Scottish Natural Heritage
Research Report No. 1022

Developing a counting methodology for mountain hares (*Lepus timidus*) in Scotland

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RESEARCH REPORT

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Developing a counting methodology for mountain hares (*Lepus timidus*) in Scotland

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This report should be quoted as:

Newey, S., Fletcher, K., Potts, J. & Iason, G. 2018. Developing a counting methodology for mountain hares (*Lepus timidus*) in Scotland. *Scottish Natural Heritage Research Report No. 1022.*

RESEARCH REPORT
Summary

Developing a counting methodology for mountain hares (*Lepus timidus*)

Research Report No. 1022
Project No: 015116
Contractor: James Hutton Institute, Game & Wildlife Conservation Trust
Year of publication: 2018

Keywords

Population assessment; survey; dung plots; lamping; trapping.

Background

In Scotland, mountain hares are a traditional game species shot for sport/recreation and sometimes killed to protect crops, forestry, woodland and for disease control. Mountain hares are listed as a priority conservation species in the UK post-2010 Biodiversity Framework and listed under Annex V of the EU Habitats Directive. Many mountain hare populations show large annual fluctuations in numbers, and some populations show regular 'cyclical' changes that make it difficult to understand long-term population trends. Despite the importance of mountain hares for both shooting and conservation, little is known about their numbers or how to ensure their sustainable management. Given concerns over the current management of mountain hares and the Scottish Government's legal responsibilities, along with recent reports that might indicate localised declines of mountain hares in response to culling, there is a clear need to develop methods for assessing and monitoring mountain hare numbers in Scotland.

The aims of the project were to: i) assess the effectiveness and reliability of some selected methods of estimating mountain hare density, and ii) recomend a 'simple and cost effective' counting methodology calibrated against a reliable independent measure of mountain hare density. Specifically, we compared the density estimates derived from a programme of capture-recapture of mountain hares with, i) indices of abundance derived from direct counts carried out during daylight, and at night with the aid of a lamp or thermal imaging equipment, and ii) indirect indices of abundance based on dung standing crop and dung accumulation. The results suggest that; i) counts of mountain hares along transect lines at night with the aid of a high power lamp (and to a similar degree, thermal imaging equipment), and ii) dung accumulation rates can both be used to provide simple and easy to use indices of mountain hare density. These indices can be applied at the local scale to obtain indices of mountain hare density to inform local mountain hare management.

Main findings

- Ten study areas were surveyed over the course of the project (2014 to 2016)
- Spatial Capture-Recapture (SCR) analysis of trapping data was used to provide reliable density estimates against which we compared the less intensive survey methods: line

transect surveys (daylight, night time lamping and thermal imaging surveys) and dung plot surveys.

- On eight sites where the SCR approach was successfully used, density estimates on moorland during the autumn varied between 18 to 146 hares km^{-2}. The coefficient of variation of the SCR estimates, for all but one sites, were below 0.25 suggesting reasonable precision.
- Low numbers of hares were recorded during daylight surveys. Our analyses suggest that counts of mountain hares during daylight walked transect surveys are unlikely to provide a reliable or repeatable population index.
- Higher numbers of hares were recorded during night time surveys than during daylight. These surveys also had a lower mean coefficient of variation between the two replicate surveys conducted at each site. Our analyses suggest that night time transect surveys of mountain hares are preferable to daylight transect counts. There was relatively little difference in performance between lamping and thermal imaging surveys, but based on our experience we suggest that lamping is simpler to conduct and therefore preferable, but we do not dismiss the potential usefulness of surveys using thermal imaging equipment.
- Dung accumulation rate also has the potential to provide an index of mountain hare abundance over winter.
- Density estimates from distance sampling analyses during lamping surveys were only weakly correlated with SCR density estimates, but there was good agreement on some sites. Distance sampling can be used to obtain mountain hare density estimates, but requires a more complex analysis.

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Acknowledgements

We should like to thank all of the estates who took part in the study for allowing us access and for their assistance. We thank Helen Allinson, Paul Davidson, Kevin Duffy, Paul Duprat, Natalie Elms, Rhodri Evetts, Debbie Fielding, Kat Finglass, Hollie Fisher, Hannah Greetham, Kayleigh Hogg, Nick Littlewood, Cristian Navarro, Nancy Parsons, Sophie Philbrick, Anna McWilliam and Amy Withers for assistance with field work; Adam Smith for advice concerning land management; Nicholas Aebischer for statistical advice; Alessandro Gimona and Laura Poggio for use of high performance computing and computing advice; and Justin Irvine and Dan Haydon for comments. This work was funded by Scottish Natural Heritage. Scott Newey, Glenn Iason and Jackie Potts were also supported by the Rural & Environment Science & Analytical Services Division of the Scottish Government.

1. INTRODUCTION

1.1 Background

Mountain hare (*Lepus timidus* L.) populations in the European range of the species are under threat from habitat loss, fragmentation, and local over-exploitation (Mitchell-Jones *et al.*, 1999; Smith & Johnston, 2008). The mountain hare is listed in Annex V of the EC Habitats Directive (Council of the European Union, 1992), as a species 'of community interest whose taking in the wild and exploitation may be subject to management measures'. This requires Member States to maintain mountain hare populations in favourable conservation status (FCS) (JNCC, 2013). In Scotland FCS is understood to mean maintaining the population across its range, and maintaining a range which is comparable to the one which was assessed when the Directive came into force in the 1990s (SNH *et al.*, 2014). To help fulfil this obligation the Scottish Government has a legal obligation to monitor mountain hare numbers and report on their status (JNCC, 2013). The mountain hare in Scotland is a priority species for conservation action under the UK Biodiversity Action Plan (JNCC, 2010), and is also on the Scottish Biodiversity List, which means that it is considered by Scottish Ministers to be of 'principal importance' for biodiversity conservation (The Scottish Government, 2013).

Mountain hares are widely distributed in Scotland, though more numerous in the central and eastern Highlands. They are strongly associated with heather moorland managed for red grouse (*Lagopus lagopus scotica*) shooting where they benefit from the associated habitat management and predator control (Hulbert *et al.*, 2008; Patton *et al.*, 2010). The distribution of mountain hares in Scotland was mapped on the basis of a questionnaire survey and found no evidence of change in their distribution since a previous survey in 1996 (Kinrade *et al.*, 2008; Patton *et al.*, 2010). The only published information on changes in mountain hare numbers are the Game & Wildlife Conservation Trust's game bag statistics from the National Gamebag Census (NGC) and, more recently, from the British Trust for Ornithology's Breeding Bird Survey (BBS) incidental mammal sightings data (Noble *et al.*, 2012; Wright *et al.*, 2014). Both of these sources provide indices of mountain hare abundance at the regional and national scale. An analysis of the NGC data on mountain hares (Aebischer *et al.*, 2011) shows a non-statistically significant decline of 40% in the number of mountain hares reportedly killed by estates in the period 1995 to 2009. Similarly, an assessment of BBS mammal data by Wright *et al.* (2014), also suggested a non-significant decline of 26% over the 18-year period up to 2012. However, the most recent NGC report suggests an increase between 2010 and 2013 (Aebischer, 2014), and the recent update of the BTO mammal data also suggests that mountain hare sightings are increasing at a UK level (Harris *et al.*, 2016). A series of daytime counts of mountain hares using dogs, on moorlands of north-east Scotland collected over a long time period of up to 60 years suggest recent declines in hare numbers on some grouse moors, but a less marked decline was observed in arctic/alpine areas (Watson, 2013). Caution is needed when interpreting indices of population abundance, as the link between the numbers of hares reported killed in the NGC and hares seen during the BBS, and the actual number of mountain hares is unknown. Furthermore, mountain hare populations in Scotland, as elsewhere in the species' range, are characterised by large annual fluctuations in numbers and exhibit 'cyclic' or 'unstable' population dynamics, where numbers for some populations can vary by a factor of 10 or more over a 7 to 15 year time period (Newey *et al.*, 2007b; Tapper, 1992). The underlying reasons for these cycles or unstable dynamics are unclear (Newey *et al.*, 2007a, 2007b 2010a; Townsend *et al.*, 2009, 2011).

Mountain hares are a game species and may be legally killed for sport and population control to protect forestry, moorland habitats, woodland regeneration and crops during the open season, and under licence during the closed season (1st March – 31st July), (Hulbert *et al.*, 2008; Kinrade *et al.*, 2008; Patton *et al.*, 2010; Tapper, 1992). Most shooting takes place in mid to late winter (December-February).The number of mountain hares that can be killed in the open season is not regulated and does not require any statutory reporting. Outside of the open season a licence from Scottish Natural Heritage (SNH) is required to legally kill hares (except for humane dispatch), for which a land owner/manager is required to provide a justification, and an indication of the numbers to be killed.

More recently, mountain hares on some moorland shooting estates have been subject to culls that aim to reduce hare numbers and maintain them at a low level as part of tick control measures to reduce the tick borne disease louping-ill (Gilbert, 2016; Harrison *et al*., 2010; Kinrade *et al*., 2008; Patton *et al*., 2010). Louping-ill is a virus transmitted by ticks which infects sheep and red grouse (Hudson *et al*., 1998; Reid, 1975). In grouse it can cause high mortality of infected birds, affecting the number of red grouse that can be shot and consequently the estate income from commercial shooting (Gilbert, 2016; Hudson *et al*., 1998; Laurenson *et al*., 2003). Although mountain hares do carry ticks and can act as a reservoir for the disease, a thorough review of the scientific literature concluded that there was insufficient evidence to suggest culling mountain hares is a useful tool for increasing grouse densities by controlling louping-ill virus and ticks, in the majority of areas in Scotland where red deer were part of the ecosystem (Gilbert, 2016; Harrison *et al*., 2010).

Harris *et al.* (1995) provide an estimate of 350,000 (+/- 50%), and the more recent review of British mammals, commissioned by Natural England, SNH and Natural Resources Wales (in prep.), provides an estimate of 132,000 (confidence limits: 79,500 to 516,000). Whilst trends are evident in the NGC and BBS data neither provides measures of actual population abundance or density. Also both the NGC and BBS only provide information at the regional and national scale, estimates are associated with wide confidence limits, and the underlying data reside with the data holding organisation and are not in the public domain. For the NGC there is also no consistent measure of effort or the area sampled. Therefore there is a need for a reliable population index, or estimate of the actual population density in order to fulfil reporting obligations for the Habitats Directive, provide evidence for evaluating applications for licensed population control, and to inform local management for any other purposes.

Since 2005 SNH has commissioned three pieces of work to improve our understanding of the status of mountain hares and the implications of their management (Kinrade *et al*., 2008; Newey *et al*., 2008, 2011). The most recent of these focused on the development of a reliable method for estimating mountain hare numbers based on dung accumulation rates (Newey *et al*., 2011). The results did not provide the necessary solution but identified the need for further work, which the current project addresses by extending that work and directly comparing the performance of different survey methods.

1.2 Aims

The aims of this project were to: i) assess the effectiveness and reliability of different methods of estimating mountain hare density, and ii) develop a simple and cost effective counting methodology calibrated against a reliable independent measure of mountain hare density. Specifically, the proposed methodology was required to be sufficiently practical for uptake and use by non-specialists following non-technical instructions, applicable at a range of spatial scales, and able to provide estimates of mountain hare density over the range typically found on upland moorland in Scotland.

2. STUDY DESIGN

The priority of the project was to assess the correlation between different methods of estimating mountain hare density and indices of mountain hare abundance (Table 1). Live trapping combined with Spatial Capture-Recapture (SCR) studies can provide reliable estimates of wild animal abundance and density along with associated measures of uncertainty, and are widely used in wildlife research, conservation and management (Krebs, 1999; Krebs *et al*., 1986; Royle *et al*., 2014a; Sutherland, 1996; Turlure *et al*., 2017). Trapping and SCR studies are however logistically demanding to carry out and their design and analysis require a high degree of specialist knowledge (Turlure *et al*., 2017). Thus, this method was felt to be unsuitable for practical wildlife management. What are needed, therefore, are simple, inexpensive, survey methods that use commonplace equipment and do not require a high level of technical skill or complex data analyses. However, before choosing any method it is important to assess and understand how different methods perform in relation to the species, habitat and questions of interest. These issues and their relevance to land managers and statutory bodies were considered when the aims and design of the study were agreed at a project partner meeting (Game & Wildlife Conservation Trust, Scottish Natural Heritage, and the James Hutton Institute) held on the 23 June 2014.

2.1 Timing of surveys

Field work was carried out from October to December each year 2014-2016. This time of year was chosen to avoid disturbance of ground nesting birds, to avoid trapping mountain hares during the breeding season, and to obtain a post-breeding population assessment of mountain hares when the population is ‘closed’ to births and to avoid peak periods of mortality associated with late summer and late winter (Flux, 1970; Iason, 1989). Population estimates at this time of year, which relate to the post-breeding and pre-shooting time period are considered by SNH and land managers to be the most useful to inform management of mountain hares for shooting and population control.

Table 1. Summary of the different survey methods compared in this study.

Measure	Survey Method
1. Density Estimate	Capture-Recapture
2. Indices of Abundance:	
(i) Encounter rate	night time transect counts – lamping night time transect counts – thermal imaging daylight transects counts
(ii) Dung	standing crop accumulation and accumulation rate

2.2 Survey methods assessed

2.2.1 Capture-recapture

Density estimates from capture-recapture offer practical and highly reliable population estimates of wild animals (Turlure *et al*., 2017). Empirical and modelling studies have demonstrated that capture-recapture methods can provide reliable density estimates for a wide variety of wildlife species (Boulanger & Krebs, 1994, 1996; Efford *et al*., 2005; Efford & Fewster, 2013). For snowshoe hares (*L. americanus*) density estimates from capture-recapture studies have been used to calibrate density estimates derived from other methods

(Krebs *et al*., 1987, 2001; McCann *et al*., 2008; Mills *et al*., 2005). Capture-recapture has been used for the study of mountain hares in Scotland with density estimates from capture-recapture showing strong agreement with density estimates from other methods applied to the same study areas (Newey *et al*., 2003). However, due to the logistical demands and complexity, this method is not expected to be widely used by the land management community but is used here **to provide reliable density estimates, against which more easily collected indices of abundance, e.g. encounter rates from surveys and dung accumulation, can be compared and potentially calibrated**.

2.2.2 Direct counts: transect surveys

Counts of animals seen whilst field surveying for hares along walked transects, can be combined with data on the distance of animals from the transect lines, in a distance sampling analysis to provide abundance and density estimates (Buckland *et al*., 2001). Distance sampling data were collected during the daylight and night time lamping surveys. Whilst previous studies have demonstrated that distance sampling of hares along transect lines can be effective, these studies have also highlighted some problems associated with acquiring adequate sightings when hares are at low density, acquiring accurate sighting measurements when hares are at high density, and of recording detections prior to movement (Newey *et al*., 2003; Shewry *et al*., 2002). Further, there were not the resources to undertake sufficient line transect surveys for reliable estimation. Therefore we did not fully assess the utility of distance sampling for estimating mountain hare density. However, noting that our survey design was limited to four transects per site (see Methods) we present the results of a distance sampling analysis of the night time survey data (when more hares were seen) for comparative purposes, in Annex 2.

However, simple counts of the number of hares seen, or encounter rate (number of hares encountered divided by the length of transects covered), might also provide an index of animal abundance. When calibrated against density estimates obtained from other methods, these encounter rates can also provide an estimate of density without the need for further more complex distance analysis. This approach is considered more reasonable by land managers, particularly if counting of hares along transects might be combined with other management activities. **Here we consider counts and encounter rates of hares along transects from; daylight walked surveys, night time lamping surveys, and night time thermal imaging surveys for their utility as indices of hare numbers or as a calibrated measure of hare density**.

2.2.3 Dung plot surveys

The use of dung plots is well established as a means of wildlife population assessment (Neff, 1968; Putman, 1984). Dung counts are typically used to provide an index of relative abundance which may be appropriate for monitoring population change (Caughley & Sinclair 1994; Krebs, 1999); but also see Anderson (2001, 2003) and Engeman (2003) for further discussion on the use of indices). However, while indices may be suitable for some purposes including long-term monitoring of trends (Aebischer *et al*., 2011; Harris *et al*., 2016), setting sustainable harvest or cull levels will benefit from a better understanding of abundance or density. With knowledge of appearance (defecation) and disappearance (decomposition) rates, dung counts can be used to derive absolute abundance or density estimates and these standing crop and dung accumulation methods are widely used in ungulate research and management (Mayle *et al*., 1999; Putman, 1984). Dung counts have also been calibrated against estimates of absolute abundance or density from, for example, capture-recapture methods via a regression model to obtain predictions of absolute abundance or density from dung counts (Krebs *et al*., 1987). This approach has been developed and widely adopted to monitor and assess snowshoe hare populations in North America, and is effective across a range of snowshoe hare densities and different habitats (Homyack *et al*., 2006; Krebs *et al*., 1987, 2001; McCann *et al*., 2008; Mills *et al*., 2005; Murray *et al*., 2002). The method has also been successfully applied to mountain hares in Sweden (Angerbjorn, 1983). **Here we assess the utility of dung standing crop and dung accumulation rate as indices of hare numbers and the potential for calibrating these against a density estimate from capture-recapture.**

2.2.4 Other methods

Counting with dogs was not used in this study because the use of dogs requires skilled handlers, and results are likely to vary between handlers and the breed and nature of the dogs used (Cablk & Heaton, 2006; Wasser *et al*., 2004). Trained pointing dogs have been used to facilitate surveys of red grouse and mountain hares on heather moorland (Jenkins *et al*., 1963; Thirgood *et al*., 2000; Watson, 2013; Watson *et al*., 1973; Watson & Hewson, 1973). Dogs are usually trained to 'quarter' the ground either side of an observer (the dog ranges up to around 100 m either side of the observer) as they walk a route or transect through a study area to provide an index of animal abundance. The use of dogs by a skilled handler to count mountain hares along transects when compared to an observer walking without a dog increases both the proportion of ground covered and number of hares seen, and with sufficient survey effort can provide an index of hare numbers (Watson, 2013; Watson *et al*., 1973). This is usually treated as a measure of the minimum number alive within an area, though in some cases where the dog and observer are considered to have effectively counted all hares in the area, the counts may be considered to be a total count of hares present.

2.3 Study sites

Ten sites were included in the study; two were surveyed in 2014, four in 2015 and four in 2016 (Table 2). We sought to ensure that study sites were geographically representative of the main mountain hare habitats and independent of each other, within the constraints of site availability, timing and budget. Study sites were in areas of extensive upland heather moorland with vegetation dominated by *Calluna vulgaris* and *Erica* sp. dwarf-shrub heath communities. All study sites were located on estates managed for red grouse shooting and red deer stalking. Access approval was given by the landowners, and to minimise the possibility of site disturbance we report the location of only the nearest village or town (Table 2). Study areas were 2 x 2 km (4 km^2, 400 ha) though two areas were smaller (300 ha and 360 ha). The size of area was logistically manageable in terms of survey design and carrying out and repeating multiple survey methods. Each area included the range of habitats typically used by mountain hares during the diurnal cycle, and annual cycle to minimise the effects of local hare movements on population estimates (Newey *et al*., 2003, 2011). Study sites were chosen to be representative of typical upland estates and habitats, and include a range of hare densities. Participating estates agreed not to kill any mountain hares within or near to the study sites over the winter they hosted the study.

Table 2. Summary of study sites, locations and the survey methods carried out at each site.

Site	Location	Area (km^2)	Transect (No.)	Thermal Imaging	Daylight Surveys	Lamping Surveys	CR	Dung Counts
2014-15								
1	Dunkeld, Perth & Kinross	4	8 km (4)	No[1]	Yes (n=2)	Yes (n=2)	Yes	Yes
2	Dunkeld, Perth & Kinross	4	8 km (4)	No[1]	Yes (n=2)	Yes (n=2)	Yes	Yes
2015-16								
3	Braemar, Aberdeenshire	4	7.2 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=2)	Yes	Yes
4	Strathdon, Aberdeenshire	4	8 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=2)	Yes	Yes
5	Strathdon, Aberdeenshire	4	8 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=2)	Yes	Yes
6	Ballater, Aberdeenshire	3	6 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=2)	Yes	Yes
2016-17								
7	Ballater, Aberdeenshire	4	8 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=2)	Yes	Yes
8	Tomintoul, Moray	3.6	7.2 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=5)	Yes	Yes
9	Nethybridge, Highland	4	8 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=5)	Yes	Yes
10	Nethybridge, Highland	4	8 km (4)	Yes (n=2)	Yes (n=2)	Yes (n=5)	Yes	Yes

Site code – study site; Year – study year, Transect – the total length and number of transects included in one replicate survey (the same transects were used for each method and replicate), thermal imaging, daylight surveys, lamping surveys and capture-recapture (CR) surveys, and dung plots marked and cleared over October-December, dung plots were revisited and cleared again April the following year; Location – nearest village or town and Scottish council area, Yes – method was applied, No – Method was not applied, n – number of replicate surveys carried out. [1] – Thermal imaging equipment was not available.

