highly vulnerable. For several decades across the entire UK there were or no annual monitoring mechanisms identifying such cyclicity. There was Hewson (1969) based on shot hares; Watson and Wilson (2018) based on flushed hares. Neither of these used spatial data to robustly estimate density. By contrast over eleven years Krebs et al. (2001) used systematic live trapping capture / recapture and were able to detect population cyclicity for Yukon snowshoe hares.

For the Peak District there is now five years published data of systematic monitoring of densities of mountain hares. A sixth year of field surveys for 2022, has been completed. This provides highly valuable information for mountain hare conservation in England, also contributing to wider lagomorph science.

6.2.2 Distribution extent

We contemplate the rationale for the definition of the distribution extent and its area (Figure 6.1). This helps conservation assessments, when considering where monitoring or management attention are required. For any species, the determination of distribution extent will vary according to data sources, assumptions and analytical objectives. Krebs (2001) suggests that measured differences in relationships of distribution and abundance are more likely to be artefacts of sampling designs than any biological cause. Of note for Peak District mountain hares, historic statements of extent were 332km^2 Mallon (2001) or 250km^2 Mathews et al. (2018).

Within this entire study other measures were presented, based on new information. Attempts to define the study extent first considered the deduplicated BRC records. This was shown to be stable over twenty years. However it would be misleading to apply a minimum convex polygon around those points (measuring 610km^2) as such includes extensive areas without mountain hares and creates unnecessary monitoring effort (Figure 6.1).

The recommended survey area is the minimum concave polygon i.e. alpha hull shape described in chapter 4 (also reprised in Figure 6.1). This shape is a purely geometric construct without reference to environmental characteristics. Added to this shape was the distance sampling survey footprint of 2019, almost identical except for minor discrepancies. The combined shape measures 358km^2 and is contiguous, except for two small patches in the far north. It contains areas without mountain hare records, which the ecological niche model predicts as absences. It is appropriate for defining the future monitoring area.

A different possibility would be the ecological niche model threshold maps from chapter 2. One might consider restricting surveys to the predicted current habitat model area of 269km^2 (repeated here in Figure 6.1) Yet this is a mosaic of large contiguous areas, many multi-hectare patches with large gaps between. It is too simplistic to suggest mountain hares never move between those patches. The alpha hull shape encompasses these patches, so is a good shape to use. One may accept that neither the alpha hull shape nor the current habitat threshold model shape will be entirely correct. Krebs (2001) suggests in these circumstances, local populations may exist, subdivided into discrete patches. This is true for Peak District mountain hares: they have a broad dispersed spread with some clumped groups (Figure 6.1). Figure 6.2 shows the Ordnance Survey map images covering this extent.

These suggest limits to the distribution of mountain hares. These may exist, simply facilitated by the geographical range of heather and limited by human infrastructure. For example, there are mountain hares at Moss Moor but not north at Rishworth Moor as there is the obvious barrier of the M62 and no contiguous heather (Figure 6.3). By way of corroborating anecdote, during 2018 an informal pellet presence / absence survey on systematic straight line transects by CM Shaw confirmed absence of mountain hares at Rishworth Moor (Bedson unpublished data).

6.2.3 Monitoring schemes

Here are suggestions for two alternative monitoring schemes. Each assumes identical survey methods as per chapter 4, conducting daylight visual sampling February to early April with approximately 15 to 20 survey days available per surveyor, covering 2 squares per day.

The first is a whole population assessment, which would enable a complete picture of the graduations of densities as well as stratifications by habitats, covering all of the alpha hull shape. This would require a systematic grid of 1-km squares which could be spaced 1km apart, with the assumption of a maximum viewing range of 780m. This amounts to 103 1-km survey squares, or if excluding edge squares, 88 1-km squares (Figure 6.4). As a bare minimum this would need three full time staff assuming fair weather. However up to ten volunteers might be more appropriate.

The second would be a more limited continued monitoring of population trajectories, following the survey footprints of Bleaklow and Margery Hill, 26 alternate 1-km squares (Figure 6.5), covering the largest portion of the population. One person may cover these areas in approximately 12 - 14 days.

6.2.4 The value of daylight visual surveys

As mountain hares are nocturnal it is sometimes recommended to survey them at night. However such methods must account for imperfect detection, or systematically measures an unimpeded visual strip, otherwise this approach is entirely devoid of merit for estimating densities. Yet if one can account for imperfect detection, one may credibly estimate density by night as per within chapter 3. Of the three compared survey "methods", my own observational and statistical preference was for thermal imaging, which provided the highest detection rates at the furthest distances with the largest group sizes. However good night-time weather occasions were few and winter darkness painfully cold. Camera traps worked well in achieving different detection rates at different locations during the extremely difficult winter weather. The number of assumptions involved in analysing camera data render this method susceptible to subjectivity. However provided the assumptions are held constant, this method can provide a useful measure of relative abundance for ongoing monitoring.

Notwithstanding these technologies, chapter 3 showed daytime distance sampling worked well, even when it was hampered with a small sample size. As further evidence, chapter 4 then showed daytime distances sampling as highly effective, accomplishing a very large number of detections (2017 to 2021 = 2,274 total observations). Chapter 4 demonstrated this method achieved very high reliability for effort. Once can cover much ground by foot, by day and record detailed observations and natural history.

There was a further suggestion (Pettigrew 2020) that counting mountain hares may be more effective at dawn, when maximum hare activity means more sightings. Whilst that contention merits consideration, it has very limited field practicality nor statistical evidence. The overall Pettigrew (2020) survey regimen and findings are not comparable. That study took place upon ~26km of path-based transects on low flat hills of managed grouse moor in the Lammermuirs, Scotland. By contrast Peak District is a much larger area. The 1-km squares of Bleaklow and Margery Hill alone require 120km of straight line transects. Each 1-km square needs ~ 4 hours plus 1 hour walk in time. Some squares are exceptionally arduous including up to 350 metres of ascent over 1 kilometre (Figure 6.6). Locally poor weather means few survey days are available (~16 days during Feb / March). Pettigrew recommended surveying during morning twilight; however in the Peak District at this hour the hills are often shrouded in fog. Accordingly daylight surveys take the whole day long (0800h to 1800h, or later by end March). As Pettigrew (2020) does not mention imperfect detection: there is no measure of detection probability i.e. what percentage of the censused population has been seen. Counts of "inactive" hares are not explained.

By contrast daylight visual surveys in the Peak District thus far reported observing ~20% of hares at 520m and >30% of hares at 100m (chapter 4 figure 4.4). These are large proportions of a population. Of all hares seen, 61% are recorded as stationary; the definition of "active" seems irrelevant. Many hares rest in gullies and do not hide in vegetation. Hares which hide in deep heather are revealed by flushing at short ranges, arising from walking straight line transects i.e. the flushing method of Watson and Wilson (2018). It is hard to see how short 90 minute dawn surveys could be logistically feasible, there is no measure of detection probability and thus it is difficult to state it would accomplish a more reliable encounter rate.

6.3 Monitoring human-caused mortality

These may be the only two mortality vectors which may be directly influenced by public policy interventions. Their effects are to limit the mountain hare population size. Data gathered during this PhD study are recorded here for the public record. Ongoing monitoring is recommended.

6.3.1 Roadkill

Information regarding roadkill was submitted to the National Infrastructure Examining Authority regarding the A57 Links Roads (previously known as Trans Pennine Upgrade Programme), see references (CPRE PDSY 2022). Elements of that report are stated here:

Introduction

Road density and traffic volumes are known vectors which contribute to roadkill, adversely affecting animal populations. In the Peak District, mountain hares are frequently killed on roads at high moorland locations Consequently the frequency of roadkill was recorded, with intention of inclusion in longer term population viability modelling.

Methods

From 2018 to 2020 I conducted tours of the road network, to record roadkill of mountain hares. This was opportunistic and not systematic. Some roads e.g. A628 Woodhead were very busy and it was likely some roadkill hares were missed. Heavy rain tended to wash away carcasses within 3 days. Some hare carcasses were obliterated so it was not always possible to identify which species of hare had been killed. Therefore observations were also recorded for brown hares (*L. europaeus*), though these were <10% of all hares. The numbers recorded were likely to be an under-representation of actual roadkill by at least 50%. Roadkill locations were mapped in ArcGIS (ESRI, USA). Roadkill numbers by month were plotted as simple column charts.

Results

Roadkill was recorded during 2017 to 2020 and subsequently estimated as ~ 200 hares per year, a substantial portion of the adult population (Figure 6.7, 6.8 and 6.9). The area with highest incidence of roadkill was where A57 Snake Summit and the Pennine Way meet. Hares were seen to actively visit the roads and follow vehicles (Figure 6.10). Separate trail camera studies showed that hares behave with curiosity and intelligence, examining fences and posts. Hares do not lick salt off roads. Hares are sometimes attracted to vehicle headlights.

Discussion

In the Peak District, roadkill of mountain hares has a substantial adverse effect on numbers, particularly affecting adults during the breeding season, which increases the pressure on a small population below viable thresholds. Roadkill is also a severe animal welfare issue.

Effect of increased traffic on A628 and A57

Is is known that the present level of roadkill does not take every mountain hare that visits the roads. The population in some of these areas can be buoyant and many individuals cross the roads and escape casualty.

It is difficult to attribute a direct relationship of increasing traffic volumes, to increased roadkill. If traffic volumes were to increase by, for example 50%, it is entirely possible that roadkill might increase by 50% also.

Mitigations

Mitigation attempts through attempting to provide overpasses or underpasses, may be counter-productive and serve to attract hares, providing shelter during poor weather, and causing them to linger at road locations. Similarly, installing fencing at key locations may be difficult. Fences would need to be totally impermeable: hares can jump to a height of 1.2 m or higher. Fences might serve to attract hares also.

Providing education to drivers, may increase their awareness of the likelihood they may accidentally kill a mountain hare. In particular, reducing driving speeds during twilight hours and at night may be helpful. It would be constructive to educate the public that during spring time, mountain hares roam at night and investigate the roads. Implementing road signs to warn the public about wild animals, may encourage some motorists to reduce their speeds. However many motorists and motorbike riders would ignore these warnings.

The most effective mitigation against mountain hare roadkill may be to introduce a 20 mph speed limit with speed cameras, at high roadkill locations. These stretches of road are mostly short: only 1,000 to 2,500 metres in length. This would increase driver journey time by perhaps 30 seconds, whilst annually saving ~ 200 hares per year from death. If one were to introduce, for example, a 20mph speed limit along the key roadkill areas of A57 Snake Pass, this could contribute to greatly reduced mountain hare roadkill, whilst only reducing driver journey times between Sheffield and Glossop by around 20-30 seconds.

Reducing driver speeds on the A628 Woodhead Road may be more challenging socially as this road is frequented by heavy goods vehicles. Nonetheless education of commercial organisations may help them to recognise they share responsibility for contributing to safe passage for wildlife.

It is also notable that the area of A57 Snake Pass and Pennine Way junction hosts a large amount of parked cars. Considerations of building a car park here might be unhelpful. Any car park infrastructure might serve as attractant to mountain hares and lead to their being habituated to humans. This would represent a kind of "Yellowstone Park" effect: a reduction of their natural evasive behaviour.

6.3.2 Persecution

Information regarding mountain hare persecution was submitted to People's Trust for Endangered Species for forwarding to the Joint Nature Conservation Committee (JNCC) as part of a data submission for the consultation on eligibility & decision criteria defined for Quinquennial Review 7 for species listed on Schedules 5 & 8 of the Wildlife & Countryside Act (1981) 27 January 2022 That report is stated below for the public record, with Table 6.1 subsequently updated in this thesis. Ongoing monitoring is recommended.

Introduction

Anecdotal mountain hare persecution data was occasionally volunteered to the author (Carlos Bedson) by members of the public. The author kept records to help understand causes of mortality.

Method

Records of mountain hare persecution events were provided to the author by various sources in confidence from January 2017 to April 2021 (updated April 2022). In May 2021 the author made further confidential enquiries of the Wildlife Trusts and a local conservation group. The author asked three landowners and an officer of the British Association of Shooting and Conservation (BASC) whether they could corroborate the events.

Results

There were more than 30 directly witnessed and evidenced persecution events dating from 2013 onward. There were 4 third party allegations made by highly reputable members of society, that miscreant persons had proactively admitted persecuting hares. See Table 6.1 and Figure 6.11. No landowner provided any evidence of shooting or persecution.

Discussion

Taken at face value, the number of detected events is low. However enquiries of landowners and BASC had yielded any admission of these events. It therefore appears likely these results under-estimate persecution levels. Much of the mountain hare range is high on hills, up to 5 km away from roads and public visibility. In February 2022 BASC published a statement on their website (BASC 2022)

"It is true that mountain hares are sometimes culled when they reach high population densities as part of a tick disease control strategy, often alongside deer management and sheep treatments."

Evidence of mountain hares being a principal vector for this disease transmission is ambiguous (Harrison et al. 2010). The disease, louping ill virus, has not been identified in the Peak District.

Persecution of mountain hares appears to take place across the whole of the Peak District in a clandestine fashion. It is difficult to state how severe this is. Historic hunting anecdotes from Scotland described how hundreds of hares could be shot in one day (Flux 1962). Without professional systematic transparent monitoring it is hard to see how shooting or trapping can have been sustainable in the Peak District (Milner-Gulland and Rowcliffe 2007).

Some complex mitigations are required. Legislation is vital. This provides the foundation for responsible apolitical members of society to objectively record hare persecution events. Without legislation, shot and trapped mountain hares are easily trivialised, dismissed as legal, can be limitless, with serious animal welfare and conservation implications, without consequence to perpetrators. By contrast many countries with highly developed hunting practices, provide careful guidance for hunting and forbid wanton waste of animals e.g. Montana Code Annotated 2019.

Yet even in the presence of legislation, during winter months great portions of Peak District upland estates receive no human visitors, meaning miscreants may shoot mountain hares without witness. Therefore objective monitoring is required, no simple task; and penalties applied, should mountain hare welfare or conservation be compromised.

6.3.3 Brown hare monitoring

Chapter 4 of this study found little competition between the two hare species at present. However one must contemplate what respective densities are required for competition to actually occur. For this chapter, Mathews et al. (2018) was referenced, assuming mountain hare densities at $10km^{-2}$, and Bolton (2013) brown hares at $1.7km^{-2}$. On that ratio, it would seem mountain hares outnumber brown hares. However, when one considers the abundance estimates of chapter 4, the mountain hare densities at the range edges are much lower and potentially on par with brown hares. This leaves some open questions. Is the brown hare density then presently high enough to cause competition? Are brown hares actually hybridising with mountain hares at these range fringes and it is not yet detected? Further observation, measurement and study are required. The genetics work has suggested some hybridisation is occurring and proliferating in to the heart of mountain hare range.

6.3.4 Forecasting Peak District mountain hares extinction risk

Conservation assessments indicate that mammal populations are vulnerable to extinction when they have limited distribution or population abundance (Mills 2013). For example the IUCN red list classification system is based on number of populations and sub-populations, extent and abundance (IUCN 2012). Many other factors may predispose a population to vulnerability. Genetic minimum effective population size may comprise only one third of total population (Mills 2012). Animal body size has been shown to be associated with minimum population threshold e.g. the 2.7kg mountain hare (*Lepus timidus*) has a threshold of 4,000 individuals (Soule 1987).

The development of population viability analysis to predict extinction risk is an urgent piece of research. This is especially true for Peak District mountain hares, given the severe range reduction forecast by the ecological niche model, the small population size and the notably lower densities on grouse moors. Such research would not only be helpful for this small group of mountain hares, yet also serve as informative case study for lagomorph and medium-sized mammal populations worldwide.

The objectives of such research would be:

1. Create a functioning population demography model
2. Identify, quantify and forecast ecological factors and anthropogenic risks
3. Predict likelihood and time to extinction

Following a brief review of analytical methods, the Bayesian approaches described by Wade are recommended (Beissinger and Mcculough 2002: 213). Rather than using point estimates for each parameter, Bayesian methods incorporate parameter ranges and their uncertainties. Simulation models then provide forecasts of a range i.e. a distribution of "time to extinction" and this range is more likely to contain the true value. Outputs can be described in simple communicable terms e.g. "There is a 0.73 probability that the population is declining at a rate of 5% per year". Such statements may provide clearer quantification and more meaningful than presently occurs in standard reporting e.g. JNCC 2019.

These forecasts would help conservation managers consider mitigating actions. Sometimes the solution to the apparent extinction risk is suggested as a new set of translocations of mountain hares from Scotland. However if the Peak District ecosystem is acting as a population sink, other mitigating actions may be more appropriate. The population viability analysis would be vital to inform these choices.

6.4 Conservation imperatives

6.4.1 Mitigating climate change

The most important conservation impact identified in chapter 2 was the prediction of the mountain hare range to shrink after climate change. The findings of mountain hares preferring cold high elevations is as expected. It is consistent with all other species occurrence reports across Europe (see chapter 2 references). The warming scenario used in the study was the mildest and may have already been exceeded. If so, the pace of mountain and brown hare range change described herein, may already be accelerated.

It cannot be surprising this study predicted climate change to cause the range of mountain hares to shrink. All other studies show this result; though they occur at larger scales of countries or the continent of Europe (chapter 2 references). By comparison, the findings for the Peak District were based on a comparably small scale and extent. Therefore this study provides an important field-based prediction of climate change impacts upon medium sized mammals. One can literally walk from 300m a.s.l to 630m a.s.l and sense where the mountain hare range extent will shift to. With less snow, there is coat colour camouflage mismatch and increased visibility to predators. The predator control practiced extensively across the uplands may mitigate some of this risk.

What can be done to alleviate these forecasted declines? The global mitigation is for human society to reduce fossil fuel consumption and slow down production of greenhouse gas emissions. Locally the mountain hares in the Peak District may act symbolically as do polar bears: evidence of climate change, indicated by the gradual disappearance of an Arctic white mammal.

Chapter 2 does not explicitly predict how heather production will be affected by a warmer, drier climate. Heather does not grow well in very wet areas, it does need some measure of dry soil to allow root growth. However when heather becomes too dry it may cede to grasses. This is a complex dynamic (Glaves et al. 2013). However, assuming the above, the reduction of heather represents a loss of winter food supply that is relied upon by mountain hares. One might expect subtle, gradual starvation: hard to directly observe and validate.

To maintain peat-based carbon storage, attempting to arrest climate change, the Peak District upland landscape is being transformed by moorland restoration. This improves the water table and vegetation, improving overall habitat quality (Buckler et al. 2013). Presently the combination of increased water levels and verdant vegetation on Bleaklow must be one of the main reasons for it hosting higher densities of mountain hares. The hares are able to access moisture and endure the hotter summers. To alleviate these impacts of climate change, the moorland restoration efforts must continue across all the Peak District hills, to improve habitat quality. This will assist mountain hares and probably most other wildlife.

6.4.2 Increasing mountain hare densities

One presupposes that higher mountain hare densities is important for their conservation. To encourage such, one might consider as follows:

1. Provide a mixture of moorland vegetation especially including heather. Grasses are good, and so are mosses. Many times hares were seen feeding or pellets were abundant on star moss (*Polytrichum* spp).
2. Engineer the land to retain water e.g. gully blocking.

Regarding mountain hares on managed grouse moor estates, interventions may include:

1. Reduction of mature / degenerative heather areas some of which are very extensive.
2. Mowing and cutting, rather than burning heather (possibly, this needs testing and measuring).
3. Increased gully blocking and water retention.
4. Independent monitoring of hare abundance.
5. Encouragement to landowners and gamekeepers to amend their philosophies to conservation of mountain hares for their own sake, rather than as a contrived pretext for predator control to protect mountain hares, about which there is no published auto-ecological evidence.
6. Cease the practice of shooting or snaring mountain hares, putting their carcasses in stink pits as bait to control predators, on the obviously disingenuous pretext of protecting mountain hares.

7. Come together with society to jointly share and place bioeconomic value on mountain hares. For example, the tax payer or conservation charities could incentivise grouse moors to have higher densities. This could be independently monitored.
8. Where grouse moors have an active hare shooting policy, must manage and monitoring this professionally and transparently (e.g. Schai-Braun et al. 2019)

Regarding acid grassland and unmanaged dwarf shrub heath: both are impoverished. Intriguing ideas for improvement include deploying bovine species to stir up the habitat. However for mountain hares, the subsequent habitat must include heather. The present heights and depths of heather on unmanaged dwarf shrub heather represent widescale fire risks hazardous to all wildlife. The risk is greater on steep valleys such as at Horse Stone.

6.4.3 Required societal approach

Stakeholders may define and agree what densities of mountain hares are appropriate and consider what factors cause fluctuations. There then needs to be an independent or transparent means of monitoring that relevant parties can rely upon. Society may consider providing financially incentives to landowners, to encourage higher numbers of mountain hares.

These interventions may be best facilitated by charitable and conservation groups working in partnership with landowners, and with landowners themselves ensuring their own staff are fully engaged. With sensible friendly discussion, all parties may agree the maintenance of prolific densities of mountain hares is a worthy conservation outcome. Each and all parties must accept their obligation to contribute to that end. By setting aside past differences, positive future outcomes can be achieved.

Acknowledgments

Grateful thanks to CM Shaw for conducting extensive pellet surveys during 2018 to confirm the northern boundary of mountain hare range.

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Tables

Table 6.1 Reported mountain hare persecution events

Year	Location	Description	Source	Evidence type
2013	Kinder Scout	Observations of men with guns with stated intention to shoot mountain hares	Land restoration charity, senior manager	Direct witness
2013	Outer Edge	Several shot mountain hares lined up in a row on heather	Land management charity, senior employee	Direct witness
2015	Moscar Moor	Mountain hare carcasses bait at fox snaring site	Conservation group	Photos
2015	Derwent Moor	Mountain hare carcass as bait in crow trap	Conservation group	Photos
2015	Foulstone Moor	Mountain hare carcass as bait in crow trap	Conservation group	Photos
2015	Bradfield Moor	Three mountain hare carcasses in stink pit	Conservation group	Photos
2015	Broomhead Moor	Dead mountain hare foot caught in Fenn trap	Conservation group	Photos
2016	Broomhead Moor	Three dead mountain hares at stink pit	Conservation group	Photos
2017	Broomhead Moor	Free roaming dog hunt, but no sighting of hares taken	National Park employee	Direct witness
2017	North America above Langsett	Free roaming beagle hunt, no sighting of hares taken	Natural History Society member with Member of Parliament	Direct witness
2017	Dukes Road	Dog-mauled mountain hare carcass in back of truck. Accompanying gamekeepers with 2 free roaming lurchers	Bedson, direct observation	Direct witness
2017	Midhope	Observation of line of gamekeepers walking along moors, shooting hares	Three ornithologists	Direct witness
2017	Bleaklow	Dog owner stated his lurcher caught ~100 mountain hares over several years	National sporting charity, chief executive	Third party allegation
2017	Kinder Scout	Gamekeeper stated he had visited Kinder Scout and shot out all hares	Wildlife journalist, national newspaper	Third party allegation
2017	Moscar Moor	Stink pit with mountain hares	Animal rights group; photos on social media	Photos
2017	Longdendale, under Lawrence Edge	Stink pit with mountain hares	Bedson, photographs	Photos
2017	Alport Moor	Farmer stated he visited end of Alport valley and shot out all hares	National sporting charity, senior official	Third party allegation
2017	Yateholme	Stink pit with mountain hares	Wildlife Trust member	Direct witness
2017	Derwent Edges	Dead mountain hares in back of truck	National Park employee	Direct witness
2018	Bleaklow, Shelf Moor	Hare coursing, at least one hare taken	Multiple witnesses on social media	Direct witness
2018	Saddleworth Moor	Mountain hare carcass as bait at trap	Bedson, photographs	Photos
2018	Saddleworth Moor	Farm owner stated to me his practice of shooting hares he saw which appeared sick	Bedson	Direct witness
2018	Broomhead	Mountain hare died in trap	Conservation group	Photos
2018	Outer Edge	Two shot mountain hares	Mountain Rescue volunteer	Direct witness
2018	Snailsden	Gamekeeper stated he had shot out the hares	Wildlife Trust senior official	Third party allegation
2019	Bleaklow	Hare coursing	Multiple witnesses on social media	Direct witness
2019	Bleaklow and Derwent Edges	Historic observations of several grouse moor tenants having shot hares, several events	Land management charity, senior employee	Direct witness
2019	Broomhead	Mountain hare leveret caught in Fenn trap, later died	Conservation group	Photos
2019	Mill Hill	Three dead hares, mauled by dogs, found by grouse butts	Bedson, photos and vet autopsy	Photos
2020	Dunford Bridge	Dead mountain hare in spring trap	Environmentalist group	Photos
2020	Moscar Moor	Several dead mountain hares at stink pits	Wildlife Trust employee	Video
2021	Peak District	Statement of practice of shooting mountain hares "for the pot" i.e. to eat	British Association of Shooting and Conservation	Direct witness

2021	Mossy Lea	Mountain hare legs as bait in traps	Conservation group	Photos
2021	Derwent Edges	Grouse moor estate, declared intention to cull hares which were "overrunning".	Wildlife charity board director	Direct witness
2020	Moscar	Free roaming beagle hunt, no record of hares taken	Conservation group	Photos
2022	Peak District	Statement of general management practice of culling hares	British Association of Shooting and Conservation	Website
2022	Mossy Lea	62 free roaming beagles on Bleaklow	Multiple independent witnesses including Wildlife Trust senior official	Photos

Figures

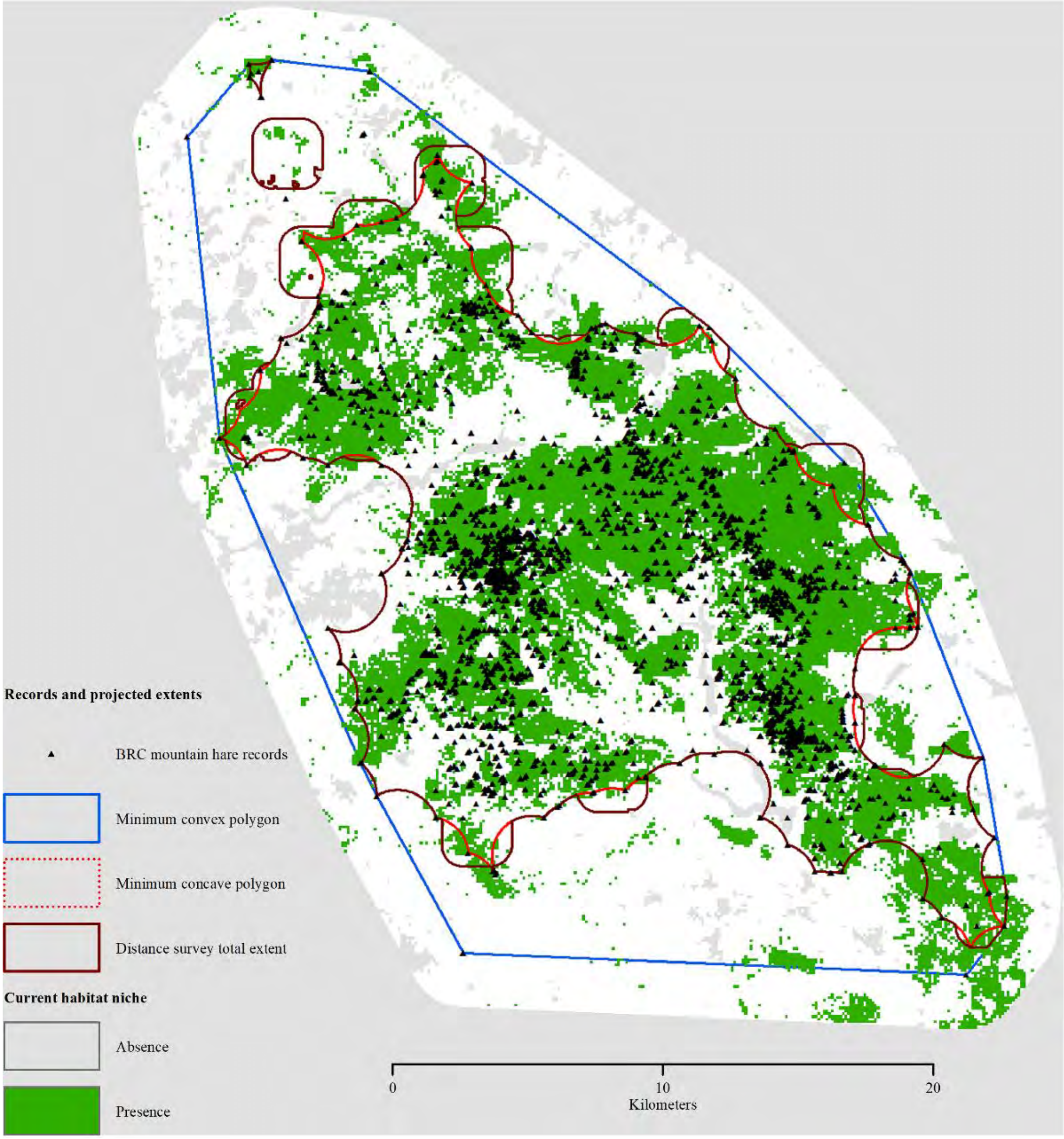


Figure 6.1 Recommendation for future monitoring based on the minimum concave polygon.

The different definitions of mountain hare range extent across the Peak District are shown. BRC mountain hare records are as used in both chapter 2 and 4: 1,690 records deduplicated to the hectare. The minimum convex polygon surrounds these points. The minimum concave polygon (alpha hull) is the conservative alternative, and excludes 6 outlying records. The distance survey total extent shows the 2019 distance sampling survey footprint which matches the minimum concave polygon, but for some very minor discrepancies, arising from some longer visual ranges. The current habitat niche predicted presence area was based on the minimum convex polygon with a 2km buffer added (enabling brown hare modelling for chapter 2). This represents the maximum theoretical area for mountain hares to occur. Grey areas are towns or water features. Future surveys should therefore cover the minimum concave polygon area and in so doing accomplish the vast majority of mountain hare ecological niche and predicted distribution range.

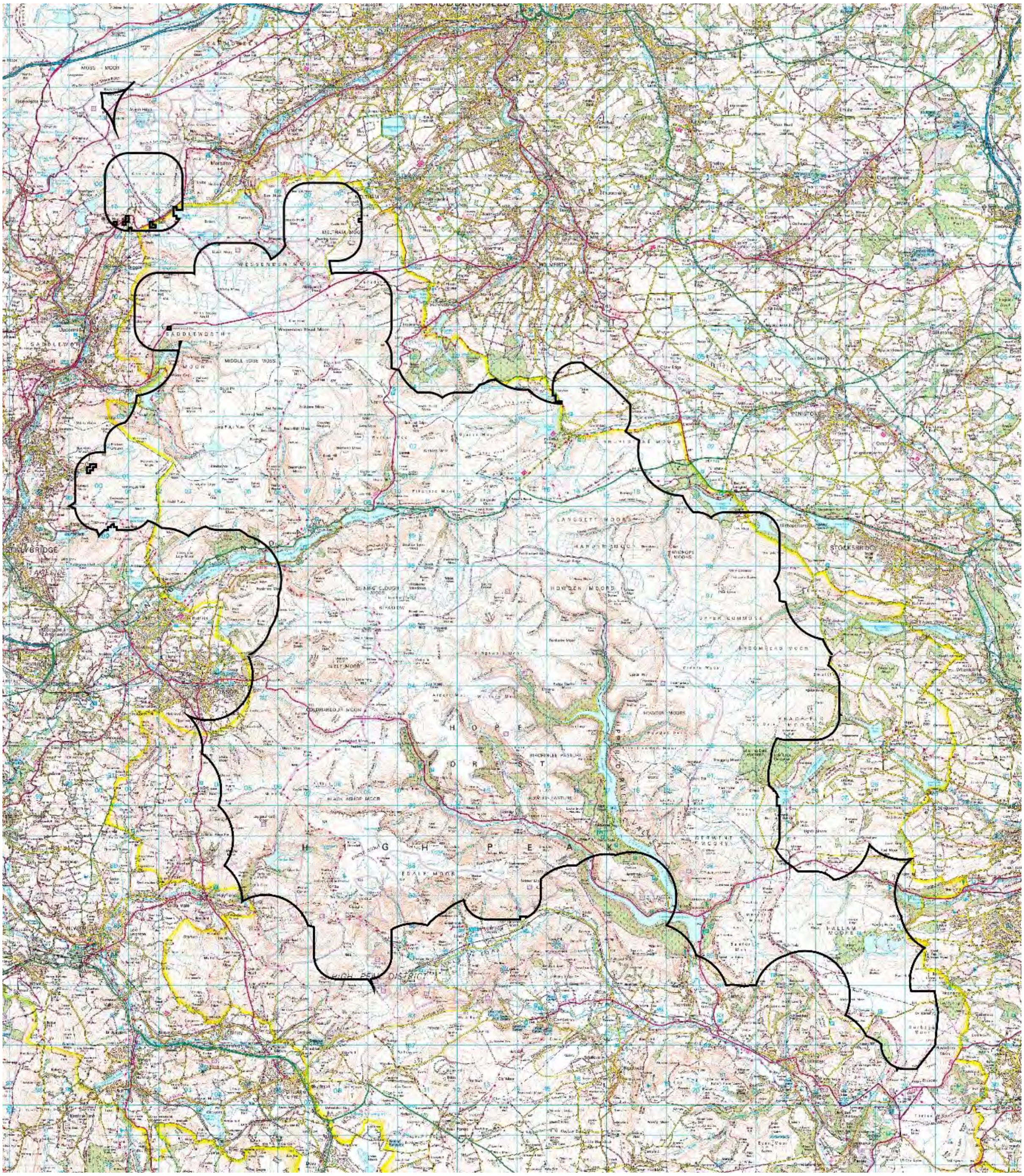


Figure 6.2 OS map with mountain hare minimum concave polygon as recommended for future monitoring.

This black outline shape is placed upon the map which is Ordnance Survey Landranger 109 and 110 at 1:50,000 scale sourced from Edina Digimap. The Peak District National Park boundary is displayed on the map by the yellow line.

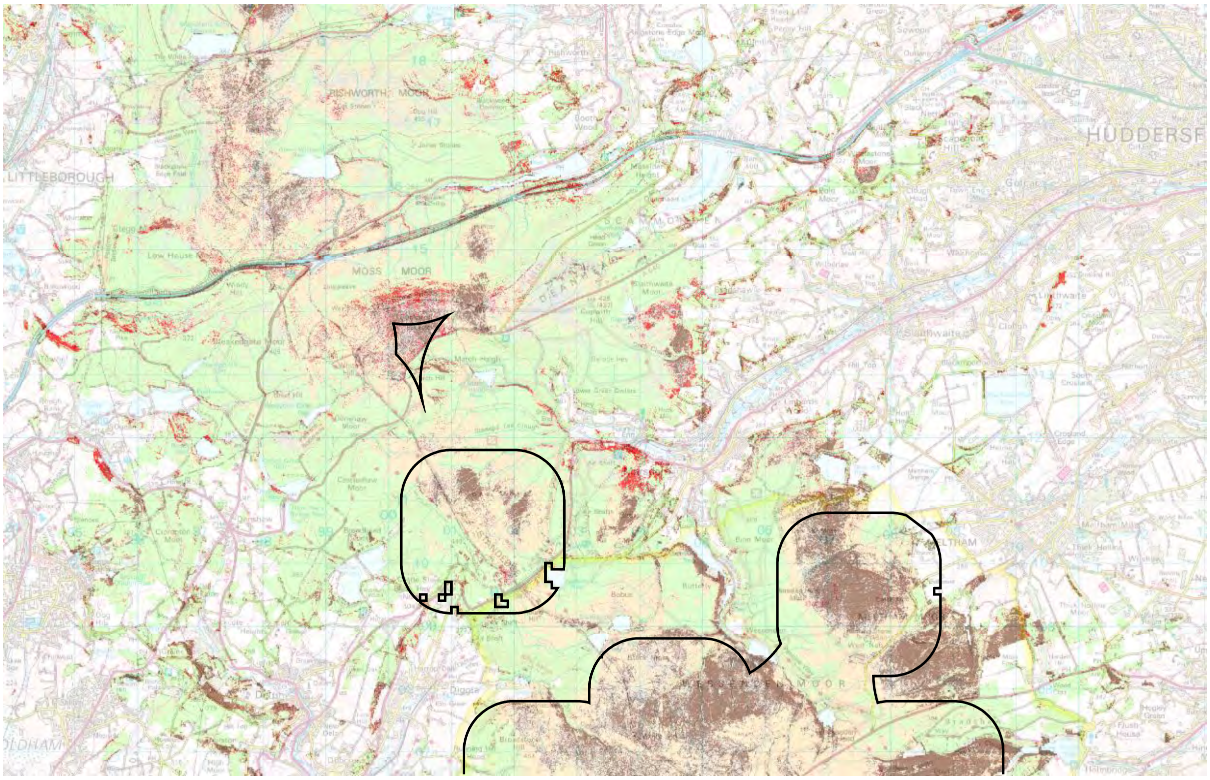


Figure 6.3 Map showing example of limits to mountain hare distribution, at the northern edge.

The Ordnance Survey map serves as background and is Landranger 109 and 110 at 1:50,000 scale sourced from Edina Digimap. The map origin occurs on tile SD with grid square 94 06 near to Oldham. Overlain is the supervised classification system at 5m pixels. Brown pixels represent mature heather; grey pixels are young heather. The distribution extent of mountain hares is represented by the curved arc lines. There is a substantial distribution of mountain hares at Wessenden Moor which becomes sparse at Moss Moor. There is little contiguous heather between the two. North of Moss Moor lies the M62 which probably prevents migration. There is little or no heather upon Rishworth Moor and further north. Hence mountain hares cannot migrate further. This pattern of occurrence continues across the entire distribution extent. Both human infrastructure and the limits of heather extent provide boundaries to mountain hare extent.

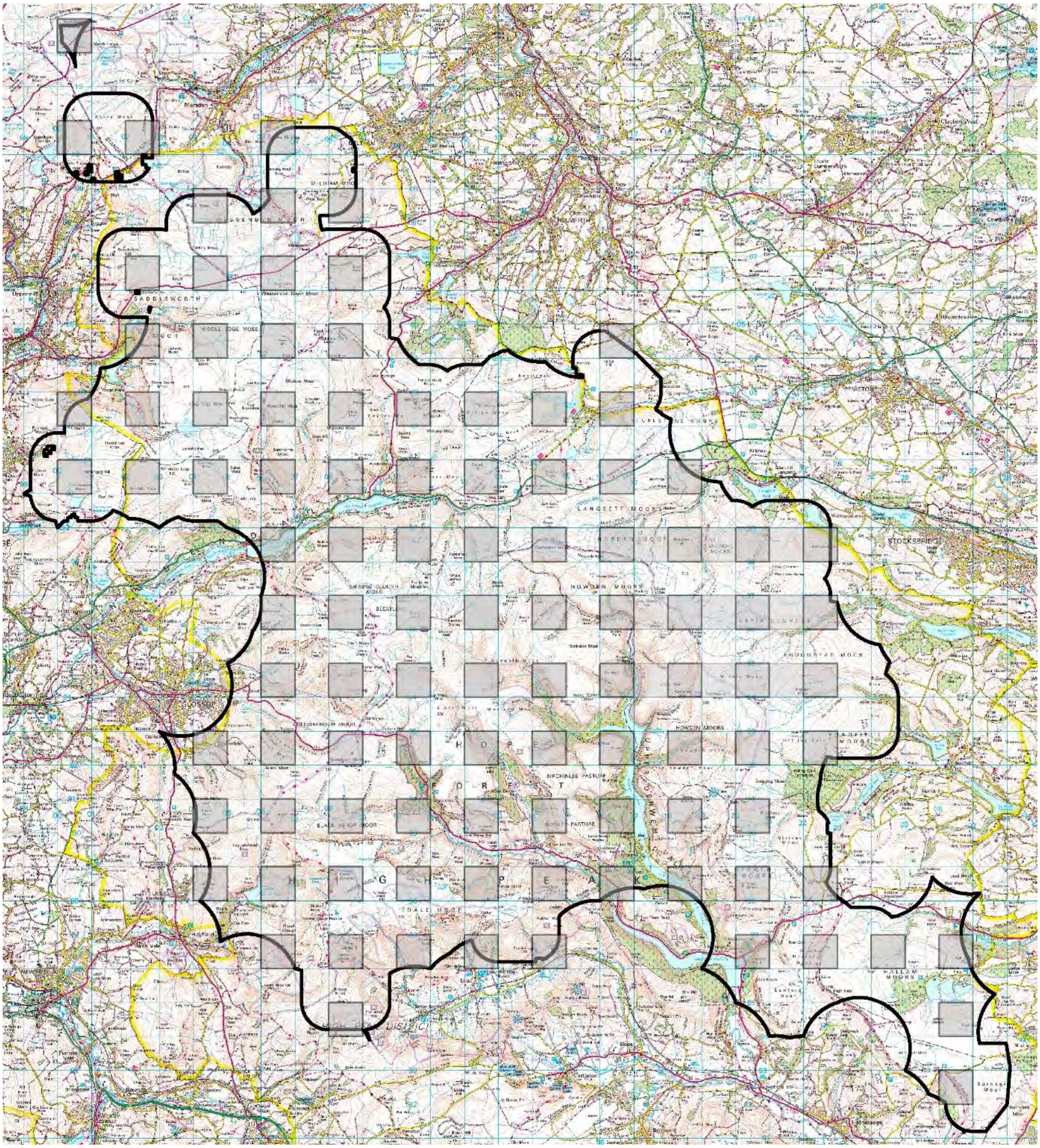


Figure 6.6.4 Design for complete survey of Peak District mountain hare distribution extent.

Black curved shape is union of minimum concave polygon and 2019 distance sampling survey footprint i.e. representing all known occurrences of mountain hares. Grey squares are target 1-km squares for surveying. Assuming a visual range of up to 780m the entirety of the distribution extent is covered.

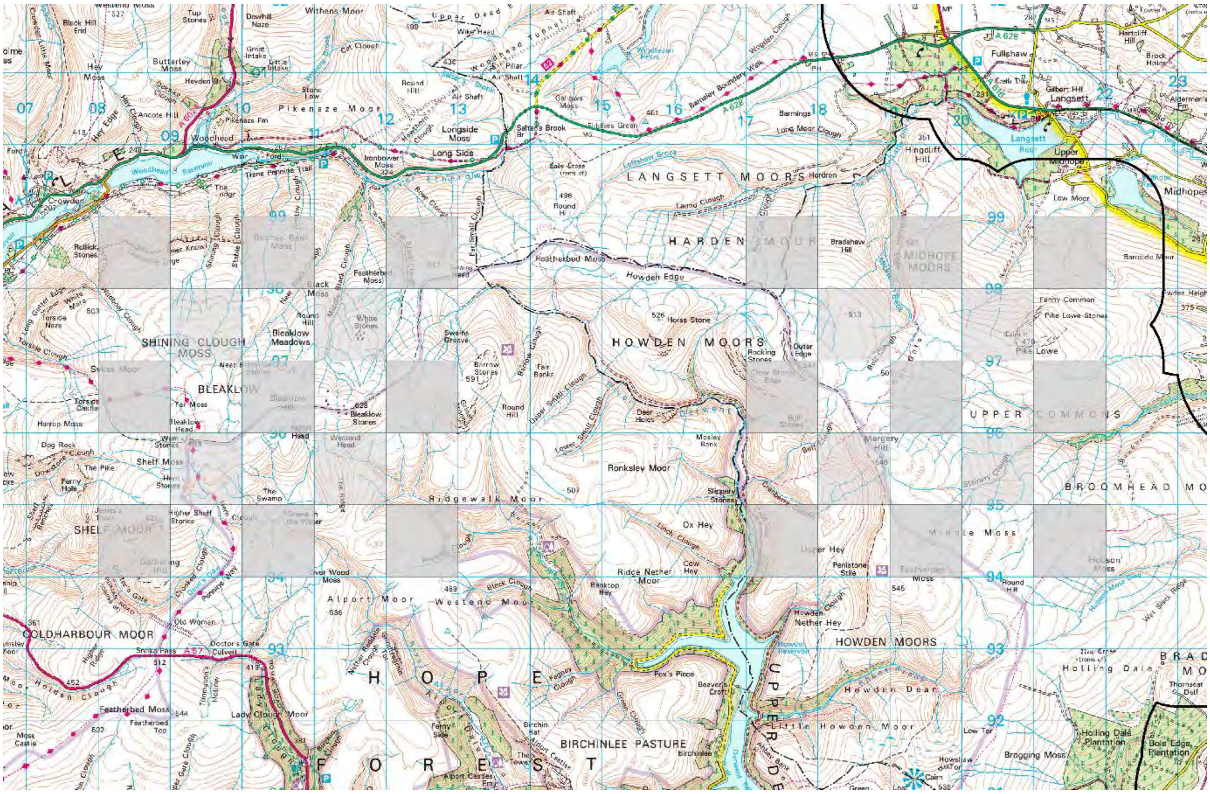


Figure 6.5 Survey footprint for Bleaklow and Margery Hill only.

Grey squares are target 1-km squares for surveying.

a)

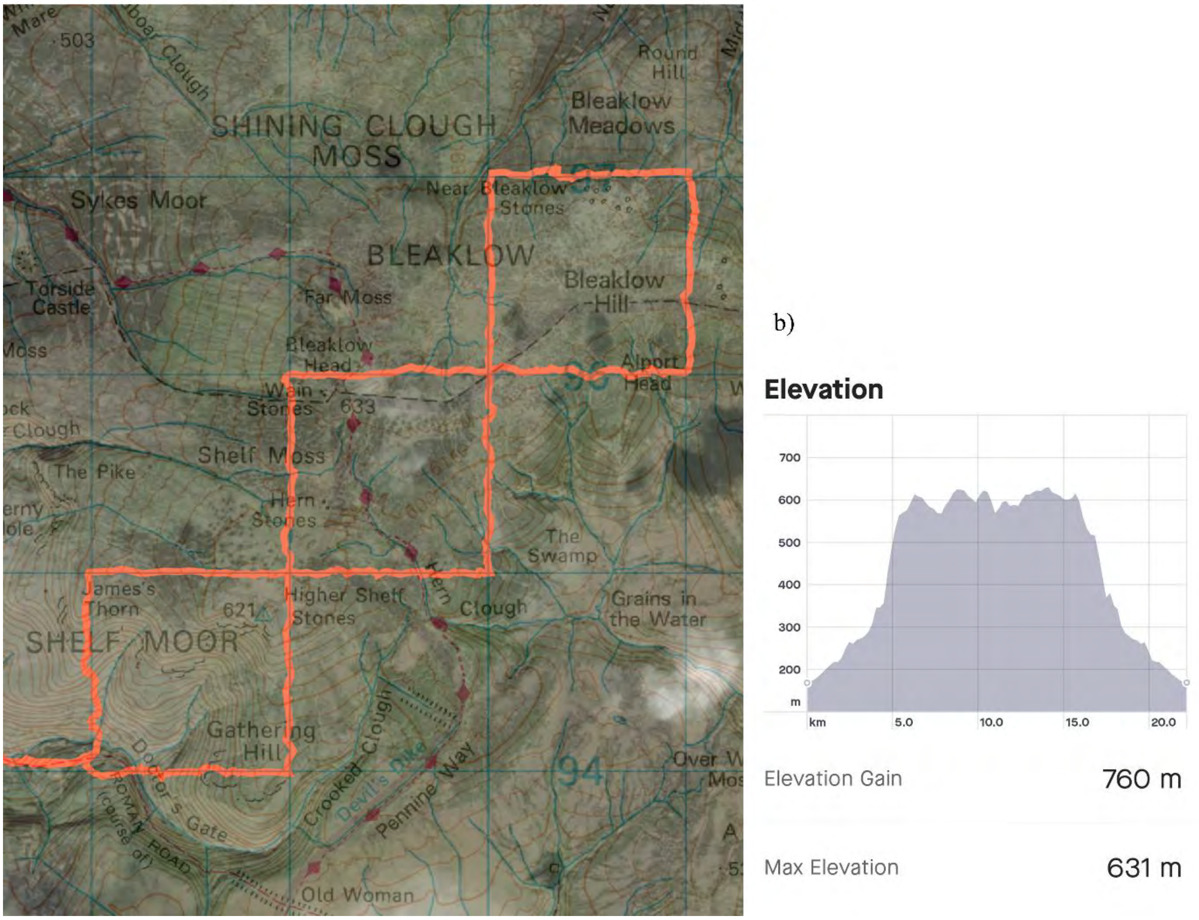


Figure 6.6 GPS trace from three survey 1-km squares surveyed on Bleaklow 30 March 2021.

a) The orange line shows the observer route which followed the Ordnance Survey gridlines (OS Landranger map 110). The map overlays a satellite photographic image with GPS trace (Source: Strava, San Francisco, USA).

b) Plot of elevation for the course of the route. Starting at bottom left, the route headed north up to James's Thorn with elevation gain >400 metres over 1 kilometre.

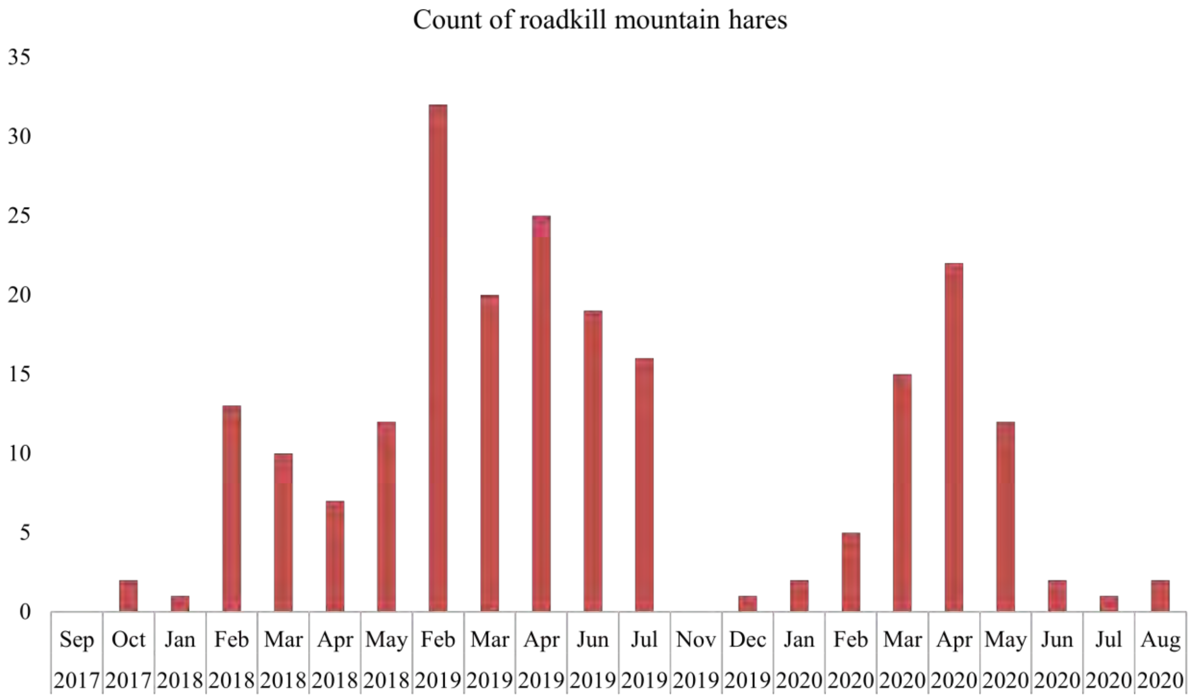


Figure 6.7 Number of mountain hares killed on roads each month.

Surveys were infrequent, opportune and under-recorded total amount of deaths. The lower numbers of 2020, compared with 2019, may be a function of an overall lower population size in 2020.

Figure 6.8 Photos of mountain hare and brown hare roadkill

a) 2017

b)

2018

c)

2019

d) 2020

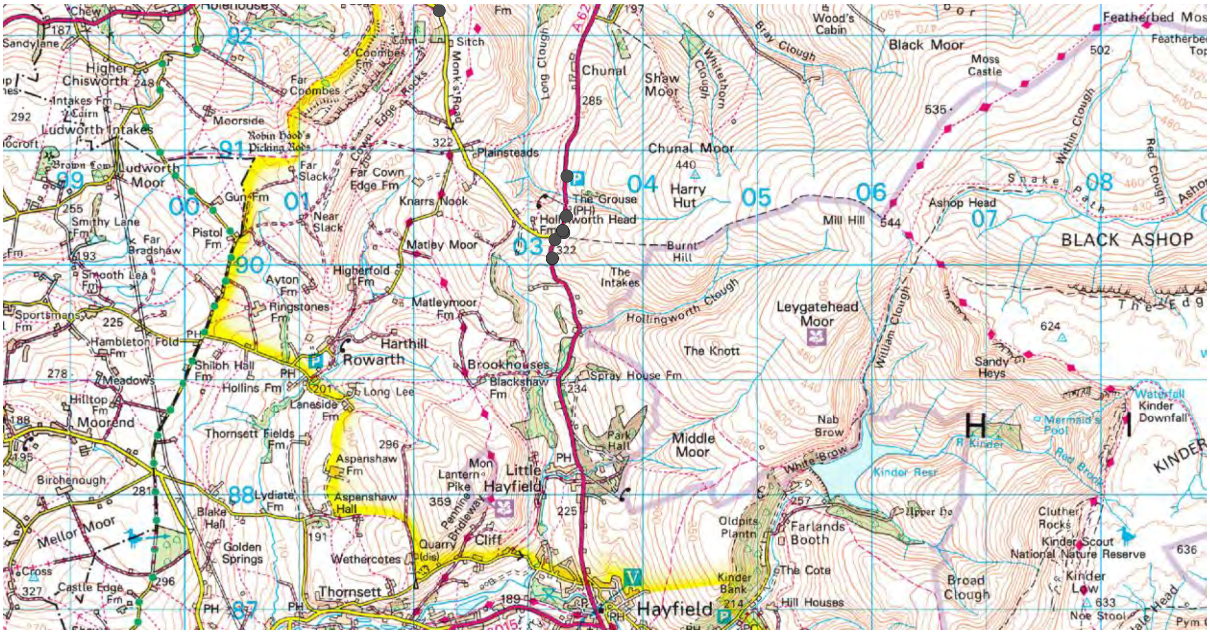
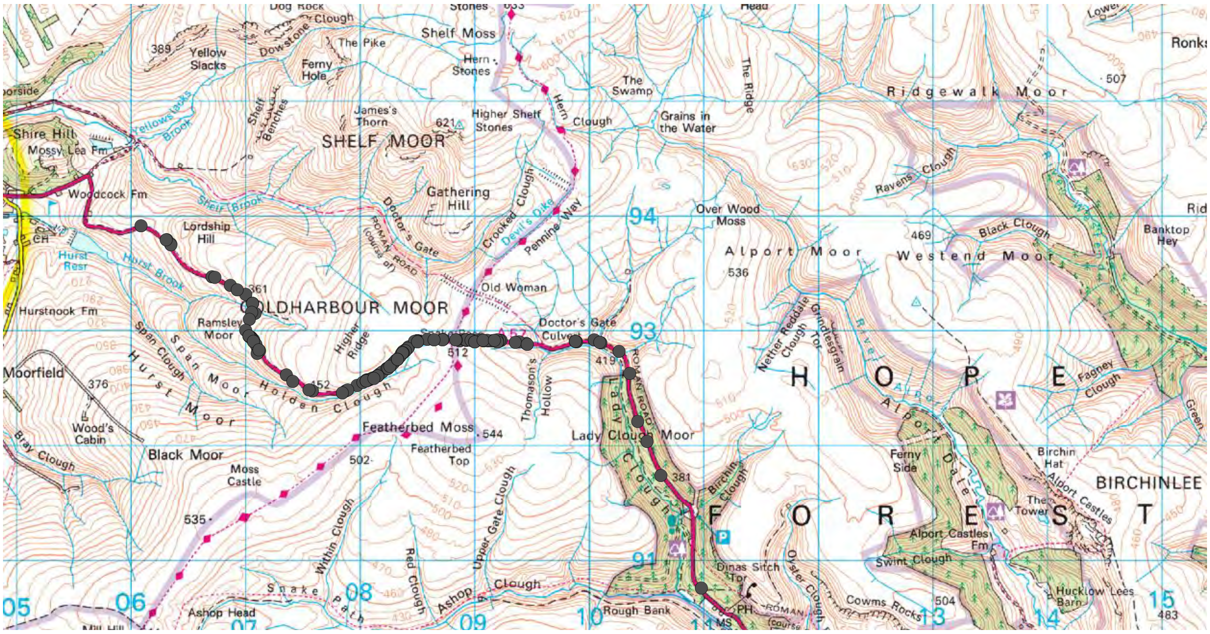


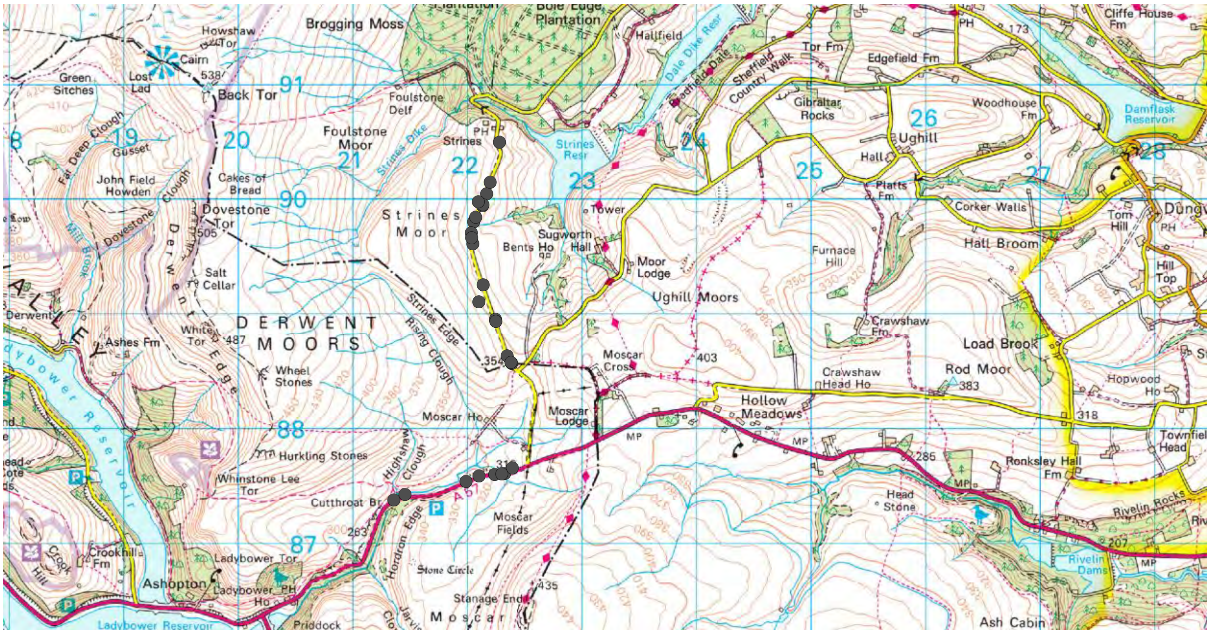
Figure 6.9 Maps of roadkill sites

a) Roadkill site A6024 Glossop Road at Chunal (minimum 6 dead hares 2017 to 2020)

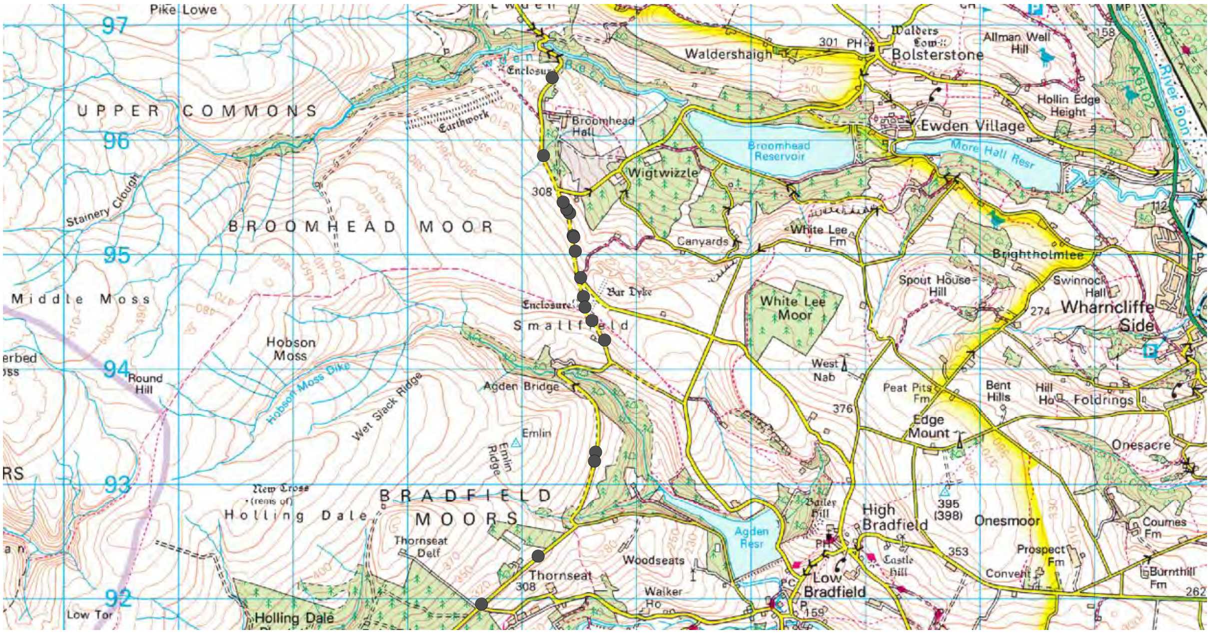
Grey dots are mountain hare and brown hare roadkill - as appear on all maps in Figure 6.9.



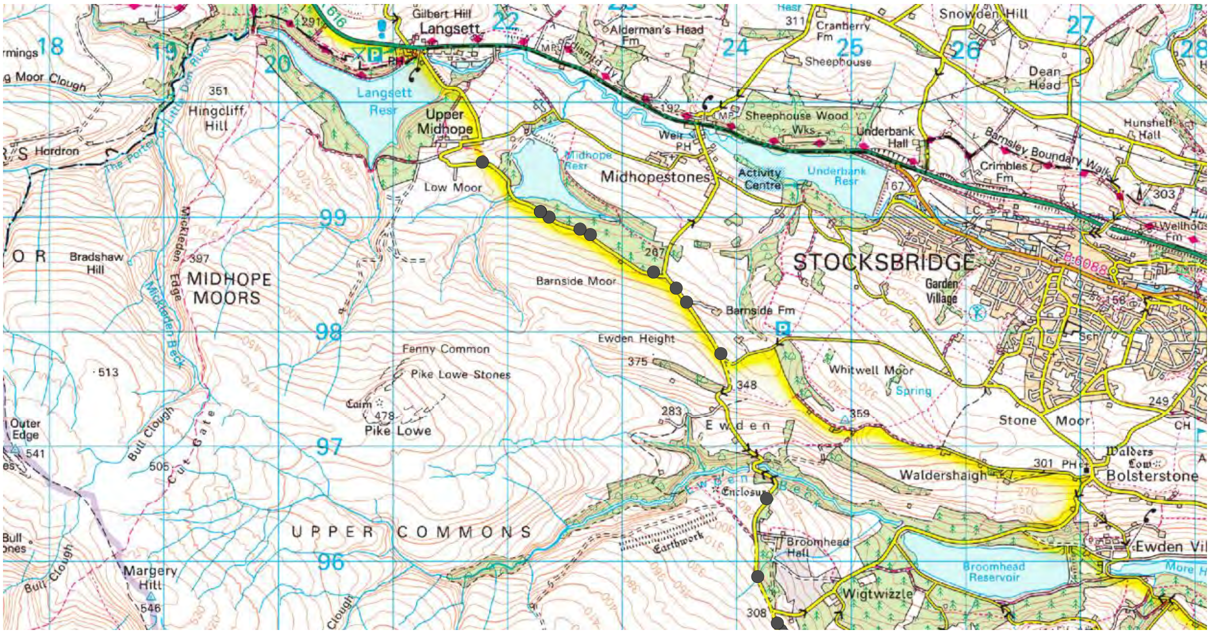
b) Roadkill site A57 Snake Pass (minimum 106 dead hares 2017 to 2020)



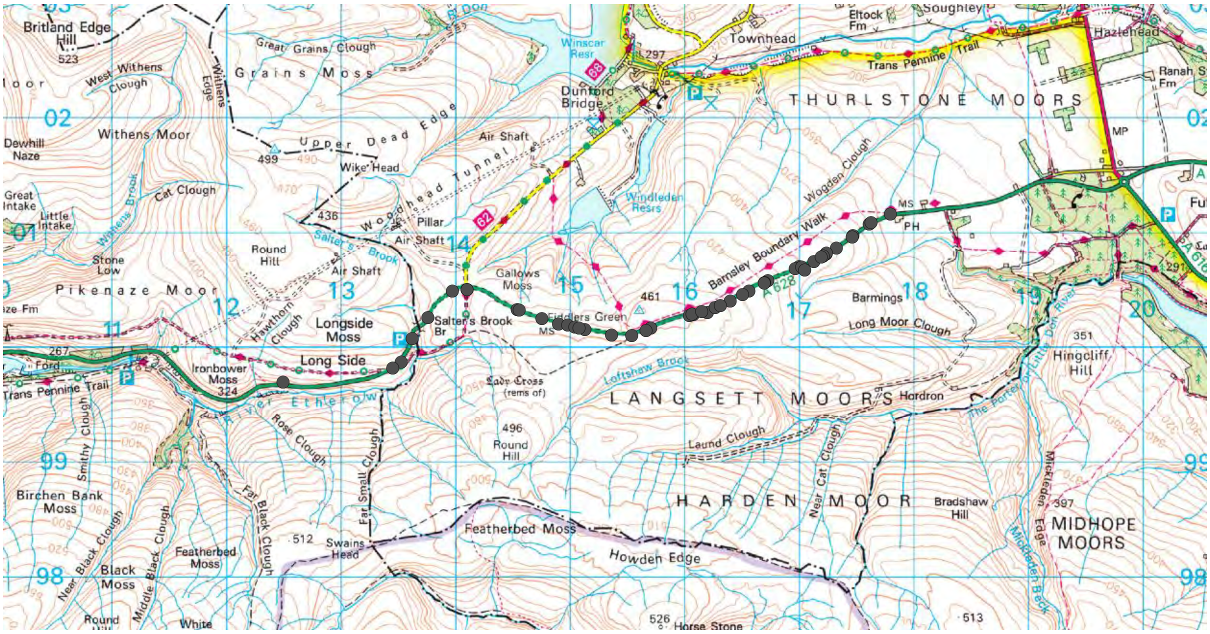
c) Roadkill site A57 Moscar (minimum 8 hares) and Strines Road (minimum 18 dead hares 2017 to 2020)



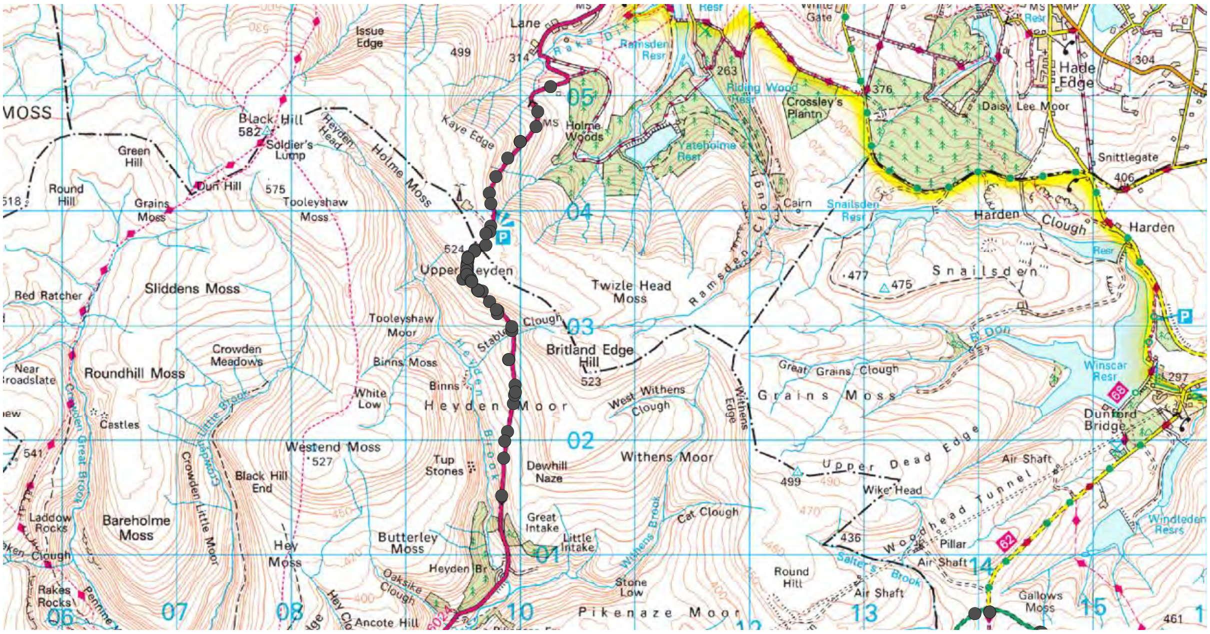
d) Roadkill site Strines Road (minimum 14 dead hares 2017 to 2020)



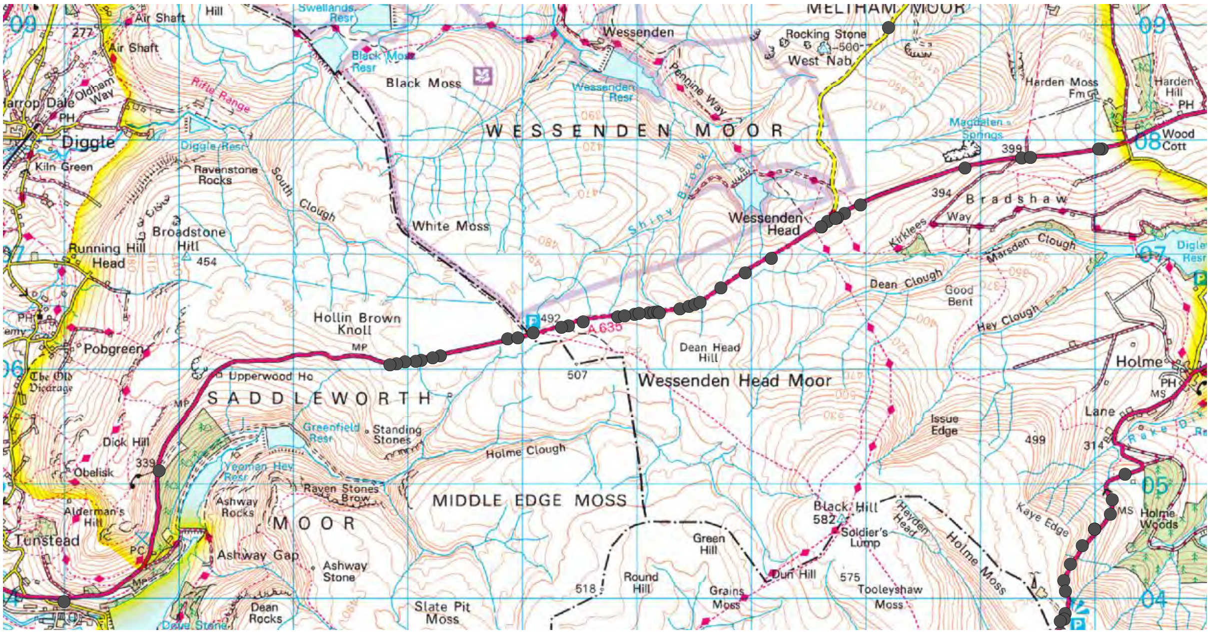
e) Roadkill site Gilroyd Road (minimum 9 dead hares 2017 to 2020)



f) Roadkill site A628 Woodhead Pass (minimum 44 hares 2017 to 2020)



g) Roadkill site A6024 Holme Moss Road (minimum 43 dead hares 2017 to 2020).



h) Roadkill site A635 Saddleworth Road (minimum 39 dead hares 2017 to 2020).

Figure 6.10 Photographs of mountain hares visiting the A6024 Holme Moss road at night

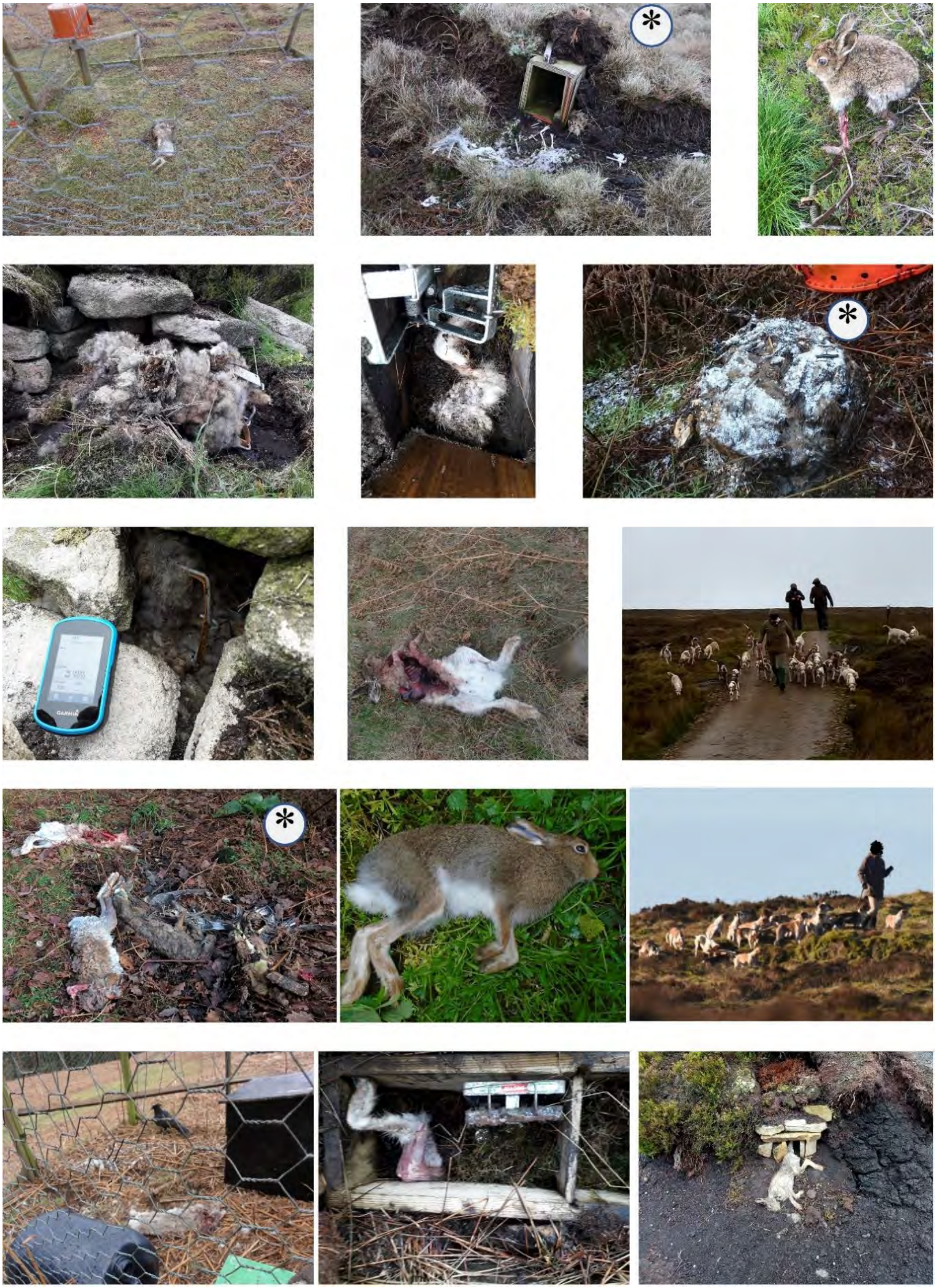


Figure 6.11 Photographs of mountain hare persecution events

Mountain hare carcasses or free roaming dogs on open moorland. The three photos marked with asterisk in circle were taken by Carlos Bedson. All other photographs provided by local conservation group.

End Page

Thank you for reading.

Carlos Bedson 9 August 2021

Amended 24 April 2022

Publications

Chapter 2, 3 and 4 appear below, as their final versions in published papers

Acta Oecologica 111 (2021) 103742

Contents lists available at ScienceDirect

Acta Oecologica

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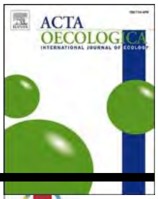

Splitting hares: Current and future ecological niches predicted as distinctly different for two congeneric lagomorphs

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ARTICLE INFO

Keywords:
Climate change
Diet
Ecological niche model
Interspecies competition*Lepus*
europaeus
Lepus timidus

ABSTRACT

The congeneric lagomorphs *Lepus timidus* and *L. europaeus* share allopatric distributions in many areas of Europe characterised by competitive exclusion and hybridisation. We investigated prospects for these species under climate change in northern England uplands. We created ensemble models predicting niche realisation for these species, influenced by abiotic and biotic factors, estimating niche overlap in geo-environmental space. The two species occupy distinctly different niches, influenced more by vegetation preferences than climatic differences.

The current climate niche for *L. timidus* featured higher elevations with cooler temperatures and 168 km^2 range extent. Its current habitat niche scale was larger at 269 km^2, comprised entirely of upland dwarf shrubs: heather, cotton grass, moorland grasses. By contrast, the current climate niche predicted *L. europaeus* occupying lowland areas with a milder climate and range extent of 252 km^2. Its current habitat niche was also greater, 401 km^2, being mostly improved grassland. Competition was presently limited. The current niche predictions showed very little geographic overlap between the species. Niche overlap measured by Schoener Index was low: current climate niche 0.16; current habitat niche 0.07. The future climate niches for 2050 (IPCC RCP2.6), predicted *L. timidus* range contracting to 19 km^2, on hilltops and *L. europaeus* range expanding to 765 km^2. Consequently *L. timidus* range would be wholly within the *L. europaeus* range. In many contact zones throughout Europe, *L. europaeus* outcompetes *L. timidus;* however, in the Peak District their distributions are largely distinct. Future replacement of *L. timidus* by *L. europaeus* may be engendered by dietary convergence, should a warmer climate cause a transition of upland dwarf shrub vegetation to grasses.

1. Introduction

1.1. Lagomorph niches and conservation status

Ecological niche models often predict opposing patterns of distribution and survival for two European lagomorph species: the mountain hare (*Lepus timidus)* and the European brown hare (*Lepus europaeus)* (Acevedo et al., 2012; Bisi et al., 2015; Leach et al. 2015a, 2015b, 2016, 2017). Despite differences in physiological adaptations and requirements, they often share distributions and compete for resources (Thulin 2003; Jansson et al., 2007). As herbivores both species are important to ecosystems for recycling vegetation nutrients, and are prey for carnivores and raptors (Harris and Yalden 2008; Barbar and Lambertucci (2018).

With a circumpolar distribution, *L. timidus* is adapted for cold temperatures and snow in hilly or mountainous areas, and is a habitat generalist, living upon boreal forest, mires, heaths and moorlands (Angerbjörn and Flux, 1995; Harris and Yalden 2008). The IUCN Red List status is Least Concern and population status is stable for *L. timidus* (Smith and Johnston 2019). Some populations are vulnerable, being quasi-cyclic (Newey et al., 2007) or limited by parasites, predation or starvation (Smith and Johnston, 2019). Climate change scenarios suggest *L. timidus* can be affected by changes in long-term weather patterns (Reid et al., 2021) and will move to higher latitudes and elevations (Anderson et al., 2009; Hof et al., 2012; Leach et al., 2015b), its range in Europe reducing by 70% (Acevedo et al., 2012).