3. METHODS

3.1 Field survey methods

3.1.1 Capture-Recapture protocol

At each site 100 double entry, weldmesh cage live traps (Jeremy Dewhurst Game & Feed Equipment, Bankfoot, Scotland) were placed in four clusters of 25 traps each centred on the study area (except site 6 where 75 traps in three clusters of 25 were used – see results) (Fig. 1). Trap clusters were 700 m apart (centre-to-centre). Each cluster consisted of a five by five grid of traps with 100 m between rows and columns of the grid. Traps were placed at suitable areas within c. 40 m of the designated trap node where there were signs of hare activity or an active hare run, and where traps could be stably secured to the ground and set to ensure the wellbeing of interned animals. Traps were covered to provide shelter for captured animals and baited with apple and vegetation from the surrounding area, and set each evening and checked the following morning. Live trapping of mountain hares was carried out over October-December each year. We aimed to set traps for four consecutive nights per week and for four consecutive weeks at each site, but logistic practicalities such as faulty or broken traps, or heavy snow fall which blocked access to the sites and prevented use of traps for animal welfare reasons (they could not be checked and trapped animals released), meant that this was not always possible. The number and layout of traps, and the number of trap nights was determined from a simulation study in which we varied the trapping regime, the distribution and density of hares, and the anticipated capture-probability to identify a trapping protocol that, given a minimum density of hares, would be expected give sufficient captures and recaptures for analysis (Annex 1).

On capture, hares were removed from the traps by allowing them to move into a dark handling bag where they were weighed. New captures were fitted with a small uniquely numbered ear tag (Monel 106, National Tag & Band, Kentucky, USA) in each ear and then released at the site of capture. Recaptures were identified then released. Live trapping was carried out under licence from Scottish Natural Heritage.

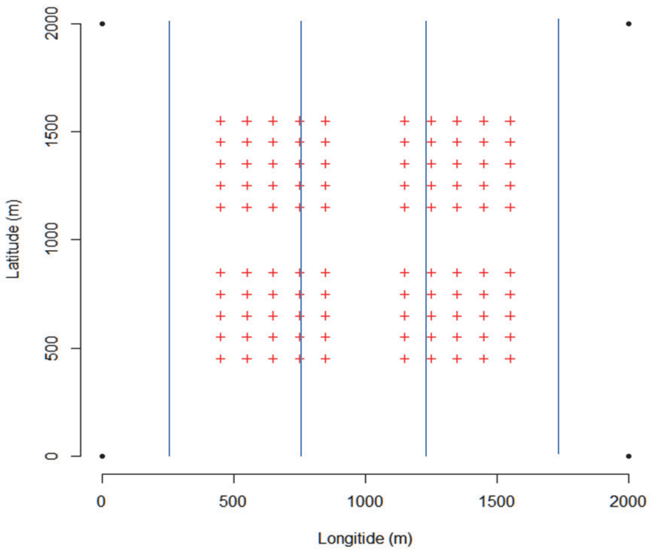


Figure 1. Schematic showing layout of study site, location of transect lines used for daylight, lamping and thermal imaging transect surveys (blue lines), and traps (red crosses) used in this study.

3.1.2 Direct counts of mountain hares

Three methods of directly counting mountain hares were employed; daylight surveys (hereafter ‘daylight’), night time surveys with the aid of a high power lamp (hereafter ‘lamping’), and night time surveys with the aid of thermal imaging equipment (hereafter ‘thermal imaging’). Four parallel transect lines, spaced 500 m apart, were mapped onto each 4 km^2 study area (Fig. 1). Transect lines were orientated parallel to the dominant altitude gradient (transects usually ran up/downhill) to minimise variance between transect lines by accommodating expected changes in hare distribution with altitude. For seven of the ten sites, four transects of 2 km each were surveyed. At site 3 transects ran diagonally across the 4 km^2 study area giving transects of different lengths (1.2 and 2.4 km) and a total of 7.2 km, while at site 6 the study area was reduced to 3 km^2 due to the presence of steep cliffs meaning the area was traversed by 6 km of transects; two each of 2 km and two of 1 km. Site 7 measured 1.8 by 2 km due to access restrictions along one edge of the site, giving a total area of 3.6 km^2. Here we used four transects each 1.8 km long (Table 2). Each study site was surveyed twice with each survey method, providing two replicates for each of the three methods; daylight, lamping and thermal imaging. Sites 1 and 2 were not surveyed using thermal imaging equipment due to a delay in delivery of the equipment. Sites 8, 9 and 10 were each surveyed 5 times by lamping, in order to investigate variation among nights in more detail (Table 2).

Lamping surveys started at least one hour after sunset. An observer walked along each transect at a steady pace (mean ± s.e. 1.37 ± 0.03 km hr^{-1}), shining a high power spot light (Tracer Light 140, Tracer, Suffolk, UK) from side to side as they traversed the transect line. Daylight surveys were similar, but were undertaken during daylight hours starting at least one hour after sunrise with an observer walking along each transect at a steady pace (mean ± s.e. 1.92 ± 0.05 km hr^{-1}) and scanning from side to side for hares. Night time surveys with a monocular style thermal imager (Recon M18, FLIR Systems Inc, Oregon, USA) also started at least one hour after sunset. It was not possible to walk safely over moorland while looking through the thermal imager, so observers therefore walked along each transect stopping regularly (approximately every 70 m) and scanning 360^{o} with the imaging equipment, for more than 10 seconds at each location recording the number of hares seen.

During daylight and lamping surveys we recorded the sighting distance and angle for each detection with a sighting compass and the sighting distance measured with a laser range finder (Yardage Pro 400, Bushnell Outdoor Products, Kansas, USA). It was not possible to measure sighting distance and angle with the thermal imager used (other models may include distance indicators) because we wanted to assess the utility of thermal imaging without the use of high powered lamps.

Transect surveys (daylight, lamping and thermal) were conducted 24 hours or more after any previous fieldwork to minimise the effect of disturbance affecting the distribution or behaviour of hares. The order in which survey methods were applied was determined in a Latin square style rotation. To minimise the effects of weather on the number of, and distance at which hares were seen, surveys were only carried out when wind speed was less than 30 km hr^{-1}, not in persistent rain or snow, or poor visibility due to low cloud cover, mist or fog. Each survey was usually carried out over two days/nights traversing alternate transect lines on each occasion. All survey visits for each site were undertaken over a ten week period immediately before, after or during the non-trapping nights of trapping work.

3.1.3 Dung plots

Dung plots were established in the autumn at each study site at approximately the same time as the trapping was being carried out, and were revisited the following spring once any snow had melted. Two hundred dung plots were established at each study site. To ensure an even distribution of dung plots in the area covered by the other survey methods, the two by two kilometre study area was divided into four 1 km^2 areas and 50 dung plot locations were randomly placed in each 1 km^2 area. We used circular dung plots which have been shown to give lower variability than equivalent square plots, and because they require only a single marker to locate the centre, are quicker to set up and survey in the field than square plots (Hodges & Mills, 2008; Murray *et al.*, 2005). Each circular dung plot had a 1.5 m^2 area (radius = 0.69 m) centrally marked with a numbered wooden stake. All mountain hare dung pellets were counted on establishment of the plot, and cleared from it along with all other dung in the plot plus a 10 cm buffer. Counts of hare pellets removed from the plots provided an estimate of dung standing crop. Dung plots were revisited and the accumulated dung pellets were counted in early April each year once any snow had cleared, except for site 6 which was revisited in May (2016) due to long lying snow cover. We believe that revisiting plots in early April avoided significant decomposition as at this time of year in the Scottish uplands it is still cold and insect activity is low.

3.2 Data analysis

3.2.1 Estimating density from Spatial Capture-Recapture analyses of trapping data

We used the R package 'secr' (version 3.0.1, Efford, 2017a; R version 3.3.3, R Core Team, 2017) to fit spatial capture-recapture (SCR, also known as spatially explicit capture-recapture, (SECR)) models to the trapping data to obtain density estimates of mountain hares (Borchers, 2010; Efford, 2004; Royle *et al.*, 2014a; see also Box 1). Spatial capture-recapture represents an extension of traditional capture-recapture analysis that explicitly incorporates the spatial heterogeneity in capture probability caused by differences in capture probabilities depending on the location of traps relative to animals, and overcomes the problem of estimating effective trapping area of a trap array (Efford, 2004). Heterogeneity in capture probability caused by the distance between an animal's notional range centre and a trap is described by a detection function defined by the probability of capture at distance zero (g0) and scale parameter (σ). These two parameters can be allowed to vary in response to, for example, sex, time, or capture experience (relating to models Mh, Mt and Mb in the classic capture-recapture framework), to accommodate other sources of heterogeneity in capture probability (Borchers & Efford, 2008; Otis *et al.*, 1978; Royle *et al.*, 2014a). Traditional capture-recapture assumes that the underlying density of population being sampled by trapping is homogenous across the study area, in secr this assumption can be relaxed and the density of animals allowed to vary spatially by, for example, habitat type, altitude, or as function of latitude and/or longitude by fitting a density surface as part of the analysis (Efford, 2017a, 2017b).

Box 1

Simple summary SCR analysis

Traps on a trap grid will have a probability of capturing animals found on the grid as well as those animals with a home range that overlaps the trap grid. The probability of an animal being caught declines with increasing distance of the animals home range centre from the trap grid. In SCR analysis a buffer is added to the outside of the trap grid to include the area in which animals are found and that have some probability of being caught. The area of the trap grid and the buffer, here referred to as a mask, is represented by a grid, or mesh, of equidistant points 'mapped' over the trap grid. To fit a model the SCR discretises ('breaks up') the area covered by the mesh. The SCR model is evaluated at each of these points and then integrated and summed, to provide an overall model estimate for the entire mask area.

Analysis of capture-recapture data as implemented in secr requires a ‘mask’ that includes the area covered by traps plus a buffer, added to the trap grid, that delimits the area of integration beyond which animals have negligible probability of capture, and mask spacing which defines the spacing of a mesh of notional points of the region of integration used to fit models by maximum likelihood (Borchers & Efford, 2008; Efford, 2017a, 2017c). The buffer needs to be wide enough to encompass all the range centres of all those individuals that may be caught, and together with the mesh spacing, defines the number of points in the region of integration and therefore the level of discretisation (conversion of a continuous variable into a discrete variable), precision of estimates and computational time. We assessed the effect of buffer width and spacing on parameter estimates by first fitting a null model with a halfnormal detection function to trapping data from each site to derive naive parameter estimates of density, and likelihood values for a range of mask values. We then used the secr ‘esa.plot()’ and ‘mask.check()’ functions to assess how bias, density and likelihood values responded to changes in buffer width and spacing. We identified the combination of buffer width and mesh spacing that resulted in low (< 0.01) bias, and stable density and likelihood values at three decimal places while aiming to ensure that the mesh for each study site also had between 1,000 and 2,000 points (Efford, 2017a; Royle *et al.*, 2014b). Using the mask parameter estimates identified above we then fitted and compared, using AIC, null models with halfnormal and exponential detection functions to identify which detection function provided the most parsimonious fit for each site.

Using the site specific mesh parameters and detection function identified above we proceeded to fit a range of SCR models using full likelihood (Table 3). Not all traps were set on every trap night and we specified whether a trap was set or not on each trapping occasion to accommodate this varying effort (Efford, 2017a). We did not expect mountain hares to be uniformly distributed over each study area, and we fitted a range of density surface models allowing density to differ with latitude and longitude using regression splines to produce smoothed density surfaces based on the underlying trapping data (Efford, 2017a, 2017b). Capture histories clearly showed large variation in the number of individuals trapped each night, and also reveal that the majority of individuals were only caught once, suggesting temporal and possibly behavioural heterogeneity in capture probability or movement. We therefore fitted models that allowed these to vary by trap day, and previous capture history. Based on previous studies there was sufficient *a priori* reason to suspect that capture probability and movement vary by individual characteristics such as sex, and age (Bisi *et al.*, 2011). In the absence of data on individual level covariates such as sex or age we attempted to model this suspected heterogeneity using 2-class finite mixture models which seek to model unobserved heterogeneity using latent classes (Efford, 2017a, 2017d). Initial model fitting identified that the ‘Nelder-Mead’ optimisation method was more robust than the default ‘Newton-Raphson’ method (Efford, 2017a). Where models failed to converge, or results suggested a problem with model fitting (e.g. missing parameter values, unusually high parameter estimates, or unusually low likelihood values), we re-ran the model, first allowing secr to identify automatic start values and then by specifying the start values using parameter estimates from a previous successful analysis of the same data set. While this improved model fitting, we found that models incorporating a density surface, those allowing capture probability and/or movement to vary with trap night, finite mixture models, and models with interaction terms, often failed to converge or parameter estimates were unstable. To overcome the problem with models incorporating ‘trap night’ sometimes failing to converge and to allow us to consistently assess time effects, we reduced the time element to ‘trap week’ and used the number of calendar weeks of trapping at a site as a time covariate in the model. We therefore considered eight candidate models: null models with no modelled heterogeneity in capture probability or movement other than that caused by the relative position of traps and animal activity centres; models allowing capture probability to vary with previous capture experience (global behavioural response), capture experience at a specific site (local behavioural response), and with trap week (‘trap week’ as a time covariate); and allowing the movement parameter to vary with trap week (Table 3). Each source of potential heterogeneity was modelled singly and in combination with each other giving eight candidate models in total (Table 3). All analyses are ‘spatially explicit’ in that they accommodate heterogeneity in capture-probability caused by the location of traps relative to animals). We used model averaging to obtain a site density estimate by averaging across all models within Δ10 of the lowest AIC thereby including all those candidate models which were to some extent supported by the data (Arnold, 2010; Burnham & Anderson, 2002, p. 70).

Table 3. Summary of Spatial Capture-Recapture candidate models considered showing all of the models originally considered but excluded from the final candidate set due to problems with model fitting, and those in the final candidate set.

	secr model parameter					
	Density (D)		Capture Probability (g0)		Movement / Scale Parameter (σ)	
Model term	Initial	Final	Initial	Final	Initial	Final
Null	Yes	Yes	Yes	Yes	Yes	Yes
spline (n=4)	Yes	No	-	-	-	-
spline (n=5)	Yes	No	-	-	-	-
spline (n=6)	Yes	No	-	-	-	-
Global behavioural response (b)	-	-	Yes	Yes*	No	No
Time covariate (trap week) (tcov)	-	-	Yes	Yes*	Yes	Yes
Local behavioural response (bk)	-	-	Yes	Yes*	No	No
2-class finite mixture model (h_2)	-	-	Yes	No	Yes	No
Time dependent effect (t)	-	-	Yes	No	Yes	No

* - also used in conjunction with allowing σ to vary with trap week.

Spline (n) – smoothed spline density surface of order n; ‘b’ – global behavioural response to previous capture experience, ‘bk’ – local behavioural response to previous capture experience, ‘t’ – time dependent response allowing parameter to vary by trap night, ‘tcov’ – time dependent response allowing parameter to vary by trap week, ‘h_2’ – finite mixture with two latent classes allowing parameter to vary for two ‘classes’ of individual within the population.

3.2.2 Estimating encounter rates derived from transect surveys

Encounter rate (number of hares detected divided by total length of transects per replicate) and associated parameters from daylight, lamping and thermal imaging surveys were estimated in DISTANCE 7 (Thomas *et al*., 2010) by specifying a Uniform key function with no adjustment series. Site-replicate specific encounter rates were produced from separate analyses of each replicate. To obtain site specific average estimates of encounter rate and associated parameters we pooled the sighting data for each replicate into a single transect and multiplied the transect length by the number of replicates. For the daylight, thermal imaging and lamping surveys we estimated encounter rates using all the sighting data – so encounter rate is based on the total number of hares detected. For daylight and lamping surveys we also explored the effects of excluding sightings of animals beyond 50 m perpendicular distance from the transect line (i.e. the data were truncated at 50 m), but found that this made little difference and do not present this.

3.2.3 Estimating a hare density index from dung counts

The counts of hare pellets from the initial clearance of dung plots were averaged and converted to pellets m^{-2} and used as a measure of 'standing crop'. Counts of pellets from the second visits represent the dung that had accumulated since the time the dung plot was cleared. This was standardised to a daily accumulation rate by dividing by the number of days between the plots being cleared and revisited and expressed as mean daily accumulation per square metre.

3.3 Assessment and Comparison of Survey Methods

A major concern with any survey methodology and the estimation of population abundance and density is the accuracy, precision, and repeatability of survey results. Accuracy refers to the magnitude of systematic errors or bias associated with an estimate. These affect how well the estimated value represents the true value. Except under controlled experimental conditions, the true abundance or density of a wildlife population is seldom known, and it is therefore not possible to directly assess accuracy. Precision refers to the variability in estimates, the spread of estimated values about the sample mean. Here we use the coefficient of variation (CV) as a measure of precision and use a value of < 0.20, to indicate an acceptable level of precision and that repeat surveys of the same population should be within 20% of the mean. A coefficient of < 0.25 was interpreted as representing moderate but adequate precision.

Each survey is assessed based on the coefficient of variation around the estimate. In the case of SCR where this is not provided, we divide the standard error of the estimate by the mean to derive an equivalent coefficient of variation. We assess the precision of each survey method by taking the mean coefficient of variation of each survey method averaged across study sites. We assessed the repeatability of the different line transect survey methods; daylight, thermal and lamping surveys, by calculating a coefficient of variation between replicates for each count method for each site. Mean and variance were not independent on the arithmetic scale. Accordingly, the coefficient of variation was calculated for each site from the mean encounter rate and its standard deviation (SD) on a logarithmic scale. The mean was obtained from a GLM with Poisson error and logarithmic link, with 'count of hares' as the response variable, $\log_e$(transect length) as an offset and constant as the sole estimated parameter. This parameter represented the mean encounter rate per kilometre of transect on a logarithmic scale. As it could be negative, all encounter rates were standardised to 8 km of transects, the total transect length on most sites, by using $\log_e(8)$ as an offset. The SD was calculated as the standard error of the parameter estimate multiplied by the square root of the number of replicates, and the coefficient of variation as SD divided by the standardised encounter rate. We tested for differences in the mean CV between methods by using a permutation test. We used Pearson's coefficient of correlation (R function; 'cor.test()', (R Core Team, 2017)) to assess the linear relationship between density estimates and indices from the different methods.

4. RESULTS

4.1 Capture-Recapture

Capture rates were low, ranging from 0.2 to 8.5 novel (previously uncaught) individuals for every 100 trap nights (Table 4). Only a small proportion of individuals were caught more than once. At two sites (6 & 7), trapping produced too few captures for analysis. At site 6 trapping was halted due to animal welfare concerns when heavy snow fall repeatedly blocked tracks to this very remote site. This resulted in few captures and recaptures (Table 4). Hare numbers at site 7 were low and too few hares were caught for analysis (Table 4). Therefore the eight candidate models (Table 3) were fitted to the data from the eight sites with sufficient data for analysis giving a total of 64 analyses. One model failed to converge, and density estimates from four analyses were associated with high standard errors (> 200, the standard errors of the other 59 analyses were < 36). In our assessment these five analyses were likely the result of problems with model convergence and were excluded for the purpose of model averaging (Table 5).

Table 4. Summary of trapping periods and trapping effort.

Site	Trapping period	Trap effort (Nights)	Individuals (Captures)	Capture rate (Individuals/100 trap nights)
1	Oct. – Nov., 2014	1,226 (9)	49 (66)	4.0
2	Nov. - Dec., 2014	849 (14)	50 (75)	5.9
3	Oct. - Nov., 2015	1,000 (12)	54 (65)	5.4
4	Oct. - Nov., 2015	1,148 (16)	58 (91)	5.1
5	Nov. - Dec., 2015	1,265 (16)	107 (138)	8.5
6	Nov. - Dec., 2015	706 (10)	22 (23)	3.1
7	Oct. - Nov., 2016	876 (11)	2 (2)	0.2
8	Oct. - Nov., 2016	1,719 (18)	51 (64)	3.0
9	Nov. - Dec., 2016	1,199 (12)	61 (80)	5.1
10	Nov. - Dec., 2016	948 (12)	55 (76)	5.8

Trap Effort – total trap nights calculated as the sum of traps set each trapping night; Individuals - number of individuals trapped; Captures - total of animals captured and recaptured. Capt. rate – capture rate, number of individuals caught divided by the number of trap nights, expressed as number of novel individuals per 100 trap nights.