By contrast *L. europaeus*, occupies temperate climate zones across Europe, is a habitat specialist, inhabiting grassland and agricultural

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https://doi.org/10.1016/j.actao.2021.103742
Received 16 February 2021; Received in revised form 30 April 2021; Accepted 9 May 2021

environments, favouring cereal, root crops or grasses (Tapper and Yalden 2010). For *L. europaeus* the IUCN Red List status is Least Concern and population status is recorded as decreasing due to agricultural intensification (Hackländer and Schai-Braun 2019). Recently some populations have revived, enabled by agricultural improvements (Viviano et al., 2021). Forecasts for *L. europaeus* under climate change suggests little response (Bisi et al., 2015) or range expansion (Hof et al., 2012; Leachet al., 2015b; Caravaggi et al., 2017).

Together, these two species form a recognised model of interspecific competition: a mechanism which acts as a determinant of species distributions (Elton 1927). Competition frequently involves one species exploiting food or shelter resources, much more effectively than another. To survive, the less effective species must either move to a different habitat or adjust its diet away from the competitor (Krebs 2001). Historic studies have reported large areas of *L. timidus* range being superseded by *L. europaeus* as a result of competition for space andresources or interspecific hybridisation with introgression, e.g. populations in Sweden and Russia (Thulin 2003), and Ireland (Caravaggiet al. 2014, 2017). Where different habitats overlap, *L. timidus* maintains high elevations and deep forests, feeding on woody browse and excludes *L. europaeus.* Alternatively *L. europaeus* maintains its dominance over optimum grassland habitats, preferring a diet of soft greens, and may displace *L. timidus* (Flux and Angermann 1990; Thulin 2003; Jansson and Pehrson 2007). However the two species may exist in sympatry,such as in Italy where they share a spatially overlapping elevation gradient, though occupying different habitats: *L. europaeus* from 500m to 1500m a.s.l. upon arable land or sparsely vegetated areas; *L. timidus* from 1300m to 3000m in areas of dwarf mountain pine (Bisi et al. 2013, 2015; La Morgia and Venturino 2017; Naldi et al., 2020).

The species *L. timidus* is native to Great Britain though died out in England around 6000 BP (Harris and Yalden, 2008) though persisted in Scotland where it is now associated with upland heather moorlands (Hewson 1984, 1989). Because of heavy culling on some moors (Watson and Wilson 2018) and a large decline in abundance, the conservation status of the UK *L. timidus* population was downgraded to ‘unfavourable-inadequate’ (JNCC, 2019a).

In England *L. timidus* was reintroduced through translocations from Scotland by sporting landowners in the 1870s and now occupies some 250 km^2 of Peak District uplands. Population density has been estimated at 10 hares km^{-2} (Mathews et al., 2018). It is isolated by 300 km from its founder population. Surveys described *L. timidus* preferring habitats of heather, cotton grass (*Eriophorum* spp.), moorland grasses (*Deschampsia flexuosa, Nardus stricta, Festuca* spp., *Juncus* spp.) and dwarf shrubs (*Empetrum nigrum, Vaccinium myrtillis*) (Mallon et al., 2003).

By contrast *L. europaeus* is thought to have been introduced to Great Britain during the Bronze Age (Thulin 2003) and certainly by Roman times (Harris and Yalden 2008) and now occupies arable landscapes.Once widespread, numbers have decreased by 80% since 1880 as a result of game-shooting and intensive farming practices, the last con-servation assessment recording the species as in decline (UK BAP, 2007). There have been no recent assessments (JNCC, 2019b). Around the Peak District extensive surveys of *L. europaeus* during 2011–12 (Bolton 2013) recorded density amongst agricultural landscapes at 1.7 hares km^{-2}, though not in upland habitats. An extensive metapopulation facilitated inward and outward migration.

Within the UK competition between these two species has received little attention. Hewson (1976a) reported in Scotland that *L. timidus* maintained dominance upon heather moorland when *L. europaeus* was present. Within the Peak District, Yalden (1971) recorded a range overlap between *L. timidus* and *L. europaeus* between elevations of 280–500m; a rough boundary between arable and moorland ecosystems. The Peak District presents an ideal model environment, to provide an important understanding of competitive dynamics between these two species (Thulin 2003; Smith and Johnston, 2019).

1.2. Study objectives

Niche model theories describe the conditions within which species maintain populations at different locations (Franklin 2009; Peterson et al., 2011). Models suggest species exist in environments having combinations of abiotic factors, topography and climate, that enable physiological survival i.e. the fundamental niche (Guisan and Zimmermann, 2000); also described as the potential niche (Sillero 2011); or the climate/geomorphological niche (Peterson et al., 2011) and it is often considered that species express such preferences over large scales (countries or continents). Species occurrence may then be facilitated, constrained or “filtered” by biotic factors: food and shelter resources, competitors, predators, parasites, human influences, this being the realised niche (Guisan and Zimmermann, 2000; Sillero 2011); the occupied or biotically reduced niche in the terms of Peterson et al. (2011) and which may be conventionally regarded as habitats (Krebs 2001: 66). However filtering processes may not always act in such a formulaic sequential hierarchy (Guisan et al., 2017: 23) and ecologicalor stochastic processes may alter species distribution in unexpected ways. Statistical models reference occurrence records, combined withenvironmental variables, to explain how species occupy these niches (Guisan et al., 2017) and the extent to which similar species co-existtogether (Broennimann et al., 2012). Such evaluations assess the sus-tainability of populations and prompt monitoring, legal protections, revision of land uses, identification of species invasions, reintroductions or translocations, or warnings of future threats (Franklin 2009).

The aims of this study were to:

1) Predict and compare the current climate niche and current habitat niche of both *L. timidus* and *L. europaeus* in northern England. We hypothesised that *L. timidus* would be associated with high elevations, a cold climate, upland heather moorland and bog vegetation and *L. europaeus* low elevations, warmer climate and grassland or woodland (Tapper and Yalden 2010);
2) Measure the extent of overlap between the two species in geographic and environmental space, to estimate the degree of competition. We did expect some competition, though were unsure how strong this might be;
3) Forecast the future climate niche for the year 2050. We anticipated that with warming climate, *L. timidus* would move to higher elevations, reducing its range. For *L. europaeus* we had no specific expectation.

2. Materials and methods

2.1. Study area

The study area encompassed the Peak District National Park, Northern England (Fig. 1). The landscape is dominated by peat uplands with vegetation of upland heath, dwarf shrubs including berries, bog grasses and mosses and grasslands. (Anderson and Shimwell 1981). Topography consists of plateau-like hills, ranging up to 631m (OS Explorer (2015). The uplands are surrounded by improved grassland areas, agriculture and cities.

2.2. Species records

Observations of species came from citizen-science sources, provided by walkers, wildlife enthusiasts, natural historians, landowners and environmental experts, sent by paper, post, email or mobile phone apps to one of eleven relevant regional or national biological recording centres (BRC’s). The BRC’s then provided to us records from 2001 to 2018 for *L. timidus* (8666 records) and *L. europaeus* (5994 records) (see Hare Data Sources). These records gave species locations from which to derive environmental data, define the study extent and provide sufficient sample and prevalence sizes for modelling (Guisan et al., 2017).

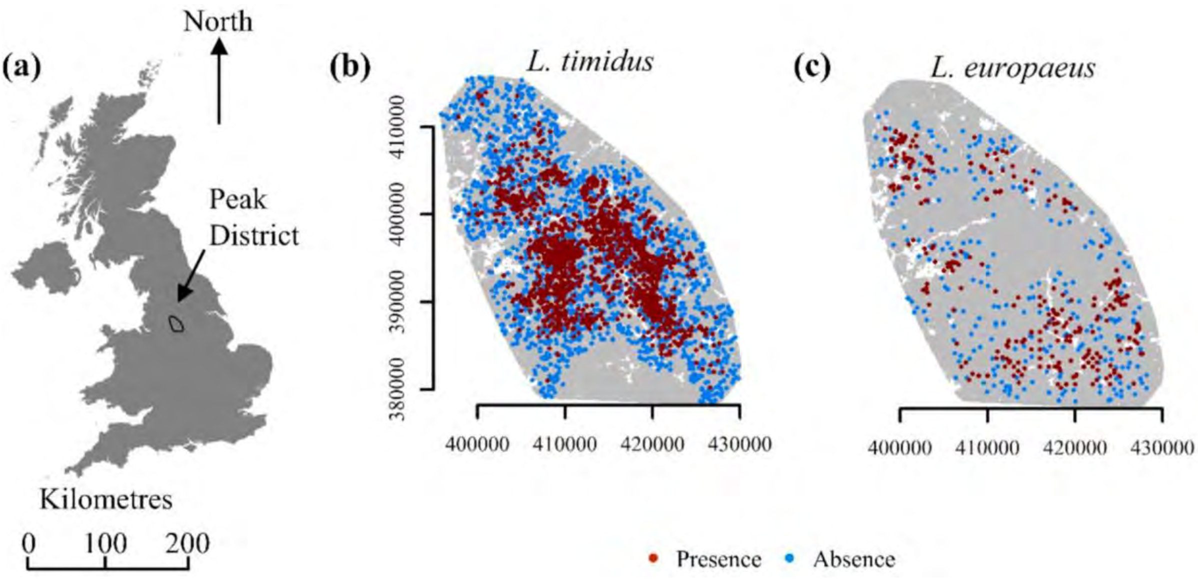


Fig. 1. Maps showing hare observation locations. **(a)** Great Britain, with Peak District; **(b)** Presence/pseudo absence data for *L. timidus;* **(c)** Presence/pseudo absencedata for *L. europaeus*. Grey shape is study extent within Peak District National Park, UK, Latitude 53.3342° N, Longitude 1.7837° W. Map axes (b) and (c) represent Ordnance Survey Eastings and Northings taken from British National Grid 100 km tiles SK and SE with ticks at 10 km intervals.

To prepare the data set we considered sources of bias including autocorrelation, pseudo-replication, duplication or observer effects (Guisan et al., 2017). Within the records we assumed correct identifi- cation of species, except discarding 5 *L. timidus* records found >10 km from the study extent as mis-identifications. We kept observations recorded to the nearest 100m, excluding records accurate only to 1000m. We used kernel density plots to assess occurrence patterns for 2001 to 2018. For *L. timidus* in particular, these showed strong annual fluctuations, with a marked nadir during 2013 (Figure S1), less so for *L. europaeus* (Figure S2). We regarded likely causes as differences of observer effort, though ecological factors were possible. Indeed fifty percent of *L. timidus* records were contributed by the late Professor Derek Yalden, until he passed away in 2013 (Table S1). To mitigate for observer effort, maintain relevance to contemporary environmental data, and alleviate possible effects of hare population dynamics (Neweyet al., 2007), we then used records for the last ten years. To reduce duplication or autocorrelation, we discarded records occurring within 100m of each other using function [ecospat.occ.desaggregation] in R package ‘ecospat’ (Di Cola et al., 2017). Thus the final data set consisted of 1690 *L. timidus* and 265 *L. europaeus* records (Fig. 1). Of these 4% *L. timidus* and 30% *L. europaeus* records were on or within 100m of roads. We acknowledged that using observations from roads might provide bias: roads being a potential deterrent or attractant to lagomorphs.

We defined potential pseudo-absences as any locations without a record for the respective species at the scale of 1 ha. We opted for ratios of 50/50 presence/absence, generating 1690 (*L. timidus*) and 265(*L. europaeus*) pseudo-absence records. This ensured prevalence was above minimum sample sizes and ratios affecting modelling errors (Jimenez-Valverde et al., 2009; Guisan et al., 2017) and ratios would not influence the accuracy measure kappa, with TSS and AUC unaffected (Allouche et al., 2006). We restricted placement of pseudo-absence lo- cations as randomly within a shape determined by designating, over- lapping and dissolving 2000m circles around each species presence point, using R package ‘dismo’ using functions [circles] and [random-Points] (Van Der Wal et al., 2009; Hijmans et al., 2017). Thus analysis utilised a randomly generated 1-ha scale grid with presence and absence points and environmental data per 1-ha.

We calculated a minimum convex polygon (MCP) of 639 km^2 based upon *L. timidus* BRC records and only employed *L. europaeus* records which occurred within this MCP. To account for environmental influences at MCP edges, we added a 2 km buffer, excluding water and urban features, to create a study extent of 805 km^2. This extent therefore encompassed the northern Peak District uplands which was the known range of *L. timidus*. By contrast *L. europaeus* could disperse in and out of the study area from surrounding populations. We assumed both harespecies were at equilibrium with environmental conditions. Haresexhibit short natal dispersal ranges and fidelity to small home ranges (Harris and Yalden, 2008; Tapper and Yalden 2010). We assumed hare records were representative of home ranges and habitat utilisation.

2.3. *Environmental parameters*

We assessed environmental factors hypothesised to influence occurrence of *L. timidus* and *L. europaeus*. Predictor variables were pre- pared within ArcMap 10.6.1 (ESRI, USA) and R (R Core Team, 2011)referencing Bivand et al., (2013); Wegmann et al., (2016); Guisan et al., (2017).

Current climate niche predictors were based upon climate and topography. Climate predictors were the WorldClim set of metrics (Fick and Hijmans 2017): temperature, rainfall and solar radiation. These were downloaded at 1 km scale, resampled using bilinear interpolation with the ArcGIS (ESRI, USA) resampling tool, providing smoothed 1-ha size values. Topography predictors were derived from OS 50m digital terrain model (Digimap 2019), used to calculate elevation, slope and aspect values. In addition the uplands contained micro-topographical features: extensive networks of peat gullies, anthropogenically caused by acid rain erosion (Bonn et al., 2009). These were used by *L. timidus* for shelter and movement. Gullies information was sourced as OS Vectordata (Digimap 2019) with a 50m buffer applied.

Current habitat niche predictors consisted of vegetation providingfood and shelter resources, roads indicating human activity, and the presence of the competitor species. Vegetation productivity indices were derived from Landsat 8 scenes (Path203/Row023, 4th May 2016), downloaded using the EarthExplorer tool of the United States Geological Survey (USGS; www.earthexplorer.usgs.gov), and resampled to 1-ha. Bands were subject to signal enhancement, to represent Normalised Difference Vegetation Index (NDVI), Normalised Difference Water Index (NDWI), Simple Ratio (SR) and Soil Adjusted Vegetation Index (SAVI).

Bands were analysed in R with at-sensor reflectance and tasselled cap transformation, representing vegetation brightness, greenness and wetness (Wegmann et al., 2016; Guisan et al., 2017). To assess the importance of habitat and vegetation types, we also created a detailed bespoke landcover map, combining the UK landcover map (Rowland et al., 2017), with data from aerial images (Digimap 2019). From the UK landcover map (Rowland et al., 2017) we included polygons for pertinent lowland categories: arable, broadleaved or coniferous woodland,improved grassland (managed or unmanaged pasture comprising *Lolium* spp and clover (*Trifolium repens),* used for sheep farming), inland rock, neutral grassland, suburban, urban, or water. However those UK landcover map (Rowland et al., 2017) types which represented upland areas (64% of the study extent) appeared homogeneous e.g. bog. Such areas consist of ecotones of young and mature heather (*Calluna vulgaris*), cotton grass (*Eriophorum* spp.), moorland grasses (*Nardus stricta, Deschampsia flexuosa, Festuca* spp.*, Molinia caerulea* etc*)*, and berries (*Empetrum nigrum, Vaccinium* spp.), pertaining to *L. timidus* food and shelter (Hewson 1962, 1989). Therefore we assembled new map data to represent these vegetation categories by supervised classification of aerial images (Wegmann et al., 2016) taking 10,527 samples, supported by 440 ground-referenced photographs, using random forest classification to create an upland vegetation raster, with 82% accuracy (Table S2; Figure S3). Each hectare was classified to its largest single dominant vegetation type, though other types might have been present. The upland vegetation raster and lowland polygons were then combined to one single map. Individual landcover classes were used as binary categorical predictors. Road information was sourced as OS Open Roads data (Digimap 2019) with a 50m buffer applied. Maps of historical *L. timidus* and *L. europaeus* records suggested a small range overlap, therefore we included the presence of each species as a predictor to the other.

Future climate niches were projected using the IPCC Fifth Assessment Report Coupled Model Intercomparison Project Phase 5 (Tayloret al., 2011) future climatic data for the Representative Concentration Pathway (RCP) 2.6 for 2050 (averaged across 2041–2060) downloaded from WorldClim at 1 km^2 grid cell resolution and resampled with bilinear interpolation to 1-ha scale. RCP 2.6 indicates a mean average global temperature increase of 2 °C by 2050. Variables were averaged across five Global Circulation Models (GCMs), CNRM-CM5, GFDL-CM3, GISSE2-R, Had-GEM-ES and MIROC-ESM-CHEM. The RCP 2.6 climate scenario is considered the mildest and least likely of global warming scenarios. Attempts to model with higher RCPs, predicted near binary absence (*L. timidus*) and presence (*L. europaeus*) which was less informative. These future climate niche projections also included the same topographical predictor variables and values as for the current climate niche i.e. elevation, slope and aspect derived from OS 50m digital terrain model and gullies information from OS Vector data (Digimap 2019). Tobe consistent with the current climate niche, the future climate niche did not include any vegetation information, which was of course unknown.

2.4. Ecological niche modelling

Niche modelling analysis followed Guisan et al. (2017) using 'biomod2' (Thuiller et al., 2014), 'ecospat' (Di Cola et al., 2017) and 'ade4' (Dray and Dufour 2007) packages in R. Predictors were normally distributed, though some were skewed, and were evaluated for collinearity with Pearson correlation coefficients using function [layerStats] from R Package 'raster' (Hijmans 2019). Strongly correlated predictors having Pearson coefficient $r > 0.75$ were removed (Guisan et al., 2017). Where choices arose, we retained those relevant to lagomorph ecology (Table 1) (Harris and Yalden 2008). For climate niche models we retained nine abiotic variables: BIO 6 minimum temperature of coldest month, BIO 7 temperature annual range, BIO 8 mean temperature of wettest quarter, BIO 9 mean temperature of driest quarter, BIO 12 annual precipitation, BIO 15 precipitation seasonality, aspect, gullies and slope (Table 1, Figure S4). For the habitat niche models we retained the following biotic variables: NDVI, brightness, wetness, all landcovertypes, roads and the presence of respective lagomorph species (Table 1, Figure S5).

Table 1

The models and variables used to predict hare ecological niches.

Species	*Lepus timidus*	*Lepus europaeus*
Species Occurrence Data	BRC data 1690 presences 1690 pseudo-absences	BRC data 265 presences 265 pseudo-absences
Current climate niche		
BIO.6 Min temp of coldest month		
BIO.7 Temp annual range		
BIO.8 Mean temp of wettest quarter		
BIO.9 Mean temp of driest quarter		
BIO.12 Annual precipitation		
BIO.15 Precipitation seasonality		
Aspect		
Gullies		
Slope		
Current habitat niche		
NDVI		
Brightness		
Wetness		
Arable		
Berries		
Broadleaved woodland		
Coniferous woodland		
Cotton Grass		
Young heather		
Mature heather		
Improved grassland		
Moorland grasses Roads		
L. timidus or *L. europaeus*		
Future climate niche		
BIO.6 Min temp of coldest month		
BIO.7 Temp annual range		
BIO.8 Mean temp of wettest quarter		
BIO.9 Mean temp of driest quarter		
BIO.12 Annual precipitation		
BIO.15 Precipitation seasonality		
Aspect		
Gullies		
Slope		

Niche models used presences and pseudo-absences for each species and relevant predictor layers (Table 1). Predictive models were assembled in 'biomod2' (Thuiller et al., 2014) which hosts a series of process steps within the function [BIOMOD_ModelingOptions] to enable use of algorithms. For these we employed three with standard settings: General Linear Model (quadratic models, no interaction terms, testing on AIC); Random Forest (500 trees, 5 nodes); MAXENT (Phillips et al., 2006) (200 iterations with linear or quadratic features). Nine runs were conducted with cross-validation, 70/30 training/test data; performance monitored with kappa, TSS (Allouche et al., 2006) and AUC scores (Fielding and Bell 1997). Because each algorithm may perform differently with different environmental predictors, making evaluation and comparison difficult, we created ensemble models retaining all information from the candidate algorithms following Thuiller et al. (2009) and Guisan et al. (2017), using function [BIOMOD_EnsembleModeling] within 'biomod2'. We chose between committee and weighted mean averaged models considering test scores for kappa, TSS and AUC. Predictor variables were ranked on average importance values for the GLM. The influence of each predictor was portrayed with evaluation strip charts (Elith et al., 2005). For each ensemble model we used optimised TSS value to determine probability threshold, predicting climate and habitat niches (Franklin 2009) using function [find.optim.stat] within 'biomod2' (Guisan et al. 17: 259). Using function [extract] in 'raster' we then measured the size of predicted niches for each species. We calculated min, max and mean abiotic values and vegetation productivity values for each species. For each landcover class we measured how much the models predicted as occupied. The future climate niche model applied the ensemble model values derived from the current climate model, to predict future climate values, forecasting for the year 2050 and quantifying range change (Fick and Hijmans 2017; Guisan et al., 2017). Some future climate variables had ranges outside those used tocalibrate the current climate models. Therefore for the future climate niche models, we recorded how many variables were invoked to form predictions, thereby indicating where predictions might be uncertain, determined with the function argument [build.clamping.mask] in 'biomod2'.

Geographic overlaps were calculated from prediction maps. Elevation overlaps were assessed with Welch's *t*-test for difference. Environmental niche overlap assessment followed Broennimann et al. (2012) predicting niche occupancy in environmental space, thereby removing geographic bias. This method was designed to detect niche overlaps in current environments. We assessed both the climate and habitat niches. Multivariate analysis of these factors applied principal components analysis to species presence points only, determining two leading components within 'ecospat' using function [ecospat.sample.envar] (Di Cola et al., 2017) and function [dudi.pca] in R package 'ade4' (Dray and Dufour 2007). Overlap of niches were tested for equivalency and similarity using Schoener and Hellinger indices (Broennimann et al., 2012) using functions including [ecospat.niche.similarity.test] in 'ecospat' (Di Cola et al., 2017).

3. Results

For both lagomorphs in all niches, ensemble modelling achieved high test scores and credible predictions of probability of occurrence(Franklin 2009; Guisan et al., 2017) (Table S3). Evaluations of maximised TSS scores provided thresholds for current climate, current habitat and future climate niches (Table 2) predicting distinctly different species niches (Fig. 2).

3.1. Lepus timidus predicted niches

The current climate niche was predicted at 168 km^2 comprising the highest elevations in the centre of the study extent (Fig. 2). Referring to GLM models, the strongest abiotic predictors associated *L. timidus* presence with a narrow temperature range (BIO 7), the wettest quarter (BIO 8), the coldest temperature of the coldest month (BIO 6), less precipitation (BIO 12) and with no apparent association for topography (Table 3, Table 4, Figure S6).

In the current habitat niche, the predictors influencing *L. timidus* presence were mid-ranges of vegetation productivity: brightness and NDVI (Table 3, Table 5, Figure S6). Broadleaved and coniferous woodland and improved grassland suggested slight negative associations. Neither roads, nor the presence of *L. europaeus* were important predictors.

The current habitat niche was predicted as actually being 60% larger than the current climate niche, 269 km^2 (Table 6, Fig. 2). More than halfof the landcover occupied by *L. timidus* was young or mature heather; moorland grasses or cotton grass made up the remainder. The current habitat niche model predicted 80% utilisation of available heather landcover (Table 6).

The future climate niche predicted for *L. timidus* a range reduction of 88% to 19 km^2, remaining only on high elevation areas (Fig. 2). The future probability of occurrence threshold was very low (Table 2). Suitable areas were mostly predicted in those locations where the model referenced at least seven abiotic variables, having ranges used to calibrate current climate niche models (Fig. 2; Figure S7).

Table 2

TSS and threshold scores for the models when projected using weighted mean ensemble modelling.

Model	Max TSS	Threshold
L. timidus current climate niche	0.66	0.57
L. timidus current habitat niche	0.46	0.49
L. timidus future climate niche	0.09	0.07
L. europaeus current climate niche	0.73	0.54
L. europaeus current habitat niche	0.44	0.37
L. europaeus future climate niche	0.04	0.23

3.2. Lepus europaeus predicted niches

The current climate niche predicted a wide lowland area of 252 km^2 encircling the uplands (Fig. 2). Referring to GLM models, the main abiotic predictors for *L. europaeus* were less precipitation (BIO 12), a colder mean temperature of the wettest quarter (BIO 8) and warmer temperatures of the driest quarter (BIO 9), (Table 3, Table 4, Figure S6). The current habitat niche was determined by vegetation productivity measures wetness and NDVI (Table 3, Table 5, Figure S6). The only important landcover predictors reported a disinclination towards cotton grass and a slight preference for improved grassland. There was a slight association with the presence of *L. timidus*. Roads provided a slight association, which we attribute to sample bias.

The current habitat niche was 401 km^2, again larger than the current climate niche by 59% (Table 6, Fig. 2). Of this, improved grassland andmoorland grasses accounted for more than 70%, woodlands at least 14% and heather 10% including slightly on to the hills. Utilisation of available improved grassland was 100%.

The future climate niche predicted expansion by *L. europaeus* across the whole study extent to 765 km^2, more than 3 times its current climate niche, and including all hill tops (Fig. 2). The predicted future probability of occurrence threshold was low (Table 2). Suitable areas were predicted by five or more abiotic variables (Figure S7).

3.3. Niche overlap

Summed kernel density plots of all years' records for *L. timidus* and *L. europaeus* showed significant weak negative correlation (Pearson $r_{\text{timidus europaeus}}$ t = −55.6, df = 81002, correlation = −0.19, *P*-value<0.001) (Fig. 3). Comparing current climate niches, there was an overlap of just 0.2 km^2 between the species. For current habitat niches, there was overlap by 38.4 km^2; 14% of *L. timidus* range and 9% of *L. europaeus* range (Fig. 2). The future climate niche space predicted *L. timidus* range wholly within and comprising 3% of *L. europaeus* range (Fig. 2).

The elevation ranges (Fig. 4) in the current climate niche predicted *L. timidus* occurring at mean elevation 491m, moving in future up to 573m. For L. *europaeus* current climate niche mean elevation was 298m, moving in future to 369m (Fig. 4). Assessment with Welch's *t*-test ofmean elevation ranges between species showed these as significantly different (Table 7). Note these forecasts are based on relationships with climate and topographical variables, without reference to vegetation.

Based on occurrence points, *L. timidus* was present at temperatures ~1° colder than *L. europaeus*, with 241 mm more annual precipitation (Table 4). Principal components analyses of abiotic variables on combined species occurrence points showed climatic variables more influential than topography; and of biotic variables, vegetation productivity indices were most important (Table 8). Kernel density plots of principal components axes showed the two species occupying separate niches (Fig. 5). Overlap indices showed the niches as very different: currentclimate niche Schoener D = 0.16, Hellinger I = 0.31; current habitat niche Schoener D = 0.07, Hellinger I = 0.20. Both metrics are probability scales from 0 (no overlap) to 1 (complete overlaps).

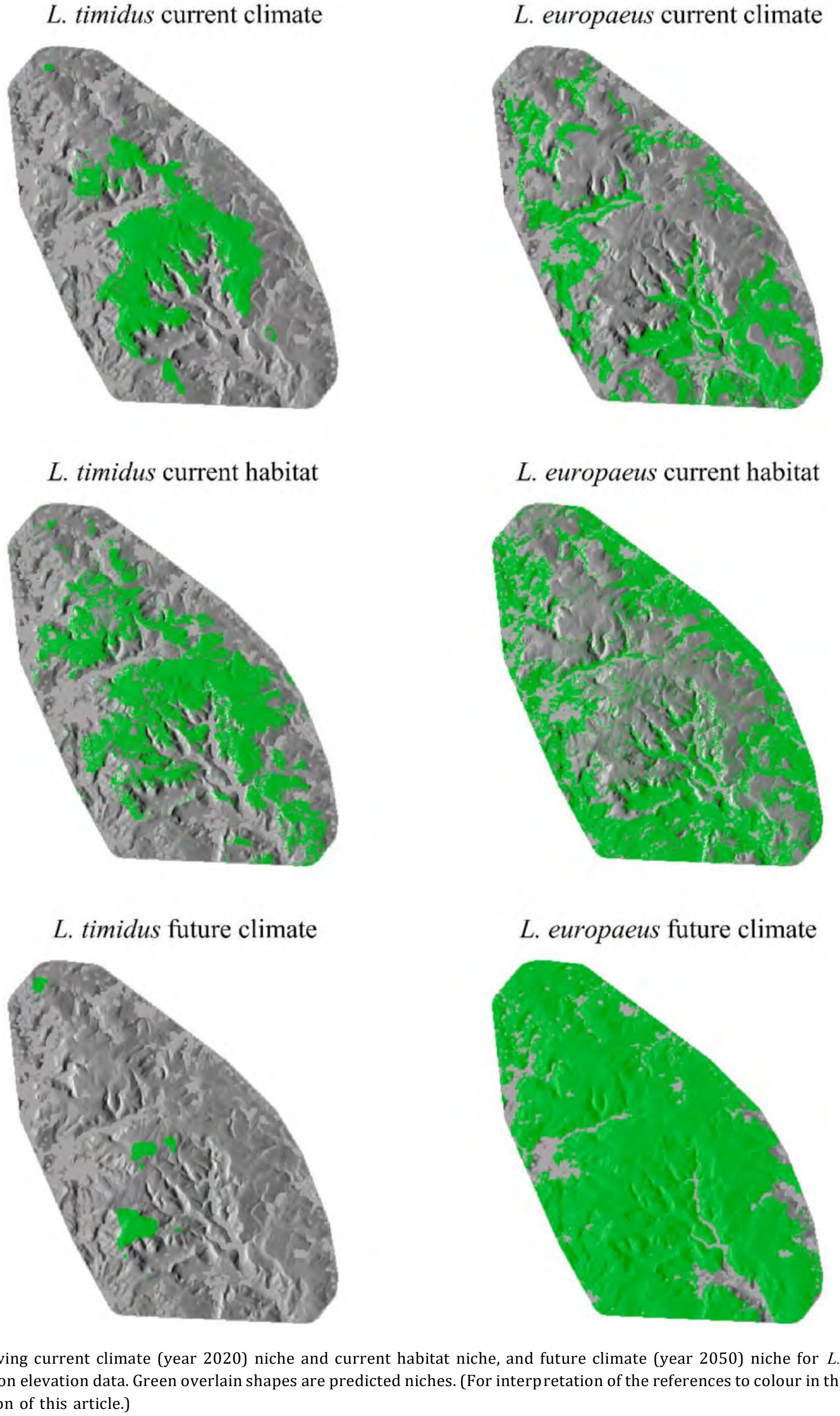


Fig. 2. Threshold maps showing current climate (year 2020) niche and current habitat niche, and future climate (year 2050) niche for *L. timidus* and *L. europaeus*. Background hill shade based on elevation data. Green overlain shapes are predicted niches. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

4.1. Two separate species, two separate niches

This study predicted two congeneric lagomorph species occupying distinctly different ecological niches in close geographic proximity with virtually no overlap. For both, their current climate niches predicted by temperature, precipitation and topography, were actually much smaller than their habitat niches predicted by vegetation productivity and composition. We found *L. timidus* occupied high elevation areas characterised by colder temperatures and higher precipitation levels. The landcover for *L. timidus* predominantly consisted of upland dwarf shrub vegetation: heather, cotton grass and moorland grasses. By contrast *L. europaeus* occupied lower elevation areas, just 1^{o} Celsius warmer, with

Variable importance was calculated with 3 permutations in biomod2, reporting by algorithm (GLM, Generalised linear model; RF, Random Forest and MAXENT). Variable importance is predicted by shuffling a single variable, then computing simple Pearson's correlation between reference predictions and the 'shuffled' one. The highest values show the more influence the variable has on the model, normalised to 100% i.e. 1.0 is most, 0.0 is no influence. Metho d does not account for in- teractions. (From package 'biomod2′, Thuiller et al., 2014). Each model is ranked by GLM score.

L. timidus current climate niche				*L. europaeus* current climate niche			
VARIABLE	GLM	RF	MAXENT	VARIABLE	GLM	RF	MAXENT
BIO.7	0.47	0.20	0.31	BIO.12	0.54	0.13	0.21
BIO.8	0.23	0.13	0.17	BIO.8	0.20	0.11	0.10
BIO.6	0.18	0.05	0.06	BIO.9	0.16	0.20	0.27
BIO.12	0.08	0.09	0.05	BIO.15	0.06	0.20	0.12
BIO.15	0.04	0.21	0.07	BIO.7	0.02	0.11	0.14
ASPECT	0.00	0.01	0.00	GULLIES	0.01	0.00	0.02
SLOPE	0.00	0.05	0.02	BIO.6	0.00	0.08	0.06
BIO.9	0.00	0.26	0.32	ASPECT	0.00	0.05	0.02
GULLIES	0.00	0.00	0.00	SLOPE	0.00	0.12	0.07

L. timidus current habitat niche				*L. europaeus* current habitat niche			
VARIABLE	GLM	RF	MAXENT	VARIABLE	GLM	RF	MAXENT
BRIGHTNESS	0.52	0.36	0.29	WETNESS	0.47	0.28	0.17
NDVI	0.32	0.29	0.12	COTTON.GRASS	0.19	0.03	0.06
BROADLEAF	0.04	0.02	0.01	NDVI	0.08	0.20	0.12
IMPROVED.GRASS	0.04	0.08	0.08	IMPROVED.GRASS	0.07	0.16	0.15
WETNESS	0.04	0.11	0.08	CONIFEROUS	0.06	0.03	0.06
CONIFEROUS	0.02	0.04	0.01	ROADS	0.05	0.09	0.09
ROADS	0.01	0.01	0.01	MATURE.HEATHER	0.03	0.02	0.05
L.europaeus	0.01	0.00	0.04	BERRIES	0.03	0.01	0.00
MOOR.GRASSES	0.00	0.02	0.10	*L.timidus*	0.02	0.01	0.05
MATURE.HEATHER	0.00	0.04	0.11	BRIGHTNESS	0.00	0.13	0.07
BERRIES	0.00	0.00	0.00	ARABLE	0.00	0.00	0.00
ARABLE	0.00	0.00	0.00	BROADLEAF	0.00	0.00	0.03
COTTON.GRASS	0.00	0.01	0.07	YOUNG.HEATHER	0.00	0.01	0.07
YOUNG.HEATHER	0.00	0.03	0.08	MOOR.GRASSES	0.00	0.02	0.07

Table 4

Mean abiotic variable values for each species, at their respective locations. Temperatures are °C, precipitation mm.

L. timidus				*L. europaeus*		
Min	Mean	Max	Min	Mean	Max BIO.6 min temp, coldest	
month	−2.20	−1.83	−0.92	−2.13	−1.47	−0.88
BIO.7 temp annual range	17.20	17.91	19.47	17.60	18.55	19.64
BIO.8 mean temp wettest quarter	3.08	3.55	4.25	3.20	3.95	5.95
BIO.9 mean temp driest quarter	9.17	11.53	13.06	10.42	12.26	13.21
BIO.12 annual precipitation	997.20	1395.40	1664.40	926.90	1154.00	1595.46
BIO.15 precipitation seasonality (CV)	17.83	21.17	22.78	16.60	19.63	22.12
Slope	0.14	6.79	30.78	0.22	8.25	23.47
Aspect°		229			221	
Species locations at gullies		43%			34%	

Table 5

Ranges of vegetation productivity at the two species' locations.

L. timidus				*L. europaeus*		
Min	Mean	Max	Min	Mean	MaxBrightness	
	0.83	0.95	1.47	0.85	1.01	1.2
Wetness	0.08	0.26	0.43	0.01	0.20	0.36
NDVI	−0.07	0.00	0.05	−0.08	−0.03	0.04

less precipitation. Its preferred landcover was improved grassland. Woodland and heather areas were also important. Whilst the margins of difference for preferred climate variables were small, they predicted strikingly separate niches across the landscape. Referencing climate values for RCP 2.6 for 2050, the *L. timidus* future climate niche was predicted to shrink to small patches at high elevations. The *L. europaeus* future climate niche was predicted to expand to higher elevations, encompassing the uplands, completely covering the range of *L . timidus*.

Interspecies competition in terms of overlaps of geographic and environmental niche ranges was presently very low and yet inferred to in- crease in future.

4.2. Reasons for niche preferences

Environmental forces are often complex and difficult to categorise or explain (Sillero 2011). There are subtle reasons for niche differences between these two lagomorphs. Our study predicted both species actu- ally occupied much larger habitat niches than climate niches. This is a different outcome to the perhaps conventional expectation that the habitat, i.e. realised niche, may be a limited version or subset of the climate, i.e. fundamental niche (Guisan and Zimmermann, 2000; Sillero 2011). This finding reflects the view that ecological forces may indeedact stochastically (Guisan et al., 2017: 23). Both species were in effect tolerating wider climatic ranges than suggested by the current climate niche models. Across the entire study extent the climate variables re- ported small variations which were not of critical physiological

Table 6
Geographic occupation of current climate and habitat niches by *L. timidus* and *L. europaeus* for each landcover type.

L. timidus						*L. europaeus*			
Landcover Available	Total	Climate niche	Habitat niche			Climate	Habitat niche		
	km^2	km^2	km^2	% of total available	% of climateniche	km^2	km^2	% of total available	% of climateniche
Arable	3.0	0.0	0.0	0%	–	0.3	2.3	78%	900%
Berries	7.4	1.0	0.1	1%	8%	3.2	0.8	11%	25%
Broadleaf	47.0	0.0	0.2	0%	1500%	26.3	30.0	64%	114%
Coniferous	33.6	1.2	0.2	1%	16%	18.2	27.0	80%	148%
Cotton grass	81.7	32.2	33.2	41%	103%	10.3	0.1	0%	1%
Improved grassland	205.9	0.2	0.0	0%	0%	97.2	205.8	100%	212%
Mature heather	143.5	58.3	115.8	81%	199%	25.2	10.7	7%	43%
Moorland grasses	201.2	41.1	54.5	27%	133%	51.9	94.0	47%	181%
Young heather	82.2	34.2	65.1	79%	190%	20.2	30.8	37%	152%
Total	805.5	168.1	268.9	33%	160%	252.8	401.5	50%	159%

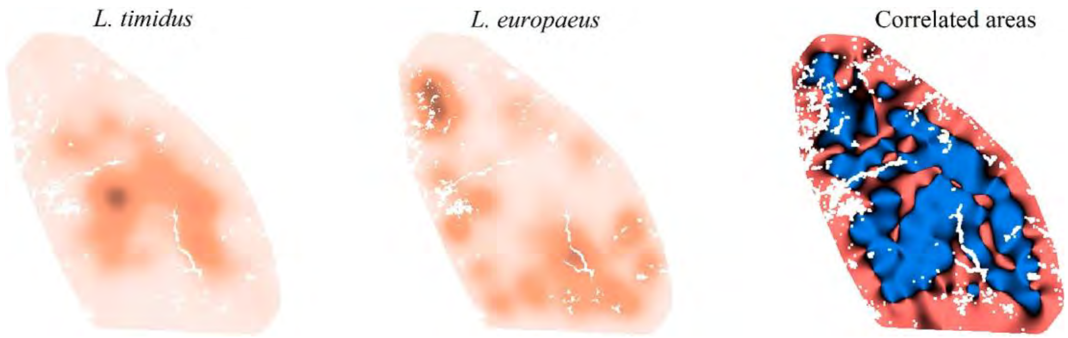


Fig. 3. Kernel density plots of summed (2000–2018) records for *L. timidus* and *L. europaeus* with darker areas indicating higher density. Correlated areas chart: blue = *L. timidus*; red = *L. europaeus*; correlated areas ("contact zones") indicated by shading increasing to black. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

importance to lagomorphs, yet could still indicate strong preferences, e.g. the widest temperature variation BIO 9 (mean temperature, driest quarter) ranged from 5.1 °C to 13.8 °C, the narrowest BIO 6 (min temperature coldest month) ranged from −2.2 °C to −0.8 °C; BIO 12 (annual precipitation) ranged 689–1666 mm. The small climatic variationsshowed distinct steep local changes, resembling the hilly topography.

Consequently, these values were sufficiently different to predict two separate climate niches for the two species. By contrast the biotic vegetation productivity variables (NDVI, tasselled cap brightness and tasselled cap wetness) showed midrange values covering a much wider geographical extent, with less severe graduations, thereby predicting much larger habitat niches.

Considering abiotic and biotic factors, it therefore appears the two species occupied separate niches because vegetation productivity, composition and associated dietary preferences, were more important than climate influences. Of note, the lagomorphs' different biotic niches were predicted by alternate aspects of vegetation productivity. Bright- ness (i.e. less exposed soil) and NDVI (i.e. actively photosynthesising plant growth) were most important for *L. timidus*, whereas, for *L. europaeus*, it was wetness (i.e. drier soil and vegetation moisture content). This then provided contrasting differences to the consequent proportion of vegetation types in the respective habitat niches of each species.

For *L. timidus*, the majority of its habitat niche was heather, with other upland bog vegetation also important (cotton grass and moorland grasses). This was consistent with reported dietary and shelter prefer- ences for *L. timidus* in the UK (Hewson 1962, 1976b, 1989). In the Peak District, much heather resource exists because of grouse moor man- agement (Anderson and Shimwell 1981). Other large areas of uplands are subject to blanket bog restoration: gully blocking to retain water and planting of upland dwarf shrubs (Bonn et al., 2009). These human interventions provide the vegetation that support the presence of *L. timidus*.

The habitat niche for *L. europaeus* was different: mostly improved grassland areas, with moorland grass, woodland and some heather also being important. This reflected the reported preferences of *L. europaeus*, favouring mixed agrarian landscapes: crops, cereals or grasses (Harris and Yalden, 2008; Tapper and Yalden, 2010).

Differences in niche preferences, and by implication diet, may be explained by vegetation qualities and productivity: energy content, moisture, digestibility of secondary compounds, terpenes, phenolic resins, and selected in an order of preference by lagomorphs (Hulbert et al., 2001; Rödel et al., 2004). The preference of *L. timidus* is grasses: *Deschampsia flexuosa, D. caespitosa, Nardus stricta, Festuca, Agrostis* spp. especially for females in summer (Harris and Yalden 2008). However, when winter grass nutritional quality is poor, *L. timidus* switches to a 90% heather diet, less digestible but tolerable. (Hewson 1962; Hulbertet al., 2001; Harris and Yalden 2008). Between the two species, *L. timidus* may be better able to detoxify phenolics occurring in shrubs and trees (Iason and Palo 1991). By contrast *L. europaeus* favours grass resources throughout the year until there is no other option. It depends on weeds in agricultural lands (Reichlin et al., 2006). Thus, whilst *L. europaeus* may venture to utilise upland grasses, when these fall senescent in winter, instead of switching to heather in the manner of *L. timidus*, (Hulbert et al., 2001), *L. europaeus* chooses improved grasslands at low elevations. Absent competition, *L. europaeus* can broaden its dietary niche to selectively include shrubs (Green et al., 2013), possiblyas a last resort (Rödel et al., 2004; Harris and Yalden 2008). Other

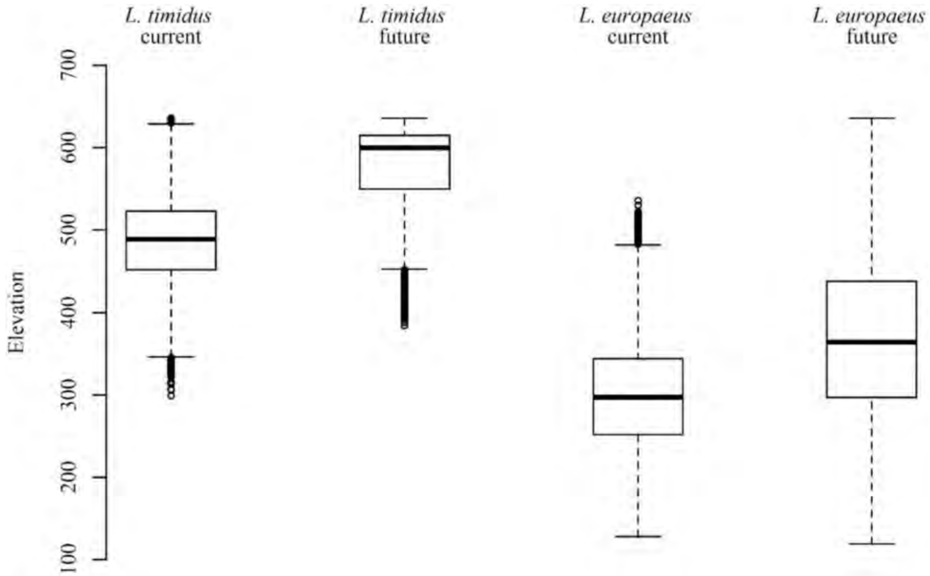


Fig. 4. Boxplots showing predicted elevation ranges for *L. timidus* and *L. europaeus* based on current and future climate niche threshold maps.

Table 7

Welch's *t*-test comparisons of predicted mean elevations (m) of hare species for current and future climate niches.

Comparison	t	df	*P*-value
L. timidus current vs *L. timidus* future	−56.8	2356	<.05
L. timidus current vs *L. europaeus* current	−313.7	38985	<.05
L. europaeus current vs *L. europaeus* future	−130.3	63858	<.05
L. timidus future vs *L. europaeus* future	−143.7	2180	<.05

Table 8

Percent contribution of each variable to principle components 1 and 2 used in the niche overlap models, values in bold as contributors.

Variable	Climate niche		Variable	Habitat niche	
	PCA 1	PCA 2		PCA 1	PCA 2
BIO.6	**11.8**	**21.6**	NDVI	**27.2**	6.6
BIO.7	**15.2**	**11.2**	BRIGHTNESS	1.9	**37.5**
BIO.8	**15.4**	5.0	WETNESS	**27.1**	1.0
BIO.9	**13.7**	0.1	ARABLE	0.1	0.0
BIO.12	**24.1**	0.1	BERRIES	0.0	0.0
BIO.15	**18.3**	4.6	BROADLEAF	0.0	1.9
ASPECT	0.0	**19.2**	CONIFEROUS	0.1	3.2
GULLIES	1.3	1.3	COTTON.GRASS	2.5	1.7
SLOPE	0.3	**37.0**	YOUNG.HEATHER	1.9	1.1
			MATURE.HEATHER	4.3	**18.8**
			IMPROVED.GRASS	**28.1**	0.0
			MOOR.GRASSES	1.9	**28.1**
			ROADS	4.8	0.1

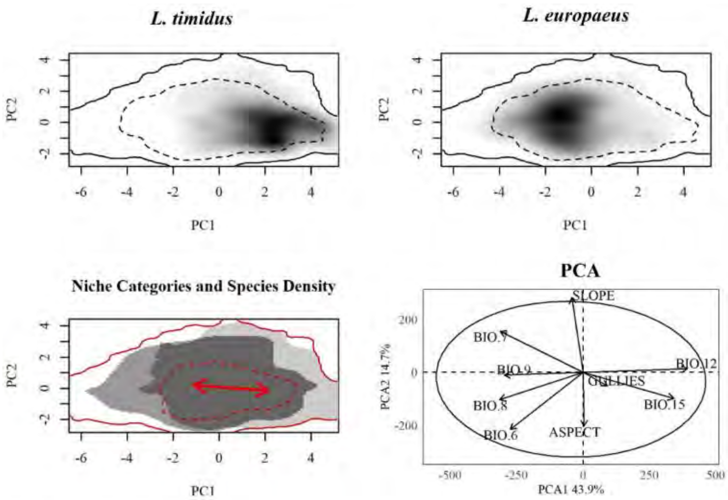
studies suggest *L. europaeus* adapts its diet when food availability is limited (Puig et al., 2017). Yet, there is ample supply of lowland improved grassland in the Peak District, providing a distinct niche for *L. europaeus*.

4.3. Level of interspecies competition

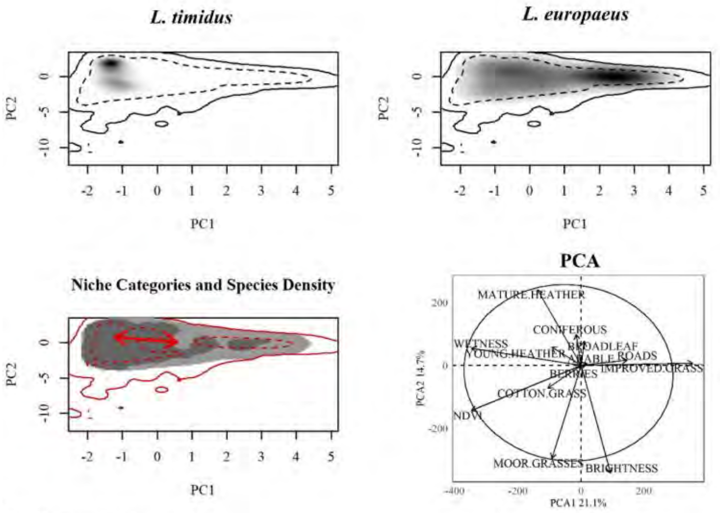
We inferred that both abiotic and biotic factors combined to determine distinct species ranges, with very small overlaps between the two. For *L. timidus*, a boreal species adapted for harsh winter climates, it was anticipated that its climate niche would occur on hilltops with the coldest wet conditions. The seasonally white pelage of *L. timidus* has high densities of air-filled hairs providing insulation that allows it to utilise colder areas during winter(Zimova et al., 2018). The heavily furred hind feet of *L. timidus* are helpful for digging through snow to reach heather (Jansson and Pehrson 2007; Harris and Yalden 2008). Yet, although *L. europaeus* does not share these adaptations, physiologicallyit can survive very cold habitats at high elevations (>2000m a.s.l.) during winter (Green et al., 2013; Puig et al., 2017). In snowscapes, *L. europaeus* restricts its diet to taller vegetation that remains visible (Green et al., 2013); but in the Peak District, only heather and berry shrubs of low height are available. So whilst *L. europaeus* could theoretically endure the cold climate of the high elevations of the Peak District, it is less well suited than *L. timidus* and may avoid the energy costs of searching for less preferable forage in poor weather or under snow, by remaining at lower, warmer elevations. Indeed where both species share territory, *L. timidus* copes more effectively with cold snow conditions (Jansson and Pehrson 2007). There may also be competitive exclusion by *L. timidus*, though the mechanism is unclear (Reid and Montgomery 2007).

Grasslands were outside the habitat niche of *L. timidus*, consistent with reports of it typically occupying heather moorland, tundra or forest (Angerbjörn and Flux 1995). Surprisingly our niche models also predicted that in woodlands, *L. timidus* were absent, and yet *L. europaeus* were present. This is different to other localities in Europe, where *L. timidus* often utilises woodlands, feeding on *Salix*, *Sorbus*, *Betula*, *Juniperus*, *Populus* and *Vaccinium* spp. (Hewson 1962; Angerbjörn and Flux 1995; Jansson and Pehrson 2007; Rehnus et al., 2013). Although this situation was recorded differently in Scotland wherein amongst mixed habitats, *L. timidus* was specifically shown to prefer heather moorland over newly planted Scots pine (*Pinus sylvestris*) woodland (Rao et al., 2003). Separate records across Europe describe *L. europaeus* pushing *L. timidus* out of forests (Flux and Angermann 1990); *L. europaeus* present in forests where clear-cuts promoted grass growth (Jansson and Pehrson 2007) or, otherwise, where *L. timidus* was absent (Rödel et al., 2004). Therefore, we are uncertain whether *L. timidus* avoids Peak District woodlands as its own preference or whether *L. europaeus* excludes them. This intriguing interspecies dynamic invites further study.

Competition occurs where dietary preferences converge. In these circumstances, *L. europaeus* often dominates, though this may depend upon local species densities (Acevedo et al., 2012). In Sweden, Jansson and Pehrson (2007) described how *L. europaeus* displaced *L. timidus* facilitated by warmer winters which increased grass availability in forests. In Ireland, the introduced *L. europaeus* outcompetes the native



(a) Current climate niche



(b) Current habitat niche

ig. 5. Niche overlap density and PCA plots **(a)** Current climate **(b)** Current habitat. ensity plots show ranges for *L. timidus* and *L. europaeus*, based onthe first two rincipal components. The solid and dotted line show 100% and 50% available nviron- mental space. Bottom left charts: Light grey area indicates the native niche or *L. timidus* only, dark grey area (centre) common (stable, shared) nichebetween *. timidus* and *L. europaeus*; and medium grey area native niche for *L. europaeus* nly. The red arrow indicates the difference in the centroid of the niche, mapping etween species. The PCA charts bottom right portray the niche variables plotted n the first two axes. (For interpretation of the refer- ences to colour in this figure egend, the reader is referred to the Web version of this article.)

L. timidus hibernicus subspecies, which feeds mainly on grasses (Car- avaggi et al. 2014, 2017). By comparison, in the Peak District, the separate improved grassland which abuts the distinctly different heather moorland and the alternate dietary preferences allow the two lago- morph species to thrive in close proximity, seemingly without compe- tition. These findings are consistent with those of Hewson (1976a) who reported that *L. europaeus* only invaded heather ranges when *L. timidus* numbers were very low. Flux and Angermann (1990) also described separate dietary niches for both these hare species.

4.4. *Future niches under climate change*

The future climate niche scenarios predicted that, by 2050, *L. timidus* would occupy a reduced geographic range of smaller patch sizes at higher elevations, consistent with studies elsewhere (Anderson et al., 2009; Leach et al., 2016; Rehnus et al., 2018). The persistence of *L. timidus* may depend on available vegetation under warmer climates. Policies and investments support both grouse moor management and blanket bog restoration, providing heather resource. However, heather requires drier soil structures. Climate forecasts for England are for wetter winters and driers summers. Notwithstanding human interven- tion, there is much uncertainty regarding future vegetation composition

(Bonn et al., 2009). Otherwise, to survive, *L. timidus* must adapt its diet (Harris and Yalden, 2008). There are scant opportunities for *L. timidus* to disperse elsewhere. Peripheral areas comprise only small patches of heather moorland and are several kilometres away. There are large areasof intervening agriculture and roads: a difficult migration for a specieswhose natal dispersal range is less than 1 km (Angerbjörn and Flux, 1995). Notwithstanding these challenges, the warming climate also re-duces snow cover, thereby increasing the vulnerability of *L. timidus* topredators, because of the camouflage mismatch arising from its whitewinter pelage (Zimova et al., 2020). The increasing number of wildfiresinevitably also threatens hares on the uplands (Albertson et al., 2010).

By contrast, we predict by 2050 the widespread expansion of *L. europaeus* to higher elevations. Being descended from central Euro-pean and Asian species, *L. europaeus* may be physiologically better abletothrive in warmer temperatures (Caravaggi et al., 2017). However, our habitat niche model and dietary evidence suggests *L. europaeus* relies on grasses. Its spread to hilltops would require upland dwarf shrub vegetation succumbing to warmer climate, the failure of human upland management interventions and a transition to grassland communities. Regardless, the dietary preference of *L. europaeus* allows it to migrate to prolific lowland agricultural landscapes of northern England.

The relationship between these species depends on whether vege-tation availability and dietary requirements converge. Should the twospecies' climatic niches merge as predicted and the upland vegetation change, this is likely to precipitate competition or hybridisation (Thulin 2003). This might occur remarkably swiftly (Caravaggi et al., 2017). We recommend ongoing monitoring of the respective niches and competitive dynamics of both lagomorph species.

Hare Data Sources

Brown and mountain hare records were kindly provided by British Trust for Ornithology, RECORD LRC (Cheshire), Derbyshire Mammal Group, Derbyshire Wildlife Trust, Greater Manchester Local Records Centre, Moors for the Future, Liverpool Museum, National Biodiversity Atlas, Sheffield Biological Records Centre, Sorby Natural History Society and West Yorkshire Ecology.

Data availability

Species records remain copyright with the Biological Record Centres listed under Hare Data Sources.

WorldClim data is open access and available from htttps://www.worldclim.org.

Both Ordnance Survey data and aerial images may be sourced fromEdina, National Data Centre, University of Edinburgh, UK.

Ordnance Survey map and topography data are available from https://www.ordnancesurvey.co.uk. Aerial images are supplied by Getmapping plc, Fleet, Hampshire UK.

Author contributions

Carlos P.E. Bedson: Conceptualisation, data curation, formal analysis, writing-original draft preparation, writing - reviewing and editing. **Christian Devenish:** Formal analysis, validation. **Elias Symeonakis:** Software, validation. **David Mallon:** Validation. **Neil Reid** Conceptualisation. **W. Edwin Harris:** Conceptualisation. **Richard Preziosi:** Supervision. All authors were involved with Writing - Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financialinterests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded by the People's Trust for Endangered Species, the Hare Preservation Trust, the British Mountaineering Council, Queen's University Belfast, Penny Anderson Associates and South-West Action for Hares. We thank N. Sillero, K. Green, A. Fielding and W. Kasworm for niche modelling advice. We dedicate this researchto the memory of Derek Yalden.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2021.103742.

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Supplementary data is recorded as Appendix A. Supplementary data and is an identical copy of the material occurring within this thesis

Estimating density of mountain hares using distance sampling: a comparison of daylight visual surveys, night-time thermal imaging and camera traps

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Source: Wildlife Biology, 2021(3)

Published By: Nordic Board for Wildlife ResearchURL:

https://doi.org/10.2981/wlb.00802

Wildlife Biology 2021: wlb.00802
doi: 10.2981/wlb.00802
Subject Editor: Luca Corlatti. Editor-in-Chief: Ilse Storch. Accepted 27 April 2021

Estimating density of mountain hares using distance sampling: a comparison of daylight visual surveys, night-time thermal imagingand camera traps

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Surveying cryptic, nocturnal animals is logistically challenging. Consequently, density estimates may be imprecise and uncertain. Survey innovations mitigate ecological and observational difficulties contributing to estimation variance. Thus, comparisons of survey techniques are critical to evaluate estimates of abundance. We simultaneously compared three meth-ods for observing mountain hare *Lepus timidus* using Distance sampling to estimate abundance. Daylight visual surveys achieved 41 detections, estimating density at 14.3 hares km^{-2} (95%CI 6.3–32.5) resulting in the lowest estimate and widest confidence interval. Night-time thermal imaging achieved 206 detections, estimating density at 12.1 hares km^{-2}(95%CI 7.6–19.4). Thermal imaging captured more observations at furthest distances, and detected larger group sizes.Camera traps achieved 3705 night-time detections, estimating density at 22.6 hares km^{-2} (95%CI 17.1–29.9). Between the methods, detections were spatially correlated, although the estimates of density varied. Our results suggest that daylightvisual surveys tended to underestimate density, failing to reflect nocturnal activity. Thermal imaging captured nocturnal activity, providing a higher detection rate, but required fine weather. Camera traps captured nocturnal activity, and oper- ated 24/7 throughout harsh weather, but needed careful consideration of empirical assumptions. We discuss the merits and limitations of each method with respect to the estimation of population density in the field.

Keywords: camera traps, cryptic animals, distance sampling, population monitoring, survey methods, thermal imager, uplands

In a global era of biodiversity crisis, conservation monitor- ing which allows us to establish trends in wild animal abun- dance, is essential. The provision of reliable census estimatesare considered vital to guide management interventions aimed at protecting vulnerable species (Krebs 1989). Effec- tive surveys must be designed to reflect species distribution and life history traits which may affect animal detection. Studies must comprise sites which represent the range of habitats, climate and topography occupied by the target spe- cies and this will both inform and constrain survey methods (Sutherland 2006).

The mountain hare *Lepus timidus* is Britain's only native lagomorph and an icon for upland habitats and their conservation. Reliable estimates of mountain hare population density are important to inform conservation assessments and to evaluate the impact of anthropogenic disturbance on population numbers (e.g. impact of roadkill or control efforts on grouse moorland). Yet hares are mostly nocturnal mammals and can be difficult to detect (Newey et al. 2011,Petrovan et al. 2011). Despite having a white pelage in win- ter, hares are adept at hiding by day in rough vegetation: they lie motionless, flattening to 15 cm height, sometimesin shallow depressions, burrows or amongst rocks and even fleeing unseen. Hares emerge at night to feed (Hewson andHinge 1990, Harris and Yalden 2008) and consequently daytime observation is characterised by low detection rates (Dingerkus and Montgomery 2002).

Surveying elusive or nocturnal animals is particularly challenging in environments such as upland terrains which often experience poor weather. Mountain hare habitats arealso frequently rugose and difficult to access, creating safetyissues for monitoring, especially at night. Mountain hares

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frequent low hills, gullies and deep vegetation, making detection difficult (Newey et al. 2018). Snow may hamper daytime observations of white camouflaged mountain hares. Effective monitoring therefore requires multiple observation points and benign weather.

Considering the suite of study methods available for wildlife monitoring, mark–recapture is regarded as the most reliable for hares (Boulanger and Krebs 1994). However, addressing welfare concerns surrounding the capture and handling of animals is resource intensive, particularly in rough terrain, making this method expensive and impracti- cal. Faecal pellet counts can provide a useful index in areas of high hare density, assuming constant accumulation rates(Newey et al. 2003). Whilst it is also possible to obtain DNAfrom faecal pellets for genetic population monitoring withmolecular mark–recapture, both plant material in the pellets and fast decay rates can reduce PCR effectiveness, requir-ing larger sample sizes and greater field and laboratory work and costs (DeMay et al. 2013). Direct observation methodsby day, such as line transect sampling, are commonly used yet are vulnerable to achieving fewer observations when such predominantly nocturnal animals remain undetected (Buck- land et al. 2001). Areas of low density may result in low encounter rates and wide variance in estimates (Newey et al.2018). Night-time spotlight surveys may miss animals as they rely on eyeshine reflections, and frequently sample along roads which animals may avoid and which locationsrepresent only a small fraction of upland habitat (Reid et al. 2007, Reid and Montgomery 2010). Thermal imaging reduces false negatives by increasing target detections, con- trasting body heat against a cold backdrop at night (Havens and Sharp 2016) but if the aim is to estimate density it also requires a means to determine distance to the object in darkness. Camera trapping provides a greater continuous survey effort including during night peak activity periodsthus increasing total numbers of detections (Caravaggi et al. 2018), and with virtually no observer field presence to dis-turb animals (Sollman 2018).

In this study we compared three survey methods of mountain hares in upland habitat to estimate density and considered factors relating to spatial variation of haredetections: 1) daylight visual surveys, 2) night-time ther- mal imaging point transects and 3) fixed position camera traps. We analysed data from each method using compa- rable distance sampling models to estimate density and associated precision. For each method we recorded sur- vey effort, observations, distances to target animals and group sizes as inputs to estimate density. As camera trap distance sampling methods are relatively recent, we also explored how different assumptions of space, time and animal behaviour affected density estimates. Since actual densities or population size were not known, we couldnot be certain which density estimate of the three meth- ods might be closest to the truth. Nonetheless the overall precision of parameters and estimates could be compared. We compared variation of estimates among methods and survey sites, the effect of terrain type and how detection rates changed throughout the study period. We evaluate the merits and assumptions of each method relative to our findings, to inform study design decisions for conservation monitoring.

Methods and materials

Study site

Surveys took place at Holme Moss, a large hill, elevation582 m a.s.l., situated in the north of England, UK (Fig. 1). Mountain hares were once native to England yet became extinct ~ 6000 years ago (Yalden 1971). They were rein- troduced to Holme Moss in the 1870s for sport shooting (Stubbs 1929, Yalden 1971). In this area historic records suggest the number of 1-km squares occupied by mountain hares as ranging from 16 (Yalden 1971) up to 35 (Mal- lon et al. 2003). This group of hares is potentially partiallyisolated from other populations elsewhere in the area by res- ervoir systems and major road networks. Whilst sightings ofmountain hares on Holme Moss have been particularly fre-quent in the past (Mallon et al. 2003), farmers and landown- ers report perceived declines across the site in the last decade.The local density on Holme Moss has never been formallyquantified. Holme Moss comprises a flat plateau with peatgullies and steep sided valleys (Fig. 1) (Tallis 1987). The areaconsists of blanket bog vegetation dominated by heather *Calluna vulgaris*, bilberry *Vaccinium myrtillis* and cotton grass *Eriphorum* spp. Over the last 200 years habitat condi- tions have deteriorated as both acid rain caused peat layerreduction and intensive sheep grazing led to widespread vegetation loss (Anderson and Shimwell 1981). Most of the hill is managed by the RSPB Dove Stone reserve engaged inblanket bog restoration.

The study focused on the entire blanket bog plateau ofHolme Moss, where elevation was above 335 m i.e. the lower elevation range of mountain hare occurrence (Yalden 1971), and as limited by major roads to the north and eastand different habitats to the south and west. This comprised 49 km^2. Within this area we selected a smaller 5 × 5 km central area for daylight visual surveys, thermal imager and camera trap surveys. This considered the area that could becovered on foot by two full time staff conducting field logis-tics: Holme Moss is largely pathless, often hazardous under-foot. Winter day lengths are short. The location of the 5 ×5 km area was chosen to be central, equidistant from roadsand habitat edges, avoiding edge areas frequented by the public, thereby reducing camera theft risk, though accepting this choice of centroid might cause bias. Within this area we then randomly selected (R-package ‘sample’) 5 × 5 1-kmsquares as the locations for random cluster samples of pointsand transects, being representative of the flat blanket bog.The location of an additional sixth site was also randomlyselected, yet at the request of wildlife agencies we altered itsshape to comprise a narrow long strip to facilitate monitor-ing of an historic high density area (Mallon et al. 2003), accepting this might bias results. Contemporary density and distribution of hares was unknown. The 1-km size of each study site enabled comprehensive continuous observa-tion of terrain, detecting potential changes in hare occur-rence over a few hundred metres. Hare home ranges can be small (0.1–0.8 km^2), non-territorial, overlapping and hares sometimes group together (Hewson and Hinge 1990, Hul-bert et al. 1996, Rao et al. 2003, Harrison 2011). The small1-km site scale facilitated efficient management of camera arrays and enabled observers to learn of local topography and

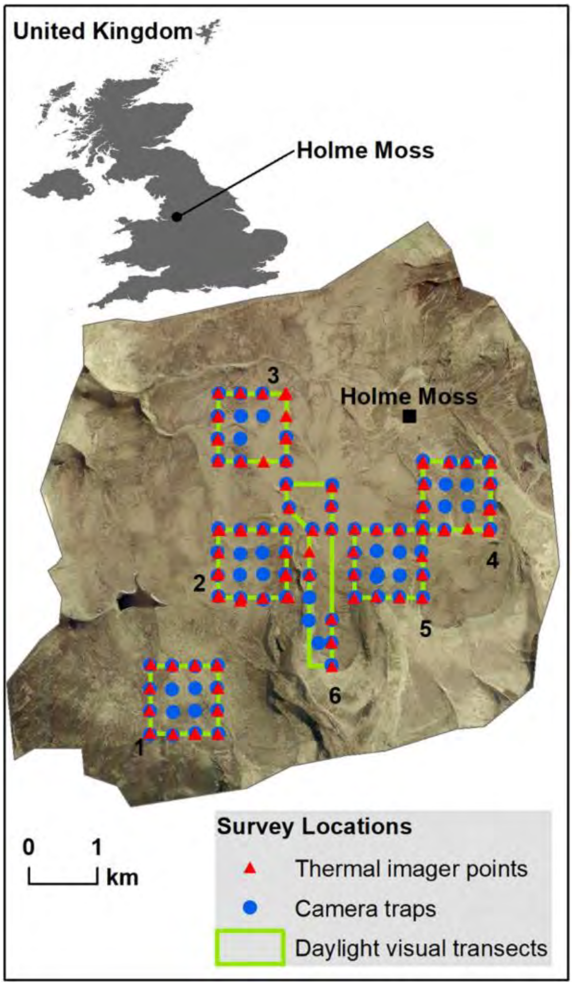

Figure 1. Location of Holme Moss study site, north west England, Great Britain. Aerial photo origin is OS SE 401398 and shows extent of Holme Moss massif, above 335 m elevation, bounded to north and east by major roads. The hill summit is indicated by the black square. Survey locations are shown, with site numbers. Sites 1–5 are 1 km squares. Site 6 is the narrow polygon running north to south between sites 2 and 5. Daylight visual transects were the perimeter of 1-km square, except site 6 being a near trapezoid shape. Thermal imager points were 333 m apart as were camera traps, though with some minor deviations for topography, standing water or perceived theft risk. Note: one thermal imager point was used in site 4 and repeated ~30 m away in site 5; 87 of 91 camera site locations are shown as 4 pairs of camera trap sites overlap; 2 were moved ~30 m mid-term because of rising standing water; 2 were moved ~30 m avoiding perceived theft risk. Three cameras were stolen from site 3 and one from site 6; their points are not shown, no data was recorded at those locations. Aerial photograph: Digimap sourced June 2019 from Digimap Ordnance Survey Collection: Getmapping aerial imagery.

hazards, prior to subsequent night surveys for thermal imaging. Within the six study sites, we chose transect and point layouts which would cover the same locations, to capture the same local variation. However some of the survey locations between methods differed slightly to account for the different observation ranges of equipment. Surveys occurred from November 2017 to May 2018 (Supporting information). The period was characterised by exceptionally severe weather including seven heavy snowfalls (UK Met Office 2019).

Daylight visual surveys

Daylight visual surveys took place using line transects following Ordnance Survey (2015) Explorer Map 1 grid lines which bounded each survey site (Fig. 1). Transects were square circuits (Buckland et al. 2001, p. 237), intended to alleviate detection bias arising from a low winter sun position when walking different cardinal directions, wind or local topography effects, whilst enabling efficient use of survey time. Whilst surveys were conducted only during good visibility, poor weather and persistent snow cover limited the survey opportunities to only one visit per site transect. Observer routes were guided by a handheld GPS. A slow, measured walk was used (~ 1 km per hour), with frequent scanning of the landscape using binoculars (Fig. 2). The location of each mountain hare was recorded, measuring radial distance from the observer with a laser range finder (maximum range 1100 m) and angle using a compass. These measurements allowed the calculation of the perpendicular distance of sightings from the line, and also enabled the location of each hare to be mapped. During these surveys, conducted when there was no snow, mountain hares bore white pelage contrasting against the green and brown moorland. Hares were often lying-up and not detected until within 30m range (Fig. 2). Whilst some hares fled from the observer, this occurred within the range of vision, so distance and angles were measured to point of origin.

Night-time thermal imaging

We conducted nocturnal surveys at point transect locations using an Armasight Command 336 HD 30 Hz 75 mm biocular (two view lenses) thermal camera, with a range of 2 km, and a refresh rate 30 Hz which enabled species identification of moving animals (Fig. 2). The camera was fitted with an Advanced Modular Range Finder 2200 which operated in darkness. In trials, distances up to 1.8 km could be measured. This assemblage was mounted on a tripod at each point location each spaced ~333 m apart (about the diameter of a single hare home range) along the same 1-km grid lines used during daylight visual surveys (Fig. 1). Thus, whilst a different survey method was used at a different time of day, survey sites were the same. Surveys did not occur at a location that had received a visit that day for other survey purposes, to ensure hares had not been disturbed. Points at sites 1–4 were visited 2–3 times over the winter; points at sites 5 and 6 were visited once only.

Surveys were conducted one hour after sunset with clear visibility though some surveys were curtailed by fog or high winds. Some surveys occurred on snow which assisted detection of hares. Walking by night from point to point took approximately 20–30 min. A red-light head-torch was used by observers to guide the way between points, minimising disturbance. Hares were seen twice only during transit. Once set up, the thermal imager assemblage was immobile; care was taken to situate it with the best field of view within 20m of the GPS point. Whilst setting up the thermal imager vantage point no hares were observed within 30 m. Surveys at each point transect consisted of complete 360° field scans and typically took 10–20 min per point. Extensive practice with the thermal imager using the setting 'white hot' ensured

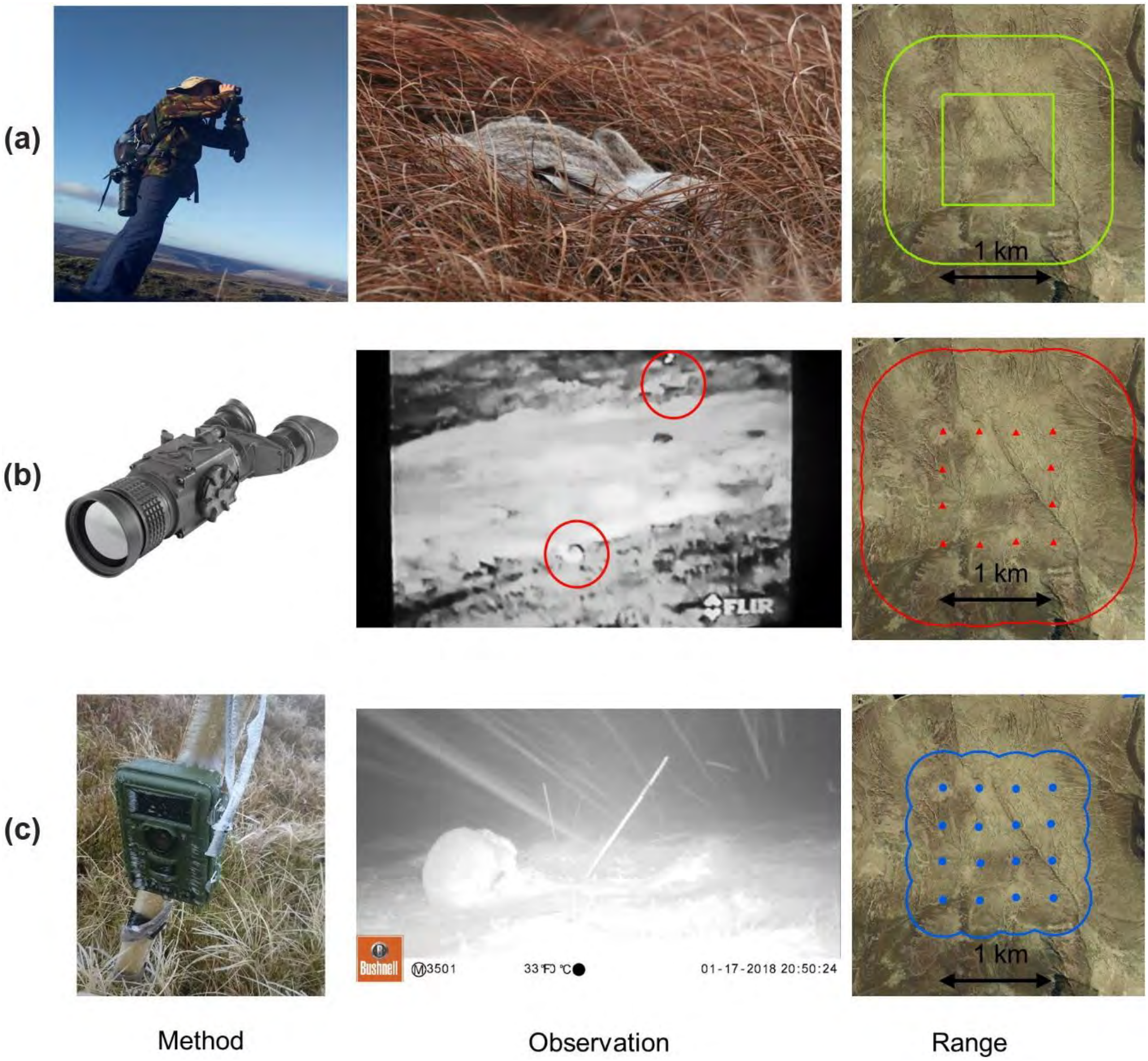

Figure 2. Photographs showing the three different methods. (a) Daylight visual surveys, (b) thermal imager, (c) camera trap. Left column shows the observation equipment. Central column shows each method's typical sighting of a mountain hare. Right hand column displays example survey location at site 1 for each method, duly surrounded by a buffer: measured to the furthest visual point (532 m) for daylight visual surveys; (740 m) thermal imager; for camera traps, buffer is portrayed to 333 m of each camera, the assumed home range of local mountain hares.

identification of hares which were easily distinguished from grouse *Lagopus lagopus* whose feathers blocked heat radiation except for beaks, and foxes *Vulpes vulpes* that were much larger (Fig. 2). For each detection, angle and distance measurements were recorded as during daylight surveys. Three sightings of leverets were excluded, to estimate adult densities only.

Camera traps

We placed between 12 and 16 camera traps at each of the six survey sites (Fig. 1). Due to logistical constraints, camera traps were deployed at site 1 before being moved sequentially to site 6 (they could not be deployed simultaneously). Cameras were left in situ for two to five weeks at each site (Supporting information), depending on weather conditions, camera performance and perceived risk of theft. Cameras were sited at the same locations as daylight visual surveys and thermal imaging surveys, along the Ordnance Survey map bounding grid lines of each site as well as several placed in the centre of each square for fuller coverage. Distances between cameras were thus 333 m, again this being the assumed home range diameter of mountain hares. Cameras were 14 MP Bushnell NatureView No Glow, set to high sensitivity. Pilot tests showed a large number of false detections would be elicited (wind blown vegetation). Capturing video might expend battery and memory capacity before revisits by staff and also make image review time excessive. Thus cameras were instead set to trigger at 1 s intervals with time-stamp recording. Camera functioning was evidenced by a 12 hourly 'field scan' setting. Cameras were installed on posts at 40 cm above ground level (Fig. 2) set facing north to avoid false triggers by sun movements. Bamboo canes were placed in a line at intervals of 2, 4, 6, 8 and 10 m in front of each camera to measure the distance of each hare to the cameraat 1 m spacing (Fig. 2) (Hofmeester et al. 2016, Howe et al.2017). Photos were managed with TIMELAPSE 2 (University of Calgary, Canada) software. Images were catalogued by location, date and time.

We reviewed the frequency of camera images of hares and considered one second as representing the survey snapshot period ('k') for point counts following advice from Howe et al. (2017) to use time periods < 3 s. For each positive detection we recorded each individual's radial distance to camera for distance sampling estimation. In a few caseswith darkness or poor focus this was difficult to determine.Images showed some hares, having appeared in the camera zone, inspected the distance marker cane or the camera itself.We considered this attraction behaviour, known to contribute to sampling bias (Corlatti et al. 2020) and discounted those images.

Unlike daylight visual surveys and night-time thermal imaging where surveys were time limited, camera traps can make detections 24/7. No detections are likely to be madewhen an animal is resting and so survey effort during day-light is highly vulnerable to false negatives, potentially lowering average density estimates. We defined the hare activity cycle using a frequency histogram of detections against eachhour of the 24-h cycle, fitting a smoothed density function for each site according to standard methods (Ridout and Linkie 2009, Rowcliffe 2014). Conservative approaches mayconsider analysis which refers to the peak diel periods when - 50% of activity occurs (Frey et al. 2017) or ≥ 55% activity (McGowan et al. 2019). However our camera sites occurred over four months, winter solstice to spring equinox, whennights became shorter. Thus when assessing the activity frequency densities and potential correlations between sites with R-package 'overlap' (Meredith and Ridout 2020) wefound different timings of bimodal activity patterns. For consistency we therefore defined the night-time period assunset-to-sunrise at the mid-term date per site (HM Nautical Almanac Office 2019) thought to provide accurate levels of activity (Vazquez et al. 2019). This night-time period encompassed > 95% of all camera trap detections.

Distance sampling

Data from each method were analysed using software distance ver. 7.2 (Thomas et al. 2010) including site, survey effort, number of detections, distance to each detection and cluster size (Buckland et al. 2001).

Daylight visual surveys were analysed using 'line transect' protocols and thermal imaging as 'points', each assuming 360° field-of-view. Camera trap surveys were also analysed as points; however survey effort had a restricted 42° field-of-view of each camera, thus distance analysis for camera trap data multiplied total effort 'k' by 42/360 following Howe et al. (2017). Model fit was optimised in each case using truncation of the most distant detections and variablebin width as appropriate. Models assessed included uniform, half-normal and hazard-rate models; and model averaging was also considered. Models were evaluated by referring to Akaike information criterion (AIC), χ^2 goodness-of-fit test values, detection probability (P) values and coefficient of variation (P CV) using established methods (Buckland et al. 2001). As sequences of camera trap detections occurring over several seconds were not independent we calculated the overdispersion factor ($\hat{c}$) and used log likelihood ($\mathscr{L}$) to calculate QAIC, i.e. the two step model evaluation approach of Howe et al. (2018).