No particular model was favoured across sites; the models best supported by the data are generally quite site specific (Table 5). On some sites capture-probability and/or movement provided the best estimate of density, while at other sites the results show that capture probability is affected (positively or negatively) by previous capture experience (Table 5). In some cases (e.g. sites 2 and 3) the AIC score for the best supported model is more than ten units lower than the next best supported model. Therefore, the site density estimate is from a single model, whereas at other sites (e.g. site 4) all eight candidate models are supported by the data and contribute to the model averaged density estimate (Table 5).

With the exception of site 3, density estimates from different models within sites are generally consistent with each other, and confidence intervals from the different models overlap (Fig. 2). Density estimates from the model incorporating a global behavioural response to capture experience (model 2) generally gives lower density estimates than the other models (Fig. 2, Table 5). In our experience, model 2 could be problematic to fit and in one case appeared not to converge, and exploratory analysis showed that this model appears sensitive to small changes in data (pers. obs). Similarly, the model that included both a global behavioural response to capture experience and a time effect on movement failed to converge or gave implausible parameter estimates in 4 cases. For site 3, the confidence intervals associated with density estimates from the model 1 (null model) and model 2 (global behavioural response to capture experience) suggest that these are significantly lower than the estimates from the other models (Fig. 2, Table 5). The reason for this is not clear, though trapping effort at this site was reduced because of animal welfare concerns due to very warm weather and the need to remove captured animals from traps as quickly as possible, and the numbers of recaptures was low (< 10). Site 3 was also unique in that a number of juveniles were caught which was unusual for this time of year (pers. obs.). Model coefficients of variation are variable, depending on both site and model (Table 5). For some sites all models show low coefficients of variation of less than 0.20 indicating low dispersion around the mean and good precision, whereas for other sites (e.g. site 9), all coefficients of variation are between 0.20 and 0.25 indicating greater dispersion around the mean and poorer precision.

Table 5. Density estimates and model summaries of each of the eight models fitted to the capture-recapture data from each site.

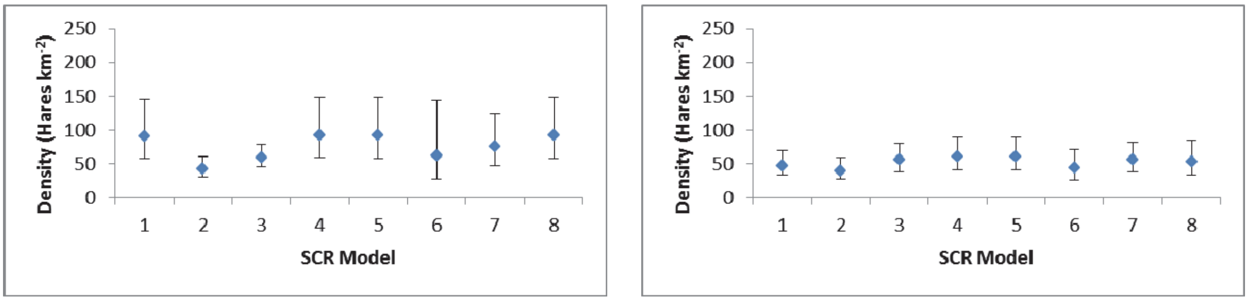
Site	Model Parameter D	g0	sigma	AIC	dAIC	AIC$_{wt}$	Density (SE, 95% CL) (Hares km^{-2})	CV
1	Null	Null	tcov$_{(wk)}$	599.69	0.00	0.31	92.74 (22.51, 58.03 - 148.22)	0.24
	Null	bk	tcov$_{(wk)}$	600.33	0.64	0.23	76.15 (19.44, 46.53 - 124.62)	0.26
	Null	b	tcov$_{(wk)}$	601.13	1.45	0.15	62.99 (27.82, 27.54 - 144.06)	0.44
	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	601.68	2.00	0.11	92.59 (22.52, 57.87 - 148.14)	0.24
	Null	tcov$_{(wk)}$	Null	601.78	2.10	0.11	93.18 (22.29, 58.69 - 147.94)	0.24
	Null	b	Null	602.59	2.91	0.07	42.52 (7.67, 29.94 - 60.38)	0.18
	Null	bk	Null	606.17	6.48	0.01	59.61 (8.61, 44.98 - 79.01)	0.14
	Null	Null	Null	614.32	14.63	0.00	91.06 (21.94, 57.16 - 145.07)	0.24
2	Null	Null	Null	613.93	0.00	1.00	47.87 (9.15, 33.02 - 69.40)	0.19
	Null	b	Null	624.12	10.20	0.00	40.34 (7.74, 27.79 - 58.55)	0.19
	Null	bk	Null	633.10	19.18	0.00	55.67 (10.47, 38.63 - 80.22)	0.19
	Null	bk	tcov$_{(wk)}$	634.95	21.02	0.00	56.16 (10.8, 38.66 - 81.59)	0.19
	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	635.42	21.49	0.00	53.14 (13.02, 33.11 - 85.31)	0.25
	Null	Null	tcov$_{(wk)}$	635.57	21.64	0.00	60.25 (12.08, 40.83 - 88.91)	0.20
	Null	b	tcov$_{(wk)}$	635.64	21.72	0.00	43.57 (11.07, 26.69 - 71.13)	0.25
	Null	tcov$_{(wk)}$	Null	635.87	21.95	0.00	60.49 (12.14, 40.98 - 89.29)	0.20
3	Null	Null	Null	350.70	0.00	1.00	18.08 (2.58, 13.68 - 23.89)	0.14
	Null	b	Null	395.24	44.54	0.00	18.2 (2.62, 13.75 - 24.09)	0.14
	Null	b	tcov$_{(wk)}$	564.05	213.35	0.00	30.9 (7.21, 19.68 - 48.53)	0.23
	Null	tcov$_{(wk)}$	Null	567.40	216.70	0.00	60.94 (10.54, 43.54 - 85.31)	0.17
	Null	Null	tcov$_{(wk)}$	568.34	217.64	0.00	60.21 (9.35, 44.5 - 81.47)	0.16
	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	569.13	218.43	0.00	61.03 (10.89, 43.13 - 86.36)	0.18
	Null	bk	Null	574.08	223.38	0.00	97.45 (35.34, 48.93 - 194.09)	0.36
	Null	bk	tcov$_{(wk)}$	574.65	223.95	0.00	95.75 (24.13, 58.88 - 155.73)	0.25
4	Null	tcov$_{(wk)}$	Null	843.30	0.00	0.30	49.14 (8.75, 34.76 - 69.47)	0.18
	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	844.19	0.89	0.19	49.58 (8.83, 35.07 - 70.10)	0.18
	Null	Null	tcov$_{(wk)}$	845.20	1.91	0.11	48.77 (8.68, 34.51 - 68.93)	0.18
	Null	bk	tcov$_{(wk)}$	845.35	2.05	0.11	50.08 (9.49, 34.66 - 72.37)	0.19
	Null	Null	Null	845.37	2.07	0.11	48.94 (8.71, 34.62 - 69.18)	0.18

Table 5 (Cont.).

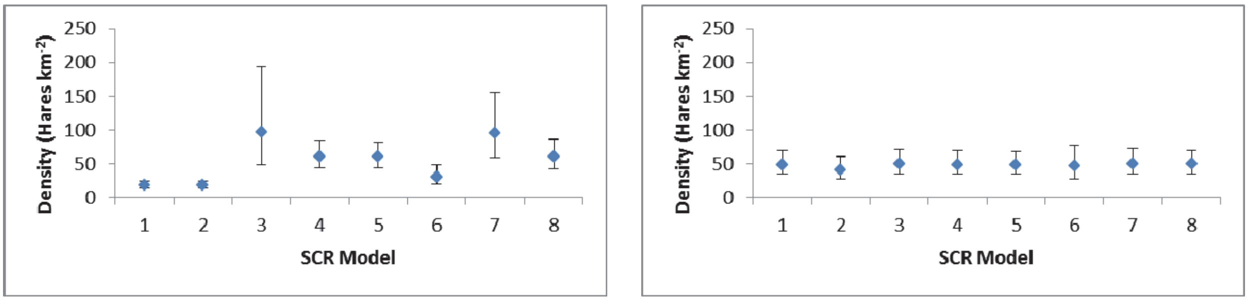
Site	Model Parameter D	g0	sigma	AIC	dAIC	AIC$_{wt}$	Density (SE, 95% CL) (Hares km^{-2})	CV
	Null	b	Null	845.97	2.67	0.08	41.58 (8.38, 28.11 - 61.49)	0.20
	Null	bk	Null	846.44	3.14	0.06	49.91 (9.32, 34.72 - 71.75)	0.19
	Null	b	tcov$_{(wk)}$	847.15	3.85	0.04	46.55 (12.38, 27.88 - 77.70)	0.27
5	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	1173.14	0.00	0.27	146.21 (26.69, 102.53-208.49)	0.18
	Null	Null	Null	1173.58	0.44	0.22	146.07 (26.88, 102.14 - 208.88)	0.18
	Null	tcov$_{(wk)}$	Null	1173.97	0.83	0.18	145.59 (26.77, 101.84 - 208.14)	0.18
	Null	bk	Null	1174.42	1.28	0.14	150.56 (29.47, 102.96 - 220.16)	0.20
	Null	Null	tcov$_{(wk)}$	1174.82	1.68	0.12	145.71 (26.8, 101.91 - 208.34)	0.18
	Null	bk	tcov$_{(wk)}$	1176.49	2.76	0.06	149.82 (29.22, 102.59 - 218.78)	0.20
	Null	b	Null	1174.77	1.63	Excl.	249.4 (290.69, 40.59-1532.36)	1.17
	Null	b	tcov$_{(wk)}$	1176.75	3.61	Excl.	186.05 (397.94, 14.2-2428.90)	2.14
8	Null	bk	tcov$_{(wk)}$	644.32	0.00	0.68	67.97 (16.92, 42.03 - 109.92)	0.25
	Null	tcov$_{(wk)}$	Null	648.10	3.78	0.10	73.88 (20.59, 43.22 - 126.28)	0.28
	Null	Null	tcov$_{(wk)}$	648.17	3.85	0.10	74.36 (20.78, 43.44 - 127.27)	0.28
	Null	bk	Null	649.04	4.72	0.06	66.46 (16.08, 41.65 - 106.06)	0.24
	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	650.06	5.74	0.04	74.15 (20.72, 43.33 - 126.9)	0.28
	Null	b	Null	652.52	8.20	0.01	37.79 (9.44, 23.33 - 61.21)	0.25
	Null	Null	Null	655.06	10.74	0.00	76.26 (21.42, 44.44 - 130.87)	0.28
	Null	b	tcov$_{(wk)}$	649.88	5.56	Excl.	27331.73 (NA, NA-NA)	NA
9	Null	tcov$_{(wk)}$	Null	733.52	0.00	0.47	77.96 (18.22, 49.61 - 122.52)	0.23
	Null	Null	tcov$_{(wk)}$	734.84	1.32	0.24	76.81 (18.01, 48.80 - 120.89)	0.23
	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	735.35	1.83	0.19	78.27 (18.28, 49.82 - 122.95)	0.23
	Null	bk	tcov$_{(wk)}$	736.83	3.31	0.09	78.26 (19.09, 48.86 - 125.36)	0.24
	Null	b	Null	741.47	7.95	0.01	41.29 (8.91, 27.18 - 62.72)	0.22
	Null	Null	Null	745.32	11.80	0.00	78.62 (18.41, 49.98 - 123.66)	0.23
	Null	bk	Null	747.81	14.29	0.00	79.02 (18.76, 49.94 - 125.05)	0.24
	Null	b	tcov$_{(wk)}$	736.56	3.04	Excl.	136.45 (508.22, 5.45-3415.99)	3.72
10	Null	tcov$_{(wk)}$	tcov$_{(wk)}$	672.15	0.00	0.95	63.82 (13.91, 41.84 - 97.33)	0.22
	Null	tcov$_{(wk)}$	Null	678.19	6.04	0.05	60.15 (12.94, 39.65 - 91.26)	0.22
	Null	Null	tcov$_{(wk)}$	686.44	14.30	0.00	58.53 (12.68, 38.47 - 89.07)	0.22
	Null	bk	tcov$_{(wk)}$	687.35	15.21	0.00	60.38 (13.96, 38.61 - 94.43)	0.23
	Null	b	Null	697.39	25.24	0.00	39.23 (8.39, 25.92 - 59.38)	0.21
	Null	Null	Null	699.27	27.12	0.00	61.05 (13.16, 40.21 - 92.69)	0.22
	Null	bk	Null	701.15	29.01	0.00	61.82 (13.84, 40.08 - 95.35)	0.22
	Null	b	tcov$_{(wk)}$	686.29	14.15	Excl.	1,051.01 (1.41x10^{64}, NA-NA)	NA

Models are ordered by increasing AIC. Model Parameter: D = density model/density surface – all analyses presented here are based on assumption of homogeneous density, g0 = capture probability model to allow for heterogeneity in capture probability, sigma - movement model – used for heterogeneity in movement, Null – no heterogeneity modelled, b – global behavioural response to capture experience, bk – local behavioural response to capture experience, tcov(wk) – weekly time covariate, dAIC – difference in AIC between highest ranking (lowest AIC) score, AICwt – AIC weight, Excl. – model was excluded from modelling average estimate, Density – estimated density, standard error and 95% confidence limits, CV – an estimate of model accuracy density SE / density estimate.

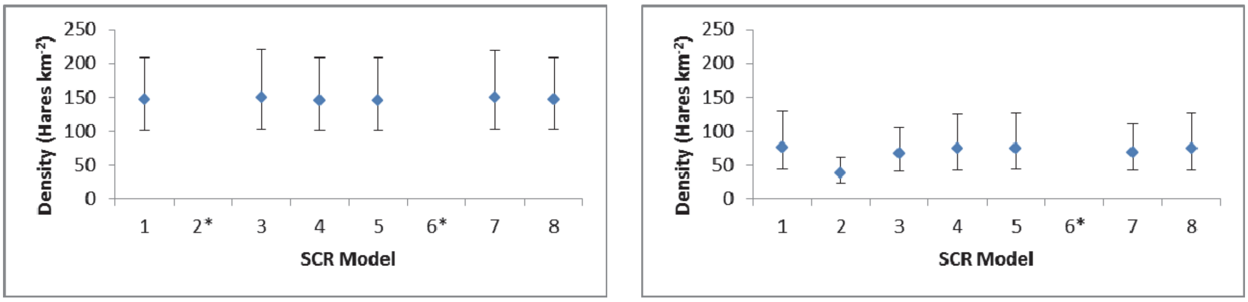
a) Site1. b) Site 2.



c) Site 3. d) Site 4.



e) Site 5. f) Site 8.



g) Site 9. h) Site 10.

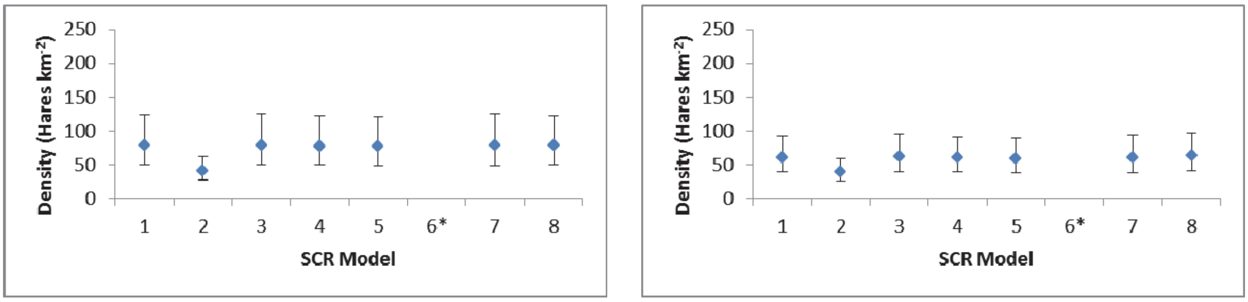


Figure 2. Spatial capture-recapture density estimates from the eight candidate models considered showing estimated density and 95% confidence intervals for each of the eight study sites where there as sufficient data for analysis. 1. Null model, 2. Capture-probability can vary globally with capture history, 3. Capture-probability can vary locally with capture history, 4. Capture-probability can vary with trapping week, 5. Scale/movement parameter can vary with trapping week, 6. Capture-probability can vary globally with capture history and scale/movement parameter can vary with trap week, 7. Capture-probability can vary locally with capture history and scale/movement parameter can vary with trap week, and 8. Capture-probability and scale/movement parameter can vary with trapping week. An '' indicates that model was excluded due to problems with convergence or implausible parameter estimates.*

Model averaged density estimates range from 18 to 146 hares per square kilometre, with four sites having density estimates between 50 and 100 hares per square kilometre (Table 6). Confidence intervals for sites 1, 2, 4, 8, 9, 10 overlap indicating that there was likely to be no real difference in density estimated by different models between these sites (Fig. 3). The density estimate for site 3 is lower than any of the other sites and confidence intervals do not overlap with other sites suggesting that this site has significantly lower density than the other sites. The confidence intervals from sites 2, 3, 4 do not overlap with those of site 5 suggesting that these sites have significantly lower hare density than does site 5 (Fig. 3). With the exception of sites 1 and 8 the coefficients of variation suggest that model estimates are reasonably precise (Table 6).

Table 6. Model averaged mountain hare density estimates for each study site.

Site	Density (SE, 95% CL) (Hares km^{-2})	CV
1	78.62 (28.73, 39.27 - 157.37)	0.37
2	47.87 (9.15, 33.02 - 69.4)	0.19
3	18.08 (2.58, 13.68 - 23.89)	0.14
4	48.56 (9.34, 33.41 - 70.56)	0.19
5	146.87 (27.39, 102.22 - 211.02)	0.19
8	68.85 (18.41, 41.13 - 115.25)	0.27
9	77.33 (18.75, 48.4 - 123.55)	0.24
10	63.64 (13.88, 41.71 - 97.11)	0.22

Density – estimated mountain hare density, standard error and 95% confidence limits, CV - coefficient of variation (calculated as density SE / density estimate).

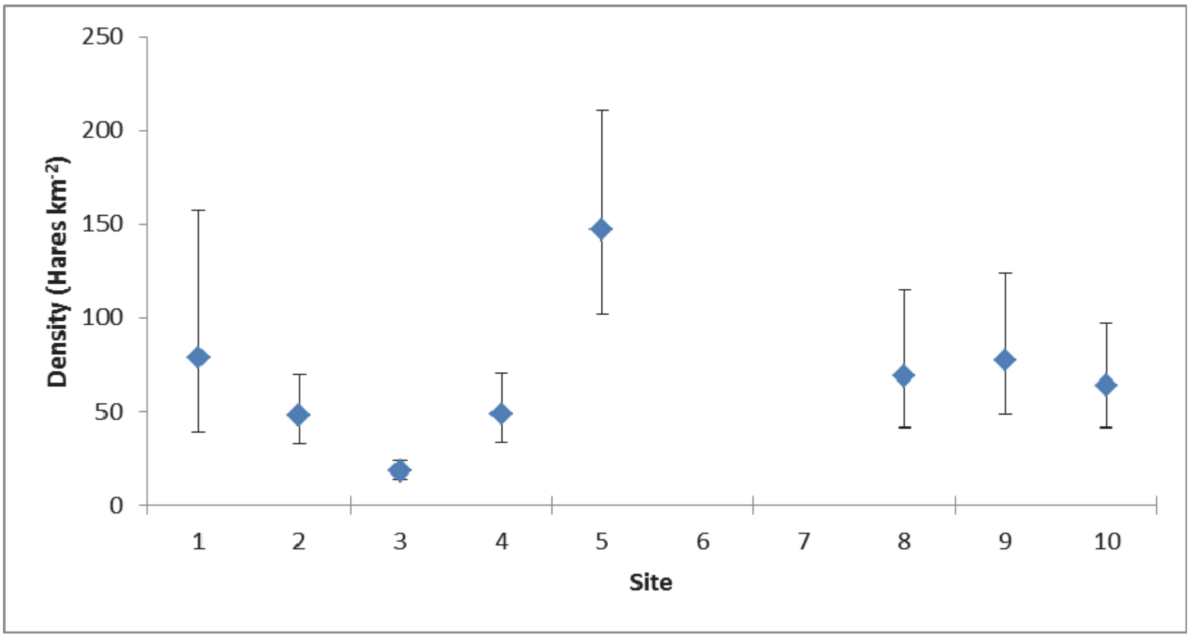


Figure 3. Model averaged density estimates with 95% confidence limits from spatial capture-recapture analysis of trapping data for each study site. There were insufficient data for analysis for sites 6 and 7.