Statistical analysis

Descriptive statistics were tabulated for a suite of parameters capturing survey effort, numbers of detections, detection distances and encounter rates for each survey method. Based on the surveys' efforts and results, we calculated and compared the level of effort to achieve a required precision of density estimate, using formulae from Buckland et al. (2001). Spatial autocorrelation of sightings (encounters) was examined with kernel density maps of detections using ArcGIS ver. 10.6.1 and tested using Moran's I index for each survey method. Comparison of sighting densities between the three methods was assessed by Pearson correlation of the kernel density maps. ArcGIS was used to map topographical gullies plotted as shapefile vector data(Ordnance Survey 2018), converted into a raster of gully density using the line density and polygon to raster toolbox functions (100 m cell size). The relationship betweenhare encounter rates and gully density was examined using linear regression for each survey method. Temporal trendsin camera trap encounter rate were examined using a separate general linear mixed model (GLMM) fitting 'Site' asa random factor to account for multiple observations per site (multiple days recording) and the sequential deployment of cameras at different sites, and with 'days since start of survey' fitted as fixed effect. Daily detections followeda negative binomial distribution. Statistical analyses were conducted using R ver. 3.6.1 (<www.r-project.org>) and R-package 'lme4' (Bates et al. 2015) for linear models following Crawley (2002).

Results

Daylight visual surveys

Over five days, the six sites were surveyed for a total of 26 h (Table 1, Supporting information). Daylight visual line transect surveys required 3–7 h per transect which were 4–8 km in length. Mean radial detection distance was 152 m and the furthest was 532 m. Thus, the survey rate was 0.98 km^2 perhour (Table 1). In total, 41 mountain hare detections wererecorded with 1 detection every 0.63 h (~38 min). Duringdaylight hours 95% of the detections were of solitary individuals, the remainder being pairs (Table 1). Owing to hiding and flushing behaviour of hares, 16 detections occurred within 30 m of the observer. Thus to enable a choice of detection function models, we truncated data at 100 mand assigned observations to bins at 5, 10, 20 and 100 m (Table 2). Candidate models showed high χ^2 goodness-of-fit (GOF) values (> 0.31) with similar detection probabilities. The half-normal model reported lowest AIC, p = 0.28, (cv) = 0.20 and was selected for density estimation. (Table 2, Fig. 3a). Following data truncation, encounter rate was0.82 km^{-1}, (cv) = 0.31 and observations were singles making

Table 1. Descriptive summary of sampling effort, detections and their distance from the observer and surveyed area (based on furthest detection distance) for daylight visual surveys, thermal imaging and camera trapping. Samples and detections are total values before truncation. Per method 'Summary' rows: Σ = column total; $\bar{x}$ = column mean. All camera trap values based on night-time (informed by Fig. 4). Calculation of area surveyed at each site for cameras = (further detection distance per site)^2 × π × camera field of view restriction (42/360) × number of cameras per site. The survey rate (km^2 per hour) for camera traps is not calculated as they are considered to be in continual operation.

Method (survey units)	Samples	Hours effort	Detections	Mean cluster size	Mean detection distance (m)	Furthest detection (m)	Detections per hour	Hours to 1st detection	Surveyed area (km^2)	Survey rate (km^2 per hour)
Daylight visual surveys Sample units = Transect length km										
Site 1	4.62	3	8	1.00	149	305	2.67	0.38	3.11	1.04
Site 2	4.82	4	11	1.09	220	446	2.75	0.36	4.92	1.23
Site 3	4.71	4	1	1.00	192	192	0.25	4.00	1.93	0.48
Site 4	4.70	4	12	1.08	172	532	3.00	0.33	5.89	1.47
Site 5	4.89	4	5	1.00	87	362	1.25	0.80	3.95	0.99
Site 6	8.16	7	4	1.00	94	263	0.57	1.75	4.51	0.64
Summary	$\Sigma = 31.91$	$\Sigma = 26$	$\Sigma = 41$	$\bar{x} = 1.03$	$\bar{x} = 152$	$\bar{x} = 350.0$	$\bar{x} = 1.75$	$\bar{x} = 0.63$	$\Sigma = 24.31$	$\bar{x} = 0.98$
Thermal imaging Sample units = points (number of replicates in brackets)										
Site 1	12 (20)	16	26	1.34	185	508	1.63	0.62	16.21	1.01
Site 2	12 (22)	22	38	1.31	256	612	1.73	0.58	25.88	1.18
Site 3	12 (27)	19	30	1.43	218	500	1.58	0.63	21.20	1.12
Site 4	12 (22)	20	87	1.44	270	682	4.35	0.23	32.14	1.61
Site 5	12 (12)	10	12	1.08	436	740	1.20	0.83	20.64	2.06
Site 6	11 (11)	10	13	1.38	220	528	1.30	0.77	9.63	0.96
Summary	$\Sigma = 71$ (114)	$\Sigma = 97$	$\Sigma = 206$	$\bar{x} = 1.33$	$\bar{x} = 264$	$\bar{x} = 595.0$	$\bar{x} = 1.96$	$\bar{x} = 0.47$	$\Sigma = 125.71$	$\bar{x} = 1.32$
Camera traps Sample units = number of cameras (total camera nights in brackets) [hours per night in square brackets]										
Site 1	16 (287) [17]	4879	768	1.00	2.33	9	0.15	6.35	0.000475	-
Site 2	16 (376) [17]	6392	550	1.00	2.60	10	0.08	11.62	0.000586	-
Site 3	12 (148) [16]	2368	213	1.00	1.92	6	0.09	11.12	0.000158	-
Site 4	16 (331) [15]	4965	1128	1.00	2.91	12	0.23	4.40	0.000844	-
Site 5	16 (386) [14]	5404	479	1.00	2.60	8	0.09	11.42	0.000375	-
Site 6	15 (272) [13]	3536	573	1.00	2.41	9	0.16	6.17	0.000445	-
Summary	$\Sigma = 91$ (1800) [varying]	$\Sigma = 27\,544$	$\Sigma = 3705$	$\bar{x} = 1.00$	$\bar{x} = 2.46$	$\bar{x} = 9$	$\bar{x} = 0.13$	$\bar{x} = 8.51$	$\Sigma = 0.002884$	-

1.00 cluster size (Table 3). The contribution to variation of density estimate was encounter rate (72.5%) and detection probability (27.5%).

Night-time thermal imaging

Over eleven nights, a total of 114 point transects located alongthe boundary of the six sites were surveyed for a total of 97 h(Table 1, Supporting information). Surveys needed 5–7 h tocover up to 12 points per night. Mean detection distance was264 m and the furthest was 740 m. Thus, the survey rate was 1.32 km^2 per hour or 0.00587 km^2 (i.e. 5870 m^2) per point (Table 1). In total, 206 mountain hare detections were made with 1 detection every 0.47 h (~28 min). During darkness 74% of detections were solitary individuals, the remainder groups of up to 8 hares (Table 1). For modelling, detections were truncated at 350 m. All candidate detection functions achieved model fit (Table 2). The hazard-rate model had low-est AIC and highest χ^2 GOF = 0.78 with P = 0.34, (cv) = 0.21and was selected for density estimation (Fig. 3b). Following data truncation encounter rate was 1.33 k^{-1}, (cv) = 0.12 and estimated cluster size 1.31, (cv) = 0.04 (Table 3). The con- tributors to variation of density estimate were encounter rate (24.5%), detection probability (73.9%), cluster size (1.6%).

Camera traps

Over four months, a total of 91 camera locations were installed throughout the six survey squares (total = 1800 days i.e. 27 544 night hours) (Table 1, Supporting infor- mation). In total, 107 000 images were captured, retrieving 5112 images of mountain hares per 1 second snapshot window. The remaining images were false triggers: wind- blown vegetation or other animals e.g. foxes, stoats *Mustela erminea*. Of these images 1329 showed hares attracted to marker canes or the camera, so were excluded, leaving 3783 separate detection events.

Of these, just 78 detections (2%) occurred by day; 3705 detections (98%) during night-time, averaging 1 detectionper 8.5 h (Table 1). Night-time showed the largest activitypeak after sunset, followed by moderate activity periods, anda distinct peak before dawn (Fig. 4). This pattern was similarat each site for the study duration: activity occurring over17 night hours late November (site 1), compressing into 13 night hours late March (site 6). However the timing ofnight-time activity peaks differed between sites. The highest correlation was 86% between sites 1 and 5; the lowest cor-relation 51% between sites 3 and 6. Based on night-time detections, the mean detection distance was 2.4 m and thefurthest was 12 m, and 95% of detections were within 5m of the camera (Table 1). Thus, the survey rate averaged0.0003 km^2 (i.e. 30.0 m^2) per camera (Table 1). Night-timedetections for distance analysis modelling assessments were allocated to bins at 1, 2, 3–4 and 5 m (Table 2). Having cal- culated QAIC and ($\hat{C}$) for candidate models, the latter was lowest for the hazard-rate model at 1.8 and χ^2 GOF = 0.18, thus was selected for reporting with P = 0.17, (cv) = 0.03(Table 2 Fig. 3c). Camera trap encounter rate was 0.00030k^{-1}, (cv) = 0.14 (Table 3, Supporting information). Cluster size was 1.00, (cv = 0.01). The contribution of variation to the density estimate was encounter rate (95.4%) and detec-tion probability (4.5%).

Table 2. Summary of models showing number of parameters (# para), AIC, Delta AIC, χ^2 values, degrees of freedom (df), and χ^2 goodness offit (GOF), detection probability (P) and co-efficient of variation values (P CV). For camera traps, log likelihood (log $\mathscr{L}$), overdispersion factor ($\hat{C}$) and QAIC are shown for assessments of over-dispersed data (Howe et al. 2018). For each survey method, data selections and number of observations (n obs) are listed. Models selected for subsequent estimations are marked with asterisk *.

	Model (key)	# para	AIC	Delta AIC	χ^2	df	χ^2 GOF	p	P CV			
	Daylight visual surveys	Data truncation at 100, bins at 5 m, 10 m, 20 m and to 100 m, n obs = 26										
	Uniform + cos	2	74.3	2.3	0.7	1	0.40	0.31	0.36			
	Uniform + polynomial	1	72.3	0.3	0.6	2	0.73	0.30	0.18			
*	Half-normal + cosine	1	72.0	0.0	0.4	2	0.82	0.28	0.20			
	Half-normal + Hermite	1	72.0	0.0	0.4	2	0.82	0.28	0.20			
	Hazard-rate	2	74.6	2.6	1.0	1	0.31	0.33	0.15			
	Thermal Imager	Data truncation at 350 m, n obs = 152										
	Uniform + cosine	2	1753.6	0.9	11.2	15	0.73	0.29	0.13			
	Uniform + polynomial	3	1755.9	3.3	11.2	14	0.66	0.31	0.12			
	Half-normal + cosine	3	1753.9	1.3	9.7	14	0.77	0.32	0.29			
	Half-normal + Hermite	1	1757.7	5.0	17.6	16	0.34	0.38	0.09			
*	Hazard-rate	2	1752.6	0.0	10.5	15	0.78	0.34	0.21			
										log $\mathscr{L}$	$\hat{C}$	QAIC
	Camera traps	Data truncation at 5 m, bins at 1, 2, 3-4, 5 m; n obs = 3506										
	Uniform + cosine	1	9371.4	875.2	876.4	2	0.00	0.30	0.01	−4684.6	438.2	12.9
	Uniform + cosine	2	8607.4	111.2	109.3	1	0.00	0.18	0.02	−4301.7	109.3	14.0
	Uniform + polynomial	1	10010.5	1514.3	1598.5	2	0.00	0.38	0.01	−5004.2	799.3	13.6
	Uniform + polynomial	2	9359.1	862.9	863.2	1	0.00	0.30	0.02	−4677.5	863.2	14.8
	Half-normal + cosine	1	8709.6	213.4	255.9	2	0.00	0.17	0.02	−4353.8	128.0	36.3
	Half-normal + cosine	2	8562.5	66.3	68.7	1	0.00	0.12	0.03	−4279.2	68.7	37.7
	Half-normal + Hermite	1	8709.6	213.4	255.9	2	0.00	0.17	0.02	−4353.8	128.0	36.3
	Half-normal + Hermite	2	8710.4	214.2	254.2	1	0.00	0.17	0.05	−4353.2	254.2	38.3
*	Hazard-rate + simple	2	8496.2	0.0	1.8	1	0.18	0.17	0.03	−4246.1	1.8	4721.9
	Hazard-rate + simple	3	8498.2	2.0	1.7	0	0.00	0.17	0.03	−4246.1	-	-

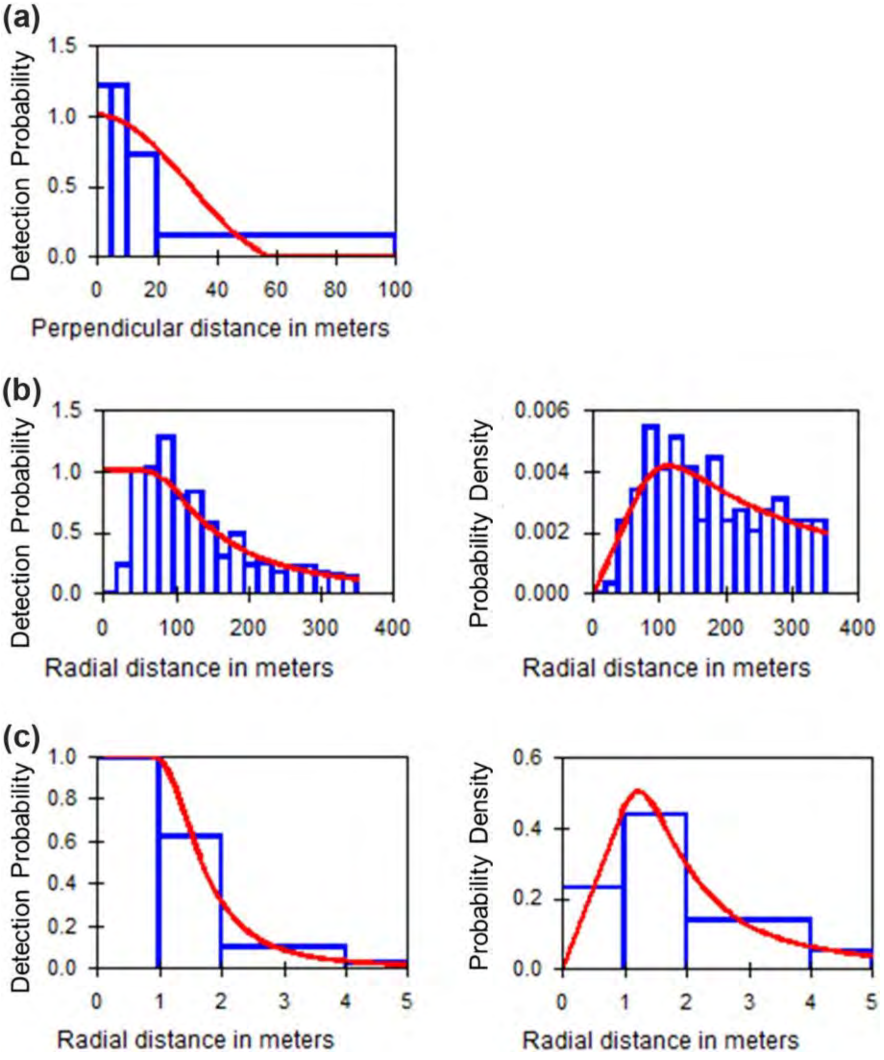

Figure 3. Distance sampling detection probability and probability density function histograms for (a) daylight visual surveys (uniform model with cosine adjustment and data allocated to bins at 5, 10, 20 and to 100 m), (b) nocturnal thermal imaging (hazard-rate model with simple polynomial adjustment and data truncated at 350 m), (c) camera traps (hazard-rate model with simple polynomial adjustment and data allocated to bins at 1, 2, 4 and to 5 m.

Comparison of methods

Distance sampling models from daylight visual surveys estimated density at 14.3 hares km^{-2} (95%CI 6.3–32.5). Nighttime thermal imaging from points estimated density at 12.1 hares km^{-2} (95%CI 7.6–19.4). Camera trapping estimated density was 22.6 hares km^{-2} (95%CI 17.1–29.9) (Table 3).

Extrapolated to the entire 49 km^2 study site at Holme Moss, density estimates suggested a total population of 705 hares (95% CI 311–1597) from daylight visual surveys, 597 hares (95% CI 374–951) from thermal imaging and 1109 hares (95% CI 839–1467) from camera traps (Table 3). Assessing the density estimates and the effort required to achieve reliable precision i.e. 20% coefficient of variation, daylight visual surveys would require 109 km of transects; thermal imagers would require 164 points; and camera traps would require 45 installations (Fig. 5). Comparing field effort daylight visual surveys surveying at 1.2 km per hour would require 89 h effort; thermal imager surveying 1.2 points per hour would need 140 h effort. Camera traps needing 3 h per installation (1 h set up, 1 h revisit, 1 h take down) would require 134 h of field effort and if a manual image review process was used (e.g. Timelapse software with auto-completing data entry, estimating 15 s per image), a further 218 h of desk time (Fig. 5).

Spatial and temporal variation

Considering sighting locations per site (untruncated data), daylight visual surveys showed large differences of sightings (encounter rates) with site 3 lowest at 0.2 km^{-1} and site 4 highest at 2.5 km^{-1}, with a sparse distribution except for sites 2 and4 (Fig. 6). Thermal imager observations occurred at a meanrate from 1.0/point (site 5) to 3.9/point (site 4) (Fig. 6) and appeared to show 2 clumped distributions around site 4 (Fig. 6). Of the thermal imager points, 99 achieved detections, 15 did not, indicating mostly widespread presence of hares acrossall sites. Camera trap observations occurred at a mean rate from 0.0002 k^{-1} (site 3) to 0.0005 k^{-1} (site 4), and showed the most intense occurrence around site 4 (Fig. 6). Of the 91 cameras, 77 achieved detections and 14 made no detection, indicating a widespread distribution though with some negative locations.

Table 3. Estimates of detection probability, density and abundance obtained from distance sampling analyses for all three survey methods. Value = point estimate; CV = coefficient of variation; LCL and UCL 95% lower and upper confidence limits. Encounter rate: Daylight visual n/km = encounters per km; Thermal imager: n/k = encounters per point; Camera traps n/k = encounters per second. Abundance estimate derived from density value projected to the 49 km^2 of Holme Moss.

Method	Value	CV	LCL	UCL
Detection probability				
Daylight visual surveys	0.28	0.20	0.19	0.42
Thermal imager	0.34	0.21	0.23	0.50
Camera traps	0.17	0.03	0.16	0.18
Encounter rate				
Daylight visual surveys (n / km)	0.82	0.31	0.36	1.81
Thermal imager (n k)	1.33	0.12	1.05	1.68
Camera traps (n/k)	0.00030	0.14	0.00023	0.00039
Cluster size				
Daylight visual surveys	1.00			
Thermal imager	1.31	0.04	1.20	1.44
Camera traps	1.00	0.01	1.00	1.00
Effective strip or radius width (m)				
Daylight visual surveys	28.3	0.19	18.9	42.2
Thermal imager	202.5	0.10	165.3	248.2
Camera traps	2.1	0.01	2.00	2.13
Density (hares km^{-2})				
Daylight visual surveys	14.3	0.37	6.3	32.5
Thermal imager	12.1	0.24	7.6	19.4
Camera traps	22.6	0.14	17.1	29.9
Abundance				
Daylight visual surveys	705	0.37	311	1597
Thermal imager	597	0.24	374	951
Camera traps	1109	0.14	839	1467

Hare detections were not spatially autocorrelated using any survey method (Moran's $I_{\text{daylight visual}} = -0.12$, Z = 0.12; Moran's $I_{\text{thermal imaging}} = 0.07$, Z = 0.99; Moran's $I_{\text{camera traps}} = -0.15$, Z = −0.27). Sighting density was strongly spatially correlated between the three methods (Pearson $r_{\text{daylight visual} \sim \text{thermal imager}} = 0.55$, $p < 0.001$, $r_{\text{thermal imager} \sim \text{camera traps}} = 0.45$, $p < 0.001$ and $r_{\text{camera traps} \sim \text{daylight visual}} = 0.52$, $p < 0.001$ (Fig. 6 and Supporting information). Site 4 was consistently estimated to have the highest sighting density regardless of the survey method (Fig. 6). Sites 1 and 2 also had substantial sighting densities.

Site encounter rates using daylight visual surveys and camera trap surveys were unaffected by gully density but encounter rates using night-time thermal imaging were significantly negatively associated with gully density ($F_{1,4} = 9.11$, β ± SE = −0.833 ± 0.0009, p = 0.039, $r^2 = 0.69$). Site 4 which had the highest density estimate of mountain hares, had the lowest gully density of any site (Fig. 7).

Camera traps ran continuously (24/7) from November to March. Sequential deployment (accounted for imperfectly using the random factor of site) reported encounter rates showing a near significant decline by 62% over the four months from 37.6 to 14.3 encounters per day (Fixed effects standardised β = −0.009, z = −1.55, p = 0.12; Random effects: Site Var = 0.10 SD = 0.324; Fig. 8).

Discussion

Our study compared three survey methods for mountain hares which provided very different kinds of observations and density estimates. Daylight visual surveys produced the fewest observations, seeing mainly single hares and appearing to under record many hares hiding by day. The method did provide sufficient observations to enable monitoring of relative density but with very wide confidence intervals. By night the thermal imager frequently observed single or large groups of hares over the furthest distances and estimated density with narrower confidence intervals. However thermal imaging opportunities were limited by bad weather. Camera traps monitored constantly and achieved the largest number of detections reflecting night time activity of hares, capturing mostly single animals at very short observation distances. Camera trap density estimates were much larger than for daylight visual sampling and thermal imaging and were more reliable, but were susceptible to many assumptions. Notwithstanding differences in detection rates the locations of sightings from each method were highly spatially correlated.

Daylight visual surveys

Daylight visual surveys for mountain hares have been criticised when used in areas of low density or during the day when hares are inactive (Petrovan et al. 2011, Newey et al. 2018). Our expectation was Holme Moss would elicit frequent occurrences of hares (Mallon et al. 2003), yet we achieved very few observations. The small sample size we achieved was below the minimum required for distance sampling and contained some heaping of detection distances. The nature of hiding and flushing hares caused many detections to occur at short range. Thus, when selecting detection function models, we were obliged to use a smaller data set with few, wide bins. This selection may have also precipitated a narrow effective strip width and this may have contributed to the overall density estimate as being higher

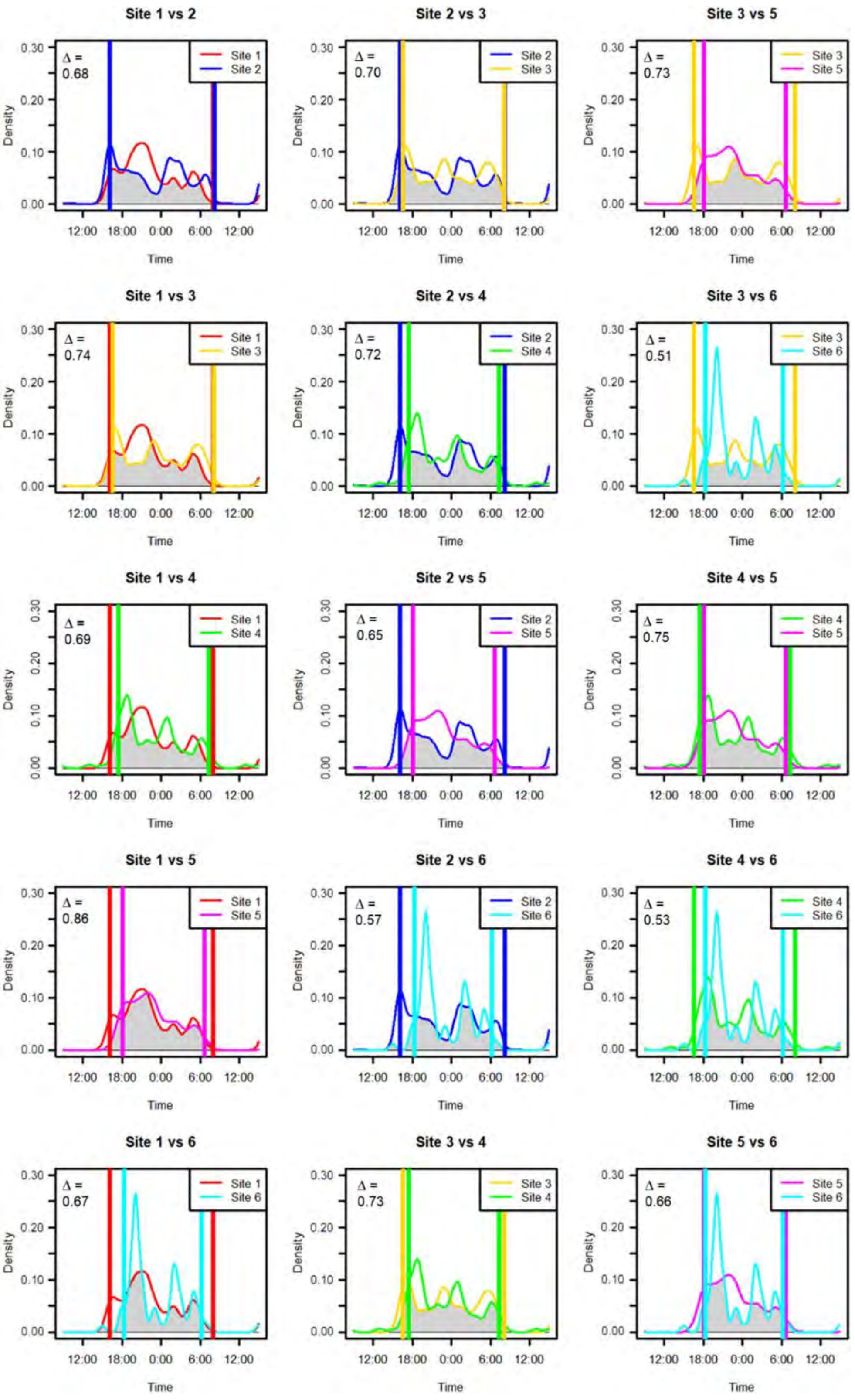

Figure 4. Diel activity at sites showing von Mises kernel densities and pairwise overlaps with other sites. The x-axis shows time of day. They-axis is the frequency estimate of detections. The overlap of densities, common to each pair of sites, is the shaded grey area below both curves. Overlap coefficient values between compared densities is top left. The mean overlap of all pairwise combinations was 68%; all exceeded 50%. Vertical lines indicate sunrise and sunset times for each site pair; night-time hours reducing with spring onset. Dates ofoperation: site 1: 24 Nov 2017–18 Dec 2017 (17 night hours); site 2: 11 Dec 2017–11 Jan 2018 (17 night hours); site 3: 9 Jan 2018–25 Jan 2018 (16 night hours); site 4: 25 Jan 2018–9 Mar 2018 (15 night hours); site 5: 16 Feb 2018–30 Mar 2018 (14 night hours); site 6: 9 Mar 2018–30 Mar 2018 (13 night hours). Images produced with R-package ‘overlap’ (Meredith and Ridout 2020) based on Ridout and Linkie (2009).

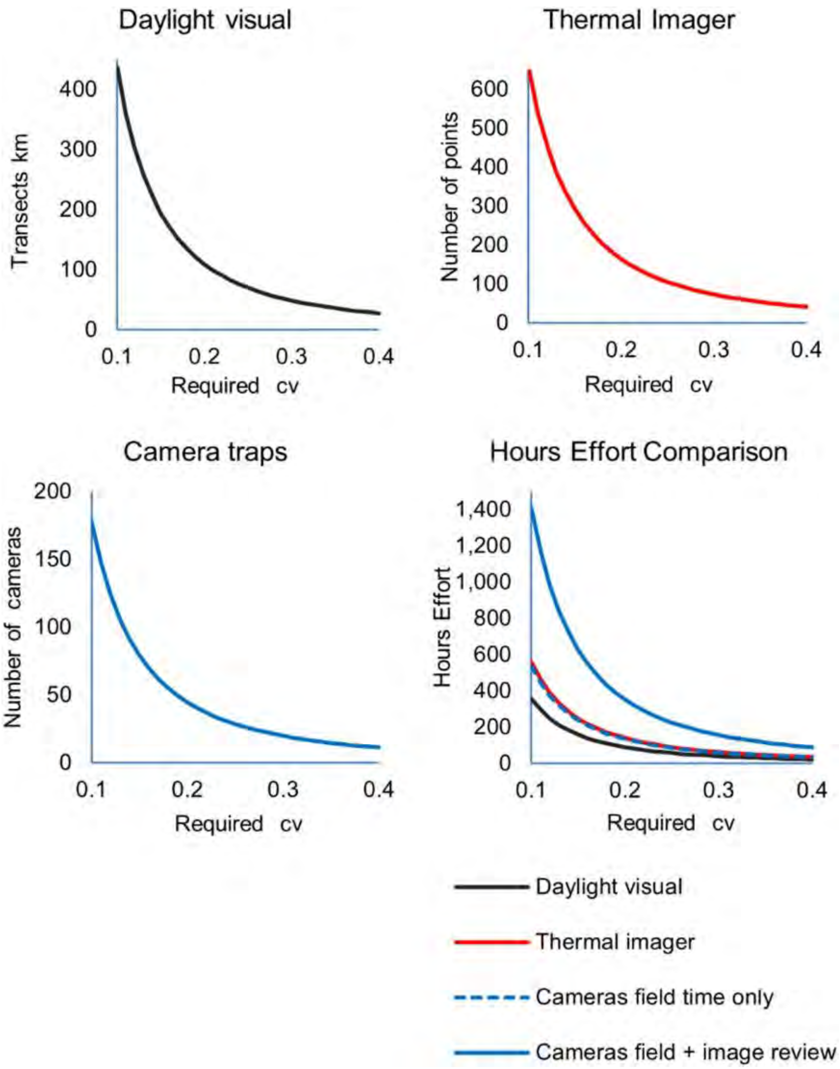

Figure 5. Effort required to achieve a target precision of density estimate, as measured by coefficient of variation. Input to the hours effort comparison is based on Table 1 and assumes for daylight visual surveys 1.2 km h^{-1} walked; for thermal imagers 1.2 point h^{-1} surveyed. Camera traps assumes cameras are in situ for average 21 days. 'Camera field time only' based on 3 h per camera being one installation visit,one maintenance visit, one retrieval visit. 'Image review' time assumes 1176 images per camera achieved with 15 s review time per image = additional 4.9 h per camera.

than for thermal imaging. This was surprising as one might expect thermal imaging to be observing more such noctur-nal animals leading to a higher encounter rate and density estimate. Although detection probability variation was moderate, encounter rate variation was high. Consequently, the density estimate possessed wide confidence intervals and variation. To achieve reliable estimates, useful for ongoing monitoring, surveys should achieve 80 or more detections (Buckland et al. 2001). This suggests that studies simi-lar to ours would benefit from replicate surveys to achieve a larger sample size to result in more accurate population density estimates, were this important for monitoring design goals. In retrospect for our own study we might have sacrificed some camera trap management time for more line transect surveys. Alternatively, daylight survey effectiveness might be improved by 3 or 4 observers walking abreast. Daylight visual surveys provided an advantage as transect routes forced the observer to traverse gullies, opening up fields of view and occasionally enabling sheltering hares to be seen.

Night-time thermal imaging

This study deployed an advanced thermal imager with mounted laser range finder for measuring distances to object in complete darkness and with point transect protocols. Whilst seemingly dangerous to walk across moorland by night, this could in fact be done as safely as by day, though slower. However, it was physically difficult to achieve 12 van- tage points, spaced 333 m apart, in a single night for a single observer. As the thermal imager was viewed through two lenses on its internal screen, it provided a 3D image and alle-viated issues of eye strain. Cold temperatures below −5°C flattened batteries within 60 min. Sinking hill fog or increas-ing winds through some nights, cut surveys short. Ther- mal imaging enabled observations of hares across a broad landscape, where they exhibited feeding and social behav- iour. The presence of the observer did not prompt evasive movement. The method worked well on snow. Encounterrates provided a sample size greater than the ~ 80 detections

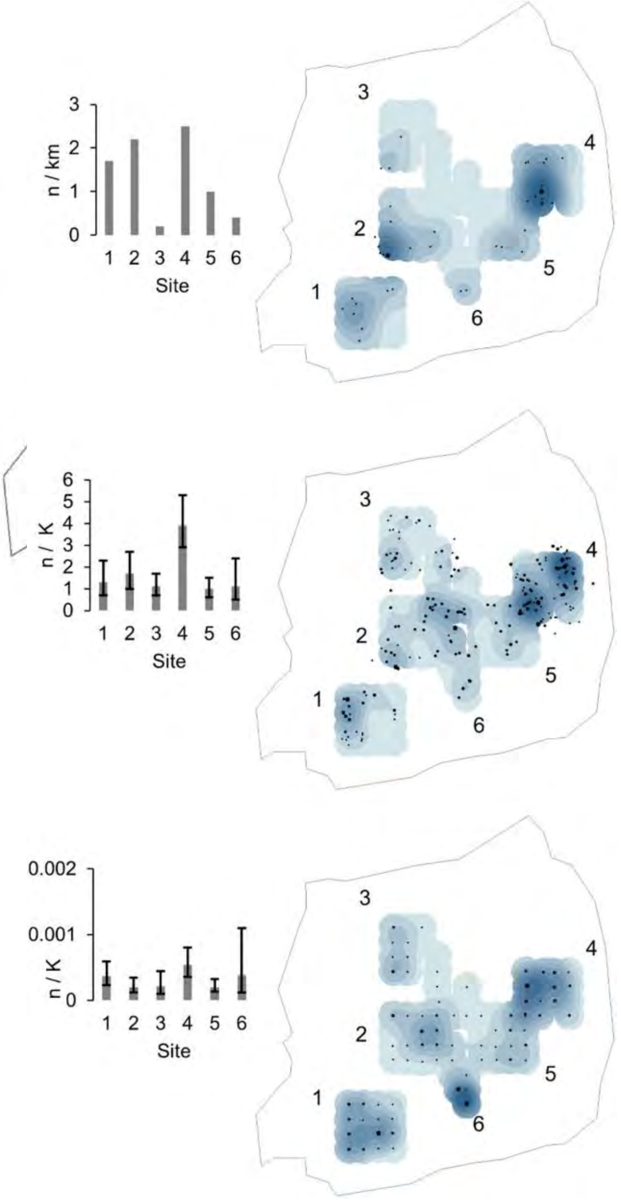

Figure 6. Sightings per method per site for (a) daylight visual surveys, (b) thermal imager and (c) camera traps. Column charts show encounter rate value estimates based on all sightings, with 95% confidence intervals for thermal imager and camera traps. Kernel density maps show spatial variation of hare sightings, with site numbers. Black dots indicate sightings, increasing in size to show clusters for daylight visual and thermal imager, (normalised for replicates) and camera traps (normalised for nights in operations). Background shading increases to dark based on sighting intensity. Kernel density boundaries are based on 333 m buffer of camera locations, hence some daylight visual sampling and thermal imager encounters fall outside this area.

Figure 7. Map of gullies (lines) with gully density (cells) across the six study sites at Holme Moss. Numbers denote each study site.

required according to distance analysis standard guidelines (Buckland et al. 2001). Distance histograms showed good model fit: a broad shoulder and gradually decreasing distance shape, providing lower variation of detection probability. The lack of detections within 30 m might suggest evasive movement by hares, although this may be expected when carrying out distance sampling with point counts (Buckland et al. 2001). Rumpled terrain occasionally meant hares might be within viewing range but hidden in gullies. Future thermal imaging studies could by day prospect for a large setof unimpeded vantage points, from which to draw a random sample to visit by night. Our findings suggested high levels of precision could be achieved with a logistically manageable number of points, requiring ~15 nights, assuming favourable weather. Such a device is a considerable investment.

Camera traps

Camera traps provided a practical method of constant surveillance in all weathers including snow. Installation of cameras across moorland was slow: often one day for two peopleto move four cameras, two kilometres. The 2–3 kg size of

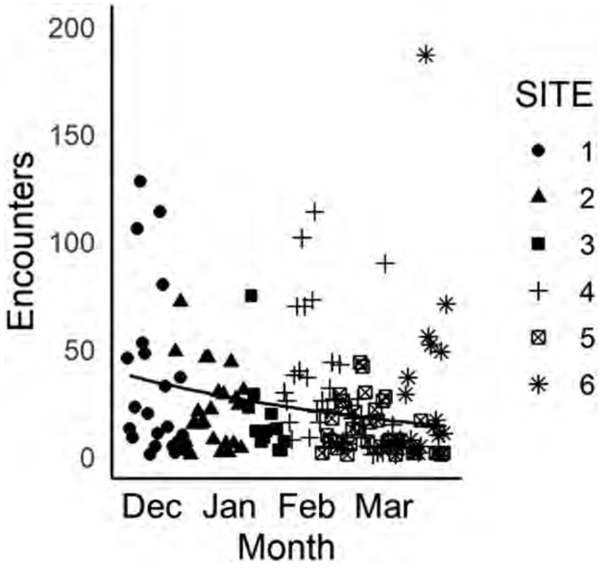

Figure 8. The regressed number of encounters (line) per camera (point shapes) is seen to decrease over the study period, end Nov 2017 to March 2018, taking into account 'Site' as a random effect.

hares required maximum camera sensitivity, also capturing blowing vegetation and 'blank' images, requiring more filtering time. However, operating 24/7, cameras appeared to avoid false negative detections. Image times conveyed peak nocturnal activity periods, even during extremely cold nights. There were two night-time peak activity phases, consistent with records for Irish hare *Lepus timidus hibernicus* Caravaggi et al. (2018). The narrow field of view captured nomore than 2 hares at a time, perhaps under recording largergroups, as observed by the thermal imager. Camera traps require financial outlay, bear theft risk and need considerable field effort. Image review time is substantial yet can be reduced using image recognition software (Schneider et al. 2020).

In our study, camera trap detections occurred at short ranges, so the detection probability histogram allocated 3506 encounters to just four distance bins, producing lowvariation of detection probability (cv = 0.03). Camera trap density estimates showed less variation than the thermal imager. Our findings suggested high levels of precision couldbe achieved with half the camera installations as we had used, with field time of ~ 20 days.

Monitoring surveys are expected to fulfil the principal assumptions of distance sampling. However, for the camera trap analysis we noted certain factors can have a large effect on density estimates (Fig. 9).

Firstly, most of our camera trap detections occurred at very short distances (≤ 5 m) creating a fine scale sensitivity in the detection function histogram for our Distance analysis. The low detection probability estimate (0.17), impliedto 5 m, 83% of hare encounters were missed and reported ashort effective strip radius (2.1 m), implying a higher densityestimate. This radius was smaller than recorded elsewhere e.g. Hofmeester et al. (2016) at 3.69 m in dense understorey. This was surprising: when siting camera traps, we saw and avoided hare trails on snow and vegetation. However camera trap passive infra-red sensors can under-record at night, at different air temperatures, and micro-topography can affect detection rates (Hofmeester et al. 2018). It is possible detections may occur at further distances if surveyingon flat arable-type land. Thus detection rates and measurement of lagomorphs in camera trap zones, merits furtherstudy within enclosure-based settings (Rowcliffe et al. 2008).