4.2 Indices

4.2.1 Daylight surveys

Daylight surveys produced very few sightings of mountain hares (mean = 7.5, range = 0 – 20; Table 7). In most cases the number of hares seen during the two replicates is similar, but in some cases there are substantial differences, for example at site 1, 7 and then two hares were seen and for site 3, 9 and then three hares were observed during the two replicate surveys (Table 7). Encounter rates were correspondingly low (mean = 1.04, range = 0 – 3.3 hares km^{-1}; Table 7). Encounter rates between replicate surveys are highly correlated (r = 0.90, t = 5.8, df = 8, p = 0.0004). Encounter rates of each replicate are also associated with a high coefficient of variation, with only one survey having a coefficient of variation of less than 0.20 (Table 7). In most cases coefficients of variation are much higher (> 0.30) indicating that the number of hares seen along each of the four different transects within a replicate could vary considerably (Table 7, Fig. 4a). Encounter rate confidence intervals between sites overlap indicating that there is little, if any real difference in daylight encounter rate between sites (Fig. 4a).

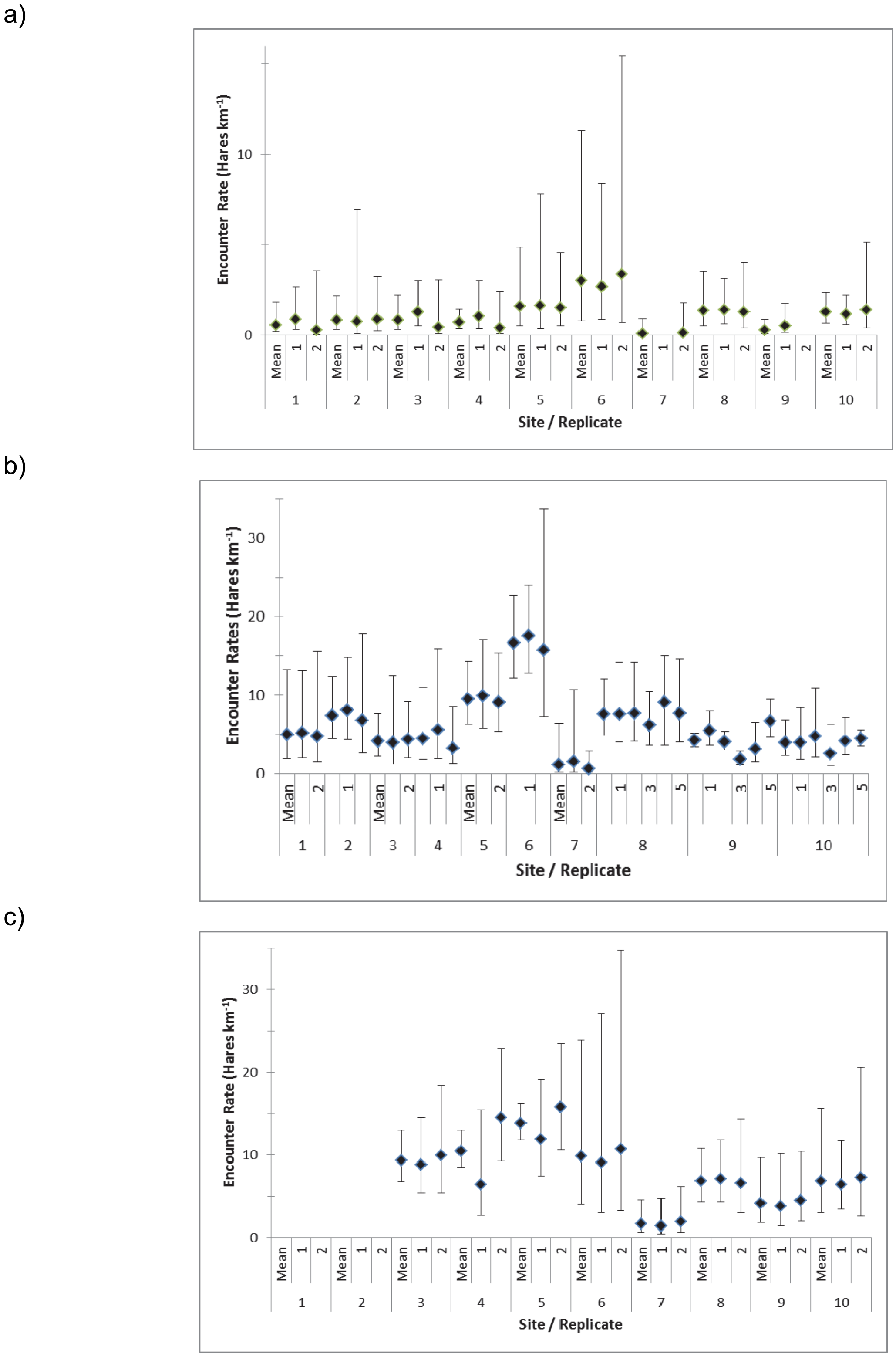


Figure 4. Encounter rates and 95% confidence limits of mountain hares along transects for the three transect survey methods used; a) daylight surveys (no hares were seen at site 7 during the first replicate survey, nor at site 9 during the second replicate survey), b) night time lamping surveys, and c) night thermal imaging surveys (there are no data for sites 1 and 2).

Table 7. Summary of details of daylight surveys, number of hares detected and encounter rate for replicate survey and site.

Site	L (km)	K	Replicate	n (mean)	n/L (95% CL) (Hares $km^{-1)}$	CV
1	16	4	Pooled	9 (4.5)	0.56 (0.18 - 1.81)	0.38
	8	4	1	7 (-)	0.88 (0.29 - 2.65)	0.36
	8	4	2	2 (-)	0.25 (0.02 - 3.54)	1.00
2	16	4	Pooled	13 (6.5)	0.81 (0.3 - 2.18)	0.32
	8	4	1	6 (-)	0.75 (0.08 - 6.93)	0.79
	8	4	2	7 (-)	0.88 (0.24 - 3.23)	0.43
3	14.4	4	Pooled	12 (6)	0.83 (0.32 - 2.19)	0.31
	7.2	4	1	9 (-)	1.25 (0.52 - 2.99)	0.28
	7.2	4	2	3 (-)	0.42 (0.06 - 3.02)	0.69
4	16	4	Pooled	11 (5.5)	0.69 (0.34 - 1.41)	0.23
	8	4	1	8 (-)	1.00 (0.34 - 2.98)	0.36
	8	4	2	3 (-)	0.38 (0.06 - 2.41)	0.64
5	16	4	Pooled	25 (12.5)	1.56 (0.51 - 4.83)	0.37
	8	4	1	13 (-)	1.63 (0.34 - 7.78)	0.52
	8	4	2	12 (-)	1.50 (0.49 - 4.56)	0.36
6	12	4	Pooled	36 (18)	3.00 (0.8 - 11.29)	0.44
	6	4	1	16 (-)	2.67 (0.85 - 8.36)	0.37
	6	4	2	20 (-)	3.33 (0.72 - 15.45)	0.51
7	16	4	Pooled	1 (0.5)	0.06 (0.00 - 0.88)	1.00
	8	4	1	0 (-)	0.00 (-)	
	8	4	2	1 (-)	0.13 (0.01 - 1.77)	1.00
8	14.4	4	Pooled	19 (9.5)	1.32 (0.50 - 3.50)	0.31
	7.2	4	1	10 (-)	1.39 (0.62 - 3.12)	0.26
	7.2	4	2	9 (-)	1.25 (0.39 - 4.02)	0.37
9	16	4	Pooled	4 (2)	0.25 (0.07 - 0.87)	0.41
	8	4	1	4 (-)	0.50 (0.14 - 1.74)	0.40
	8	4	2	0 (-)	0.00 (-)	
10	16	4	Pooled	20 (10.0)	1.25 (0.67 - 2.35)	0.20
	8	4	1	9 (-)	1.13 (0.58 - 2.2)	0.21
	8	4	2	11 (-)	1.38 (0.37 - 5.09)	0.43

L – Survey effort, length of transects multiplied by number of replicates, K – number of transects, Replicate) – whether the parameter estimates relate to the first or second replicate, or combined replicates 1 & 2 (pooled), n – number of sightings, with mean for the combined/pooled analyses, n/L – encounter rate; number of sightings divided by survey effort, CV – coefficient of variation, '-' no value possible.

4.2.2 Lamping surveys

Lamping surveys were repeated twice on sites 1-7, and five times on sites 8-10 in order to better investigate variation between replicate surveys. All lamping surveys yielded hare sightings and consistently produced many more, often five or ten times more, sightings of mountain hares than daylight surveys along the same transects over the same period of time (mean = 47.3, range = 5 – 105 hares per survey; Table 8). The number of hares seen between replicate surveys was also more consistent compared to daylight surveys, though there are notable exceptions; at site 4, 44 hares were seen during the first replicate and 26 hares during the second replicate, and for site 8 the lowest number of hares recorded over the course of the five replicates was 14 and the highest 53, a nearly 4-fold difference (Table 8).

Encounter rates were correspondingly higher than daylight surveys (mean = 6.45, range = 0.63 – 17.50 hares km^{-1}). Encounter rates for the first two replicate surveys (when all sites were surveyed twice) were highly correlated ($r = 0.98$, $t = 12.55$, $df = 8$, $p < 0.001$) (Table 8, Fig 4b). Coefficients of variation were generally lower compared to daylight surveys, indicating more consistent counts of hares between transects of the same replicate, but many individual replicate surveys were associated with very high coefficients of variation (Table 8). Sites 8, 9 and 10, where five replicate surveys were completed, show the variability that can be found in both estimated encounter rate and associated coefficients of variation; for example at site 9 the lowest encounter rate of the five replicates was 1.75 (95% confidence limits; 1.11 – 2.75) compared to the highest of 5.38 (95% confidence limits; 3.65 – 7.92) (Fig. 4b, Table 8). The 95% confidence limits of estimated encounter rates for both replicate specific and pooled samples were largely overlapping indicating there is unlikely to be a real difference in encounter rate between these sites (Fig. 4b). It is striking to compare encounter rate estimates for sites 5 and 7 because although there is a very marked and consistent difference in the point estimate of encounter rate, depending on the replicate compared the confidence limits still overlap (Fig. 4b).

Table 8. Summary of details of night time lamping surveys, number of hares detected and encounter rate for each replicate survey and site.

Site	L (Km)	K	Replicate	n (mean)	n/L (95% CL) (Hares km^{-1})	CV
1	16	4	Pooled	79 (39.5)	4.94 (1.84 - 13.22)	0.32
	8	4	1	41 (-)	5.13 (2.02 - 13.08)	0.30
	8	4	2	38 (-)	4.75 (1.45 - 15.53)	0.38
2	16	4	Pooled	118 (59)	7.38 (4.41 - 12.34)	0.16
	8	4	1	64 (-)	8.00 (4.34 - 14.76)	0.19
	8	4	2	54 (-)	6.75 (2.56 - 17.81)	0.31
3	14.4	4	Pooled	59 (29.5)	4.10 (2.2 - 7.62)	0.20
	7.2	4	1	28 (-)	3.89 (1.21 - 12.52)	0.38
	7.2	4	2	31 (-)	4.31 (2.02 - 9.19)	0.24
4	16	4	Pooled	70 (35)	4.38 (1.74 - 10.99)	0.30
	8	4	1	44 (-)	5.50 (1.91 - 15.86)	0.34
	8	4	2	26 (-)	3.25 (1.24 - 8.54)	0.31
5	16	4	Pooled	151 (75.5)	9.44 (6.22 - 14.33)	0.13
	8	4	1	79 (-)	9.88 (5.73 - 17.01)	0.17
	8	4	2	72 (-)	9.00 (5.29 - 15.31)	0.17
6	12	4	Pooled	199 (99.5)	16.58 (12.14 - 22.66)	0.10
	6	4	1	105 (-)	17.50 (12.77 - 23.98)	0.10
	6	4	2	94 (-)	15.67 (7.26 - 33.8)	0.25
7	16	4	Pooled	17 (8.5)	1.06 (0.18 - 6.37)	0.61
	8	4	1	12 (-)	1.50 (0.21 - 10.68)	0.68
	8	4	2	5 (-)	0.63 (0.14 - 2.84)	0.51
8	36	4	Pooled	273 (54.6)	7.58 (4.76 - 12.07)	0.15
	7.2	4	1	54 (-)	7.50 (3.97 - 14.16)	0.20
	7.2	4	2	55 (-)	7.64 (4.12 - 14.15)	0.20
	7.2	4	3	44 (-)	6.11 (3.57 - 10.46)	0.17
	7.2	4	4	65 (-)	9.03 (3.57 - 14.96)	0.16
	7.2	4	5	55 (-)	7.64 (3.99 - 14.64)	0.21
9	40	4	Pooled	167 (33.4)	4.18 (3.4 - 5.12)	0.06
	8	4	1	43 (-)	5.38 (3.65 - 7.92)	0.12
	8	4	2	32 (-)	4.00 (3.02 - 5.30)	0.09
	8	4	3	14 (-)	1.75 (1.11 - 2.75)	0.14
	8	4	4	25 (-)	3.13 (1.52 - 6.43)	0.23
	8	4	5	53 (-)	6.63 (4.63 - 9.47)	0.11
10	40	4	Pooled	157 (31.4)	3.93 (2.24 - 6.86)	0.18
	8	4	1	31 (-)	3.88 (1.81 - 8.32)	0.24
	8	4	2	38 (-)	4.75 (2.08 - 10.82)	0.26
	8	4	3	20 (-)	2.50 (1.00 - 6.26)	0.29
	8	4	4	33 (-)	4.13 (2.38 - 7.15)	0.17
	8	4	5	35 (-)	4.38 (3.48 - 5.50)	0.07

L – Survey effort, length of transects multiplied by number of replicates, K – number of transects, Replicate – whether the parameter estimates relate to the first or second replicate, or to both replicates combined (pooled), n – number of sightings, with mean for the combined/pooled analyses, n/L – encounter rate; number of sightings divided by survey effort, CV – coefficient of variation, '-' no value possible.

4.2.3 Thermal imaging surveys

Night time surveys of transects with the aid of thermal imaging equipment were carried out twice at sites 3 to 10. Number of hares seen (mean = 58.69, range = 11 – 126) and encounter rates (mean = 7.85, range = 1.38 – 14.5 hares km^{-1}) were much higher than for daylight surveys and slightly higher though similar to lamping surveys and showed much the same pattern (Fig. 4c, Table 9). Encounter rates between replicate surveys were strongly correlated (r = 0.83, t = 3.62, df = 6, p = 0.01). Coefficients of variation for each replicate thermal surveys are similar to those from lamping surveys for sites 4, 5, 6 and 8, but substantially lower for site 7 and higher for site 9 (Tables 8, 9).

Table 9. Summary details of night time surveys using of thermal imaging equipment, number of hares detected and encounter rate for replicate survey and site

Site	L (km)	K	Replicate	n (mean)	n/L (95% CL) (Hares km^{-1})	CV
3	14.4	4	Pooled	134 (67.0)	9.31 (6.68 - 12.96)	0.10
	7.2	4	1	63 (-)	8.75 (5.30 - 14.44)	0.16
	7.2	4	2	71 (-)	9.86 (5.30 - 18.35)	0.20
4	16	4	Pooled	167 (83.5)	10.44 (8.39 - 12.99)	0.07
	8	4	1	51 (-)	6.38 (2.63 - 15.44)	0.29
	8	4	2	116 (-)	14.50 (9.22 - 22.79)	0.15
5	16	4	Pooled	221 (110.5)	13.81 (11.77 - 16.21)	0.05
	8	4	1	95 (-)	11.88 (7.38 - 19.10)	0.15
	8	4	2	126 (-)	15.75 (10.61 - 23.38)	0.12
6	12	4	Pooled	118 (59.0)	9.83 (4.06 - 23.83)	0.28
	6	4	1	54 (-)	9.00 (2.99 - 27.06)	0.36
	6	4	2	64 (-)	10.67 (3.28 - 34.67)	0.38
7	16	4	Pooled	26 (13.0)	1.63 (0.58 - 4.59)	0.34
	8	4	1	11 (-)	1.38 (0.40 - 4.73)	0.40
	8	4	2	15 (-)	1.88 (0.58 - 6.09)	0.38
8	14.4	4	Pooled	98 (49.0)	6.81 (4.32 - 10.73)	0.14
	7.2	4	1	51 (-)	7.08 (4.25 - 11.80)	0.16
	7.2	4	2	47 (-)	6.53 (2.99 - 14.25)	0.25
9	16	4	Pooled	66 (33.0)	4.13 (1.76 - 9.67)	0.27
	8	4	1	30 (-)	3.75 (1.39 - 10.12)	0.32
	8	4	2	36 (-)	4.50 (1.94 - 10.42)	0.27
10	16	4	Pooled	109 (54.5)	6.81 (2.98 - 15.58)	0.26
	8	4	1	51 (-)	6.38 (3.47 - 11.72)	0.19
	8	4	2	58 (-)	7.25 (2.56 - 20.53)	0.34

L – Survey effort, length of transects multiplied by number of replicates, K – number of transects, Replicate – whether the parameter estimates relate to the first or second replicate, or to both replicates combined – pooled, n – number of sightings, with mean for the combined/pooled analyses, n/L – encounter rate; number of sightings divided by survey. effort, CV – coefficient of variation. There were no surveys for sites 1 and 2

4.2.4 Dung surveys

Dung plots were established, cleared and revisited to establish estimates of standing crop in late summer/early winter, and over winter accumulation. It was not always possible to establish the intended 200 dung plots due to, for example rabbit-proof exclosures at one site associated with woodland planting, or in the cases of sites 6 and 8, the study sites were smaller than the nominal 4 km^2 or it was not practical to establish and clear dung plots in the time available due to snow cover (site 6). Snow cover into late spring 2016 also delayed revisiting the dung plots on site 6. In some cases dung plots could not be relocated in the spring if the markers had been knocked out by animals. At site 2 a small number (not more than 5%) were accidently burnt in spring during muirburn (prescribed heather burning) and were excluded from the analysis. Counts of dung in late summer/early winter and spring were highly over dispersed with variances greater than the means (Table 10). With the exception of one site, site 6, dung counts were between two and four times higher in spring when the plots were revisited and cleared than when the plots were established and first cleared in late summer/early winter (Table 10). Dung standing crop was poorly correlated with the dung accumulated ($r = 0.30$, $t = 0.91$, $df = 8$, $p = 0.39$) and the dung accumulation rate ($r = 0.23$, $t = 0.66$, $df = 8$, $p = 0.53$).

Table 10. The number of dung plots established and cleared on each site, with the mean number of pellets removed at the first and second visits, and the associated mean daily accumulation rate per plot.

	First Clearance		Second Clearance		
Site	No. Plots Cleared	Mean dung count (variance)	No. Plots Cleared	Mean dung count (variance)	Mean accumulation (pellets day^{-1})
1	175	6.39 (105.6)	171	23.39 (624.69)	0.16
2	190	6.84 (49.7)	177	21.98 (440.05)	0.18
3	194	9.99 (177.8)	194	27.63 (801.73)	0.15
4	199	9.31 (157.7)	197	16.05 (393.55)	0.10
5	200	12.86 (194.3)	199	57.68 (1,617.75)	0.43
6	96	22.00 (342.2)	93	17.84 (228.94)	0.10
7	198	1.57 (16.4)	191	5.94 (272.64)	0.03
8	190	15.06 (427.9)	189	38.06 (2,462.86)	0.21
9	200	10.32 (222.6)	200	61.90 (2,653.91)	0.45
10	202	12.87 (312.4)	198	46.83 (4,061.30)	0.35

4.3 Comparison of methods

4.3.1 Correlation between survey methods

Density estimates from SCR show weak, positive but non-significant correlations with both replicate specific and pooled encounter rates from daylight and thermal surveys (Table 11, Fig. 5). The correlation between SCR density and encounter rates from individual replicates and pooled estimates from lamping surveys is much stronger, and significant at $p < 0.1$ (Table 11, Fig. 5, 6a). There is only a weak, positive non-significant correlation between SCR density estimates and dung standing crop (Table 11, Fig. 5). The correlation between SCR density estimates and accumulated dung and dung accumulation rate show moderate positive correlations, but these are not significant at $p < 0.05$ (Table 11, Fig. 5, 6b).

Table 11. Pearson correlations between density estimates from spatial capture-recapture and indices from daylight, night surveys with a lamp, night surveys with thermal imaging equipment, and dung plots; standing crop, accumulation, and accumulation rate.

		Density from SCR analysis of trapping data. Correlation coefficient ($t_{(df)}$, p)
Daylight Encounter Rate		Not truncated
	Replicate 1	0.37 ($t_6 = 0.99$, $p = 0.36$)
	Replicate 2	0.58 ($t_6 = 1.61$, $p = 0.17$)
	Mean	0.45 ($t_6 = 1.22$, $p = 0.27$)
Lamping Encounter rate		
	Replicate 1	0.67 ($t_6 = 2.26$, $p = 0.06$)
	Replicate 2	0.64 ($t_6 = 2.06$, $p = 0.08$)
	Mean	0.68 ($t_6 = 2.29$, $p = 0.06$)
Thermal Encounter Rate		
	Replicate 1	0.47 ($t_4 = 1.07$, $p = 0.34$)
	Replicate 2	0.35 ($t_4 = 0.74$, $p = 0.50$)
	Mean	0.42 ($t_4 = 0.93$, $p = 0.41$)
Dung		
	Standing crop	0.32 ($t_6 = 0.85$, $p = 0.43$)
	Accumulation	0.64 ($t_6 = 2.01$, $p = 0.09$)
	Accumulation rate	0.66 ($t_6 = 2.18$, $p = 0.07$)

Mean = the mean encounter rate from pooled transect surveys.

It was not possible to establish a statistically rigorous regression calibration between SCR density estimates and lamping encounter rates or dung accumulation (Fig. 6a,b). The regression of SCR density and both lamping encounter rate and dung accumulation rate exhibit a good linear and monotonic relationship. Doubling the value of either index is matched by an approximate two fold increase in the density point estimate, although the confidence intervals overlap (Fig. 6c). For example an index value of four hares per km of transect from a lamping survey corresponds with a density estimate of 45 hares with lower and upper 95% confidence limits of 10 and 82 hares per square kilometre. An index value of eight hares per km of transect from a lamping survey indicates a density estimate of 95 hares with lower and upper 95% confidence limits of 57 and 136 hares per square kilometre. While this suggests that there may be twice as many hares present, the confidence limits overlap, indicating that there is likely to be no real difference in the inferred density estimates (Fig 6c). **The relationship between SCR density and indices is not currently suitable to be used to infer exact density with sufficient confidence.** In addition to the fact that the sample size is small, correlations are not statistically significant, and the confidence intervals are wide, the regression is heavily influenced by the site with the highest SCR density estimate and lamping encounter rate.

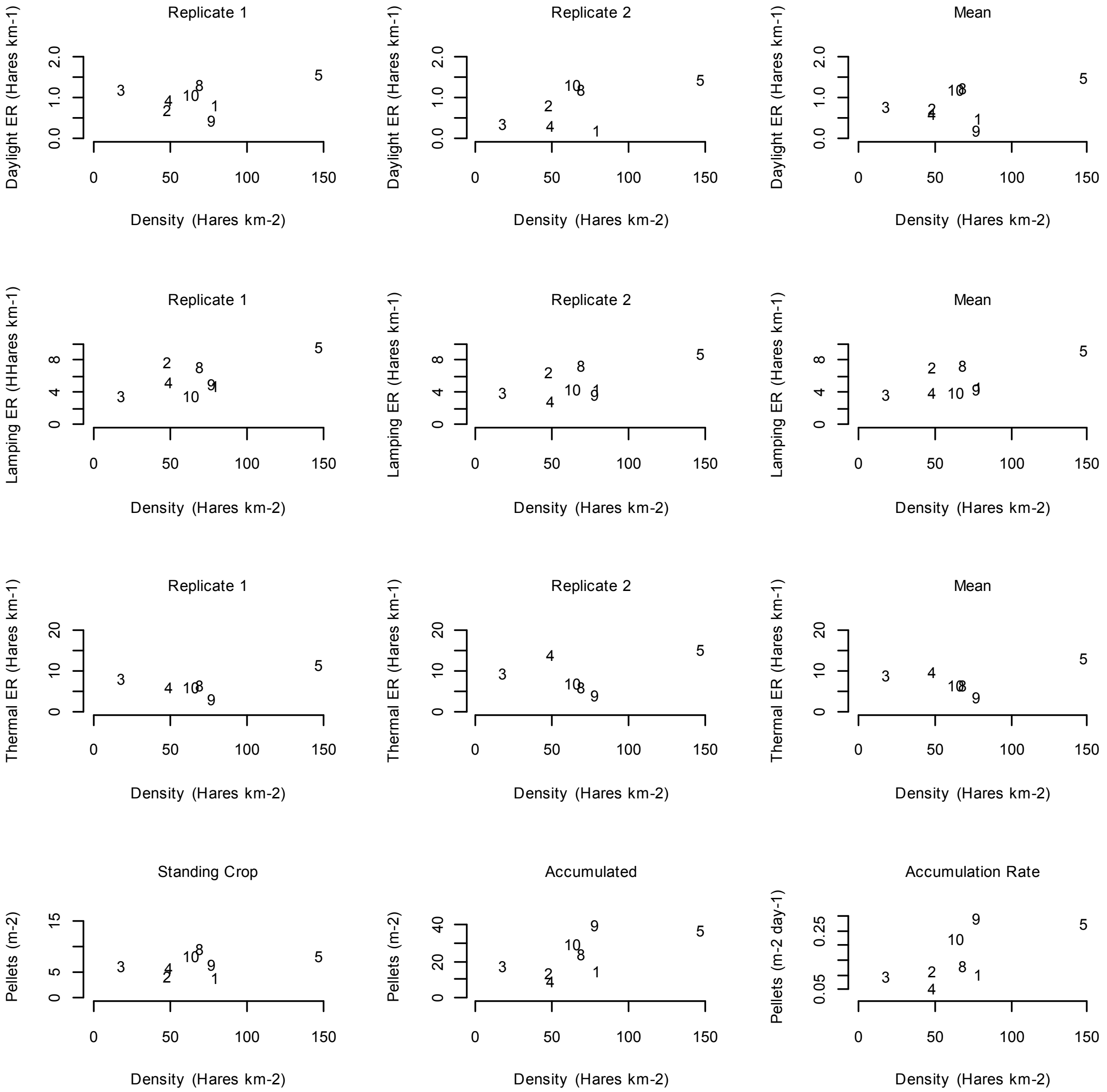


Figure 5. Scatter plots showing relationship between density estimates from spatial capture-recapture, and other indices; encounter rates from daylight (DaylightER), lamping (LampingER) and thermal imaging surveys (ThermalER) along transects, dung standing crop, dung accumulation, and dung accumulation rate for each replicate and the mean estimate from pooled samples. Plots show the site number. Density = estimated density of mountain hares per square kilometre, ER – Encounter Rate = estimated mean number of hares encountered per one kilometre of transect line. Standing Crop and Accumulation plots show mean pellets per square metre. Accumulation rate shows the mean dung accumulated per square metre per day.

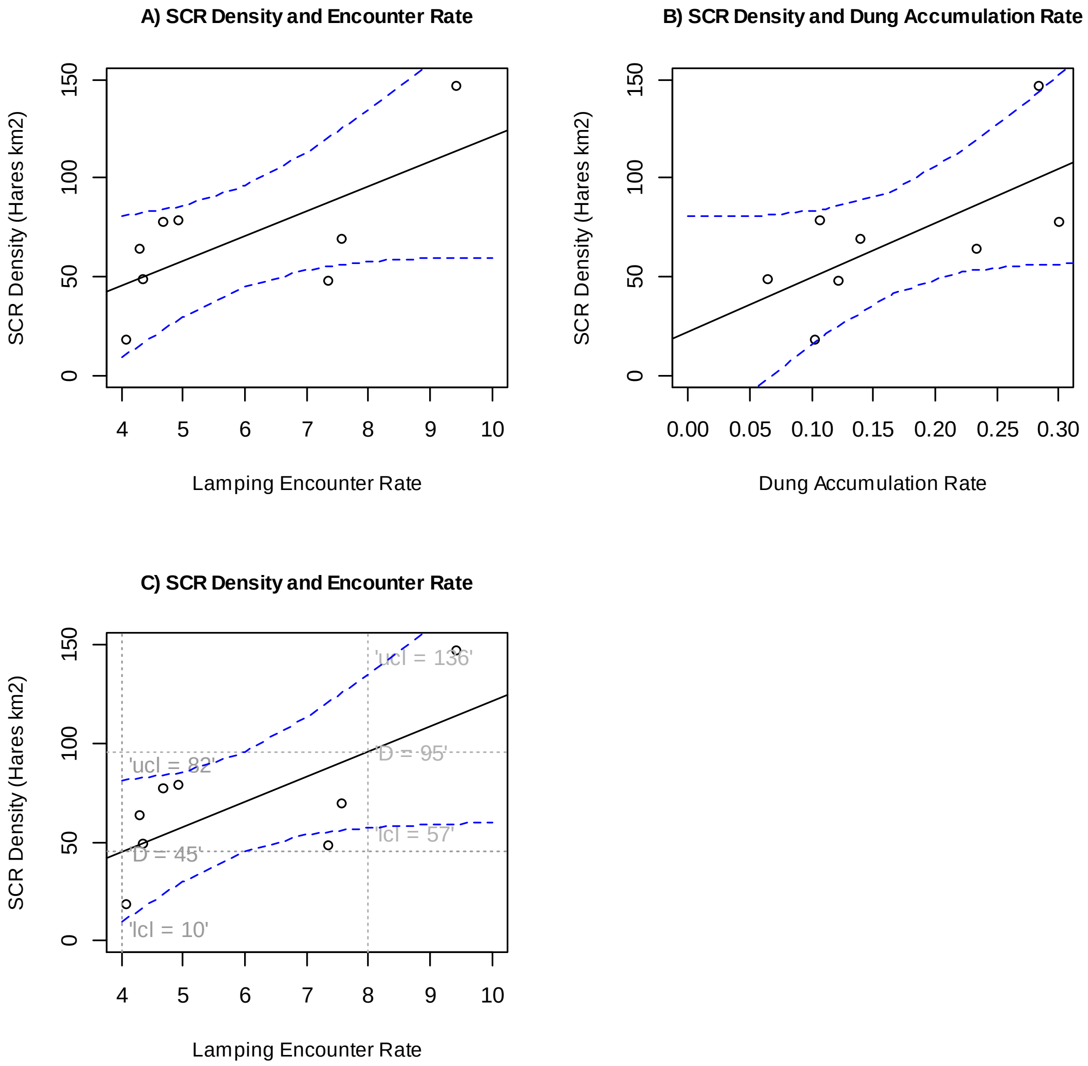


Figure 6. Regression plots with 95% confidence limits for Spatial Capture-Recapture (SCR) density (hares km^{-2}) for; a) lamping encounter rate (hares km^{-1}), b) dung accumulation rate (pellets m^{-2} day^{-1}), and for illustrative purposes only c) presents density against lamping encounter rate showing the density point and confidence limits for lamping encounter rates of 4 and 8 hares km^{-1}. D = Inferred hare density and associated 95% lower confidence limit (lcl) and upper confidence limit (ucl).

4.3.2 Precision and repeatability

Daylight surveys show higher within-replicate coefficients of variation than lamping or thermal surveys indicating that there is greater variation in the number of hares encountered between transects during daylight surveys than during either of the night time surveys (Table 12, Fig. 4). Method precision and repeatability are lower for daylight surveys compared to either of the night time survey methods suggesting that daylight surveys can be more variable, prone to larger inter-replicate variation, and poor precision and repeatability (Table 12, Fig. 7). However, while daylight surveys are associated with higher inter-replicate variability, which is particularly pronounced at sites 1, 3, and 4, compared to the night time surveys the permutation test shows that this difference is not significant (Tables 13, Fig. 7).

Table 12. Method precision and repeatability of each method and each survey. The table shows the mean coefficient of variation of each method (method precision) and survey (Method Repeatability).

Method	Method Precision			Method Repeatability
	Replicate 1	Replicate 2	Pooled	
Daylight	0.39	0.60	0.40	0.19
Thermal	0.25	0.26	0.18	0.07
Lamping	0.27	0.27	0.22	0.06
SCR	-	-	0.23	-

Method Precision – mean coefficient of variation of each method across all sites surveyed. Method Repeatability – mean inter-replicate coefficient of variation of each method. Daylight – daylight surveys along walked transects, Thermal – night time surveys with thermal imaging equipment along walked transects, Lamping - night time surveys with a lamp along walked transects. SCR – Spatially Capture-Recapture. Replicate 1, 2, Pooled – indicates whether the mean coefficient of variation applies to a replicate or the pooled/mean estimate. '-' – no estimate.

The coefficients of variation associated with replicate thermal surveys are similar, though marginally lower, than corresponding lamping surveys (Fig. 7, Table 12). The difference in inter-replicate variation was not significant (Tables 12, 13). Both thermal and lamping surveys show reasonable precision and repeatability (Table 12). The coefficients of variation associated with lamping surveys on sites 8, 9 and 10 when five replicate surveys were included are higher (Fig. 7). This represents the increased probability of an extreme value with increasing sample size, and suggests that the coefficients of variation based on two replicates are likely to be under estimating variability. The precision, estimated by the coefficient of variation of SCR density estimates, varied with site, with six of eight estimates showing good or moderate levels of precision (Table 6). On average, SCR density estimates show moderate precision (Table 12).

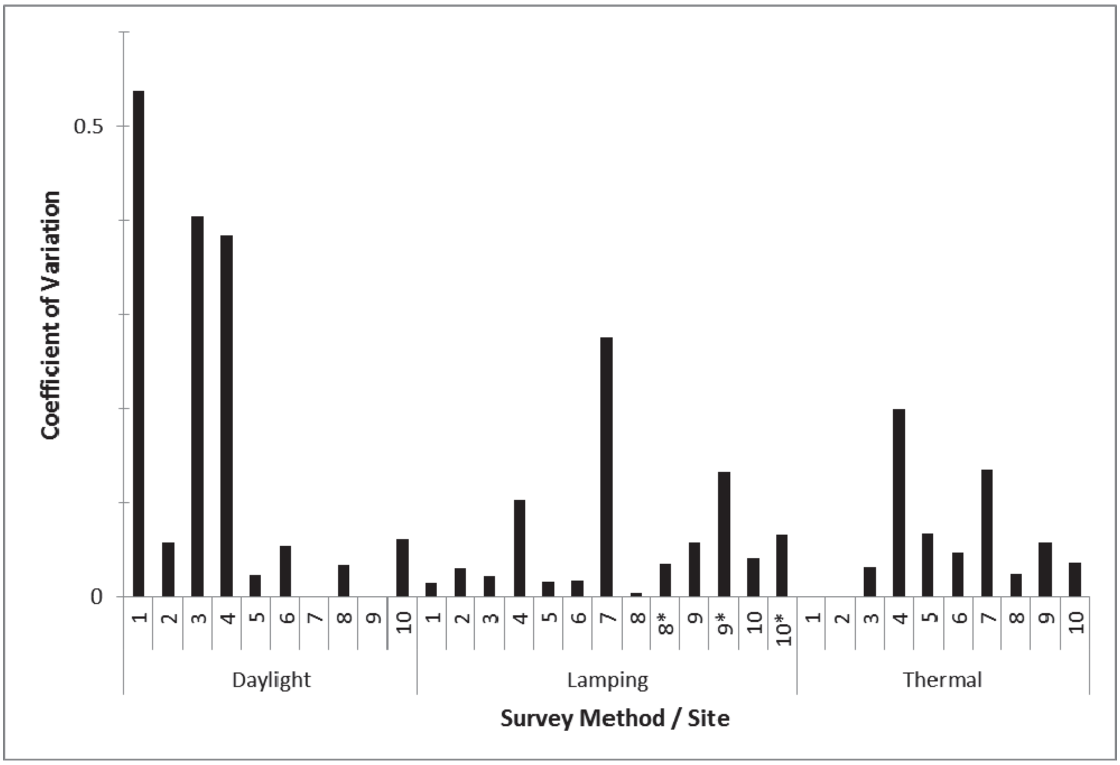


Figure 7. Inter-replicate coefficients of variation in encounter rate for each of the three direct count methods; daylight surveys, night time lamping surveys, and night time thermal surveys along line transects. Coefficients of variation are based on two replicate surveys. For the lamping surveys carried out on sites 8, 9 and 10 where extra replicates were carried out these are shown marked with an ''.*

Table 13. Results of a permutation test comparing the mean coefficients of variation (CV) of the encounter rates for the three direct count methods. A significant result indicates that the mean CVs differ at the given p-value.

Survey Method	Daylight	Thermal
Daylight surveys	-	-
Thermal surveys	p = 0.164	-
Lamping surveys (2 replicates for all sites)	p = 0.087	p = 0.647
Lamping surveys (including. extra replicates)	p = 0.111	p = 0.922

'-' – no data entry

5. DISCUSSION AND RECOMENDATIONS

5.1 Discussion

Wildlife population assessment is necessary for informed, transparent, evidence-based management. Population assessment and monitoring embraces areas of social and economic as well as ecological science and remains one of the most challenging areas of wildlife ecology (Elphick, 2008; Newey *et al*., 2010b). There have been huge advances in technology, field and especially analytical approaches in recent years which have led to the development of a range sophisticated tools and methods for collecting and analysing data from wildlife populations (Borchers & Efford, 2008; Buckland *et al*., 2001, 2015; Efford *et al*., 2004; Elphick, 2008; Long *et al*., 2008; Meek & Fleming, 2014; Rovero & Zimmermann, 2006; Royle *et al*., 2014a; Thomas *et al*., 2010). While these methods offer researchers and managers a wealth of tools and methods to monitor wildlife populations, in the face of limited and often decreasing resources, practical wildlife management often requires simple and easy to use methods. We aimed to identify one or more indices that could be validated and potentially calibrated against robust density estimates to provide an easy to use method for assessing mountain hare populations in the Scottish uplands.

Using a capture-recapture approach based on marked individuals, we estimated the density of mountain hares at ten moorland study sites. At the same sites we also quantified indices of mountain hare abundance based on the number of animals seen per unit of effort over the course of line transect surveys carried out during; a) daylight hours, b) night time with the aid of a high power lamp, and c) night time with the aid of thermal imaging equipment, as well as indirect indices of abundance using standing crop, and over winter accumulation of mountain hare dung. A comparative analysis of these indices with the SCR approach shows that night time lamping and dung accumulation rates show a reasonable correlation with the capture-recapture estimates, lamping more so than accumulation rates, and may be the best options for practical mountain hare monitoring.

Population density estimates from SCR analyses were based on four weeks of intensive mountain hare trapping and probably represent the most reliable density estimate practicable. However, even with the level of effort invested there are limitations due to the volume and characteristics of the data which can limit the analyses that can be carried out, as well as affecting the precision and accuracy of the calculated density estimates. For eight out of the ten sites where we attempted SCR analyses, we caught at least 49 individual hares, and obtained recaptures of between nine and 25 individuals. This indicates that in most cases the large majority of individuals were only caught once, and only a small proportion was caught twice or more. The relatively low number of recaptures provides limited information to inform the spatial component of the SCR model as well as limited data on the effects of capture history on capture probability. The low number of recaptures is probably the reason why we were unable to reliably fit some SCR models (density surfaces, finite mixture, and time dependent models) to our trapping data. Notwithstanding this, the density SCR estimates within sites are consistent, except for site 3 where there were only nine individuals recaptured and trapping effort had been reduced due to animal welfare concerns associated with unusually warm weather. The mean coefficient of variation of the SCR estimates of 0.23 suggests reasonable precision and repeatability.

Despite the high number of hares detected during transect counts, on site 6 the number of captures (n = 22), and especially the recaptures (n = 1) were too low for SCR analysis. This may be due to a combination of factors. First, trapping effort in this area was lower than at any other site because the size and shape of the area meant we only deployed three trapping grids (75 traps compared to 100 traps at the other sites). Second, trapping effort was further curtailed when access was reduced due to snow fall blocking vehicle tracks and it was decided to pause trapping for animal welfare reasons because it was not possible to guarantee being able to release interned animals within a reasonable time. Whilst twenty two individual captures for the trapping effort is not in itself especially low, the proportion of recaptures is particularly low and may suggest that the population in this area is more transitory than other areas.