Secondly, snapshot window (k) definition greatly affected effort values and the number of defined detections. We opted for k = 1 second, which provided both the highest number of absolute encounters and also the most conservative estimate of encounter rate. Other studies have used

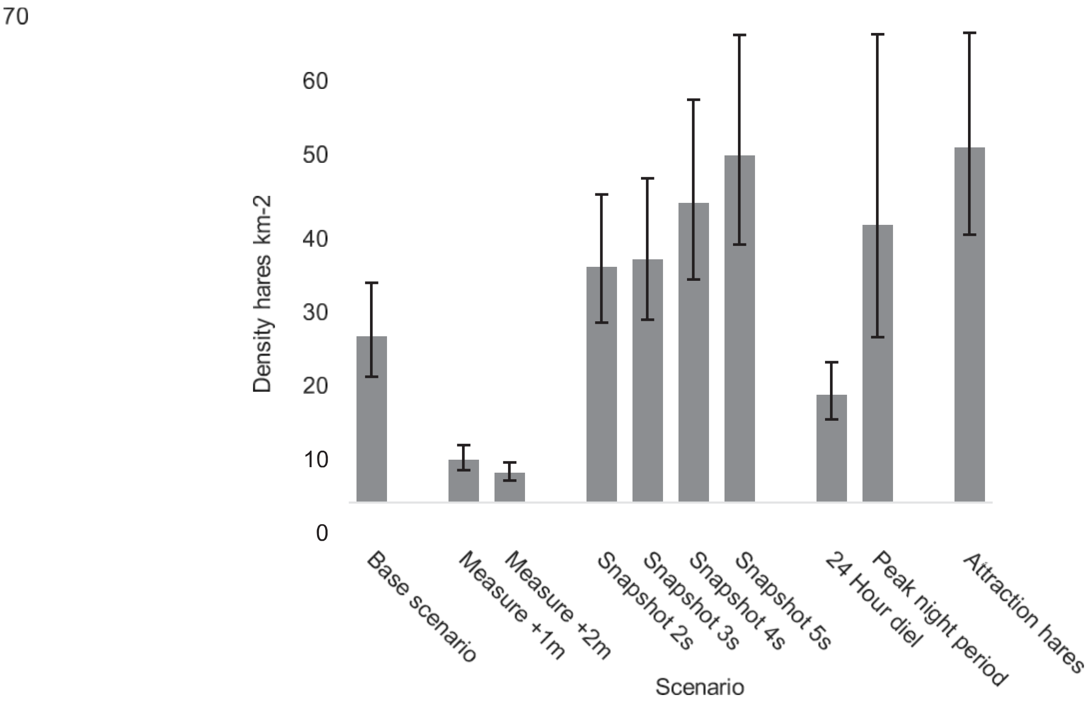

Figure 9. Analysis of alternate scenarios providing camera trap density estimates. The x-axis shows different data treatments or assumptions.The y-axis shows consequent density of hares km^{-2}. Columns are density values with 95% confidence interval error bars. To maintain consistency amidst the comparisons, all scenarios used the same data filter with detection distances binned at 1, 2, 4 and to 5 m with theHazard-rate model with simple polynomial, which in all cases achieved lowest AIC scores of candidate models. 'Base scenario' was the scenario eventually chosen for our camera trap estimate for comparison with daylight visual sampling and thermal imager. This assumes correct measurements (metres) of distance to hare; k snapshot window = 1 second; diel period is sunset-to-sunrise (Fig. 4); and hare imagesshowing attraction behaviour are discounted. The alternate scenarios each use the same assumptions and change one factor as follows: 'Measure +1 m, +2 m' highlights the effect of increasing the measured distance to camera of all hare detections by 1 m or 2 m which wouldlead to an increase in detection probability and lower density estimate. This is an exaggerated scenario, yet serves to demonstrate the sensitivity. 'Snapshot 2s, 3s, 4s or 5s' shows the effect of increasing snapshot window k, which reduces effort to a much greater degree thanencounters, thus increasing density. '24 hour diel' uses full 24 hour period, correspondingly greater effort, very few additional detections. 'Peak night period' uses a 55% peak night activity period per site (McGowan et al. 2019) with consequently reduced effort. 'Attractionhares' includes a further 1318 images (after truncation) when dwelling behaviour observed.

longer durations: k = 2 seconds of Howe et al. (2017), k = 13 seconds (Corlatti et al. 2020). Our alternative scenarios suggested a gradual increase of k value brought fewer encounters, though disproportionate to the larger decrease in k units, thereby increasing encounter rates and thus density estimates. This effect diminished with increasing values of k. Further assessments of this relationship may require consideration of animal movement duration relative to camera detections, possible behavioural biases; or when modelling, setting thresholds for the influence of different values of k.

Thirdly, encounter rate estimation may be impacted bythe number of night hours, varying by time of year and latitude or alternatively affected by choice of peak activity period (Frey et al. 2017, McGowan et al. 2019, Vazquez et al.2019). Our activity frequency estimates showed different peak activity periods at different sites. This might have beencaused by hares altering their feeding patterns because of changes to day length, or varying snow cover requiring longer foraging periods. Hence we chose sunset-to-sunrise for consistency between sites.

Fourthly, some images showed individual hares 'dwelling' on the camera trap site. Even with videos, it is hard to definesuch behaviour as happenstance or genuinely biased. A rulesset may assist for rejecting such images. For example, we discarded any image where the hare's nose was within ~ 5 cmfrom the bamboo cane or camera. Attraction behaviour may be mitigated with marker canes used as reference photo, then removed, reprojecting their positions on ensuing computer images (Caravaggi et al. 2016), using video or having two cameras facing each other.

Ecological inferences

Between the methods we found a strong correlation between sighting density, and the similarity of detection probabilities for each method lend credibility to reported densities. The spatial correlation suggests the methods detected similar patterns of animal distribution even though they exhibited different detection rates. Methodological constraints (e.g. timing delay due to inclement weather) may explain some variation in our findings: some sites were surveyed early or late in the winter, during which time hare behaviour and consequent detectability changes. By late March, daytime hare activity often changes from dormant isolation to social grouping and mating. The assessment with the camera traps, statistically mitigating for site differences, showed encounter rates largely decreasing throughout the survey season. This may be understandable: an exceptional season of high winds and deep snow falls may have caused winter mortality.

These findings represent important indicative baselines for local monitoring and may inform assessments of other groups of native or reintroduced mountain hares. Notwithstanding its remarkable 150 year tenure, the Holme Moss mountain hare densities may be considered low comparedto many populations in Scotland which commonly reach 20–50 hares km^{-2} (Watson et al. 1973, Newey et al. 2018).

Conclusions

We report the practical survey effort, scale, encounter rates, density estimates and measures of precision which may be helpful for the planning of studies of elusive or nocturnal animals in difficult terrain. Daylight visual sampling is low cost, is logistically simple, can rapidly cover much ground and can achieve precise density estimates, yet, transpiring byday, may fail to observe cryptic nocturnal animals, thereby reporting lower encounter rates and thus underestimating abundance. For somewhat more effort, a high power thermal imager achieves potentially more observations of nocturnal animals including at long distances and consequent higher density estimate precision. It is recommended when surveying accessible areas, with dependable fog and wind free weather. By contrast camera traps can provide constant monitoring and at night over long periods in all weathers. They are thus useful for long term surveys, placed in locations which are difficult to access frequently or where it would be hazardous to venture in darkness. Camera traps can achieve large numbers of detections, including at night, recording the peak activity levels of nocturnal animals.

However between the methods, daylight visual sampling and thermal imager surveys both work well in applying the principles of distance sampling. Practically speaking, camera trap distance sampling operates effectively in achieving large data sets and can adopt distance sampling principles. However the consequent models need contemplation of additional assumptions and sensitivity modelling. Where there is insufficient empirical data, inferences may require subjective analytical decisions, potentially rendering camera trap distance sampling estimations less robust.

Acknowledgements – We thank RSPB Dove Stone, United Utilities and Upperwood Estate for fieldwork permissions and J. Mann of FLIR for advice on thermal imagers. We thank G. Pettigrew, M. Kocsis, J. Minshull, K. Boyd, C. Rice, D. Hogg and A. Oliver for support with fieldwork and M. Jones, A. Reuleaux and A. Hashmi for comments which improved earlier drafts.

Funding – Research funding was kindly provided by the People's Trust for Endangered Species (PTES), the Hare Preservation Trust, the British Mountaineering Council, Queen's University Belfast (QUB), Penny Anderson Associates, South-West Action for Hares and Manchester Metropolitan University (MMU).

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3r2280gg0> (Bedson et al. 2021).

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Supporting information is available at the Dryad repository is an identical copy of the material occurring within this thesis

Received: 20 March 2021 | Revised: 5 February 2022 | Accepted: 24 February 2022

DOI: 10.1002/ece3.8744

RESEARCH ARTICLE

Ecology and Evolution Open Access WILEY

Highest densities of mountain hares (*Lepus timidus*) associated with ecologically restored bog but not grouse moorland management

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Funding information

Hare Preservation Trust, Grant/Award Number: HPT Grant 2017-20; Queen's University Belfast, Grant/Award Number: QUB.NR.2017; Penny Anderson Associates, Grant/Award Number: S.R.2017; People's Trust for Endangered Species, Grant/Award Number: PTES

MMU 2017; Action For Hares SouthWest, Grant/Award Number: RO201720; British Mountaineering Council, Grant/Award Number: DT1720

Abstract

Over the last 20 years, ecological restoration of degraded habitats has become common in conservation practice. Mountain hares (*Lepus timidus scoticus*) were surveyedduring 2017–2021 using 830 km of line transects in the Peak District National Park, England. Historically degraded bog areas were previously reported having low hare numbers. Following bog restoration, we found hare densities of 32.6 individuals km^{-2},notably higher than neighboring degraded (unrestored) bog with 24.4 hares km^{-2}. Hare density on restored peatland was 2.7 times higher than on bogs managed for grouse shooting at 12.2 hares km^{-2} and 3.3 times higher than on heather moorland managed for grouse shooting at 10.0 hares km^{-2}. Yearly estimates varied most on habitats managed for grouse, perhaps indicative of the impact of habitat management, for example, heather burning and/or possible hare culling to control potential tick-borne louping ill virus in gamebirds. Acid grassland used for sheep farming had asimilar density to grouse moorland at 11.8 hares km^{-2}. Unmanaged dwarf shrub heathhad the lowest density at 4.8 hares km^{-2}. Hare populations are characterized by significant yearly fluctuations, those in the study area increasing by 60% between 2017 and 2018 before declining by *ca*. 15% by 2020 and remaining stable to 2021. Duringan earlier survey in 2002, total abundance throughout the Peak District National Parkwas estimated at 3361 (95% CI: 2431–4612) hares. The present study estimated 3562(2291–5624) hares suggesting a stable population over the last two decades despite fluctuations likely influenced by weather and anthropogenic factors. Mountain hares in the Peak District favored bog habitats and were associated with restored peatland habitat. Wildlife management should be cognizant of hare density variation between habitats, which may have implications for local extinction risk.

KEYWORDS

blanket bog, distance sampling, grouse moor, habitat degradation, landscape restoration,monitoring, mountain hare, peatland

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Ecology and Evolution. 2022;12:e8744.
https://doi.org/10.1002/ece3.8744

TAXONOMY CLASSIFICATION

Population ecology

1 | INTRODUCTION

Across the world, many ecosystems are suffering anthropogenic damage with wide-ranging impacts (IPBES, 2019). Among these are peatlands, wetland ecosystems where decomposing vegetation has taken thousands of years to accumulate as peat layers. These are often vulnerable to human activities (e.g., cutting, grazing, burn-ing, and indirect erosion) and sensitive; their replacement may require millennia (Page & Baird, 2016; Yu et al., 2016). In the northern hemisphere, peatlands experience cold-wet climates, providing the conditions for peat layer development. Peatland habitat stores approximately 50% of total global soil carbon storage (Evans et al., 2006), while hosting environmentally sensitive plants and animals of high conservation importance. Across Europe, many peatlands are degraded (Urak et al., 2017) and substantial funds (e.g., ~ €167 m in EU Life projects) have been invested in peatland restoration in recent decades, recognizing its importance for carbon sequestration, water retention, and biodiversity (Andersen et al., 2017).

The South Pennine Moors contains 650 km^2 of UK upland peatland distribution (Bonn et al., 2009; JNCC, 2015) and received Special Areas of Conservation (SAC) designation in 2005 for its unique upland plant community and population of breeding waders (Natural England, 2005, 2019). This area features peatlands which have suffered extensive human-caused degradation (Evans, 2009). Over the last two centuries, atmospheric pollutant deposition from the surrounding industrial cities including Sheffield and Manchester led to local soil acidification and loss of sphagnum, severely harming vegetation, leaving bare peat and extensive gully erosion (Alderson et al., 2019; Andersen et al., 2017; Natural England, 1993; Tallis, 1997, 1998). Within the SAC are ~350 km^2 of grouse moor estates practicing rotational heather burning and predator management, creating an ecosystem supporting red grouse (*Lagopus lagopus*) for shooting (Phillips, 2012; Sotherton, 2009). There are also areas, which have seen extensive sheep (*Ovis aries*) overgrazing, where former upland dry heath has transitioned to acid grassland (Anderson& Yalden, 1981). The frequency of accidental or deliberate wildfires has also increased (McMorrow et al., 2009). All these anthropogenic mechanisms have been implicated in causing extensive moorland degradation, precipitating much loss of diversity of flora and fauna (Anderson & Shimwell, 1981; Pearce-Higgins et al., 2006; Sim et al.,2005; Tallis, 1998; Thompson et al., 1995; Tucker, 2003). Recent evaluation of habitat conditions for the South Pennine Moors SAC rated the area as 99% “unfavorable-recovering” or “unfavorable-no change” (Natural England, 2021).

From 2003, a well-funded (~ €35 m) restoration program managed by the Moors for the Future Partnership commenced in the South Pennine Moors SAC (Alderson et al., 2019; Bedson *in litteris*.). Conservation measures included fencing out grazing animals, reduced burning and trampling, and removal of species, for example, *Molinia*. Hydrology was re-established with gully blocking. Bare peat was restored with netting, fertilizers, liming, mulches and reseeding and replanting with grasses, rushes, mosses, dwarf shrubs, heather, and eventually *Sphagnum* moss (Alderson et al., 2019; Buckler et al.,2013). Many bare peat areas recovered their vegetation (Alderson et al., 2019). However, little was known about the effects on wildlife(Andersen et al., 2017; Shepherd et al., 2013).

The mammal species mountain hare (*Lepus timidus scoticus*) has been regarded as a useful habitat quality indicator (JNCC, 2008). This cold-adapted lagomorph is associated with UK upland peatlands, playing an important role as both herbivore and prey forfoxes (*Vulpes vulpes*), stoats (*Mustela erminea*), and raptors (Yalden, 2009). Elsewhere across Europe and Asia, mountain hares occupya range of elevations, inhabiting tundra, taiga, boreal forests, bogs, and grasslands at low population densities of 1–6 individuals km^{-2}, though higher, on some Baltic islands (25–60 km^{-2}) and far east Russia (200–400 km^{-2}) (Angerbjorn & Flux, 1995). Mountain hare density is high (50–200 km^{-2}) on managed grouse moor habitat in Scotland. Rotational heather burning provides early-stage heather favored by hares (Flux, 1962; Hewson, 1976, 1989; Savory, 1986). Predator control (e.g., shooting or trapping of foxes, stoats, weasels (*M. nivalis*), corvids, or historically, raptors) to protect grouse was also purported to support hares (Patton et al., 2010; Stoddart & Hewson, 1984). However, many grouse moor estates also shot hares for sport(Hesford et al., 2020; Patton et al., 2010). More recently, culls were organized to substantially reduce hare numbers, on the grounds thathares transmit ticks carrying louping ill virus to grouse (Patton et al.,2010; Watson & Wilson, 2018); although evidence of mountain hares being a principal vector for this disease transmission is ambiguous (Harrison et al., 2010). Annual hunting of hares until 2016 averaged 39,000 individuals (95% CI: 16,000–70,000) (Aebischer, 2019). The recent assessment under Article 17 1992 EC Habitats and Species Directive described UK mountain hare status as “deteriorating” and “unfavorable-inadequate” (JNCC, 2019). Populations cycle with up to 80% amplitude, confounding conservation monitoring (Newey, Dahl, et al., 2007). Yet, the central tendency of census estimates hasdecreased from 350,000 (95% CI: 93,000–709,000) (JNCC, 2007) to

132,000 individuals (95% CI: 79,000–516,000) (JNCC, 2019).

In England, mountain hares became extinct around 6000 bpand were reintroduced to areas of the South Pennines Moors lying within the present-day Peak District National Park, by landowners with sporting interests in the 1870s (Harris & Yalden, 2008). From the 1970s, studies described a small, stable population of ~1000 individuals (Mallon, 2001; Yalden, 1971, 1984). The last field study estimated ~10,000 individuals, inconsistent with previous research (Mallon et al., 2003). The most recent estimate was 2500 individuals(Mathews et al., 2018). Mountain hares were associated with mixed

Calluna/*Eriophorum* areas or *Calluna* areas on grouse moors (Mallon et al., 2003; Yalden, 1971), and there were concerns about the per-sistence of these habitats (JNCC, 2007).

The aim of this research was to estimate mountain hare densi- ties in different upland habitats. We surveyed mountain hares over5 years and evaluated evidence whether habitat restoration and/or grouse moor management was concomitant with high hare popula- tion density. In 1 year, we also surveyed the whole National Park to report overall mountain hare abundance. This research was intended to accomplish investigations recommended by the UK Biodiversity Action Plan (JNCC, 2008) and to inform future conservation status assessments.

2 | MATERIALS AND METHODS

2.1 | Study area

Fieldwork was conducted on upland habitats in the Peak District National Park, lying within the South Pennine Moors SAC (Figure 1). These uplands are underlain by acidic gritstone and shale rocks forming hills up to ~630 m. The annual average temperature is 10.3°C and precipitation 1025 mm, creating a wet substrate on hill tops (UK Met Office, 2020). The hills are covered with peat, up to2 m deep (Anderson & Shimwell, 1981). The study extent was in- formed by UK Biological Record Centre (BRC) mountain hare obser- vations (See Acknowledgments) for the period 1998–2018, eliciting 8666 records. From these, we mapped a minimum convex polygon 610 km^2 constituting the observed mountain hare range in our studyarea (Figure 1).

2.2 | Habitat classes

We developed a habitat classification map by layering several data sources and mapping with a 1-ha scale cell grid (i.e., 100 cells km^{-2})in ArcGIS (ESRI USA) (Figure 2). Habitat classes pertaining to moun-tain hare occupancy were acid grassland, upland dwarf shrub heath,and wet upland blanket bog (Jackson, 2000; Natural England, 2005,2019), with extent informed by the UK landcover map (Rowlandet al., 2017). Other habitats had very few mountain hare records andwere deemed irrelevant.

Acid grassland occurred at 300–550 m elevation, comprisinga broad habitat type of calcifugous swards dominated by grasses (*Festuca ovina*, *Nardus stricta*), sedges, and herbs on lime-deficientsoils, pH <5.5 (Jackson, 2000; Rowland et al., 2017). In winter (when mountain hares were surveyed), grasses and bracken (*Pteridium*) were senescent; *Calluna* reaching to 80 cm height, *Juncus* and *Molinia* reach 120 cm height (Stace, 2010). These areas were used for sheep rearing.

Blanket bog comprised ombrotrophic wetlands supporting veg- etation forming deep peat overlaying hill plateaus (Natural England, 1993). *Eriophorum vaginatum* was dominant, with *Sphagnum* mosses and bog pools present (Anderson & Shimwell, 1981; IUCN, 2014; Natural England, 2005; Rowland et al., 2017). These areas had been extensively eroded (Natural England, 1993). We subdivided theblanket bog landcover area to “grouse moor bog,” “restored bog,” and “unrestored bog” described below. Upland dry heath occu-pied lower slopes of moors on mineral soils or shallow peat areas, strongly dominated by *Calluna vulgaris*-*Deschampsia flexuosa* and *C. vulgaris*-*Vaccinium myrtillus* heath. (Anderson & Shimwell, 1981; Elkington et al., 2001; Natural England, 2005; Rowland et al., 2017) and we subdivided this to “grouse moor heather” or “unmanaged dwarf shrub heath” described below.

To identify grouse moor areas, we followed methods from Yallopet al. (2006) and assembled a mosaic of 1:500 scale aerial images dated for 2018 (Digimap, 2019). Any 1-ha cell showing a burn or mowed patch was designated as “grouse moor bog” or “grouse moor heather” depending on underlying landcover (Rowland et al., 2017). Grouse moors featured rotationally burned areas, shooting butts,grit trays, quad bike tracks, and predator (corvid and mustelid) traps. “Grouse moor bog” at elevations 350–530 m was wet heath overly- ing deep peat with eroded gullies, *Calluna*, more *Eriophorum* spp. and mosses. “Grouse moor heather” at elevations 280–510 m was drier areas with shallow peat, few gullies, and extensive *Calluna* (Allenet al., 2016). Burned heather comprised different succession stages:suppressed (“pioneer”) heather, height to 15 cm; sub-dominant heather, age to 10+years, height ~15 cm, coverage ~40%; dominant heather, age up to 25 years, height ~30–120 cm coverage, 60+% (Allen et al., 2016; Bardgett et al., 1995; Stace, 2010; Whitehead et al., 2021). Also present were *Eriophorum*, *Sphagnum* and other mosses, cross-leaved heather *Erica tetralix*, bell heather *Erica cine-rea*, bilberry *Vaccinium myrtillus*, and crowberry *Empetrum nigrum* (Bardgett et al., 1995; Whitehead et al., 2021). The Peak District was recorded with burns as 29% of total potential burn area and patch sizes 500–1000 m^2 (Allen et al., 2016).

The remaining heather area not grouse moor was classified as “unmanaged dwarf shrub heath” at elevations 250–520 m includ-ing steep slopes and few gullies. This comprised mosaics of 70% dense/30% open heather, predominantly *Calluna* (Rowland et al., 2017), height to 120 cm (Bardgett et al., 1995; Stace, 2010). There was no predator control and few sheep.

We identified “restored bog” from shapefiles provided by the con-servation partnership “Moors for the Future” (Acknowledgments), designating their recovery work to 2016. These areas measured ~20 km^2, occurring at elevations 480–630 m and comprised previ-ously degraded bare peat. From 2007, restoration efforts included gully blocking, fertilizer, liming, laying of jute textiles, reseeding, plant-ing, and spreading heather brash (Alderson et al., 2019). By 2016, this work achieved 75% vegetation cover (Alderson et al., 2019); much was in lush, verdant condition. Vegetation comprised a wide variety of moorland species, which shifted frequently in composition over thespace of a few meters, including *Calluna*, *Eriophorum*, and *Sphagnum* spp., shrubs (e.g., *Erica tetralix*, *E. cinerea*, *Rubus chamaemorus*, *Vaccinium mytrillus*, and *Empetrum nigrum*), ferns (e.g., *Oreopteris lim- bosperma* and *Blechnum spicant*), herbs (e.g., *Potentilla erecta*, *Viola*

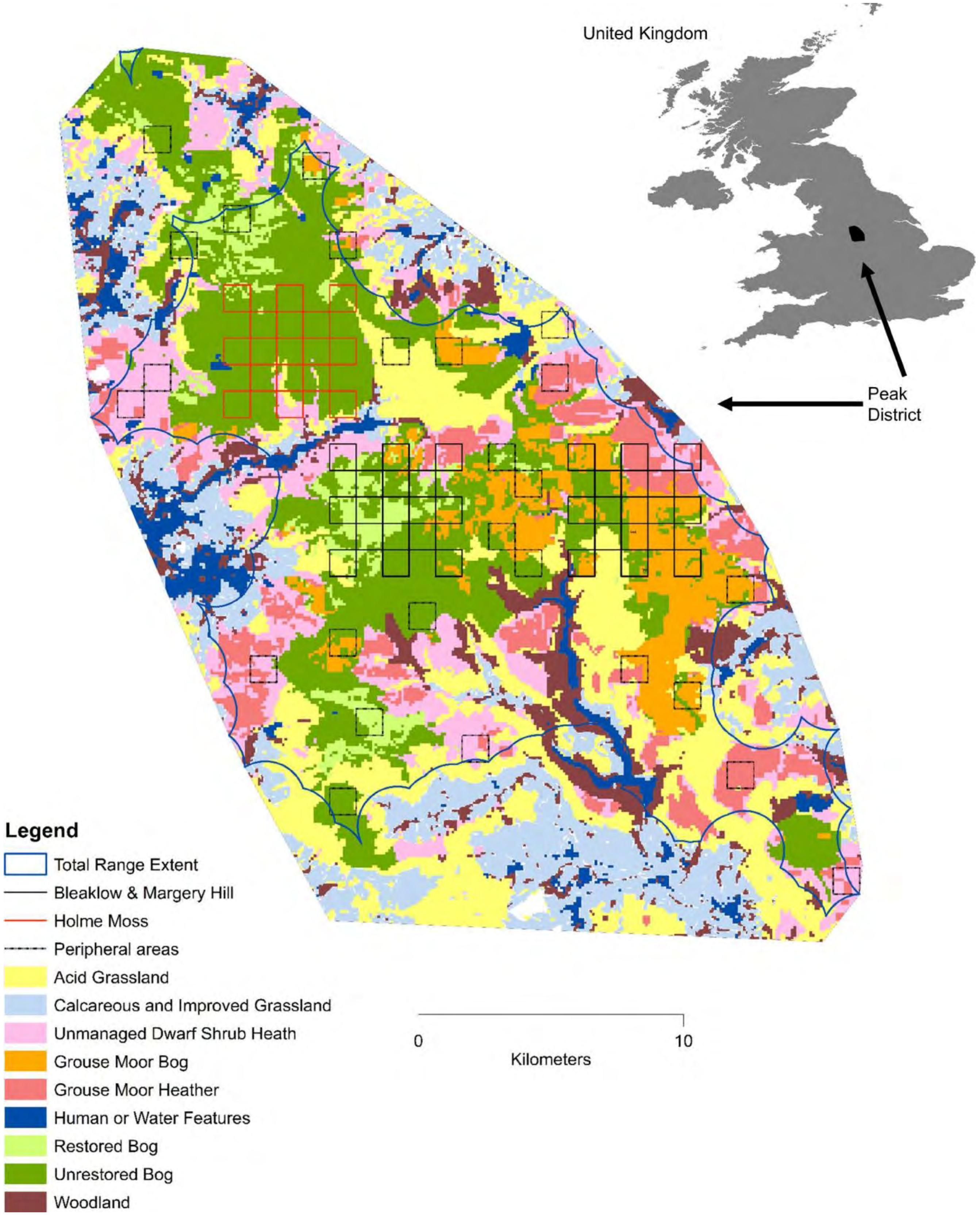


FIGURE 1 Map of study area. The locations of 10 years of BRC mountain hare records informed the minimum convex polygon, being the outer shape. The extent of hares for abundance projection was the alpha hull shape, shown by the blue line and also the survey areas. The survey transects are shown for Bleaklow and Margery Hill (black squares); Holme Moss (red squares); and peripheral areas (dotted squares).Legend shows habitat classes. Inset map shows location of Peak District in the United Kingdom. Peak District map origin is British National Grid Reference SK Easting 390000 Northing 370000. North at top

palustris, *Chamerion angustifolium*, and *Galium saxatile*), and mosses(e.g., *Hypnum jutlandicum* and *Polytrichum spp*). *Calluna* height was up to ~100 cm; winter grasses were senescent reaching heights ~30 cm(Stace, 2010). The extensive networks of eroded gullies were revege-tated, and the water table was high (Alderson et al., 2019). There was no predator control practiced, and sheep were fenced out.

The remaining bog areas were classed as "unrestored bog" at elevations 300–630 m. These had not historically deteriorated tothe point of comprising bare peat, yet nonetheless appeared eco- logically impoverished, that is, "unfavorable-recovering" condition (Natural England, 2019). They consisted mostly of extensive fields of *Eriophorum* spp. and *Molinia caerulea* grass, winter height ~30 cm, and some *Calluna* patches height ~100 cm (Stace, 2010) with lowerspecies diversity than restored bog areas. They featured eroded gul- lies, without gully blocking as was the case for "restored bog," there-fore drier with water run-off. No predator control was practiced, andthere were some sheep.

Ground and aerial photographs showing habitat classes appearin Figure 3. Table 1 lists vegetation communities. Habitat class data for hare observations, transect lengths, and surveyed area size werethen determined using "extract" function in package Raster (Hijmans& van Etten, 2012) within R (R Core Team, 2021).

2.3 | Surveys

When planning surveys, we perceived a random stratified approach (Morrison et al., 2010) might miss local concentrations of mountain hares (Flux, 1962) with typical small home ranges from ~10 ha (Raoet al., 2003) to ~100 ha (Hewson & Hinge, 1990). We, therefore, designated survey sites as 5 × 5 km, potentially identifying hare density patterns over a few hundred meters and large enough to encompass all habitat classes. During pilot surveys, we observed mountain hares up to 700 m range and so conducted transects in sampled 1 km squares of the Ordnance Survey grid (OS Explorer Map1, 2015), achieving continuous coverage probability >.01. The perimeter of each square was surveyed as a circuit, walking all four sides as one continual transect. By walking all cardinal directions, we intended this to account for sampling differences arising from slope,weather, or lighting. We considered each 1-km transect to be inde- pendent. At adjoining corners of squares, there was overlap of visualcoverage (at a subsequently modeled range 520 m), meaning corners were surveyed twice a year compared with remaining areas sur- veyed once. We assessed this coverage (Table A1) using Pearson's chi-square test, which reported no significant difference in propor- tion of habitat classes surveyed twice, versus once: χ^2 (5) = 3.588, p = .61. Hence, we did not modify estimates for differing coverage probabilities. Therefore, we met standard distance sampling as- sumptions with survey effort acting as denominator for encounter rate (Buckland et al., 2001, 233–235; Buckland et al., 2004, 224; Buckland et al., 2015, 27).

To meet our aim of surveying the entire mountain hare popula- tion at our sites, our study sampling was designed to make efficient use of limited staff time and good weather days. From BRC records, we noted 37% of historic observations were on 23% of the study area: Bleaklow and Margery Hill, with 4 km of non-surveyed land between them (Figure 1). Thus, we configured the 5 × 5 km sites atop these two hills, acknowledging that ensuing density estimates might be higher than elsewhere in the wider park. We surveyed al- ternate 1 km^2 squares, that is, 13 squares on Bleaklow, 13 squares on Margery Hill. Surveys commenced for 2017, repeated in 2018, 2019,2020, and 2021 with the same 26 squares being surveyed each year(Figure 1).

We added an additional 5 × 5 km site on Holme Moss with13 more squares in 2018, repeated in 2019. During 2019, we ex- tended surveys to achieve an estimate for the entire Peak District. Because the remaining park was much larger, for logistical reasons we configured remaining surveys of areas as 26 random 1 km^2 squares ("peripheral areas"), with 6 squares deliberately chosen as pairs, for efficiency (Figure 1).

Survey transects followed each 1 km^2 square perimeter, guided by GPS (Garmin 64MapST, 15m accuracy), and were conducted January through April. The survey schedule randomized squaresthe first year, maintaining the same schedule each year as logistics allowed. Each side of the square was surveyed once, looking onboth sides of the transect, walking very slowly, and taking 2–5 h. Surveyors scanned ahead with binoculars every 200 m to locate hares or groups of hares in the undulating terrain. Only observa- tions made while walking along the transect line were included inthe analysis.

Mountain hare observations were made using standard distance sampling methods, recording date, time, grid reference, clustersize, distance to hare (Nikon ProStaff7i laser range finder, accuracy 1m), and angle (compass and angle board) (Buckland et al., 2001). Potential double counts for observation were discounted. Previous studies described difficulties of daytime surveys for mountain hares, as this nocturnal species often hides by day, revealing itself by flush-ing from cover, a difficulty associated with tall heather on grouse moor habitats, contributing to imprecise density estimates (Bedson, Thomas, et al., 2021; Newey et al., 2003, 2018) To evaluate whether this behavior affected the detection process, we categorized hare activity upon first being observed, as stationary (lying or sat up); moving (walking, running, or feeding); or flushing (emerging from cover). Surveys were conducted under similar conditions for com- parable previous studies in clear weather with wind speed <20 mph (e.g., Newey et al., 2018). We assumed stronger winds did not influ-ence hare detections (e.g., Flux, 1962), but caused difficulties hold- ing the laser range finder steady. No surveys were conducted with snow present.

2.4 | Distance modeling

For Bleaklow and Margery Hill, mountain hare observations were attributed to the habitat class on which the animal was first seen (as represented in Figure 1). To consider the possibility of field

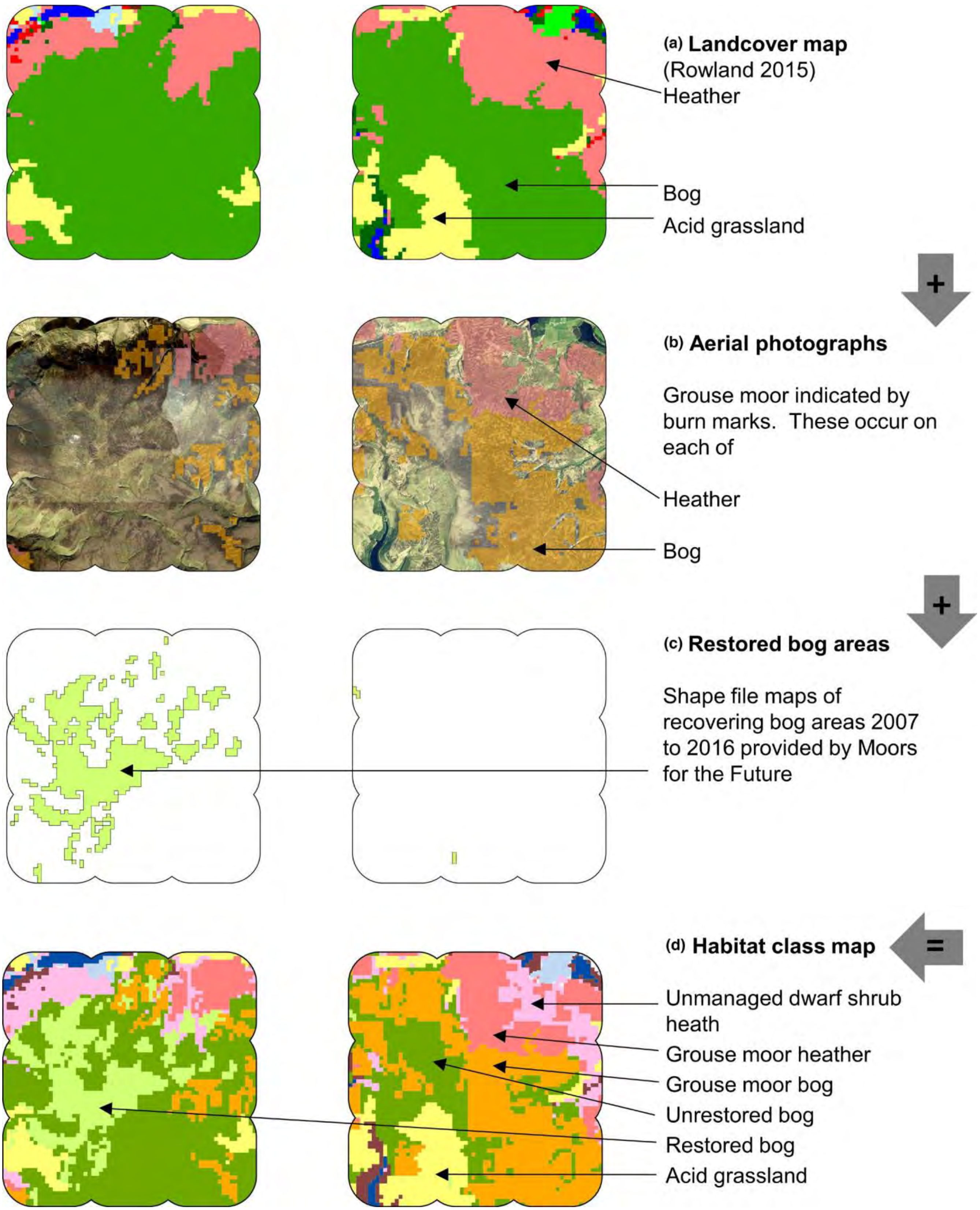


FIGURE 2 Step-by-step construction of habitat class map for surveyed extent (5 × 5 km with 800 m buffer) with 1-ha pixel, for each of Bleaklow (left) and Margery Hill (right) (British National Grid origin SK Easting 408000 Northing 394000). Map (a) shows landcover classification system of Rowland et al. (2017), which is used as starting point. Map (b) Aerial photographs are assessed and any with burn mark within any hectare denoted as either grouse moor bog or grouse heather, referencing the underlying landcover determined by Rowland et al. (2017). Map (c) Shapefiles provided by Moors for the Future, showing recovering bog areas which received treatment up to 2016. Map (d) The final map with all habitat classes pertinent to mountain hares. Any heather without burn mark is, therefore, regarded as unmanageddwarf shrub heath

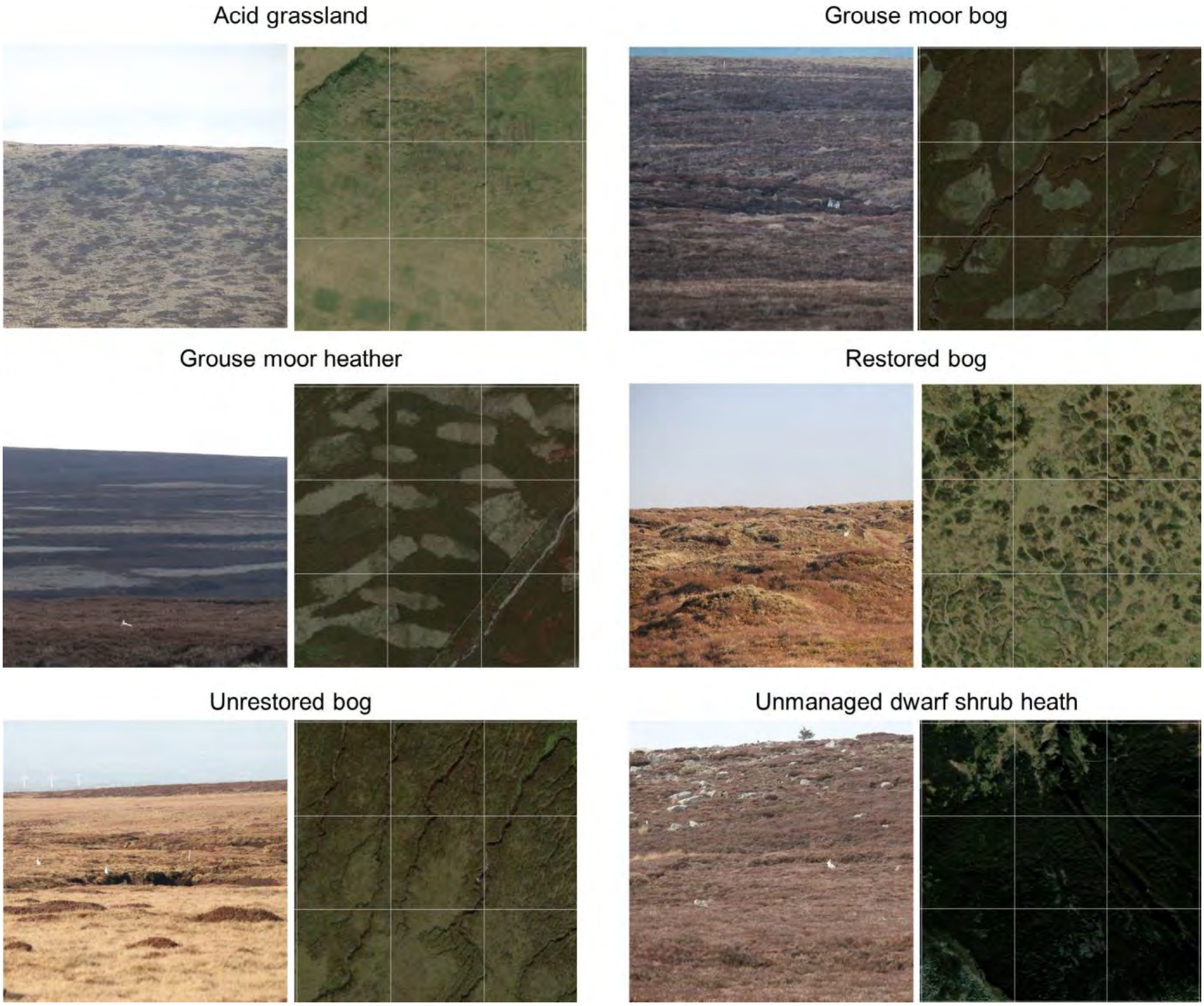


FIGURE 3 Photographs of each of the habitat classes. For each habitat class, the left field photograph is taken from the ground. The right side photographs are aerial images at 300 m by 300 m with a 100 m fishnet grid overlain, for scale. Source: ArcGIS ESRI "WorldImagery" downloaded 3 August 2021. Colors are natural, not enhanced. Note each field photograph also contains an example mountain hare observation

measurement errors (GPS, laser range finder, and angle board) affecting habitat class assignment, within ArcGIS we applied buffers of25 m circles to all observations and found 97.3% of these lay whollywithin the observation's extracted habitat class; 2.7% straddled two habitat classes. We accepted this as tolerable systematic error. We excluded Holme Moss and peripheral areas from habitat analyses as they were not surveyed every year, retaining them for discrete "area only" estimations.