Site 3 also appears as an outlier in the scatter plots due to the low SCR density estimate relative to the encounter rates, dung counts and dung accumulation. The density estimates from the different candidate SCR models gave some quite different results for this site, with the null model and the model allowing capture probability to vary globally in response to capture history, giving much lower density estimates and very narrow confidence limits compared to the other candidate models. The density estimate for this site is based entirely on the null model as all the other models were more than 10 AIC scores greater than the null model. Recaptures at site 3 (n = 9) were lower than any of the other seven sites for which trapping data were analysed, and the data for this site may be too sparse for reliable model fitting. Trapping effort at site 3 was reduced on animal welfare grounds which may at least partly explain the low number of recaptures. Certainly the evidence from the other surveys suggests there may have been more hares present on this site than the SCR analysis suggests.

Encounter rates of mountain hares during daylight surveys are low, typically one to two hares per kilometre of transect, detecting only a fraction of the hares present during the night time surveys of the same transects with the aid of a lamp or thermal imaging equipment. The associated coefficient of variation for each replicate and pooled samples are high and in all but three cases are greater than 0.25, indicating poor repeatability. Daylight encounter rates are only weakly positively and non-significantly correlated with SCR density estimates. Daylight surveys of mountain hares in winter, using any method, will invariably be counting them while they are inactive and sheltering. Therefore detection is mainly of hares that have been flushed – individuals that are disturbed by the observer, or another hare, before fleeing. The flushing distance of mountain hares varies with habitat, vegetation, weather, age, sex, and time of year and is shortest around November when hares are often moulting and when our surveys were mostly carried out (Hewson & Hinge, 1990; Shewry *et al*., 2002). Differences in flushing behaviour due to vegetation, terrain and even weather may make it more difficult to compare the results of daylight surveys from different sites, and even different surveys within the same study area. **Our evidence suggests counts of mountain hares during daylight walked transect surveys, not only sample a small proportion of the hares present, but are unlikely to provide an accurate repeatable population index.**

Mountain hares are generally more active at night, especially during the winter. Encounter rates during night time surveys with either a lamp or thermal imaging equipment are much higher, typically four to eight hares per kilometre of transect walked, and the lower (though in some cases still high) coefficients of variation indicate better precision and repeatability than daylight surveys; with thermal surveys showing slightly better precision than lamping surveys. Counts of hares while they are active at night may be less influenced by site differences in vegetation and terrain than counts during the day when hares are inactive. **Our evidence suggests that night time transect surveys of mountain hares are preferred to daylight transect counts.** Encounter rates from thermal imaging surveys, though marginally more precise, are only weakly positively correlated with SCR density estimates, whereas lamping encounter rates are more strongly and positively correlated with SCR density estimates, though the relationship is not statistically significant at a probability of less than 0.05. **There was relatively little difference in performance between lamping and thermal surveys, but based on the evidence available and our experience we suggest that lamping is preferable due to its ease of implementation, but we do not dismiss surveys using thermal imaging equipment.** Lamping has the advantage that the equipment is relatively cheap compared to thermal imaging equipment (and could be readily combined with collection of distance data if desired). On the other hand thermal imaging equipment is much lighter and easier to carry around in the field and some types may allow easy simultaneous collection of distance data.

Neither of the dung counts indices were significantly correlated to SCR density estimates although there was a better relationship with dung accumulation rates. With the exception of site 6, mean dung counts were higher when plots were revisited in the spring than when first cleared in the preceding winter, suggesting that dung accumulates over the winter when temperatures, insect activity and decomposition are low. Site 6 is the only site where the accumulated dung counted in the spring was lower, indeed much lower, than the standing crop measured in the previous autumn. Site 6 is at high elevation (> 650 m) in the eastern Cairngorms and comprises an exposed area of peat hags and short vegetation, bounded by steep low ground to one side and higher ground to the other. The area represents good habitat for mountain hares and is also very popular with hill walkers and other outdoor recreationalists year round. We hypothesise that this area may have been highly disturbed by visitors over the winter using a track which bisected the site, the area was also snow covered for some of the winter, during which time hares may have made more extensive use of the adjacent lower-lying areas and may not have been present in this area for much of the winter. Alternatively, the later clearance date in spring 2016 may also have allowed some dung to decompose. The comparison of SCR density estimates and dung accumulation does not include site 6 because too few hares were caught here for inclusion in the SCR analyses and therefore are not influenced by the very low accumulation of dung at site 6, and though not significant, there is a moderately strong correlation between dung accumulation rate and SCR density. **We therefore suggest that dung accumulation rate could form a suitable index of hare abundance,** and this would be particularly useful where observational methods were not possible. However, the timing of these surveys, if implemented overwinter and in spring, means their results may not be suitable to inform management of hares for sport shooting. Further research on the methods, particularly to take account of higher decomposition rates in other seasons, would be needed before it could be applied.

The size of the study area was chosen to balance the requirements for; i) an area large enough to accommodate the daily and seasonal needs of mountain hares so as to minimise the movement of hares into and out of the study area, during surveys or over the course of the winter between clearing and revisiting dung plots, ii) the logistic constraints and practicalities of carrying out intensive live trapping, and repeated surveys and iii) an area that represented a realistic management unit ‘typical’ of upland estates. **We suggest that monitoring of mountain hares should take place over similar areas/scales, and certainly not at any smaller scales.** Mountain hares are crepuscular, active at night but mostly active at dawn and dusk when they feed, in north-east Scotland, predominantly on grasses and heather (Hulbert *et al*., 2001; Iason & Van Wieren, 2006). While they can be also active during the day, they generally rest in areas adjacent to or near their feeding areas in tall vegetation, peat hags, among rocks, or in shallow scrapes or depressions (Hewson & Hinge, 1990; Thirgood & Hewson, 1987). Mountain hares are caecotrophic and re-ingest their own faeces; during the day hares produce soft faecal material which is re-ingested directly from the anus (Iason & Van Wieren, 2006; Pehrson, 1983).They produce the commonly seen hard, fibrous pellets as they feed and move around between dawn and dusk. It is these fibrous pellets that are counted during dung surveys. The distribution of daylight and night time habitats can therefore not only affect the distribution of dung pellets, but also the areas and habitats where mountain hares are more likely to be trapped. The size of study sites and their locations were chosen to include a range of habitats that hares would typically favour over the course of their diurnal cycle. Dung plots were located with random placement of 50 plots within each 1 km^2 of the study site, to try to capture the distribution of dung. Similarly, traps were clustered in grids to provide a reasonable coverage of the whole study site, while keeping the distance to traverse all traps manageable and allowing time to process and release captured hares (see Annex 1). Mountain hares are not thought to move long distances (Dahl & Willebrand, 2005; Harrison, 2011; Hulbert *et al*., 1996; Kauhala *et al*., 2005; Rao *et al*., 2006). In Scotland the typical mean annual home ranges are around 10-20 ha and juveniles typically establish their own home range overlapping their maternal home range (Harrison, 2011; Hulbert *et al*., 1996; Rao *et al*., 2006). However, the spatial ecology of mountain hares is poorly understood and how mountain hares move in response to weather and disturbance, particularly during winter, is not well documented. Therefore, while the size and locations of study sites were chosen so as to try to keep the population closed or at least minimise movement into and out of the study site, short and long term movements of hares in response to short-term weather changes, or over the course of the winter, could have affected trapping, transect surveys and spatial and temporal dung accumulation.

The study design here used ten sites over three field seasons with different sites used each year. While this provided a range of independent study sites, it also brings in another source of variation in that some methods may be more suitable on some sites than others, or more effective in some years due to the prevailing conditions, and the risk that differences in density between sites may be conflated by site characteristics. Another approach would have been to use fewer sites over a longer time period using the same sites each year, but this was not an option for this study. We used ten study sites as this was the maximum number of sites we could run in the time and with resources available. Ten study sites is a small sample size, a problem confounded by effectively losing two of the study sites from the SCR analysis due to sparse data, and not being able to carry out thermal surveys in the first year of the study. More study sites would clearly have been beneficial. The small sample of sites, conflated by missing samples, is likely to have contributed to the lack of significant correlation results and to the fact that the results obtained do not allow us to formally statistically calibrate any of the indices against SCR. **The results do however strongly suggest that night time surveys with either a lamp or thermal imaging equipment can provide a good index of hare abundance. The results also suggest that dung accumulation rate could also be used to provide an index of hare abundance.** These methods are simple and inexpensive to carry out, the data do not require complex analysis, and can therefore be used by a wide range of stakeholders to assess mountain hare populations. Furthermore, whereas the BBS and NGC provide indices of mountain hare abundance at the regional or national scale, the methods tested here can be applied at the local scale to inform local management of mountain hares. Lamping surveys can be carried out quickly thereby enabling rapid, and if required, multiple assessments over short periods of time to, for example, assess a population before and after a cull. At the same time, these survey methods could be applied to a sample of survey sites to establish indices of mountain hare numbers which could be up-scaled to provide indices of hare numbers over larger areas, including the regional or national scales.

5.2 Summary and Recommendations

We found that the number of hares seen along transects when lamping or using thermal imaging equipment is greater when SCR estimates indicate higher densities and less when SCR estimates indicate low densities. The areas where we tested these methods were open habitats and terrain, and counts along transects of known length can be used in these circumstances to provide an estimate of encounter rate, which the results here suggest can provide a reasonable index of hare density. We also demonstrate that dung accumulation and dung accumulation rate show a moderate, though non-significant, positive correlation with SCR density estimates. Dung accumulation rate may be potentially useful as an index of abundance when access or disturbance is an issue. However, surveys were restricted to ten upland areas of heather moorland in Perthshire, Strathspey, and Deeside, and these methods have not been trialled in other areas or habitats, for example woodland or less intensively managed heather moorland. Guidelines on how to plan and carry out lamping and dung plot surveys are provided in Annex 3.

5.3 Distance Sampling Summary

We did not set out to formally assess the utility of distance sampling to estimate mountain hare density, because there were insufficient resources to undertake the recommended 20 transects needed to obtain reliable density and variance estimates. However, whilst acknowledging this, we analysed distance sampling data from nine of the ten study sites collected during the night time lamping surveys (Annex 2). Although there is a poor correlation between distance sampling density estimates and SCR density estimates, there is good agreement in the density estimates for four of the eight sites where it is possible to compare. Distance sampling density estimates based on pooled surveys and a global detection function give reasonably precise density estimates (mean coefficient of variation = 0.14). Our results concur with previous studies that have applied distance sampling to mountain hare surveys on heather moorland in identifying problems with hares moving away from the transect line before detection, obtaining sufficient sightings when hare density is very low, and the problem of obtaining accurate sighting measurements when hare density is very high (Newey *et al.*, 2003; Shewry *et al.*, 2002). Though there are problems with applying distance sampling to mountain hares on heather moorland, and the lack of a stronger correlation with other methods raises concerns, the method provides a survey option if density estimates are required.

5.4 Further development

The results presented here, to our knowledge, provide for the first time, validated survey methods for mountain hares in open heather moorland. We were, however, unable to calibrate indices against SCR density estimates. We therefore suggest two areas of further development. Firstly, the methods could be repeated in other areas, in order to establish more significant statistical correlations between the methods. The applicability of these, and potentially other methods, in different habitats (e.g. woodland or less intensively managed heather moorland), where visual detection of hares is likely to be more difficult) should be undertaken. The effect of seasonal hare behaviour on the effectiveness of transects surveys, in different seasons, or the effect of season on dung accumulation and decay, should be assessed. We also require information on the performance of the methods in an extended range of population densities. Secondly, there is a need to trial this approach as part of a wider pilot mountain hare monitoring scheme to assess the long term status of the mountain hares in Scotland, and inform statutory reporting requirements.

Further development of survey methods to establish a calibration could be achieved by adding more sites and surveys to the results of this study. Alternatively, the methods described here could be calibrated using different survey methods, for example lamping encounter rates could be calibrated by comparing encounter rates before and after a known number of hares have been killed during a cull or sporting shoot. Advances in molecular, genetic, and remote sensing techniques (e.g. use of camera traps, and aerial surveys from drones) could also be explored further.

A driving motivation for this study was the need to obtain national and regional population estimates of mountain hares. The methods described here now need to be applied in a wider pilot survey. A key step before implementing a monitoring programme will be to formulate clear and explicit monitoring objectives, and then design a monitoring programme to meet those objectives. Mountain hare populations vary considerably in space and time, and in many parts of their range show large multi-annual fluctuations in population size that makes monitoring and identification of trends difficult. Careful survey design and consideration of statistical power will be required. The data provided here can be used to aid the design of effective and efficient surveys.

In addition we believe there is a need to systematically study and ascertain movement patterns of mountain hares, particularly in winter and in response to weather conditions in different landscapes. A better understanding of the spatial ecology of mountain hares would inform survey and monitoring, as well as local management of mountain hares.

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ANNEX 1: USING SIMULATIONS TO OPTIMISE TRAPPING PROTOCOLS

A1.1 Background

This annex comprises a report on a preliminary desk-based study to inform the design of the capture-recapture study described in the main body of this report. The work was undertaken between May and July 2014.

A1.2 Aims

Against a back drop of growing concern over the conservation status of mountain hares, in order to effect appropriate conservation and management of mountain hares, Scottish Natural Heritage (SNH) and wildlife managers require simple and effective survey methods for the species. To this end, and since 2005, SNH have commissioned two relevant pieces of work to; i) review and make recommendations on survey methods for mountain hares (Newey *et al*., 2008), ii) test and calibrate dung counts as a method to assess mountain hare populations (Newey *et al*., 2011). The latter contract reported in Newey *et al.* (2011) however found no correlation between either dung standing crop or dung accumulation and mountain hare density estimated by capture-recapture.

In order to develop reliable, robust methods to assess mountain hare populations in a variety of habitats, it has been suggested that a range of methods, be calibrated against a standard method. Capture-Recapture (CR) is a widely used survey method for small and medium sized mammals, has been widely used to estimate abundance and density in hare research, and has been used to calibrate survey methods for other hare species (Hodges & Mills, 2008; Krebs *et al*., 2001; McCann *et al*., 2008; Mills *et al*., 2005; Murray *et al*., 2002), and shown to be effective for assessing mountain hare populations in Scotland (Newey *et al.*, 2003). Capture-Recapture methods have therefore been suggested as a method against which to calibrate other survey methods (Newey *et al*., 2008). However prior to implementing a large scale study that cross-references a range of methods against this technique, it is necessary to assess whether CR is likely to yield sufficient data for reliable density estimation and identify the most appropriate design for the trapping programme. This will ensure that the appropriate and efficient trapping effort is applied and will provide the understanding of the sources of error necessary to interpret results with a known level of confidence.

This study uses data from previously implemented trapping studies of mountain hares (Newey *et al*., 2011) to quantify the effects of; i) number of traps, ii) spacing of traps and the area covered, iii) duration of the trapping programme, and iv) mountain hare density on the performance of CR density estimates.

A1.3 Methods

We investigated the effects of CR survey design on the likely number of animals caught and the performance of density estimates using simulation features in the R packages ‘secr’ and ‘secrdesign’ (Efford, 2014a, 2014b). The set of parameter values to be considered was identified in discussion with SNH and the GWCT (Table A1.1).

Table A1.1. The parameter and parameter values used for simulations of mountain hare capture-recapture surveys.

Factor	Description	Value
Sigma (σ)	Sigma is a biological parameter relating to animal movement and the scaling parameter of the detection function. With a Halfnormal detection function sigma scales to animal movement so that approximately 2.5 x sigma = 99% home range radius. Based on published autumn/winter mountain hare home ranges in the Scottish uplands of between 10 and 20 ha (Hulbert *et al*., 1996; Rao *et al*., 2003) we set sigma to equal 100 m equating to home ranges of 20 ha. A sigma value of 100 m is also consistent with the range of values found from the analysis of the Newey *et al.* (2011).	100 m*
Density (D)	Represents the known density used in the simulations. Mountain hare densities vary widely in time and space (Hewson, 1976; Newey *et al*., 2007a; Watson *et al*., 1973). For simulation purposes we used densities of 0.1 and 0.5 hare per ha (equating to 10 and 50 hares per km^{-2}) as this is believed to represent a realistic range of densities of hares found on grouse moors and which are amenable to CR studies.	0.1 and 0.5 per ha.
Probability of capture (g0)	Represents the probability of an individual being caught if a trap were at zero metres from that individuals home-range centre. For simulations we used values of 0.1 and 0.2 which represent the lower, and thus more challenging, end of the spectrum of capture probabilities found in the Newey *et al.* (2011) study.	0.1 and 0.2

Size of trapping grid	The size of trapping grid is determined by the number of traps, trap spacing and the layout of the traps. Previous work trying to estimate mountain hare density from CR used 42 traps in a 6 by 7 grid with 85 m spacing between traps sometimes failed to catch sufficient hares (Newey *et al.* 2010). Here we investigate trap grids based on 64 and 100 traps arranged in a single grid or 4 clusters. One hundred traps (dependent on trap spacing) is considered the maximum number and represents the number that one field worker could cover in one day. For single grid layouts we explored the effects of 100, 150 and 200 m trap spacing. For the traps deployed as clustered grids we used 4 grids of 5 by 5 traps and initially kept trap spacing constant at 100m, but varied the distance between cluster centres; 600, 700 and 800 m representing 200, 300 and 400 m grid edge to edge separation (Fig. A1.1). In the later stages of the analysis we also considered an inter trap spacing of 125 m with cluster centres 700 and 800 m apart (200 and 300 m edge to edge separation) and 150 m inter trap spacing with cluster centres 900 and 100 m apart (300 and 400 m edge to edge separation) (Fig. A1.1).	100 m trap spacing 8 x8 grid 10 x 10 grid 4 x (5 x 5) clustered grids (with 600, 700 and 800 metres between cluster centres). 150 m spacing 8 x 8 grid 10 by 10 grid 4 x (5 x 5) clustered grids (with 900 and 1,000 metres between cluster centres). 200 m spacing 8 x 8 grid 10 by 10 grid 125 m trap spacing* .(clustered grids only) 4 x (5 x 5) See Table A1.2 and Fig. A.1.1f or details.
Number of occasions	We assumed 12 or 16 nights trapping representing 3 or 4 weeks of trapping, at 4 nights per week. These figures are based on knowledge from previous trapping programmes while also allowing for the closure assumption required for closed population CR methods to be met, and practicalities of access and deployment of staff. Later stages of the simulations focused on the 16 sampling occasions only because at low density and capture probability the longer survey period was considered necessary.	12 and 16 sampling occasions (nights).

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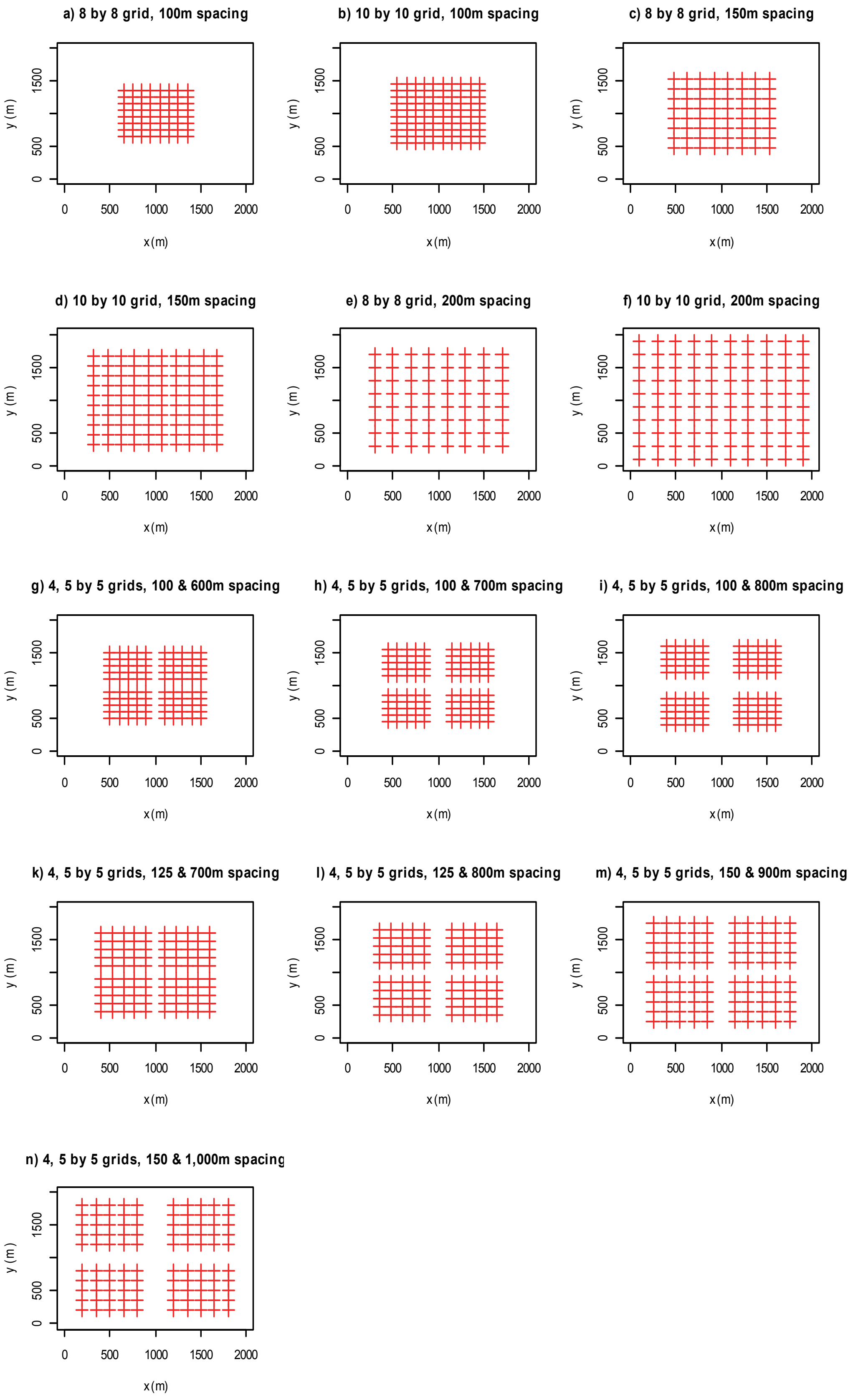
*200 m was also initially agreed, but was dropped due to time constraints, and because the literature strongly suggests winter upland home ranges of around 20 ha which equates to a sigma value of 100 m. There is also evidence that trap grids perform better when spacing is approximately the same as sigma.

Table A1.2. Details of the trapping grids used for simulations. Area refers to the area physically covered by the grid or grids.

	No. Traps				Spacing (m)				To traverse traps	
Layout	Total	x-axis	y-axis	No. clusters	Inter-trap	Cluster Centres	Cluster Edges	Area (ha)	Km	Hrs
single grid	64	8	8	1	100	na	na	490	7.1	1.8
single grid	64	8	8	1	150	na	na	1,103	10.7	2.7
single grid	64	8	8	1	200	na	na	1,960	14.2	3.6
single grid	100	10	10	1	100	na	na	810	10.9	2.7
single grid	100	10	10	1	150	na	na	1,823	16.4	4.1
single grid	100	10	10	1	200	na	na	3,240	21.8	5.5
clustered	100	5	5	4	100	600	200	640	12.4	3.1
clustered	100	5	5	4	100	700	300	640	12.8	3.2
clustered	100	5	5	4	100	800	400	640	13.2	3.3
clustered	*100*	*5*	*5*	*4*	*125*	*700*	*200*	*1,000*	*15.3*	*3.8*
clustered	*100*	*5*	*5*	*4*	*125*	*800*	*300*	*1,000*	*15.7*	*3.9*
clustered	*100*	*5*	*5*	*4*	*150*	*900*	*300*	*1,440*	*18.6*	*4.7*
clustered	*100*	*5*	*5*	*4*	*150*	*1000*	*400*	*1,440*	*19.0*	*4.8*

‘To traverse traps’ refers to the shortest walking route around all the traps in kilometres and to the estimated time taken to walk around all the traps using this route walking at 4 km h^{-1}.


a) 8 by 8 grid, 100m spacing

b) 10 by 10 grid, 100m spacing

c) 8 by 8 grid, 150m spacing

d) 10 by 10 grid, 150m spacing

e) 8 by 8 grid, 200m spacing

f) 10 by 10 grid, 200m spacing

g) 4, 5 by 5 grids, 100 & 600m spacing

h) 4, 5 by 5 grids, 100 & 700m spacing

i) 4, 5 by 5 grids, 100 & 800m spacing

k) 4, 5 by 5 grids, 125 & 700m spacing

l) 4, 5 by 5 grids, 125 & 800m spacing

m) 4, 5 by 5 grids, 150 & 900m spacing

n) 4, 5 by 5 grids, 150 & 1,000m spacing

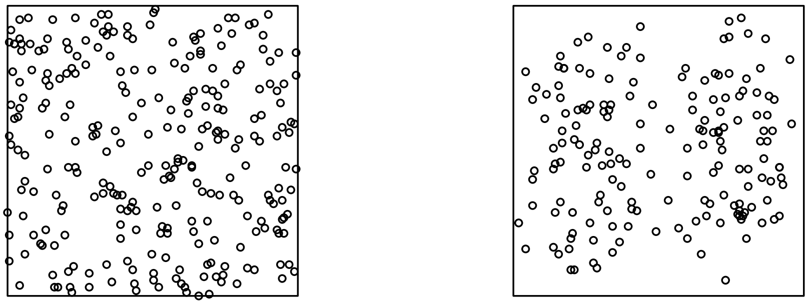
Figure A1.1. Diagrams of the different trapping grids used in simulations. The boxed area represents the 2 by 2 km study area. The crosses represent the trap locations.

Simulations were carried out in two phases.

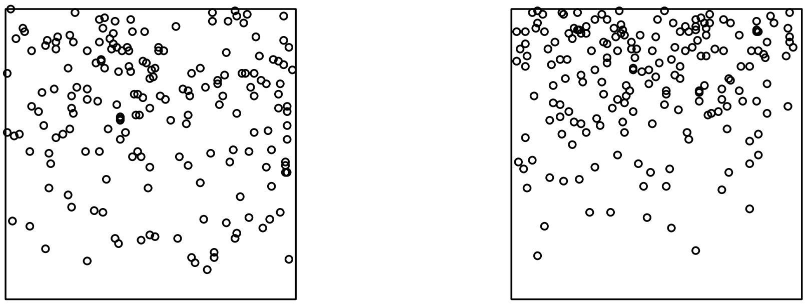
Phase 1
Initially we assumed that mountain hares were distributed homogeneously (individuals are placed according to a homogeneous Poisson distribution) across the study area (Fig. A1.2(a)). We also assumed, apart from spatial heterogeneity, constant capture probability (i.e. no behavioural, time or individual heterogeneity in capture probability except that caused by the location of individuals relative to traps). We generated scenarios for each combination of parameters; D = 0.1, 0.2, g0 = 0.1, 0.2, sigma = 100, number of occasions = 12, 16 for each trap layouts 1-9 and ran 100 simulations for each scenario.

Phase 2
In the second phase we introduced inhomogeneity in the underlying distribution of hares across the study area. Without detailed information on how mountain hares might distribute themselves over a study area we investigated two 'built in' inhomogeneous distributions; 'hills' where density across the study area is described by a sine curve in the x- and y-directions where density varies between 0 and 2 x D along each axis (Efford, 2014a), and the 'coastal' distribution where the distribution of individuals is concentrated along the x- and/or y- axis of the study area (Fewster & Buckland, 2004). We considered one scenario using hills where individuals were distributed across two 'hills' along the x-axis (described by the '2,1' postfix) (Fig A1.2(b)), and four coastal scenarios representing increasing concentration of individuals along the y-axis (representing, for example, an altitudinal gradient in distribution where the level of aggregation is described by the postfix number where the larger first number represents increasing aggregation such that the coastal 5,1 distribution approximately represents 50% of the population in the top 10% of the study area) (Fig. A1.2(c-f)).

a) Homogeneous b) Hills 2,1



c) Coastal 2,1 d) Coastal 3,1



e) Coastal 4,1 f) Coastal 5,1

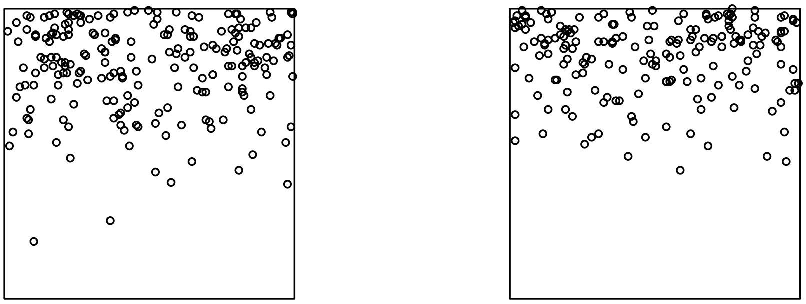


Figure A1.2. Distributions used to describe the underlying distribution of mountain hares over the study areas. a) Homogeneous distribution, b) Hills with individuals distributed into two 'hills', c-f) Coastal distributions with individuals distributed so that an increasing proportion of the population is distributed in the upper area of the plot area. For illustration Density = 5 hares per ha. (The figures following the distribution are the parameter values describing the distribution; 'coast 2,1 codes for 2 hills in the x-axis and one hill in the y-axis; the 'Coastal' a,b codes for increasing aggregation of the population along the y-axis, 'Coastal 5,1' approximately represents 50% of the population in the upper 10% of the study area).

For each of the five cases of inhomogeneous distributions we generated scenarios for all parameter combinations; D = 0.1, g0 = 0.1, sigma = 100, number of occasions = 16, and trap configurations 1-13 with the trap grid centred in the middle of the study area. Apart from the heterogeneity arising from the placement of traps relative to animals we assumed a constant capture probability and ran 100 simulations for each scenario.

In both phases we assessed the results from each scenario based on the predicted number of individuals caught, the number of recaptures and the number of individual recaptures at a different trap to that originally caught at, and for the density estimates associated with each scenario we assessed:

• estimated relative bias;	(observed – truth) / truth,
• relative standard error;	standard error / estimate, and
• coverage;	the proportion of simulations where the confidence intervals embrace the true estimate.

Reliable parameter estimates from capture-recapture studies are dependent on both capturing and recapturing sufficient individuals. In addition SECR methods require sufficient recaptures of individuals at different traps. It is therefore most critical to understand the performance of capture-recapture surveys at the lower spectrum of mountain hare density and capture probability when fewest animals are likely to be caught. We therefore focus on results from the lowest values of density and capture probability, to test the limits of applicability of the methods.

A1.4 Results

Phase 1

Given a homogeneous distribution of mountain hares, both survey periods and trap configurations except the eight by eight grid with 100 m trap spacing performed reasonably well. For both the 12 and 16 day sampling regimes the number of individuals caught on the single grids increased with increasing trap spacing. Increasing the distance between clusters for the clustered layouts had only a small positive effect on the number of individuals caught (Fig. A1.3 (a)). For any given give trap layout, more individuals were caught during the 16 day than the 12 day trapping period (Fig. A1.3 (a)). The eight by eight single trapping grid produced the fewest captures for any given trap spacing and sampling duration, and captures only 10 individuals with 100 m and 15 individuals at 150 m trap spacing with 12 days sampling (Fig. A1.3 (a)). The longer sampling period appears to have only a small positive effect on the number of individuals caught (Fig. A1.3 (a)).

The number of recaptures and recaptures at novel trap locations are greater for the 16 day compared to the 12 day sampling period (Fig. A1.3 (b)). For the single grids the number of recaptures increases with trap spacing, but the number of recaptures at novel traps decreases. Cluster spacing has minimal effect on either number of recaptures or number of recaptures at new trap locations (Fig. A1.3 (b). In terms of number of individuals, number of recaptures and number of recaptures at novel traps the clustered grids perform better than the eight by eight grid, but not as well as the 10 by 10 grid for any given sampling period (Fig. A1.3 (a-b)).

Except for the eight by eight grid with 100 m with 12 days sampling all trap configurations and the two survey periods provided reasonable density estimates with low (<5%) relative bias and good coverage (Fig. A1.3 (c-d)). However, the high (> 25%) relative standard error associated with the single eight by eight and 10 by 10 trapping grids suggests that these trap configurations at the shorter survey duration do not yield reliable density estimates, even with the longer 16 night survey duration; neither the smaller eight by eight nor 10 by 10 grids performed well at 100 m spacing (Fig. A1. 3 (e-f)).

Summary of Phase 1

Overall the eight by eight and 10 by 10 grids with 150 and 200 m spacing along with the clustered grids seem to perform the best, particularly with the longer survey period. For the single grids greater trap spacing tends to produce captures of more individuals. The number of recaptures and particularly recaptures of individuals at novel trap locations decreases with increasing trap spacing. In addition there appears to be little difference in the number of individuals caught between 150 and 200 m spacing, but the 150 m spacing tends to produce more recaptures than the same grid with 200 m trap spacing. For the clustered grids the overall size of the grid is determined by both the trap spacing and the distance between clusters. Here we have only changed the cluster spacing, making it difficult to compare the effect of trap spacing on the performance of density estimates. However, clustered grids overall performed better than all the eight by eight grids and as well as the 10 by 10 grid with 100 and 150 m trap spacing. While the 10 by 10 grid with 200 m spacing seems to perform best, the practicalities of deploying and checking daily 100 traps with 200 m spacing between them probably makes this layout impractical. Moreover while a 10 by 10 trap layout with 200 m trap spacing produces the most novel captures the clustered grids produce more recaptures and recaptures at novel trap locations.

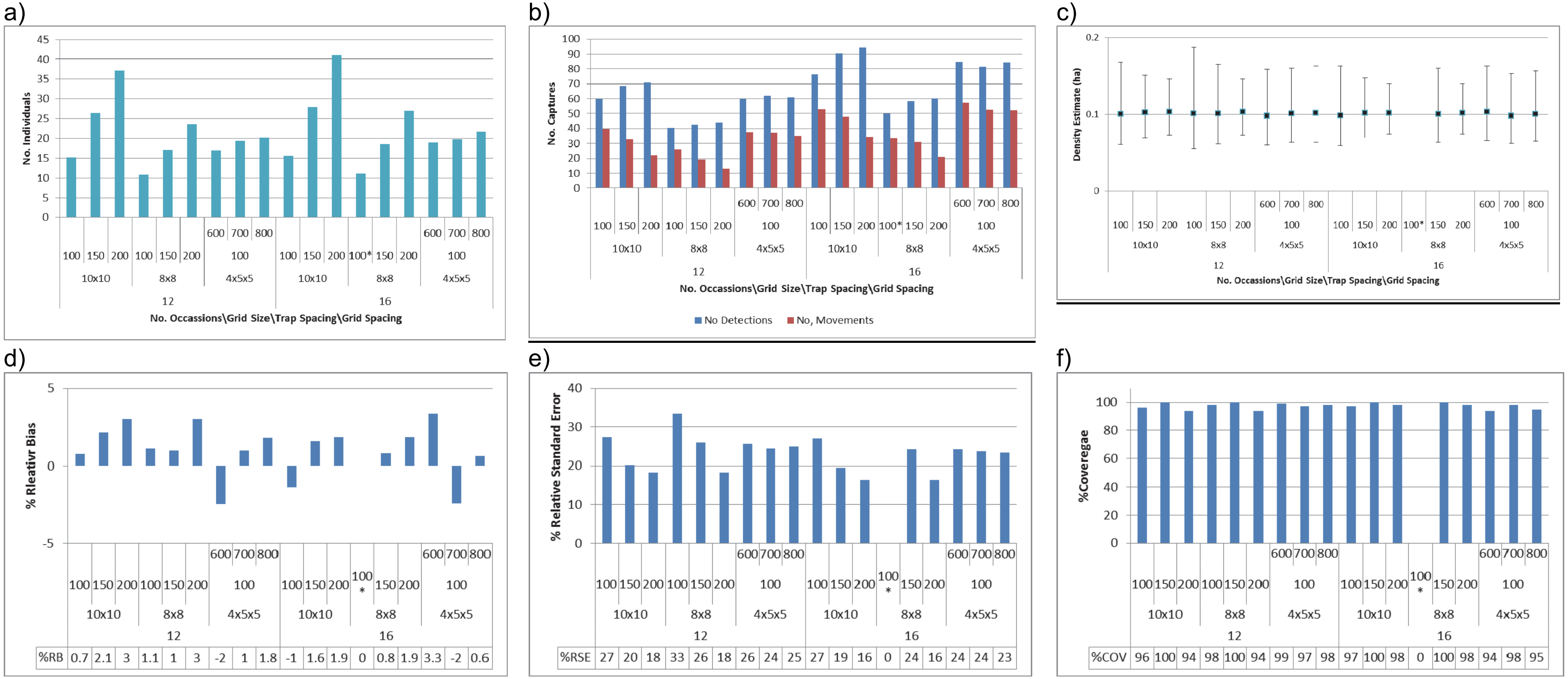


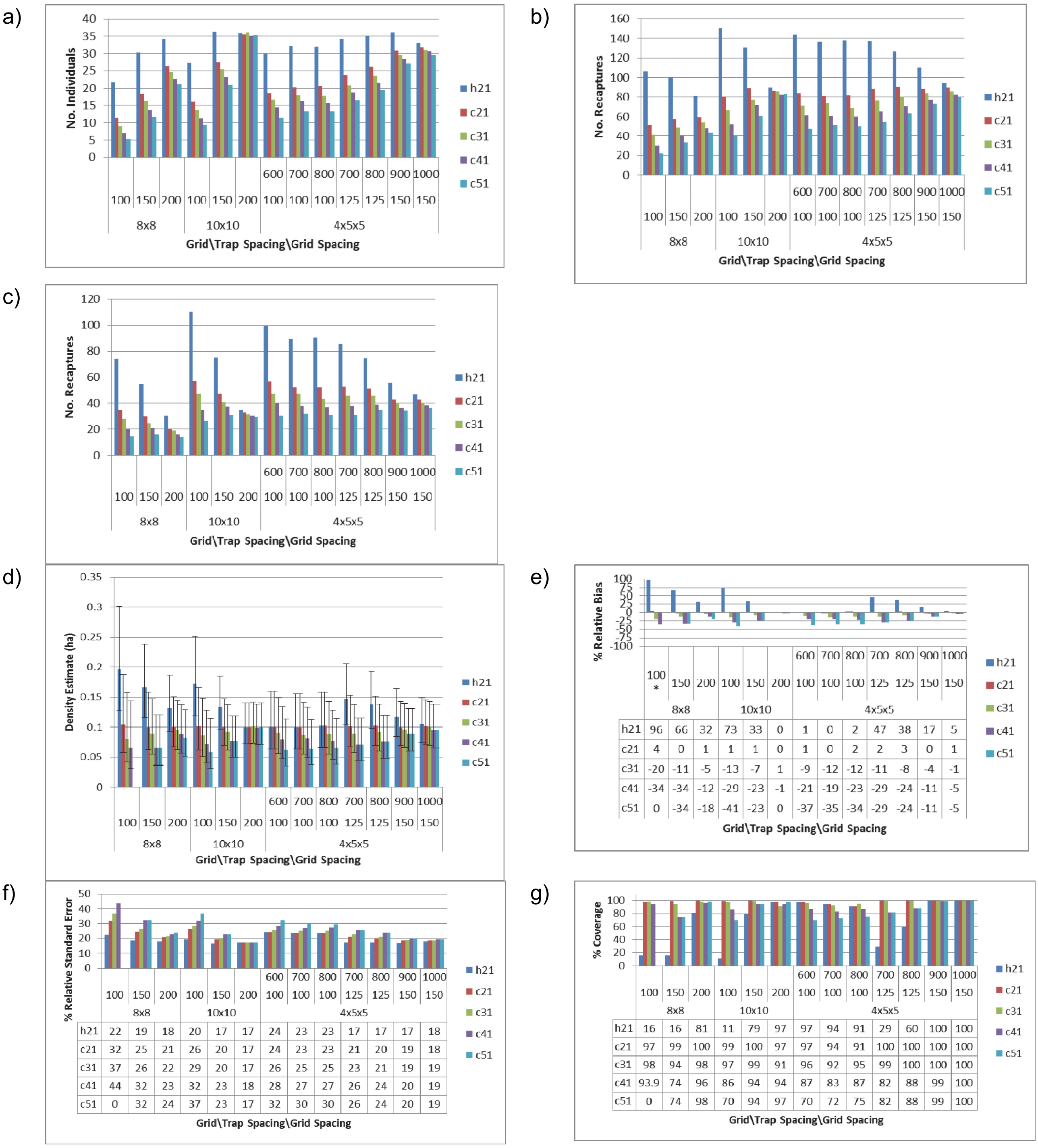
Figure A1.3. Graphs summarising the performance of simulations of inhomogeneous distributions; a) number of individuals caught, b) total number of recaptures and total number of recaptures of individuals at a novel trap, c) density estimates with 95% upper and lower confidence limits, d) relative bias (%), e) relative standard error (%), and f) coverage (%). %RB = Percentage Relative Bias, %RSR = Relative Standard Error, %COV = Percentage Coverage, D = 0.1, g0 = 0.1, sigma = 100.