We analyzed our data with DISTANCE v.7.3 (Thomas et al., 2010), using different data filtering and model selections. We assessed different truncation distances and bin widths. We compared detection models with three key functions: uniform, half-normal, and hazard rate, with cosine or polynomial expansion terms (Buckland et al., 2001, 47; Williams & Thomas, 2007). We assessed the suitability of assumptions and models using histograms, quantile-quantile plots,χ^2 goodness of fit statistics, and the fit of the detection function close to the transect line g(0). We compared and sought simple mod-els with few parameters, lower AIC values between models usingthe same data selection, higher χ^2 goodness of fit statistics, and lower detection probability *cv* values (Buckland et al., 2001). The furthest observation distance was 780 m. We truncated the data ata range of 520 m. The hazard-rate model provided its characteristic wide shoulder and steep drop off of the detection function with increasing perpendicular distance. With data truncated at 520 m, this provided a high χ^2 goodness of fit statistic (0.77) for the detection function, with $p = .18$ and low detection probability $cv = 0.04$ (TableA2, Figure 4). Both the uniform and half-normal models failed to achieve a suitable (i.e., >0.05) χ^2 goodness of fit statistic with most data selections.

We compared two approaches to stratification by habitat: (1) global detection function using pooled data, this required three parameters, reporting AIC 22,148.43, global P $cv = .04$; (2) strata

TABLE 1 Ecosystems and habitat classes used in this research and the plant communities within these areas,as described by the British National Vegetation Classification (NVC) (Elkingtonet al., 2001; Hall et al., 2004; Jackson, 2000; JNCC, 2015; Natural England, 2005; Rowland et al., 2017)

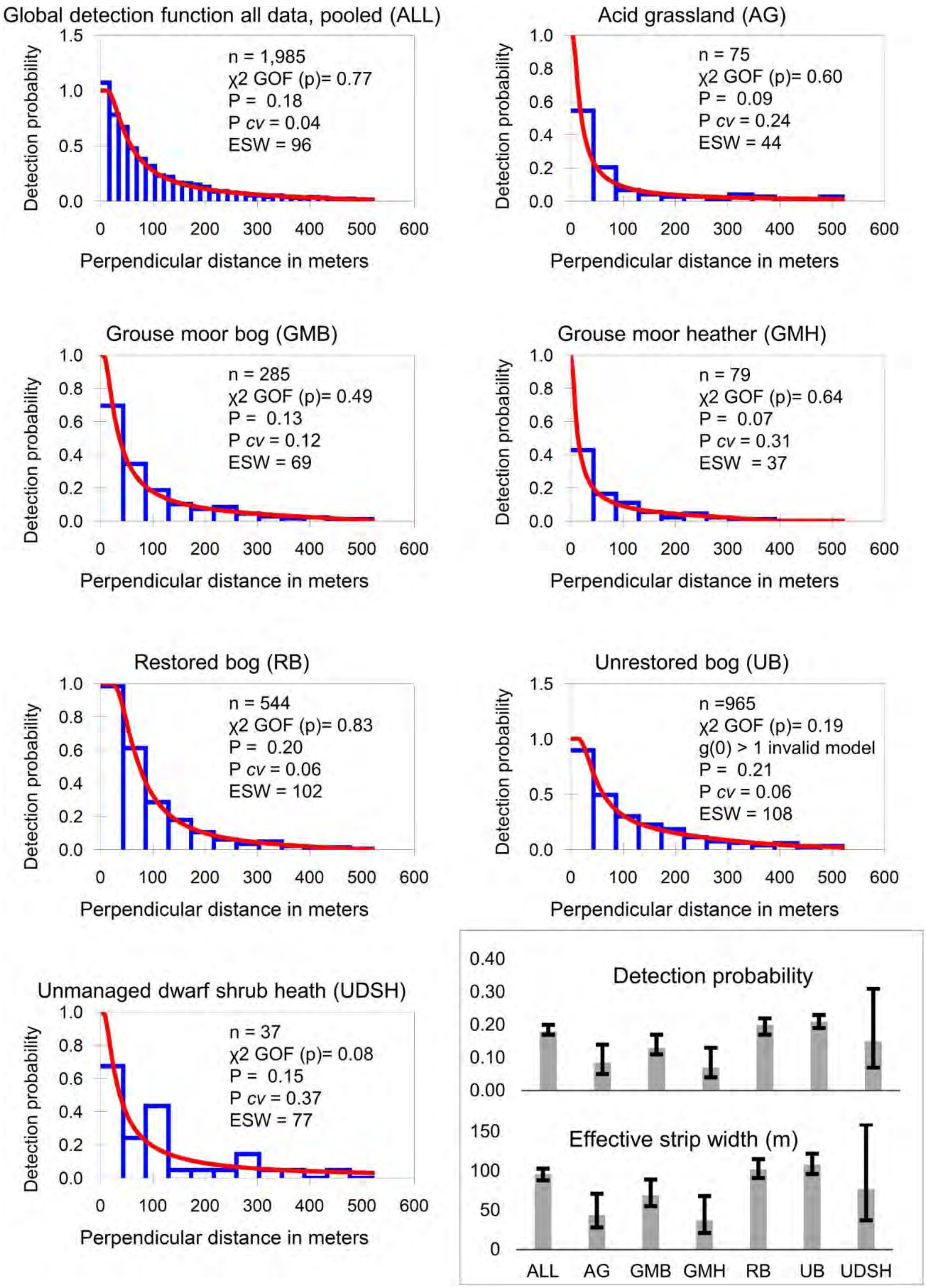
Ecosystem	Habitat class	NVC category
Blanket bog	Restored bog	M1 and M2 *Sphagnum* bog pools
		M3 and M20 *Eriophorum* bog pools
		M4 Carex rostrata—*Sphagnum recurvum* mire M5 Carex rostrata—*Sphagnum squarrosum* mireM6 *Carex*–*Sphagnum* mires
		M9 Carex rostrata—*Calliergon cuspidatum*/*giganteum* mire
		M15 *Scirpus cespitosus*–*Erica tetralix* wet heath
		M16 *Erica tetralix*–*Sphagnum compactum* wet heath
		M19 *Calluna*–*Eriophorum* blanket mires
	Unrestored bog	As for restored bog
	Grouse moor bog	As for restored bog
Upland dry heath	Grouse moor heather	H1 *Calluna*–*Festuca* heath
		H8 *Calluna*–*Ulex* heath
		H9 *Calluna*–*Deschampsia* heath
		H10 *Calluna*–*Erica* heath
		H12 *Calluna*–*Vaccinium* heath
	Unmanaged dwarf shrub heath	H18 *Vaccinium*–*Deschampsia* heath
		M19 *Calluna*–*Eriophorum* blanket mires
		H1 *Calluna*–*Festuca* heath
		H8 *Calluna*–*Ulex* heath
		H9 *Calluna*–*Deschampsia* heath
		H10 *Calluna*–*Erica* heath
		H12 *Calluna*–*Vaccinium* heath
		H18 *Vaccinium*–*Deschampsia* heaths
Acid grassland	Acid grassland	U1 *Festuca ovina*–*Agrostis capillari* - *Rumex acetosella* grassland
		U2 *Deschampsia flexuosa* grassland
		U4 *Festuca ovina*–*Agrostis capillaris*–*Galium saxatile* grassland
		U5 *Nardus stricta*–*Galium saxatile* grassland U6 *Juncus squarrosus*–*Festuca ovina* grassland*W16 Quercus* spp.–*Betula* spp.–*Deschampsia flexuosa* woodland (for bracken)

(i.e., habitat class)-specific detection function, this required 16 parameters, reporting AIC = 22,110.73, ΔAIC = 37.70 (Figure 4). The lower AIC of the strata-specific detection function indicated this model was best. However, for some habitats this estimated high *Pcv* values: acid grassland = .24; grouse moor heather = .30; and un-managed dwarf shrub heath = .36, leading to greater uncertaintyfor density estimates. Additionally, the detection function for unrestored bog was invalid ($g(0) > 1$) and the sample size for unmanaged dwarf shrub heath was 37 observations, below that recommended by Buckland et al. (2001), exacerbating doubts about estimate validity. Meanwhile, attempts to use strata as covariates resulted in greater AIC values and were dismissed.

We considered how the strata-specific detection function varied by habitat class. Outlying hare observations were achieved at long ranges: acid grassland 747 m; grouse moor bog 623 m; grousemoor heather 565 m; restored bog 780 m; unrestored bog 732 m; and unmanaged dwarf shrub heath 566 m. Figure 3 shows example long-range detections. Effective strip widths varied considerably:acid grassland 44 m; grouse moor bog 69 m; grouse moor heather 37 m; restored bog 102 m; unrestored bog 108 m; and unmanaged dwarf shrub heath 77 m.

We assessed whether hare detectability (hiding behavior) varied between habitat classes. For all observations, hare activity was recorded as 61% stationary, 21% moving, and 19% flushing from

FIGURE 4 Histograms for Bleaklow and Margery Hill distance sampling data from 2017 to 2021 (1985 observations) fitted with the hazard-rate model truncated at 520 m. The first histogram shows all data, pooled, as used for reporting. The subsequent six histograms show detection functions when stratified by habitat class with parameters: n = sample size; χ^2 GOF (p) = chi-square goodness of fit p-value;P = detection probability P cv = coefficient of variation; ESW = effective strip width in meters. Detection function for unrestored bog reports detection probability at the transect line >1, that is, invalid model. The column charts bottom right show detection probability and effective strip width estimates with 95% confidence intervals. All = from global detection function all data, pooled, showing much narrower confidence intervals than the subsequent six columns where the detection function is stratified by habitat class


Global detection function all data, pooled (ALL)
n = 1,985
χ2 GOF (p)= 0.77
P = 0.18
P cv = 0.04
ESW = 96
Acid grassland (AG)
n = 75
χ2 GOF (p)= 0.60
P = 0.09
P cv = 0.24
ESW = 44
Grouse moor bog (GMB)
n = 285
χ2 GOF (p)= 0.49
P = 0.13
P cv = 0.12
ESW = 69
Grouse moor heather (GMH)
n = 79
χ2 GOF (p)= 0.64
P = 0.07
P cv = 0.31
ESW = 37
Restored bog (RB)
n = 544
χ2 GOF (p)= 0.83
P = 0.20
P cv = 0.06
ESW = 102
Unrestored bog (UB)
n =965
χ2 GOF (p)= 0.19
g(0) > 1 invalid model
P = 0.21
P cv = 0.06
ESW = 108
Unmanaged dwarf shrub heath (UDSH)
n = 37
χ2 GOF (p)= 0.08
P = 0.15
P cv = 0.37
ESW = 77
Detection probability
Perpendicular distance in meters
0
100
200
300
400
500
600
0.0
0.2
0.4
0.5
0.6
0.8
1.0
1.5
Detection probability
0.00
0.10
0.20
0.30
0.40
Effective strip width (m)
0
50
100
150
ALL
AG
GMB
GMH
RB
UB
UDSH

cover, varying per habitat class and radial distance. To test for relationships between these factors, we calculated encounter rate, allocating untruncated observations to 18 radial distance bin widths of ~43 m (Figure A1), that is, resembling habitat stratified detection function histograms (Figure 4). Some activities were not observedat certain ranges, so log-linear analysis was not possible (Field et al.,2012, 837). Therefore, we grouped observations as within or be- yond 43 m, evaluating with Pearson's chi-square test (multiplyingto encounters per 100 km). This showed significant association of activity, habitat class, and observation distance $\chi^2(16) = 224.76, p < .001$. Hares were more likely to flush on unmanaged dwarf shrub heather (33% of observations) grouse moor heather (32%), grouse moor bog (25%), than on acid grassland (21%), restored bog (16%),and unrestored bog (16%). On unmanaged dwarf shrub heath and grouse moor heather, proportionally more hares flushed at greater distances. However, absolute encounter rates (hares km$^{-1)}$ of flush- ing hares were as follows: acid grassland 0.38, grouse moor bog 0.54, grouse moor heather 0.51, restored bog 0.91, unrestored bog 0.67, and unmanaged dwarf shrub heath 0.26. These findings did notsupport the hypothesis that more hares might be lying undetected, that is, perhaps hiding and not flushing, on grouse moor areas. For allthe above reasons, we did not believe a stratified detection function would be more informative. Therefore, we used the same global de-tection function using pooled data for all stratification queries, with only encounter rate and cluster size varying by strata per habitat class and or year (Buckland et al., 2001, 89–91).

We stratified the sampling data and reported in four ways: (1) by habitat class, that is, pooling all observations in each habitat class over the 5 years together; (2) by year, that is, pooling all observationsin each year, without habitat information; (3) by habitat and by eachyear, that is, 6 habitats × 5 years = 30 strata; and (4) by area only and to enable the 2019 population estimate. This was accomplished within software distance, using the same data, each time allocating transects and observations to different strata definitions (Thomas et al., 2010). Estimates for the survey year 2019 also used data trun-cated at 520 m and the hazard-rate model; inevitably its global de- tection function $f(0)$ differed slightly from the smaller data set of Bleaklow and Margery Hill. We reported parameters and estimates with 95% confidence intervals. Comparisons between strata used the t-statistic based on the Satterthwaite approximation, accounting for unequal sample sizes (Buckland et al., 2001, 84–86). This test takes into account the lack of independence of data arising from using a common detection function between strata. We evaluated significance with a Bonferroni-corrected p-value and also calculated effect sizes (Field et al., 2012).

Abundance for the Peak District National Park was calculatedfor 2019 based on the additional survey effort. The 2019 survey showed very strong density fall off from center to edge of the Park. Therefore, to determine the extent for calculating abundance, we created an alpha hull shape measuring 325 km^2, from BRC hare re- cords (Figure 1). We discarded six outlying records to cover only theknown range of hares. This alpha hull shape differed very slightly from our survey area, so we merged them based on habitat classes to total 358 km^2. Abundance was calculated for each of Bleaklowand Margery Hill and Holme Moss and peripheral areas, multiplying density estimates by area.

3 | RESULTS

3.1 | Observations

In 2017, Bleaklow and Margery Hill surveys covered 121 km of transects, recording 304 detections; 2018 covered 122 km with 504 detections; 2019 covered 113 km with 401 detections; 2020 covered 123 km with 402 detections; and 2021 covered 121 km with 374 detections (Table 2; Figure 5). Encounter rate estimates varied from highest 7.5 (95% CI: 3.8–14.7) mountain hares km^{-1} on restored bog in 2020 to lowest 0.2 (95% CI: 0.0–1.8) mountain hares km^{-1} onunmanaged dwarf shrub heath 2017 (Table A3, Figure A2). Cluster sizes were slightly above 1.0; most encounters were single hares (Table 2, Table A3, Figure A2). The surveys of 2018 on Holme Moss covered 60 km with 89 observations and 2019 covered 58 km with
50 observations. Peripheral areas in 2019 covered 113 km with 101 observations (Table 2, Figure A3).

3.2 | Density and abundance

On Bleaklow and Margery Hill, the 5-year mountain hare pointestimates of density hares km^{-2} per habitat class were restoredbog = 32.6 (95% CI: 25.2–42.2), unrestored bog = 24.4 (20.6–29.0), grouse moor bog = 12.2 (9.4–15.8), acid grassland = 11.8 (7.3–19.2), grouse moor heather = 10.0 (6.1–16.6), and unmanaged dwarf shrub heath = 4.8 (2.6–8.8) (Table 2, Figures 5 and 6). There were signifi- cant differences for 10 paired comparisons of habitats (Table A4).
Hare densities on restored bog were significantly higher ($p < .05$) than all other habitats except unrestored bog; densities in the for- mer were 34% higher than the latter: $t(1.92) = 99.03, p = .057, r = .19$. Unrestored bog also showed significantly higher densities than the other classes. Acid grassland, grouse moor heather, and grouse moor bog were similar. Grouse moor bog hare density was not sig- nificantly higher than grouse moor heather $t(0.76) = 47.19, p = .449, r = .11$. Acid grassland and grouse moor bog were significantly higher than unmanaged dwarf shrub heath. Grouse moor heather was higher than unmanaged dwarf shrub heath $t(1.90) = 43.10, p = .064, r = .28$. When comparing habitats within each individual year, many of these differences were often apparent in individual years (Tables A3 and A5).

From 2017 to 2018, unrestored bog showed a significant in- crease in hare density from 18.7 hares km^{-2} (95% CI: 13.0 to 26.7) to 30.5 hares km^{-2} (95% CI: 24.3–38.6), $t(2.64) = 57.93, p = .011, r = .33$ (Tables A3 and A4). From 2017, grouse moor bog reported hare density increasing significantly from 8.7 hares km^{-2} (95% CI: 4.5–16.8) to 21.4 hares km^{-2} (95% CI: 16.4–28.0), $t(3.29) = 40.07, p = .002, r = .46$. On grouse moor bog, hare density from 2019 to

TABLE 2 Stratified distance sampling survey parameter estimates. Data selection based on 520 m truncation with hazard rate model

	n	L	n/L	n/L cv	n/L LCL	n/L UCL	K	E(s)	E(s) cv	D	D cv	D LCL	D UCL
Habitats													
Acid grassland	75	42.3	1.8	0.23	1.1	2.8	36	1.28	0.05	11.8	0.24	7.3	19.2
Grouse moor bog	285	133.9	2.1	0.12	1.7	2.7	85	1.09	0.01	12.2	0.13	9.4	15.8
Grouse moor heath	79	48.6	1.6	0.23	1.0	2.6	23	1.18	0.03	10.0	0.24	6.1	16.6
Restored bog	544	97.8	5.6	0.12	4.4	7.1	54	1.12	0.01	32.6	0.12	25.2	42.2
Unrestored bog	965	233.0	4.1	0.07	2.6	4.8	117	1.12	0.01	24.4	0.08	20.6	29.0
Unmanaged heath	37	45.3	0.8	0.30	0.4	1.5	47	1.12	0.04	4.8	0.30	2.6	8.8
Years													
2017	304	120.9	2.5	0.20	1.7	3.8	26	1.18	0.02	15.5	0.21	10.1	23.9
2018	504	121.6	4.1	0.10	3.3	5.2	26	1.14	0.01	24.7	0.11	19.6	31.5
2019	401	112.5	3.6	0.14	2.6	4.8	26	1.13	0.01	21.1	0.15	15.4	29.0
2020	402	123.1	3.3	0.25	1.9	5.5	26	1.05	0.01	17.9	0.26	10.6	30.8
2021	374	120.8	3.1	0.18	2.1	4.4	26	1.13	0.01	18.3	0.18	12.6	26.8
Survey areas 2019													
Bleaklow	246	56.7	4.3	0.14	3.2	5.9	13	1.09	0.01	27.2	0.15	19.9	37.9
Margery Hill	155	55.8	2.8	0.30	1.5	5.3	13	1.16	0.03	18.6	0.30	9.7	35.5
Holme Moss	50	57.5	0.9	0.26	0.5	1.5	13	1.22	0.03	6.1	0.27	3.4	10.9
Peripheral Squares	101	113.0	0.9	0.19	0.6	1.3	26	1.19	0.04	6.2	0.20	4.1	9.4

Note: n = encounters; L = line length km; K = number of transects; E(s) = mean cluster size; D = density estimate km^{-2}; cv = parameter coefficient of variation; LCL & UCL = 95% confidence intervals. D is calculated with probability density function $f(0)$ and $f(0)$ cv. (Buckland et al., 2001, 84,85). "Habitats" data source is Bleaklow and Margery Hill only with probability density function $f(0) = 0.010467$ and $f(0)$ $cv = 0.0407$ and represents 2017 to 2021 totalled effort and encounters, mean cluster size and density estimate values. "Years" data source: Pooled by year (not by habitat) for

Bleaklow and Margery Hill only with same probability density function. Survey areas 2019 is modelled with all data for all areas for all areas (2225 observations) with probability density function $f(0) = 0.011522$ $f(0)$ $cv = 0.0407$. However the table just reports estimates for the surveyed areas for 2019 only.

2020 decreased significantly from 18.3 km^{-2} (95% CI: 11.2–30.3) to 5.5 km^{-2} (95% CI: 3.2–9.4), $t(2.88) = 21.65$, $p = .009$, $r = .53$ and this was the only significant decrease in any habitat type between years.On Bleaklow and Margery Hill, annual density estimates showed a significant increase by 59% from 2017 to 2018 from 15.5 hares km^{-2} (95% CI: 10.1–23.9) to 24.7 hares km^{-2} (95% CI: 19.6–31.5), $t(2.29) = 57.56$, $p = .025$, $r = .29$) (Table 2). Density then dropped 15% to 21.1 hares km^{-2} (95% CI: 15.4–29.0) in 2019 and by 15% to 17.9 hares km^{-2} (95% CI: 10.6–30.8) in 2020. From 2020 to 2021, density reported an increase by 2% to 18.3 hares km^{-2} (95% CI: 12.6–26.8).

Of the 2019 survey areas, the highest density of hares was reported for Bleaklow with 27.2 hares km^{-2} (95% CI: 19.9–37.9), significantly higher than any other area (Tables 2 and A4, Figure A4). Margery Hill density was also high at 18.6 hares km^{-2} (95% CI: 9.7–35.5). Holme Moss had low density of mountain hares 6.1 hares km^{-2} (95% CI: 3.4–10.9), and this was similar to the peripheral areas6.2 hares km^{-2} (95% CI: 4.1–9.4).

For 2019, abundance for the Peak District study area (alpha hull shape + surveyed areas) estimated 3562 hares (95% CI 2291–5624) (Table A6; Figure A5). Bleaklow was 11% of area and accounted for 31% of hares; Margery Hill was 11% of area and 21% of hares; Holme Moss 11% area and 7% of hares; and peripheral areas 66% area and 41% of hares.

4 | DISCUSSION

We report strong evidence that mountain hare density differs between peatland habitat types. We found intensely localized hare abundance, which we attribute to characteristics of the habitat classes. There appears a clear association between restored bog habitat and high mountain hare densities. Many studies of peatland restoration describe levels of degradation and potential effects of recovery interventions upon hydrology, water tables, soil quality, carbon and methane storage, and vegetation (Aldersonet al., 2019; Bain et al., 2011; Holden et al., 2007; Page & Baird, 2016). Few studies show how vertebrates, particularly mammals, may benefit from peatland improvement (Andersen et al., 2017; Littlewood et al., 2021). Our research suggests that restored bogs can have a measurable conservation impact on vertebrate populations. This is encouraging, because many sensitive ecosystems are in such poor condition and resources for restoration are limited (Andersen et al., 2017).

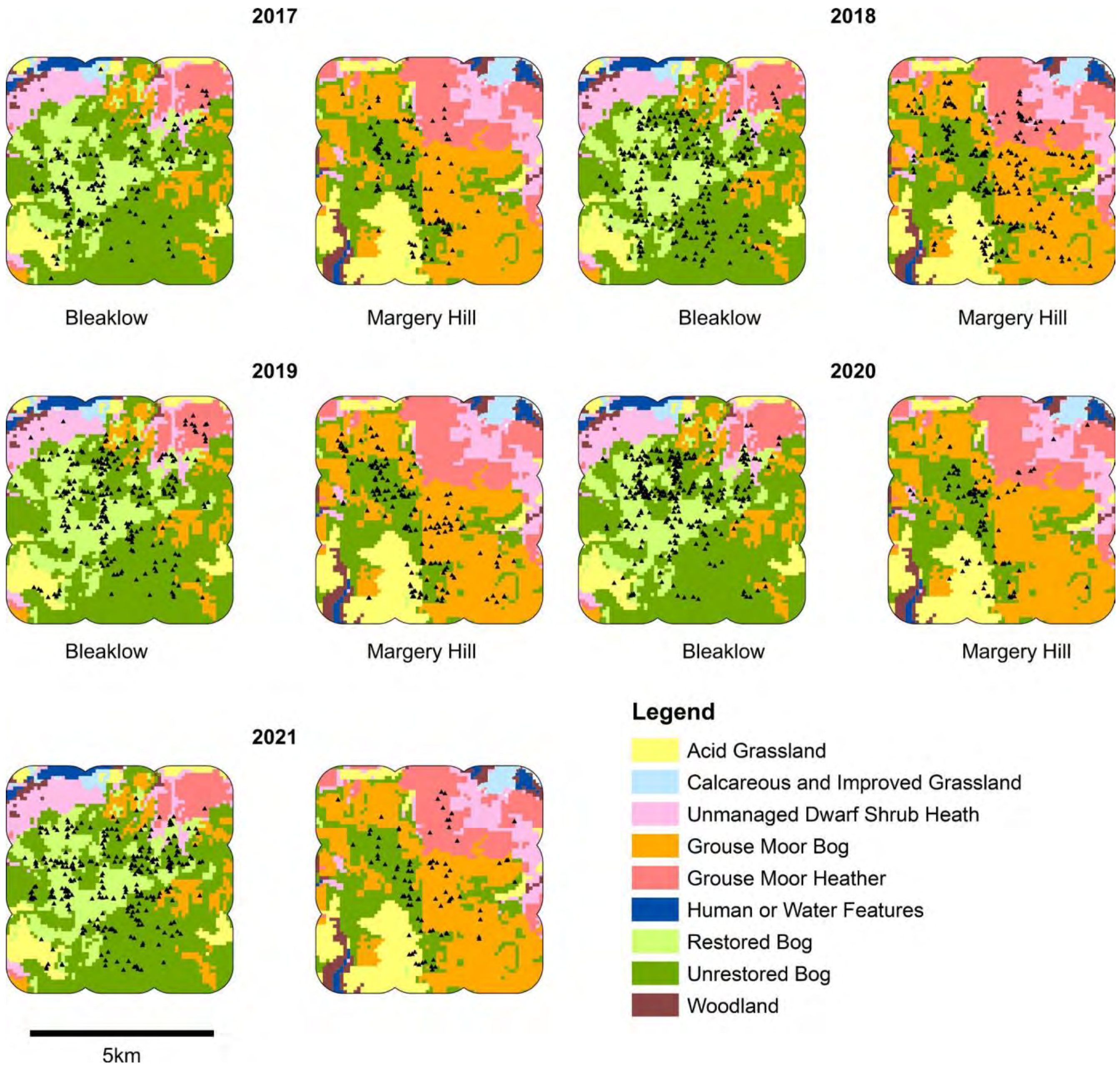


FIGURE 5 Distance sampling observations for Bleaklow and Margery Hill survey sites with 800 m buffer, for years 2017 to 2021. Habitat classes as legend. Bleaklow map origin is British National Grid Reference SK Easting 308000 Northing 394000. Margery Hill survey site is duly positioned 4 km to east. Black triangles indicate all observed mountain hares (untruncated data)

For the United Kingdom, this study represents the first such density estimate comparison based on surveys of live mountain hares (i.e., not game bags), using geospatial measurements of animal occurrence and comparing densities across the full range of habitat classes used by this species. Our findings complement other research in Europe that describe mountain hare habitat utilization: preferences for thickets of *Salix*, *Betula*, and *Picea* with dense under-storey in Scandinavian woodland (Hiltunen et al., 2004); preference for dwarf mountain-pine (*Pinus mungo*) regardless of patch size in the Alps (Bisi et al., 2013); and preference for moorland over woodland in Scotland (Rao et al., 2003). The mountain hare densities we recorded are higher than many comparable populations in Europe. Notable high densities elsewhere include populations on heather moorland in Scotland (Watson & Hewson, 1973 ~280 km^{-2}; Watson et al., 1973 ~200 km^{-2}; Newey et al., 2018 ~200 km^{-2}) and on predator-free heather dominated islands off mainland Sweden (~400 km^{-2}, Angerbjorn & Flux, 1995). Separately, snowshoe hare (*L. americanus*) densities reach up to 300 km^{-2} in boreal forests (Krebs et al., 2001).

4.1 | Degraded habitats

We observed wide variation of hare density between habitat types. We found significant differences between habitat classes, which

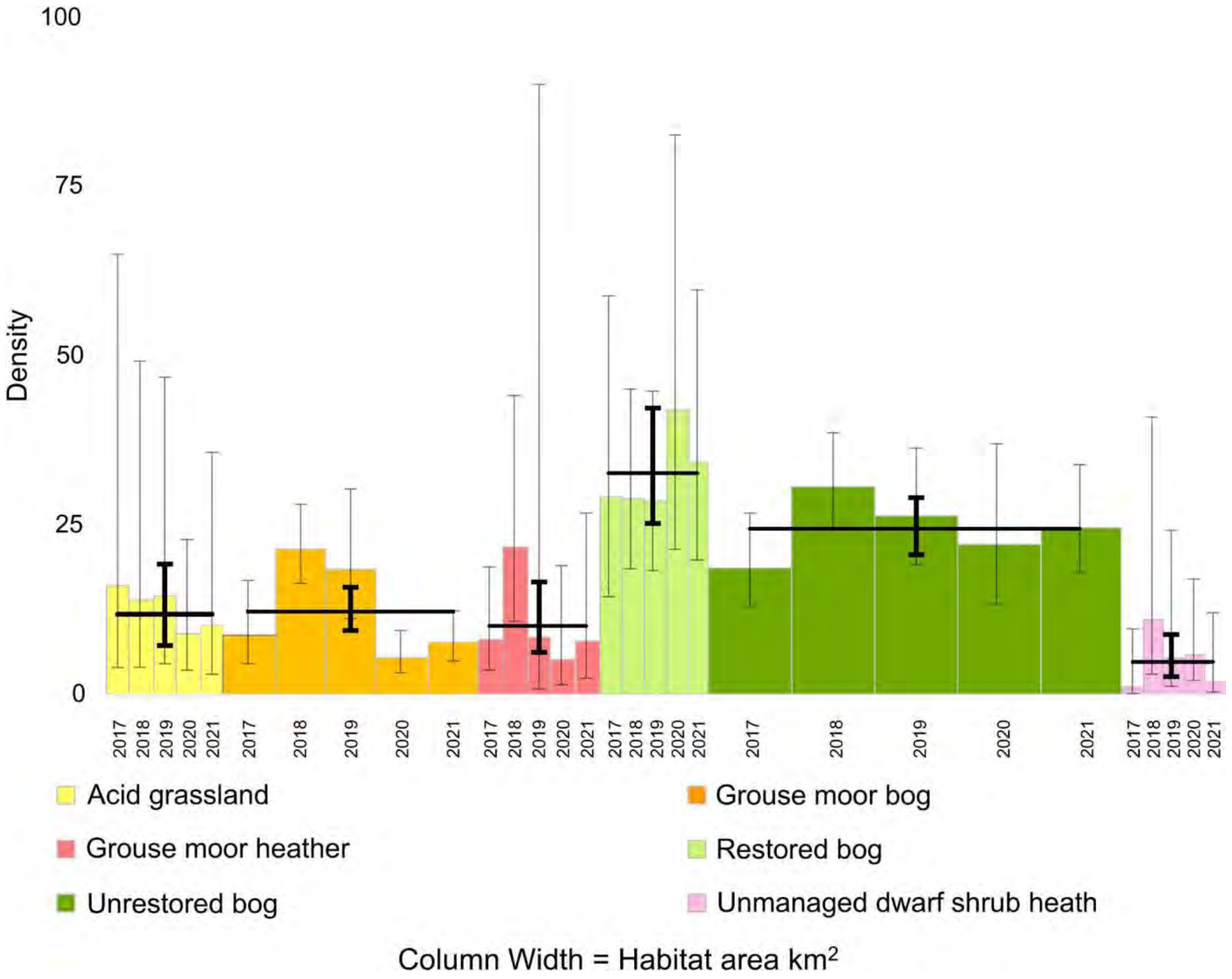


FIGURE 6 Estimates of abundance of mountain hares by habitat class, each year, as reported by distance sampling analysis for Bleaklow and Margery Hill only. *x*-axis column widths represent habitat area in km^2 which were as follows: acid grassland 8.5; grouse moor bog 18.4; grouse moor heather 18.7; restored bog 7.9; unrestored bog 29.8; and unmanaged dwarf shrub heath 7.4. Column height is mean density estimate (D). Column error bars indicate lower and upper 95% confidence limits on D. The shaded column area, therefore, represents the abundance of hares on each habitat type each year based on point density values. Black horizontal bars indicate mean density value for each habitat over the 5 years, with black vertical error bars showing 95% confidence limits (following Clymo, 2014, 230)

imply contrasts in vegetation diversity, forage quality, or attractiveness to hares. We detected a significant increase in density between 2017 and 18 followed by 2–3 years of decrease.

The Bleaklow surveys included 20 1-km^2 squares, which up to 2003 comprised eroded bare peat (Proctor et al., 2013) or low lev- els of co-dominant heather (Anderson & Yalden, 1981). On those, Yalden (1971) recorded hares in only 8 1-km squares, and as single hare observations. By contrast, our surveys of 2017–21 in those same areas, now as restored bog, showed high densities of moun- tain hares, that is, 32.6 (95% CI: 25.2–42.2) hares km^{-2}; in 2019 forBleaklow overall 27.2 (95% CI 19.9–37.9) hares km^{-2}. This clearly sug-gests a positive impact of bog restoration on hare density. These restored areas have been shown to support higher floral diversity (Pilkington et al., 2016), which we suggest is attractive and bene- ficial to hares. Restoration, lime, and fertilizer applied to bare peat, potentially provided a lingering amount of phosphorous and nitro- gen in the vegetation (Alderson et al., 2019), affording nutritional benefits to hares (Hewson, 1989; Miller, 1968; Watson et al., 1973).Such might contribute to animal health and higher numbers (Watsonet al., 1973). However, it is not clear whether food availability or nu-tritional quality limits hare populations (Keith, 1983; Newey et al., 2010) so it is hard to make inferences that food is the main cause ofdifferences in hare density between habitats. It is also conceivable that where restoration elevated the water table this created more water and moisture availability for mountain hares, particularly im- portant during summer. Restored bog areas contained eroded gulliesused by mountain hares for shelter and movement pathways. Taking advantage of the intricate micro-topography, during bad weather, hares could simply move ~20 m to new shelter among peat hags andgullies. The eroded gullies also existed in 1971 (Bower, 1961), and again this implies the restoration efforts themselves contributed to high hare numbers.

Unrestored bog areas also showed consistently high mountain hare encounter rates and density estimates. Density on restoredbog was 34% higher than unrestored bog, implying restoration ben-efits were proving supportive. Unrestored bog areas were similar to restored bog with many eroded gullies. However, unrestored bog areas featured extensive swathes of cotton grass with small pock- ets of heather; not the diverse micro-mosaic patchwork of assorted grasses, heather, ferns, and moss species seen on restored bog. Therefore, peat fertilization and diverse vegetation replanting on restored bog may have contributed to higher numbers of hares. Theabsolute extent of unrestored bog and its high densities made this the most important habitat for sustaining this hare population.

The presence of grouse moors was not associated with the high-est mountain hare densities. Grouse moor bog showed significantly lower density than unrestored bog, despite having similar vegeta- tion and with gullies present as potential shelter. Hare density on grouse moor bog was slightly higher than grouse moor heather. Both reported densities similar to acid grassland, noted as ecologically im-poverished (Anderson & Yalden, 1981). Density on grouse moor bog was significantly higher than unmanaged dwarf shrub heath. Density on grouse moor heather was also notably higher than unmanaged dwarf shrub heath, so the benefit to mountain hare density from heather burning and associated management activities described by Hesford et al. (2019) seemed apparent, as previously reported (Yalden, 1971). Yet, we observed the lower slopes of grouse moor heather were often dry, as also reported by Holden et al. (2015). Frequent extensive heather burning reduced vegetation diversityand cover (Bonn et al., 2009, 178). On some of these areas, no hares were seen. On less frequently burned areas, groups of hares were occasionally observed feeding upon pioneer heather (Hewson, 1962, 1989). The grouse moor bog included deeper mature heather, where some hares hid, though finding movement difficult (Hewson, 1989; Stoddart & Hewson, 1984). Indeed, Yalden (1971) recorded fewer hares in areas of pure *Calluna*. We were unable to ascertain whether predator control on grouse moors was reducing levels of predation and contributing to higher densities of hares.

We estimated lower mountain hare densities on grouse moors than reported in Scotland (Hesford et al., 2019; Newey et al., 2003, 2018). In Scotland, high densities of mountain hares on grouse moors were first reported in four studies. Hewson (1965) reported game bags of 43–295 hares, annually 1955–63 on a 2 km^2 area. Watsonet al. (1973) produced raw count data estimating up to 300 hares km^{-2}. Stoddart and Hewson (1984) suggested an association of hares with grouse moors from game bags, estimating hares 42 km^{-2}.Watson and Hewson (1973) reported count data, comparing den- sity by habitat, with high densities in valleys 26.3 hares km^{-2}, on grouse moors in the Cairngorms 32.6 hares km^{-2}; lower at arctic- alpine areas 7.9 km^{-2}, suggesting grouse moor as optimum habitat. More recently, studies in Scotland have shown the persistence of mountain hares measured in terms of occupied range and count in- dices as associated with moors managed for driven grouse shooting (Hesford et al., 2019, 2020). Very high densities (18–249 hares km^{-2}) were recorded on grouse moors in northeast Scotland (Newey et al., 2018). In the Peak District, Yalden (1971, 1984) and Wheeler (2002) found highest counts on heather moorland, followed by bog and acid grassland.

It was, therefore, unexpected to find lower mountain hare den- sity on grouse moors in the Peak District. Possibly mountain hares had shifted habitat use to high elevations, making for higher densi- ties on the biologically diverse and higher altitude bogs. This could be a response to climate change and the rise in annual average tem-peratures observed in the Peak District (Caporn & Emmett, 2009, 47) and has been forecast across Europe (Leach et al., 2015). On re- stored and unrestored bog, patches of heather resource were ample, dispersed amidst a variety of other vegetation species and easyfor hares to move around. Grouse moor bog had similar vegetation species to unrestored bog; grouse moor heather was characterized by heather species. Yet on both grouse moor bog and heather, the *Calluna* existed in such large deep expanses that movement for hares could be difficult. It may be that intense heather burning resultedin inferior vegetation quality or diversity compared with Scotland. We speculate that Peak District heather moorland overlays acidic rock, which may contribute to lower forage quality and lower hare densities (Watson et al., 1973). On grouse moor bog, there was a significant increase in mountain hare density 2017–18 and a signif- icant decrease in 2019–20. On grouse moor heather, there were large reductions in mountain hares in 2018–20. These fluctuations contrasted with the other habitat types, though heather was foundin all of them. The forces which govern populations ought to have been similar: weather, availability of food resource within each hab- itat class, disease, and parasites (Newey, Willebrand, et al., 2007), contributing to similar dynamics. We reflect that in Scotland, grouse moor estates have conducted lethal removal of mountain hares (Patton et al., 2010). We then speculate whether the same occurredon grouse moors within the Peak District, causing lower and fluctu- ating mountain hare densities.

Mountain hare density on acid grassland showed high variation. While containing much *Nardus* and *Molinia* disliked by mountain hares, some areas contained *Calluna* patches, enabling hares to feed, without trapping them within it. Unmanaged dwarf shrub heathareas mostly reported lowest hare densities. Its deep mature woody *Calluna* was frequently impenetrable. These findings are consistent with previous work by Yalden (1971), Watson et al. (1973), Hewson (1989). Acid grassland and unmanaged dwarf shrub areas were mostly at extent edges, possibly experiencing human pressure from higher road densities, walking paths, sheep farms, and settlements.

4.2 | Survey efficacy

The use of daylight distance sampling for mountain hares has been criticized as hares are nocturnal and rest up, hiding by day, resultingin lower observed encounter rates (Newey et al., 2018). However, our research achieved large sample sizes and encounter rates with narrow confidence intervals, a function of high densities on Bleaklow and Margery Hill, and demonstrating distance sampling by day can be effective. That said, we had deliberately chosen those areas for survey efficacy. By contrast, in mountain hare surveys on the Scottish Lammermuir hills, Pettigrew (2020) recommended 90- min surveys by dawn light as hares are more active and visible at thistime rather than by midday when dormant. However, this suggestion lacked information regarding imperfect detection process or detec- tion probability so is hard to compare; and those surveys occurred on small accessible areas ~26 km^2 of relatively flat elevation 420– 520 m. By contrast, the Peak District required >120 km of transects and featured steep hills elevation 630 m with transect elevation changes >350 m over 1 km. These hills were often fog shrouded early morning, so dawn surveys were not possible. Consequently, Peak District surveys took up the whole day (2–4 h per square, two squares in a day). Bedson, Thomas, et al. (2021) compares noctur- nal survey methods for mountain hares, showing daytime surveysas effective.

We also considered differences in detection process between different habitat classes. Our surveys went on straight line tran- sects, following the Jenkins et al. (1963) method of flushing hares from cover and were applied consistently to all habitat classes. Of note, the assessment of hare activity, that is, numbers of flush-ing hares, did not provide evidence that our surveys were missing hares hiding in deep heather. Indeed, all habitat classes contained winter vegetation up to ~100 cm height. Given that mountain hares can lie themselves down to ~15 cm height, they can hide in any habitat.

When assembling these analyses, we also considered several alternative habitat class definitions, for example, merging restored and unrestored bog; grouse moor bog and grouse moor heather. Such alternatives did not change the substantive findings that bog habitats reported significantly higher density than managed grouse moor or acid grassland habitats. During surveys, when walking fromone habitat to another, we typically observed an immediate abrupt change of encounter rates within <200 m.

We acknowledge that mountain hares may move between habitat classes and we did not employ telemetry to measure this. Hewson (1962, 1989) suggested hares would move by dusk to feed on grouse moor pioneer heather patches. We rarely observed such movement. Both the high elevation restored and unrestored bog areas contained some heather resource, obviating the need for a nightly migration. We analyzed habitat classes based on where eachhare was first seen. We acknowledge field measurement factorsmay have contributed to small errors of habitat class allocation. Harehome ranges may be very small ~0.1 km^2 (Hewson & Hinge, 1990; Rao et al., 2003). Because our visual range exceeded 700 m and thestudy layout meant transects were 1000 m parallel to each other, wefelt that coverage of home ranges was likely to be comprehensive. Our surveys occurred without snow lie present, which might other- wise prompt hares to seek for heather which might better protrude out of the snow. Notwithstanding these challenges, our surveys achieved global detection probability of 18% of hares, that is, seeing nearly 1 in 5 hares to a range of 520 m. We duly consider distance sampling by day as effective across habitats.

4.3 | Population fluctuations

In the Peak District since 1971, there were four previous reports of mountain hare abundance suggesting a population of up to ~1000 individuals (Mallon, 2001). The distance sampling survey of winter 2001–2002 using different methods to this paper estimated abun- dance at ~12,000 hares (CI: 7000–20,000) (Mallon, 2001; Mallonet al., 2003; Wheeler, 2002). We retrieved that data and applied thesame analyses as for 2017–21. This revised 2002 density estimateto 9.4 hares km^{-2} (95% CI 6.8 to 12.9); abundance for survey ex-
tent 3361 (95% CI 2431–4612) individuals. However, we recommend caution with 2002 values as its survey methodology differed from that of 2017–21: that is, different transect shapes, different loca- tions, no use of binoculars, no laser range finder for measuring the distance to object, no GPS measurement of transect length, and all observations recorded as singles, that is, no clusters.

Estimates for 2017 to 2021 reported high densities upon Bleaklow and Margery Hill. We acknowledge that using these two high-density areas for 2019 surveys (i.e., as 40% of survey areas), may bias the park-wide estimate upwards. The Peak District mean abundance estimate for 2019 refers to densities from the wider survey and alpha hull shape, reporting as 3562 (95% CI 2291–5624)individuals.

Therefore, estimates for 2002 compared with 2019 appear similar and suggest a stable population. We speculate whether the increase in densities seen on restored bog has been balanced by a decrease in densities in other areas. Otherwise, the length of this study (2017–21) is too short to detect population cycles, whichare subject to complex factors (Newey, Willebrand, et al., 2007). Population dynamics for congeneric snowshoe hare suggest an-nual fluctuations with observed increases by 25%, or decreases by as much as 75%, linked to food supply and predation (Krebs et al., 2001). Cycle periodicity of mountain hares in Scotland has a range of4–15 years, with amplitude of up to 90% (Newey, Dahl, et al., 2007),8 years historically for Irish hare (Reid et al., 2021).

We cannot identify explicit causation for the population fluctu- ations we observed. Winter 2017–18 was exceptionally severe (UK Met Office, 2020), possibly causing additional mortality. Summer 2018 was extremely hot, potentially contributing to difficult breed- ing conditions arising from dry vegetation and reduced water avail- ability. Under climate change, the range of mountain hares is forecast to move northwards and to higher elevations (Bedson, Devenish,et al., 2021; Leach et al., 2015; Rehnus et al., 2018), which may result in lower abundances.

This Peak District mountain hare population assessment shows how their confinement to the uplands, and sensitivity to differ- ent habitats, makes them a useful mammal species for ecosystem monitoring. They provide an understanding of mammalian responses to climate change: a cold-niche specialist at the periphery of their climatic range (Harris & Yalden, 2008). We suggestboth degrading forces and restoration efforts impact upon hare density. There is substantial variation of density between habitat classes, predisposing the population to local extinction events (Patton et al., 2010). Management agendas should consider how future changes to habitat landcover and land use may affect this mountain hare population.

ACKNOWLEDGMENTS

This research was funded by the People's Trust for Endangered Species, the Hare Preservation Trust, the British Mountaineering Council, Penny Anderson Associates, South-West Action for Hares, Queen's University Belfast, and an MMU matched-fundedPhD scholarship to CB. We thank RSPB Dove Stone, The National Trust, United Utilities, and Upperwood Estates for access support. We thank Moors for the Future for shapefiles showing restoredbog areas. We thank E. Rexstad of University of St. Andrews for R code enabling the t-test analyses. We thank J. Minshull, D. Hogg, K. Boyd, I. Commerford, C. Shaw, M. Moore, and C. Thelier for field- work. Mountain hare BRC records kindly provided by British Trust for Ornithology, Cheshire Record LRC, Derbyshire Mammal Group, Derbyshire Wildlife Trust, Moors for the Future, Liverpool Museum, National Biodiversity Atlas, Sheffield Biological Records Centre, Sorby Natural History Society, and West Yorkshire Ecology. We thank Anna Reuleaux and two anonymous reviewers who advisedon earlier drafts of this paper.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

Carlos P. E. Bedson contributed to conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); validation (lead); visualization (lead); and writing—original draft (lead); and writing—review and editing (lead). **Philip M. Wheeler** contributed to data curation (supporting); validation (equal); and writing—review and editing (supporting). **Neil Reid** contributed to conceptualization (supporting); funding acquisition (supporting); methodology (supporting); validation (supporting); visualization (supporting); writing—original draft (supporting); and writing—review and editing (supporting). **Wilson Edwin Harris** contributed to writing—review and editing (equal). **David Mallon** contributed to conceptualization (supporting); investigation (sup- porting); validation (supporting); and writing—review and editing (supporting). **Simon Caporn** contributed to validation (support- ing) and writing—review and editing (supporting). **Richard Preziosi** contributed to conceptualization (supporting); formal analysis (supporting); funding acquisition (supporting); methodology (sup- porting); project administration (supporting); resources (lead); software (supporting); supervision (lead); validation (supporting); visualization (supporting); and writing—review and editing (supporting).

DATA AVAILABILITY STATEMENT

Observation data are available from the corresponding author upon reasonable request.

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How to cite this article: Bedson, C. P. E., Wheeler, P. M., Reid,N., Harris, W. E., Mallon, D., Caporn, S., & Preziosi, R. (2022). Highest densities of mountain hares (*Lepus timidus*) associated with ecologically restored bog but not grouse moorland management. *Ecology and Evolution*, *12*, e8744. https://doi.org/10.1002/ece3.8744

APPENDIX

TABLE A1 Coverage of surveyed area arising from square survey design (Figure 1)

Habitat class	Total surveyed area	Of which Area visited once	 Area visited twice	Total area visited
Acid grassland	8.5	7.4	1.2	9.6
Grouse moor bog	18.4	11.9	6.5	24.9
Grouse moor heather	8.7	6.8	2.0	10.7
Restored bog	7.9	2.7	5.2	13.1
Unrestored bog	29.8	18.9	10.9	40.6
Unmanaged dwarf shrub heath	7.4	6.4	1.0	8.4

Note: Those areas at adjoining vertices effectively received two visits in each year. Values are km^2.

TABLE A2 Range of candidate models based on all data for Bleaklow and Margery Hill, pooled. (2017, 2018, 2019, 2020, and 2021)

Data selection	*n*	Model (key)	# para	AIC	ΔAIC	χ^2 GOF (*p*)	*P*	*P cv*
Truncate at 520 m	1985	Uniform + cosine	3	22353.25	204.82	.00	.30	.01
		Uniform + poly	3	22672.06	523.63	.00	.40	.01
		Half-normal + cosine	3	22260.09	111.66	.00	.25	.02
		Half-normal + Hermite	1	22619.32	470.89	.00	.35	.01
		Hazard rate + cosine	3	22152.52	4.09	.61	.19	.04
		Hazard rate + poly	3	22148.43	0.00	.77	.18	.04
Truncate at 500 m	1980	Uniform + cosine	3	22234.13	185.62	.00	.30	.01
		Uniform + poly	3	22533.32	484.81	.00	.40	.01
		Half-normal + cosine	3	22153.85	105.34	.00	.26	.02
		Half-normal + Hermite	1	22503.44	454.93	.00	.36	.01
		Hazard rate + cosine	3	22050.69	2.18	.62	.19	.04
		Hazard rate + poly	3	22048.51	0.00	.70	.19	.04
Truncate at 480 m	1970	Uniform + cosine	3	22025.26	165.86	.00	.30	.01
		Uniform + poly	0	0.00	0.00	.00	.00	.00
		Half-normal + cosine	3	21952.22	92.82	.00	.26	.02
		Half-normal + Hermite	1	22278.42	419.02	.00	.36	.01
		Hazard rate + cosine	3	21863.44	4.04	.19	.20	.04
		Hazard rate + poly	3	21859.40	0.00	.37	.20	.04

Note: *n* = number of observations; Model (key) = Key function with series expansion; AIC = Akaike information criterion; ΔAIC = delta AIC value within comparable data selections; χ^2 GOF (*p*) = chi-square goodness of fit *p*-value; P = detection probability function; P *cv* = detection probability coefficient of variation. We chose to use data truncated at 520 m with the hazard-rate model and polynomial, for all analyses.

TABLE A3 Stratified distance sampling survey parameter estimates for habitat classes each year for Bleaklow and Margery Hill

	n	*L*	*n*/*L*		*n*/*L*	*n*/*L*	*K*	*E* (s)	*E* (s) *cv*	D̂	D̂ *cv*	D̂ LCL	D̂ UCL
AG17	11	8.3	1.3	0.61	0.3	5.3	7	2.31	0.25	16.0	0.67	3.9	64.8
GMB1	41	27.0	1.5	0.31	0.8	2.9	17	1.10	0.05	8.7	0.31	4.5	16.8
RB17	93	19.8	4.7	0.32	2.3	9.4	11	1.19	0.03	29.3	0.32	14.4	58.8
UH17	2	8.7	0.2	1.12	0.0	1.8	9	1.00	0.00	1.2	1.12	0.1	9.6
GMB18	102	27.2	3.8	0.12	2.9	4.8	18	1.09	0.03	21.4	0.13	16.4	28.0
RB18	99	19.9	5.0	0.20	3.2	7.7	12	1.11	0.02	28.9	0.20	18.5	45.0
UH18	12	8.9	1.3	0.62	0.4	5.0	10	1.56	0.11	11.0	0.63	3.0	40.9
GMB19	80	25.1	3.2	0.23	1.9	5.2	17	1.10	0.03	18.3	0.24	11.2	30.3
RB19	86	18.3	4.7	0.19	3.0	7.3	10	1.16	0.03	28.5	0.20	18.2	44.7
UH19	8	8.1	1.0	0.73	0.2	4.4	9	1.04	0.11	5.4	0.74	1.2	24.2
GMB20	25	27.6	0.9	0.25	0.5	1.5	17	1.15	0.05	5.5	0.26	3.2	9.4
RB20	150	20.0	7.5	0.30	3.8	14.7	11	1.07	0.01	42.0	0.31	21.4	82.5
UH20	10	8.9	1.1	0.48	0.4	3.2	9	1.00	0.00	5.9	0.48	2.0	17.0
GMB21	37	26.9	1.4	0.20	0.9	2.1	16	1.08	0.05	7.8	0.22	4.9	12.3
RB21	116	19.7	5.9	0.24	3.4	10.2	10	1.11	0.03	34.2	0.25	19.8	59.6
UH21	5	10.5	0.5	0.91	0.1	2.8	10	0.82	0.18	2.0	0.93	0.3	12.0

Note: *n* = encounters; *L* = line length km; *K* = number of transects; *E*(*s*) = mean cluster size; D̂ = density estimate km^{-2}; *cv* = parameter coefficient of variation; LCL & UCL = 95% confidence intervals. D̂ is calculated with probability density function *f*(0) = 0.010467 and *f*(0) *cv* = 0.0407 (Buckland et al., 2001, 84,85). AG = acid grassland; GMB = grouse moor bog; GMH = grouse moor heather; RB = restored bog; UB = unrestored bog;

UH = unmanaged dwarf shrub heath and each year shown as suffix, for example, AG17 is acid grassland in 2017 survey.

TABLE A4 Pairwise *t*-tests comparing strata based on values from Table 1

S1	S2	$\hat{D}$ Difference	SE diff	*t* Stat	df *t* stat	*p* Value	Significant	Bonferonni-corrected significant	Effect size
Habitats									
Acid grassland	Grouse moor bog	−0.26	3.2	0.08	66.04	.934			0.01
Acid grassland	Grouse moor heather	1.84	3.6	0.50	64.44	.615			0.06
Acid grassland	**Restored bog**	**−20.73**	**4.9**	**4.26**	**105.67**	**.000**	*	**	**0.38**
Acid grassland	**Unrestored bog**	**−12.44**	**3.3**	**3.75**	**86.17**	**.000**	*	**	**0.37**
Acid grassland	**Unmanaged heath**	**7.09**	**3.2**	**2.23**	**61.53**	**.029**	*		**0.27**
Grouse moor bog	Grouse moor heather	2.10	2.8	0.76	47.19	.449			0.11
Grouse moor bog	**Restored bog**	**−20.46**	**4.2**	**4.83**	**85.35**	**.000**	*	**	**0.46**
Grouse moor bog	**Unrestored bog**	**−12.18**	**2.3**	**5.28**	**313.71**	**.000**	*	**	**0.29**
Grouse moor bog	**Unmanaged heath**	**7.35**	**2.1**	**3.53**	**139.46**	**.001**	*	**	**0.29**
Grouse moor heather	**Restored bog**	**−22.57**	**4.6**	**4.89**	**90.60**	**.000**	*	**	**0.46**
Grouse moor heather	**Unrestored bog**	**−14.28**	**2.9**	**4.86**	**66.43**	**.000**	*	**	**0.51**
Grouse moor heather	Unmanaged heath	5.25	2.8	1.90	43.10	.064			0.28
Restored bog	Unrestored bog	8.29	4.3	1.92	99.03	.057			0.19
Restored bog	**Unmanaged heath**	**27.82**	**4.2**	**6.55**	**82.52**	**.000**	*	**	**0.58**
Unrestored bog	**Unmanaged heath**	**19.53**	**2.3**	**8.40**	**222.27**	**.000**	*	**	**0.49**
Comparison of habitats year to year									
AG17	AG18	2.1	13.1	0.15	14.11	.877			0.04
AG18	AG19	0.6	10.7	0.05	12.96	.957			0.01
AG19	AG20	5.6	8.2	0.67	9.30	.510			0.21
AG20	AG21	−1.2	6.8	0.18	12.43	.859			0.05
GMB17	**GMB18**	**−12.7**	**3.8**	**3.29**	**40.07**	**.002**	*	**	**0.46**
GMB18	GMB19	3.0	5.0	0.60	31.19	.549			0.11
GMB19	**GMB20**	**12.9**	**4.6**	**2.88**	**21.65**	**.009**	*	**	**0.53**
GMB20	GMB21	−2.3	2.1	1.09	35.64	.283			0.18
GMH17	GMH18	−13.6	5.9	2.31	5.59	.063			0.70
GMH18	GMH19	13.3	10.3	1.29	6.54	.239			0.45
GMH19	GMH20	3.3	9.1	0.35	4.58	.738			0.16
GMH20	GMH21	−2.8	4.4	0.62	7.28	.554			0.22
RB17	RB18	0.4	11.1	0.03	17.95	.975			0.01
RB18	RB19	0.4	8.0	0.05	22.45	.964			0.01
RB19	RB20	−13.5	13.8	0.97	14.28	.344			0.25
RB20	RB21	7.8	15.1	0.51	17.82	.612			0.12

TABLE A4 (Continued)

S1	S2	$\hat{D}$ Difference	SE diff	*t* Stat	df *t* stat	*p* Value	Significant	Bonferonni-corrected significant	Effect size
UB17	**UB18**	**−11.9**	**4.5**	**2.64**	**57.93**	**.011**	*	**	**0.33**
UB18	UB19	4.2	4.9	0.86	55.74	.393			0.11
UB19	UB20	4.2	65.0	0.65	43.63	.518			0.10
UB20	UB21	−2.4	6.3	0.38	41.99	.705			0.06
UH17	UH18	−9.8	7.1	1.38	10.37	.195			0.39
UH18	UH19	5.6	8.1	0.69	15.80	.498			0.17
UH19	UH20	−0.5	4.9	0.10	15.09	.919			0.03
UH20	UH21	3.8	3.4	1.12	14.58	.279			0.28
Years (Bleaklow and Margery Hill combined)									
2017	**2018**	**−9.21**	**4.0**	**2.29**	**57.56**	**.025**	*		**0.29**
2018	2019	3.65	3.9	0.94	61.36	.350			0.12
2019	2020	3.13	5.4	0.58	47.34	.563			0.08
2020	2021	−0.36	5.6	0.06	49.37	.948			0.01
Survey areas 2019									
Bleaklow	**Margery Hill**	**8.68**	**6.8**	**1.27**	**23.31**	**.214**			**0.25**
Bleaklow	**Holme Moss**	**21.13**	**4.2**	**5.03**	**18.78**	**.000**	*	**	**0.76**
Bleaklow	**Peripheral Squares**	**21.10**	**4.1**	**5.20**	**16.90**	**.000**	*	**	**0.78**
Margery Hill	Holme Moss	12.45	5.8	2.13	14.76	.050			0.48
Margery Hill	**Peripheral Squares**	**12.42**	**5.7**	**2.16**	**13.89**	**.049**	*		**0.50**
Holme Moss	Peripheral Squares	−0.03	2.0	0.01	27.84	.987			0.00

Note: S1 = Stratum 1; S2 = Stratum 2. $\hat{D}$ difference subtracts S2 $\hat{D}$ from S1 $\hat{D}$. A positive value indicates Stratum 1 is larger; a negative value means Stratum 2 is larger. SE is the standard error of $\hat{D}$ difference. Values are assessed with Satterthwaite *t*-test reporting *t*-statistic and degrees of freedom. Asterisk * and bold lines indicate *p*-value significant and using Bonferroni within-cohort correction. Effect size calculated with Cohen's *d* and considered as $r = .10$ (small); $r = .30$ (medium); $r = .50$ (large) (Field et al., 2012).

Abbreviations: AG, acid grassland; GMB, grouse moor bog; GMH, grouse moor heather; RB, restored bog; UB, unrestored bog; UDSH, unmanaged dwarf shrub heath.

TABLE A5 Pairwise *t*-tests comparing habitat class strata each year based on values from Table A1 for Bleaklow and Margery Hill

Comparison between habitats within each year									
S1	**S2**	**$\hat{D}$ Difference**	**SE Diff**	***t* Stat**	**df *t* stat**	***p*-Value**	**Significant**	**Bonferroni-corrected significant**	**Effect size**
AG17	GMB17	7.3	10.9	0.66	9.23	.521			0.21
AG17	GMH17	7.8	10.9	0.72	9.17	.492			0.23
AG17	RB17	−13.2	14.1	0.93	17.59	.360			0.22
AG17	UB17	−2.7	11.0	0.24	9.72	.810			0.08
AG17	UH17	14.8	10.7	1.39	8.37	.200			0.43
GMB17	GMH17	0.5	3.9	0.14	16.60	.891			0.03
GMB17	RB17	−20.5	9.8	2.09	12.31	.058			0.51
GMB17	**UB17**	**−9.9**	**4.2**	**2.34**	**43.72**	**.023**	*		**0.33**
GMB17	**UH17**	**7.5**	**3.1**	**2.44**	**23.74**	**.022**	*		**0.45**
GMH17	RB17	−21.0	9.8	2.14	12.17	.053			0.52
GMH17	**UB17**	**−10.5**	**4.2**	**2.48**	**22.51**	**.021**	*		**0.46**
GMH17	UH17	7.0	3.1	2.28	8.00	.052			0.63
RB17	UB17	10.6	9.9	1.06	13.11	.307			0.28
RB17	**UH17**	**28.0**	**9.5**	**2.94**	**10.92**	**.013**	*		**0.66**
UB17	**UH17**	**17.5**	**3.5**	**4.98**	**32.92**	**.000**	*	**	**0.66**
AG18	GMB18	−7.4	8.2	0.90	8.18	.393			0.30
AG18	GMH18	−7.9	9.4	0.83	9.99	.422			0.25
AG18	RB18	−14.9	9.7	1.53	13.63	.148			0.38
AG18	UB18	−16.6	8.4	1.97	9.00	.080			0.55
AG18	UH18	2.9	10.4	0.28	14.60	.782			0.07
GMB18	GMH18	−0.4	5.8	0.07	5.87	.940			0.03
GMB18	RB18	−7.5	7.5	1.17	17.67	.256			0.27
GMB18	**UB18**	**−9.1**	**4.1**	**2.22**	**55.33**	**.030**	*		**0.29**
GMB18	UH18	10.4	7.4	1.39	12.86	.186			0.36
GMH18	RB18	−7.1	7.8	12.61	12.61	.380			0.25
GMH18	UB18	−8.7	6.1	1.44	7.03	.193			0.48
GMH18	UH18	10.8	8.7	1.24	12.73	.235			0.33
RB18	UB18	−1.6	6.6	0.24	20.39	.806			0.05
RB18	UH18	17.9	9.1	1.97	20.27	.062			0.40
UB18	**UH18**	**19.5**	**7.6**	**2.56**	**14.43**	**.022**	*		**0.56**
AG19	GMB19	−3.8	8.5	0.44	11.14	.664			0.13
AG19	GMH19	6.1	11.5	0.52	9.00	.613			0.17
AG19	RB19	−14.0	9.2	1.51	13.28	.153			0.38
AG19	UB19	−11.8	8.3	1.42	10.31	.184			0.40
AG19	UH19	9.2	8.4	1.09	10.09	.300			0.32
GMB19	GMH19	9.9	9.8	1.00	6.17	.354			0.37
GMB19	RB19	−10.2	7.0	1.46	21.70	.158			0.30
GMB19	UB19	−8.0	5.7	1.41	40.21	.166			0.22
GMB19	**UH19**	**13.0**	**5.8**	**2.22**	**24.00**	**.036**	*		**0.41**
GMH19	RB19	−20.0	10.4	1.91	7.52	.094			0.57
GMH19	UB19	−17.9	9.6	1.85	5.76	.115			0.61
GMH19	UH19	3.1	9.7	0.32	5.77	.760			0.13
RB19	UB19	2.2	6.6	0.32	20.71	.746			0.07

TABLE A5 (Continued)

Comparison between habitats within each year									
S1	S2	$\hat{D}$ Difference	SE Diff	*t* Stat	df *t* stat	*p*-Value	Significant	Bonferroni-corrected significant	Effect size
RB19	**UH19**	**23.2**	**68.0**	**3.40**	**17.78**	**.003**	*	**	**0.63**
UB19	**UH19**	**21.0**	**5.5**	**3.82**	**24.96**	**.001**	*	**	**0.61**
AG20	GMB20	3.5	3.8	0.92	8.51	.381			0.30
AG20	GMH20	3.7	4.2	0.89	9.39	.393			0.28
AG20	**RB20**	**−33.0**	**13.1**	**2.51**	**11.96**	**.027**	*		**0.59**
AG20	**UB20**	**−13.1**	**6.4**	**2.05**	**28.48**	**.049**	*		**0.36**
AG20	UH20	3.1	4.5	0.68	13.00	.507			0.19
GMB20	GMH20	0.2	2.6	0.08	5.88	.930			0.03
GMB20	**RB20**	**−36.5**	**12.7**	**2.87**	**10.64**	**.016**	*		**0.66**
GMB20	**UB20**	**−16.7**	**5.5**	**3.02**	**26.49**	**.006**	*	**	**0.51**
GMB20	UH20	−0.4	3.1	0.13	12.28	.894			0.04
GMH20	**RB20**	**−36.8**	**12.8**	**2.86**	**10.99**	**.015**	*		**0.65**
GMH20	**UB20**	**−16.9**	**5.8**	**2.92**	**26.21**	**.007**	*	**	**0.50**
GMH20	UH20	−0.6	3.6	0.18	10.59	.860			0.06
RB20	UB20	19.9	13.7	1.45	14.25	.168			0.36
RB20	**UH20**	**36.1**	**12.9**	**2.79**	**11.41**	**.017**	*		**0.64**
UB20	**UH20**	**16.2**	**6.0**	**2.68**	**31.19**	**.011**	*		**0.43**
AG21	GMB21	2.4	6.1	0.40	8.94	.690			0.13
AG21	GMH21	2.2	7.0	0.31	12.19	.756			0.09
AG21	**RB21**	**−24.0**	**10.2**	**2.36**	**16.68**	**.031**	*		**0.50**
AG21	UB21	−14.3	6.8	2.10	14.13	.054			0.49
AG21	UH21	8.2	6.2	1.32	9.34	.216			0.40
GMB21	GMH21	−0.2	4.2	0.05	6.66	.961			0.02
GMB21	**RB21**	**−26.4**	**8.5**	**3.12**	**10.56**	**.010**	*		**0.69**
GMB21	**UB21**	**−16.8**	**3.9**	**4.34**	**38.25**	**.000**	*	**	**0.57**
GMB21	**UH21**	**5.7**	**2.5**	**2.29**	**22.79**	**.032**	*		**0.43**
GMH21	**RB21**	**−26.2**	**9.1**	**2.86**	**13.19**	**.013**	*		**0.62**
GMH21	**UB21**	**−16.6**	**5.2**	**3.18**	**15.04**	**.006**	*	**	**0.63**
GMH21	UH21	5.9	4.3	1.38	7.42	.208			0.45
RB21	UB21	9.7	9.0	1.08	13.62	.300			0.28
RB21	**UH21**	**32.2**	**8.5**	**3.77**	**10.81**	**.003**	*	**	**0.75**
UB21	**UH21**	**22.5**	**4.0**	**5.61**	**37.44**	**.000**	*	**	**0.68**

Note: S1 = Stratum 1; S2 = Stratum 2. $\hat{D}$ difference subtracts S2 $\hat{D}$ from S1 $\hat{D}$. A positive value indicates Stratum 1 is larger; a negative value means Stratum 2 is larger. SE is the standard error of $\hat{D}$ difference. Values are assessed with Satterthwaite *t*-test reporting *t*-statistic and degrees of freedom. Asterisk * and bold lines indicate *p*-value significant and also when applying Bonferonni within-cohort correction. AG = acid grassland;

GMB = grouse moor bog; GMH = grouse moor heather; RB = restored bog; UB = unrestored bog; UH = unmanaged dwarf shrub heath and each year

shown as suffix, for example, AG17 is acid grassland in 2017 survey.

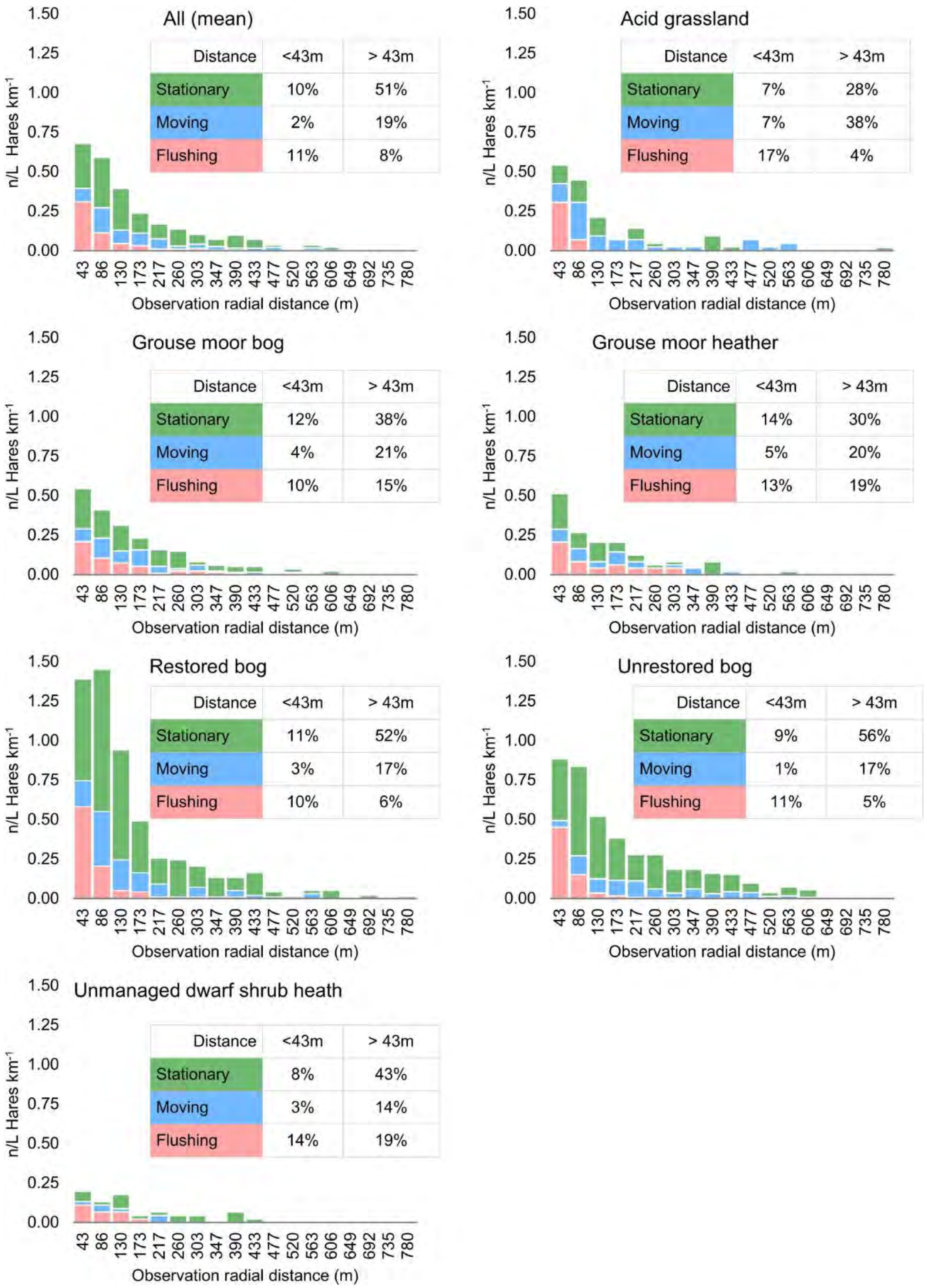
TABLE A6 Abundance of mountain hares for Peak District for year 2019, based on density estimates derived from pooled observations for each of the four denoted surveyed areas

	Bleaklow	Margery Hill	Holme Moss	Peripheral areas	
Density km^{-2}	27.4	18.6	6.1	6.2	
Density LCL	19.9	9.7	3.4	4.1	
Density UCL	37.8	35.5	10.9	9.4	
					Total
Area km^2	40.4	40.4	40.4	236.3	357.5
Abundance	1107	750	247	1458	3562
Abundance LCL	802	393	139	957	2291
Abundance UCL	1528	1433	442	2221	5624

Note: Calculation of km^2 for each surveyed areas is based on relevant habitat classes only, thatis, acid grassland; grouse moor bog; grouse moor heather; restored bog; unrestored bog; and unmanaged dwarf shrub heath. Thus non-relevant types, for example, woodland are excluded.

Density estimate is shown with 95% confidence limits; abundance also with 95% confidence limits.

FIGURE A1 Encounter rate (hares km^{-1}) by habitat class, by activity first observed for all Bleaklow and Margery Hill detections n = 1999. If groups, activity recorded as that of majority of hares. Histogram distance bin widths arranged at ~43 m increments as Figure 4. Note x-axis = radial distance observer to object, whereas Figure 4 x-axis represents perpendicular distance, hence differences between the two charts. When comparing summed encounters occurring either within or beyond 43 m for each habitat class, the highest proportion of activity was 56% of hares on unrestored bog beyond 43 m as stationary. Proportionately nearly twice as many observations on grouse moor bog or heather were of flushing hares, compared with restored or unrestored bog. Chart excludes records of 11 hare encounters where activity went unrecorded: 3 on restored bog and 8 on unrestored bog



All (mean)

Distance	<43m	> 43m
Stationary	10%	51%
Moving	2%	19%
Flushing	11%	8%

Acid grassland

Distance	<43m	> 43m
Stationary	7%	28%
Moving	7%	38%
Flushing	17%	4%

Grouse moor bog

Distance	<43m	> 43m
Stationary	12%	38%
Moving	4%	21%
Flushing	10%	15%

Grouse moor heather

Distance	<43m	> 43m
Stationary	14%	30%
Moving	5%	20%
Flushing	13%	19%

Restored bog

Distance	<43m	> 43m
Stationary	11%	52%
Moving	3%	17%
Flushing	10%	6%

Unrestored bog

Distance	<43m	> 43m
Stationary	9%	56%
Moving	1%	17%
Flushing	11%	5%

Unmanaged dwarf shrub heath

Distance	<43m	> 43m
Stationary	8%	43%
Moving	3%	14%
Flushing	14%	19%

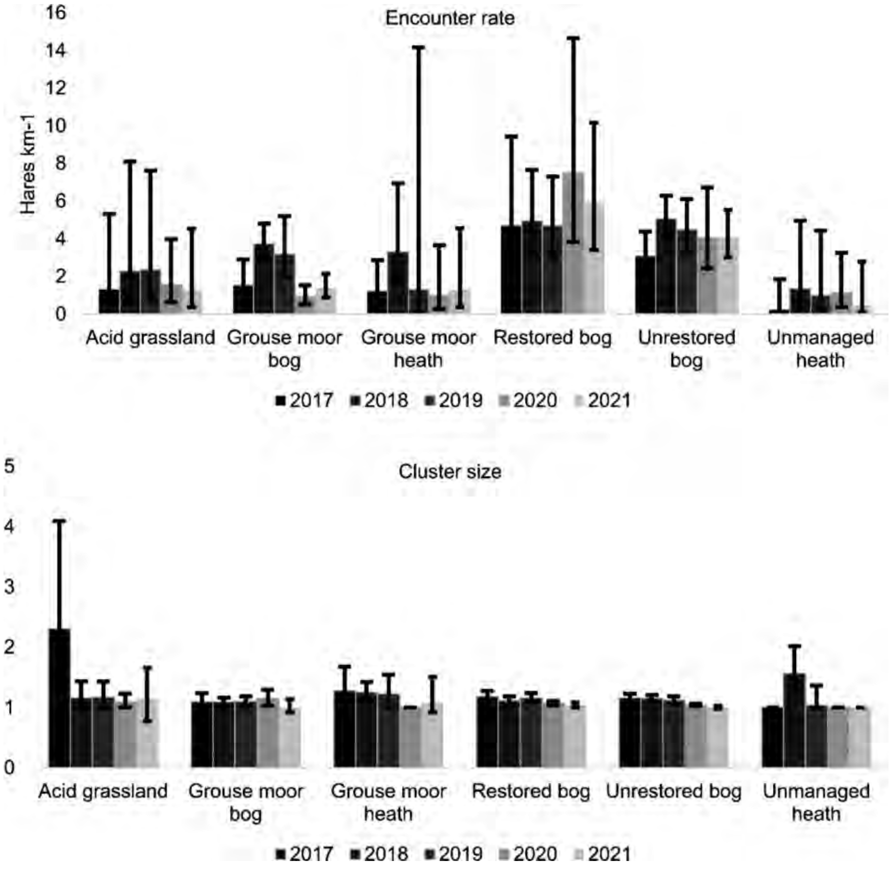


FIGURE A2 Encounter rate (mountainhares km^{-1}) and cluster size estimates for each habitat class and year based on Bleaklow and Margery Hill data. In total the number of hares recorded (before data truncation) was 385 in 2017; 622 in 2018; 517 in 2019; 434 2020; 458 in 2021

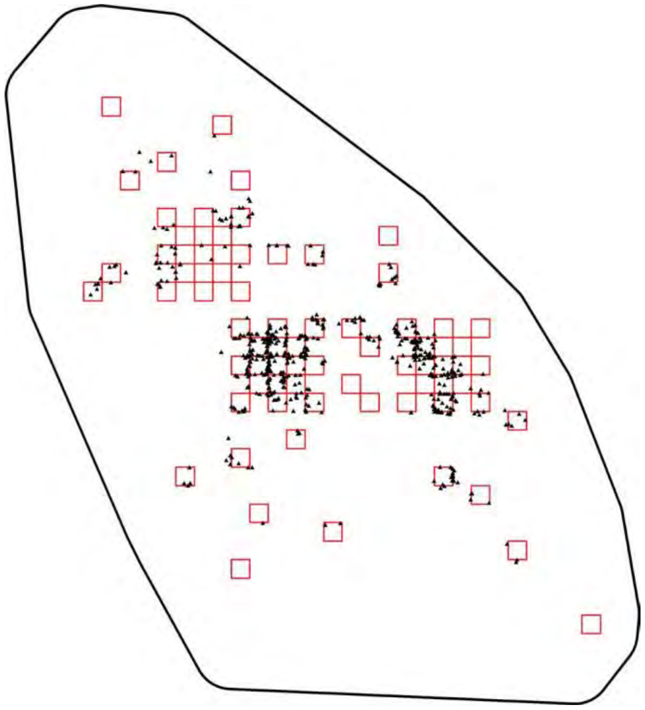


FIGURE A3 Distance sampling observations for the entire Peak District survey for 2019. Map origin is British National Grid Reference SK Easting 390000 Northing 370000. Transects are red 1 km squares. Black triangles indicate all observed mountain hares (untruncated data)

FIGURE A4 Estimates of total

mountain hare density per year per surveyarea, based on pooled observations each year. Error bars indicate 95% lower and upper confidence limits. Upon Bleaklow and Margery Hill there was a 59% increase in density from 2017 to 2018.
This was followed by a 15% decrease 2018–19%; 15% decrease 2019–20; 2%
increase 2020–21. Density upon Bleaklowand Margery Hill was significantly higher than Holme Moss when it was surveyed in 2018 and 2019 and also significantly higher than peripheral areas in 2019

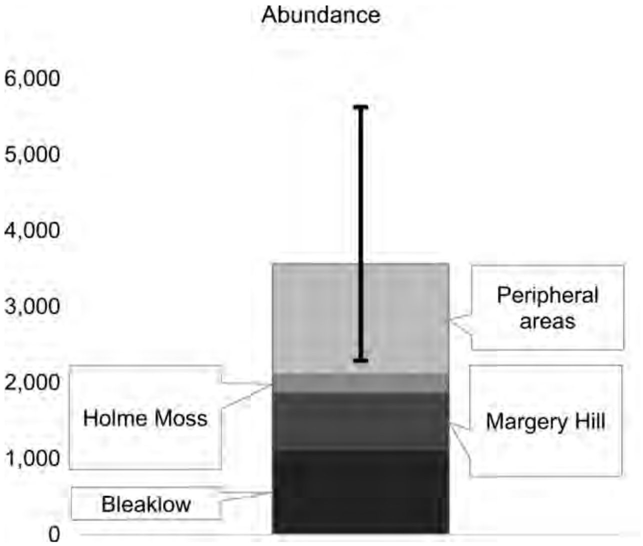


FIGURE A5 Abundance estimate for Peak District for year 2019, based on density estimates derived from pooled observations for the four different survey areas indicated by callouts. Error
bars indicated 95% lower and upper confidence limits for total abundance. Source data from Table A6