Phase 2

The effects of introducing inhomogeneity into the distribution of hares are dependent on the type of inhomogeneity and trap layout and trap\grid spacing. With the exception of the 10 by 10 grid with 200 m spacing which effectively covers the whole (2 x 2 km) study area the single grids do not perform well (Fig. A1.4). While the number of individuals caught, recaptures and spatial recaptures for the ‘hills’ distribution is adequate, fewer individuals are caught and recaptured under the ‘coastal’ distributions and decline with increasing concentration along the y-axis (Fig. A1.4 (a-c)). While a similar pattern is found for the clustered grids the number of captures and recaptures are all higher compared to, all except the 10 by 10 grid with 200 m spacing, the single grids and increase with increasing trap and grid spacing (Fig. A1.4 (a-c)). Though the 10 by 10 grid with 200 m spacing produces a high number of captures and recaptures, the number of recaptures at novel trap locations is low compared to all the clustered grids under all distributions (Fig. A1.4 (a-c)).

Density estimates and the performance of density estimates are also greatly influenced by the underlying distribution of mountain hares. Again, with the exception of the 10 by 10 grid with 200 m trap spacing the single grids tend to perform poorly (Fig. A1.4 (d-e)). Under the ‘hills’ distribution single grids produce highly positively biased density estimates with high relative bias (Fig 4 (d-e)); although the relative standard error is acceptable, the coverage is poor (Fig. A1.4 (f-g)). The large 10 by 10 grid with 200 m spacing produces unbiased density estimates with acceptable relative standard error and good coverage (Fig. A1.4 (f-g)). Under the ‘coastal’ distributions all the eight by eight and two smaller 10 by 10 single grids (i.e. with 100 and 150 m trap spacing) tend to produce biased density estimates with high relative standard errors that increase with increasing concentration of the population along the y-axis (Fig. A1.4 (d-f)).

The clustered trap layouts produced less biased results than did the single grids with layouts, with 100 and 150 m trap spacing producing the least biased results (Fig. A1.4 (e)). Bias increased with increasing concentration of the population, and it decreased across all distributions with increasing grid spacing (Fig. A1.4 (d-e)). Similarly, relative standard error and coverage increased with increasing concentration of the population, but decreased with increasing trap and grid spacing (Fig. A1.4 (f-g)), though the clusters with 125 m trap spacing show low coverage compared to the other clustered layouts (Fig. A1.4 (f-g)). Overall the relative standard error decreases and coverage increases with increasing trap and grid spacing, though the smaller clustered grids with 100 m trap spacing and 700 and 800 m grid spacing perform adequately up to moderate (coastal 3,1) levels of aggregation in the ‘coastal’ distributions (Fig. A1.4 (f-g)).



e)

	8x8			10x10			4x5x5						
	100 *	150	200	100	150	200	100	100	100	125	125	150	150
							600	700	800	700	800	900	1000
h21	96	66	32	73	33	0	1	0	2	47	38	17	5
c21	4	0	1	1	1	0	1	0	2	2	3	0	1
c31	-20	-11	-5	-13	-7	1	-9	-12	-12	-11	-8	-4	-1
c41	-34	-34	-12	-29	-23	-1	-21	-19	-23	-29	-24	-11	-5
c51	0	-34	-18	-41	-23	0	-37	-35	-34	-29	-24	-11	-5

Grid\Trap Spacing\Grid Spacing

f)

	8x8			10x10			4x5x5						
	100	150	200	100	150	200	100	100	100	125	125	150	150
							600	700	800	700	800	900	1000
h21	22	19	18	20	17	17	24	23	23	17	17	17	18
c21	32	25	21	26	20	17	24	23	23	21	20	19	18
c31	37	26	22	29	20	17	26	25	25	23	21	19	19
c41	44	32	23	32	23	18	28	27	27	26	24	20	19
c51	0	32	24	37	23	17	32	30	30	26	24	20	19

Grid\Trap Spacing\Grid Spacing

g)

	8x8			10x10			4x5x5						
	100	150	200	100	150	200	100	100	100	125	125	150	150
							600	700	800	700	800	900	1000
h21	16	16	81	11	79	97	97	94	91	29	60	100	100
c21	97	99	100	99	100	97	97	94	91	100	100	100	100
c31	98	94	98	97	99	91	96	92	95	99	100	100	100
c41	93.9	74	96	86	94	94	87	83	87	82	88	99	100
c51	0	74	98	70	94	97	70	72	75	82	88	99	100

Grid\Trap Spacing\Grid Spacing

Figure A1.4. Graphs summarising the performance of simulations of inhomogenious distributions; a) number of individuals caught, b) total number of recaptures, c) total number of recaptures of individuals at a novel trap, d) density estimates with 95% upper and lower confidence limits, e) relative bias (%), f) relative standard error (%), and g) coverage (%). The distributions are coded as; h21 = 'hills' 2,1 where 2,1 represents the number of hills of the x- and y- axes; c21 = 'coastal 2,1; c31 = 'coastal' 3, c41 = 'coastal 4,1, and c5,1 = 'coastal' 5,1 where the figures represent the Beta parameter values along the y-axis. For all simulations D = 0.1, g0 = 0.1, sigma = 100, number of occasions = 16.

A1.5 Discussion and Recommendations

We have restricted our assessment of the performance of different live trapping regimes to scenarios which are likely to represent low hare density (0.1 hares per ha) and low capture probability (g0 = 0.1), as these are the scenarios that represent the greatest challenge. This also leads to conservative estimates of the trapping effort needed to secure sufficient initial captures and recaptures for meaningful analysis. Live trapping on study areas where hares are more numerous and/or exhibit higher capture probability may require fewer traps and/or a shorter survey period.

Larger trapping grids that cover a larger area due to larger inter-trap distances will on average capture more individuals than smaller trapping grids because larger grids will encompass more individual home ranges. However, as trap spacing increases relative to home range size (i.e. sigma), larger trapping grids will tend to yield fewer recaptures because there are fewer traps per home range and the distance between individuals' home range centres and traps increases. These observations can be clearly seen in the results of the simulations presented here, where the number of individuals caught increases with increasing trap spacing and grid size while the number of recaptures decreases.

Here we have set density to 0.1 hares per ha which, assuming a 2 by 2 km study area means that the entire hare population in the study area is around 40 hares. Where hares are distributed uniformly in the study area, trap grids that cover a larger proportion of the study area will tend to catch more individuals. Hence the 10 by 10 trapping grid with 200 m trap spacing tended to perform better than all the other trapping grids as it essentially covered the entire study area. This large trapping grid also performed well when we introduced inhomogeneity in the underlying distribution of hares because it, again, covered all of the survey area and so encompassed the underlying variation in distribution.

It is important to note that for convenience all trapping grids were centred on the study area giving rise to a symmetrical spatial coverage. This is likely to be one reason why the smaller and single trap grids performed worse than larger trap grids with increasing inhomogeneity. For example under the 'hills' distribution, smaller grids were likely to only include a limited range of the underlying density distribution leading to lower than expected captures and recaptures. The sub-grids of the clustered layouts may have only included areas with a higher than average density. Similarly, moving a small grid 'north' in the 'coastal' scenarios may have reduced bias and increased coverage.

Assessing the theoretical performance of different trapping grids is only one element that needs to be considered in making recommendations on the 'best' trap layout. Practical considerations based on the available resources must also be considered. It is quite clear that it is unrealistic for one person to manage 100 traps deployed in a 10 by 10 grid with 200 m between traps as this means the shortest route around all the traps is nearly 22 km, which assuming a walking speed of 4 km per hour would take over five hours to just walk round all the traps. Adding just two minutes per trap to bait and set the trap adds just over three hours. Assuming it takes a competent person 10 minutes to process a captured hare, and assuming (based on the predicted number of captures and recaptures) a 7.5% occupancy adds another 75 minutes to the time it takes to go round the traps. Assuming it should not take a person longer than 3.5 hours to traverse a trapping grid, of the trap layout considered, the following trap arrays are possible (Table A1.4).

Table A1.4. Details of the trap layouts considered here that can be traversed in 3.5 hours or less.

	No. Traps				Spacing (m)				To traverse traps	
Layout	Total	x-axis	y-axis	No. clusters	Inter-trap	Cluster Centres	Cluster Edges	Area (ha)	Km	Hrs
single grid	64	8	8	1	100	na	na	490	7.1	1.8
single grid	64	8	8	1	150	na	na	1,103	10.7	2.7
single grid	100	10	10	1	100	na	na	810	10.9	2.7
clustered	100	5	5	4	100	600	200	640	12.4	3.1
clustered	100	5	5	4	100	700	300	640	12.8	3.2
clustered	100	5	5	4	100	800	400	640	13.2	3.3

Of these, the simulations carried out here suggest that the clustered design with four grids of five by five traps with 100 m trap spacing and 700 m grid spacing is a good compromise. This trap layout with 16 sampling days produced density estimates with low bias, acceptable relative standard error and good coverage for all but the most extreme distributions assessed here. We advocate further investigation of this and similar trapping grids to assess how, for example, reducing the number of traps and (slightly) increasing trap spacing might affect performance. In addition we suggest an informal 'adaptive' approach whereby survey design and duration may be modified in response to conditions prevailing at the time, the number of animals caught and ongoing 'live' analysis.

Modelling and simulation studies play an important and useful role in ecology allowing us to explore scenarios and hypotheses before embarking on labour intensive field studies. However, simulations are only that and need to be considered with due regard to the implicit and explicit assumptions, and modelling framework. None of the simulations here, for example, accommodate for the vagaries and challenges of Scottish winter mountain weather! While many of the assumptions here are design-based and therefore within our control to stipulate, two key parameters g0 and sigma, are biological parameters that we have estimated from previous studies and the literature. Both of these parameters are likely to be habitat and site dependent and vary by individual and will influence the efficacy of live trapping studies. We have used informed and conservative estimates of g0 and sigma to minimise the effect of miss-estimation.

Simulations have assumed a constant and regular study area where traps can be placed according to the survey design. Of course, trap placement will have to accommodate the geography of study sites and considerable deviation from the proposed design might be needed. Where possible we suggest that modifications should be informed by further simulations that accommodate local information before implementation.

ANNEX 2: DISTANCE SAMPLING ANALYSIS OF NIGHT TIME LAMPING SURVEYS

A2.1 Introduction

Daylight surveys produced too few sightings to estimate density from distance sampling analyses (see Results) and it was not possible to collect suitable distance data from night time thermal imaging surveys. Distance sampling analyses are therefore confined to night time lamping surveys.

A2.2 Methods

During lamping surveys we collected distance data; for each detection the sighting angle from transect line was measured with a sighting compass and the sighting distance measured with a laser range finder (Yardage Pro 400, Bushnell Outdoor Products, Kansas, USA).

The recorded sighting angle and sighting distance were transformed to perpendicular distance from the transect line prior to analysis. Histograms of perpendicular distances were examined for evidence of 'spikes' or 'heaping' in the data that might suggest violation of the assumptions; i) that animals at distance zero from the transect line are detected, ii) that animals do not move before detection, and to also check for any obvious rounding of measurements (Borchers *et al*., 2002; Buckland *et al*., 2001), and to assess the need for truncation or possible 'binning' (grouping) of perpendicular distances into distance categories. We always excluded the largest 5% of sighting distances as recommended and used this as a starting point for further truncation (Buckland *et al.*, 2001). Where exploratory analyses revealed spikes and heaping of perpendicular distances, distance data were truncated to exclude detections at larger perpendicular distances where spikes and heaping tended to occur. In some cases heaping, associated with very few observations close to the transect line, was extreme (see results) and the data required 'binning' to improve fit though our preference was to analyse non-binned data and binning was used where fit was otherwise very poor. Exploratory analyses also identified cases where there were too few sightings and/or data were too heaped to enable analysis (see Results). After truncating or binning the data as necessary, candidate models were then fitted using the DISTANCE 7 package (Thomas *et al*., 2010).

To obtain density estimates for each site we analysed the data from all the replicate lamping surveys completed for each site together, fitting a common, global, detection function and used post-stratification by replicate to produce a weighted average density estimate for each site. Exploratory analyses revealed that in some cases the optimal detection function differed between replicates, and that a global detection function may not be the most appropriate. We therefore compared AIC scores from analyses with a global detection function to analyses with replicate specific detection functions. This comparison showed that in all cases analysis with a global detection was better supported by the data based on the lowest AIC (Annexes A2.5 and A2.6). To assess the reliability and repeatability of lamping surveys we obtained site-replicate specific density estimates by separate analysis for each replicate fitting a site-replicate specific detection function for each analysis (i.e. each replicate survey of four transects).

For each analysis we fitted the candidate models; 'uniform' key function with either 'cosine' or 'simple polynomial' adjustment series, 'halfnormal' key function with 'cosine' adjustment series, and 'hazard rate' key function with cosine adjustment series to the distance data. Choice of these models was based on assessment of the distribution of distances, previous experience and published literature and the merits of different models (Buckland *et al*., 2001; Newey *et al*., 2003). We considered the goodness of fit of each model and the need for further truncation or binning based on visual inspection of sighting histograms, qq-plots, and the Kolmogorov-Smirnov test, and the weighted and uniform Cramer-von Mises family tests of goodness of fit test statistic, or in the case of 'binned' data we used the Chi-sq goodness of fit test (Buckland *et al*., 2001; Thomas *et al*., 2010). Once we had identified a suitable level of truncation or grouping of distances into distance categories we used AIC alongside goodness of fit tests to identify the most parsimonious model and inform the choice of the 'best' model as the lowest AIC score did not always identify the model with the best fit to the data. Our survey design comprised only four transects per site which is too few to make use of bootstrapping to estimate variance, or to allow use of bootstrapping for model averaging. Indeed we acknowledge that four transects is a small sample size to estimate variance between transects and overall variance.

A2.3 Results

Histograms of perpendicular distances show 'spikes' and 'heaping' caused by more animals being seen at certain distances, than would be expected if placement of the transects was random relative to animal distribution, and detection probability declined with distance from the transect line (Fig. A2.1). For many sites this effect is particularly pronounced at around 30 or 50 m from the transect line. The higher than expected frequency of hares seen away from the transect line, suggests that mountain hares may have being moving away from the transect line before they were detected and recorded.

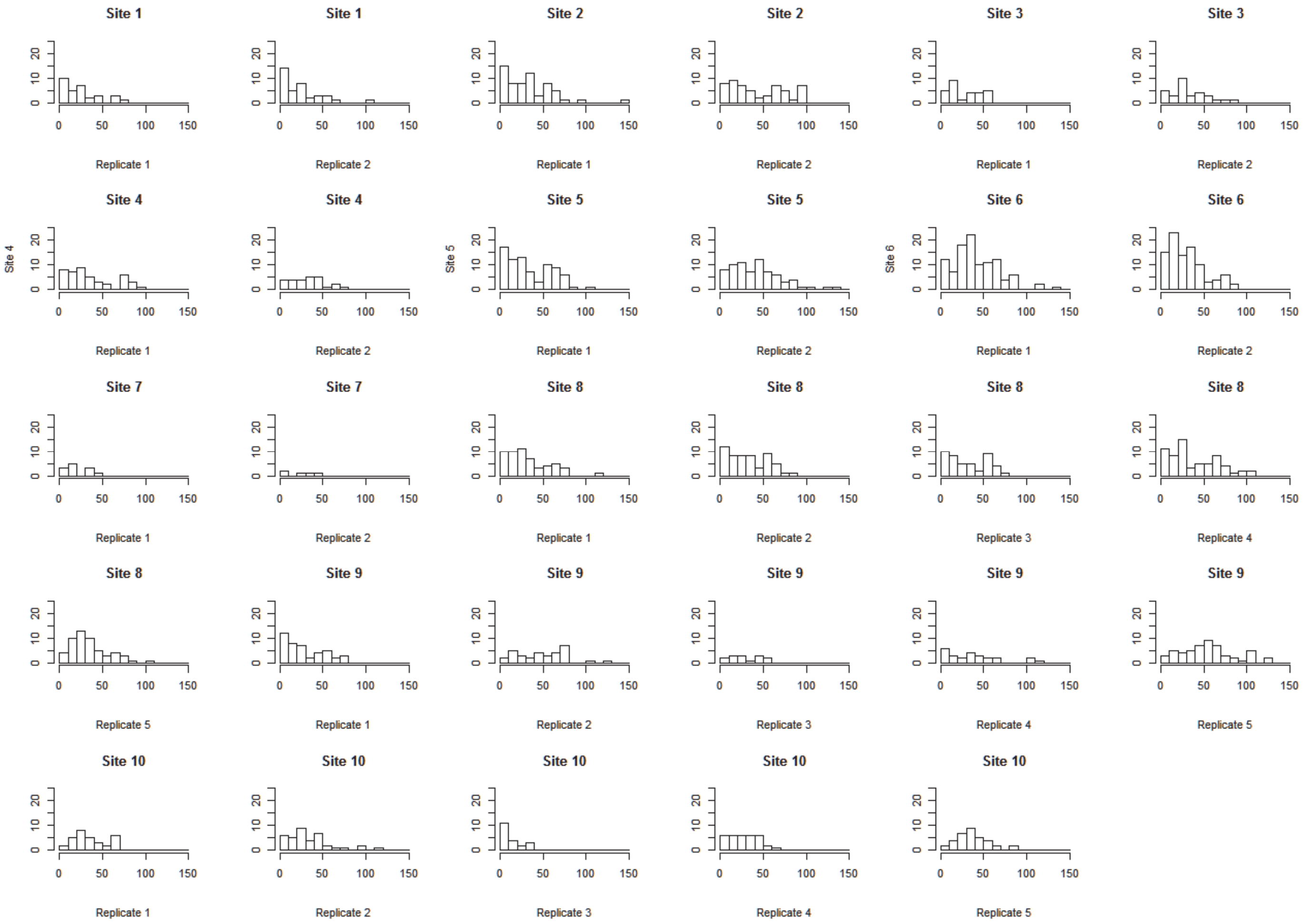


Figure A2.1. Histograms of perpendicular distances of mountain hare sightings for each replicate of night time lamping surveys carried out at the ten sites in this study showing, on the vertical y-axis, the count of sightings in each 10 m distance category. The vertical, y-axis, and horizontal, x-axis, are constant to facilitate comparison.

A2.3.1 Replicate and site specific density estimates

Replicate specific density estimates were obtained by analysing each replicate (i.e. each replicate of four transects) separately. Analysing each replicate lamping survey separately means that there are fewer sightings to fit the detection function, and accentuates the presence of spikes and heaping in the data requiring greater truncation, and in two cases binning of the data to obtain a good model fit to the data, and meant that in six cases there were too few data to fit an adequate detection function (Table A2.1).

Replicate specific density ranged from 31 to 153 hares km^{-2} (Fig. A2.2, Table A2.1). Density estimates are, in most cases, associated with high coefficients of variation (> 0.20) indicating appreciable differences in number of hares seen on different transects within replicate surveys, and correspondingly wide confidence intervals (Fig. A2.2, Table A2.1). The intra-site difference between highest and lowest density estimates from replicate surveys differ by between 18-41% (representing a difference of between 15 and 22 hares km^{-2}) for those replicates for which there were sufficient data to obtain an estimate (Table A2.1). Density estimates from replicates 1 and 2 are strongly positively and significantly correlated with each other ($r = 0.82$, $t = 3.31$, df = 5, $p < 0.05$).

The pooled density estimates show, with exception of site 2, much narrower confidence limits resulting from the larger number of transects used to estimate the global detection function and better estimate between transect variability (Fig. A2.2). Compared to the site mean densities produced from pooled and post-stratified analysis (Table A2.2) replicate specific estimates are similar for all sites except 9 where the mean estimate (31.24 hares km^{-2}) is substantially lower, less than half, than the one replicate specific estimate available (65.66 km^{-2}) (Fig. A2.2, Tables A2.1, A2.2). This discrepancy appears to be due to the very low number of detections of hares at site 9 during replicate surveys 2-5 which were too low to enable replicate specific estimates to be obtained and which seem to lower the weighted mean estimate, (the weighted mean estimate is the pooled estimate of the five replicates because a global detection function was used which enabled a density estimate to be calculated for each replicate survey) (Tables A2.1, A2.2).

Table A2.1. Replicate specific density estimates and summary results of distance sampling analyses of lamping data for each replicate survey showing the best model chosen for each site replicate.

Site	Replicate	Truncation/Bins	n	Key-Exp	ESW (dMax) (m)	D (SE, 95% CI) (Hares km^{-2})	%Diff.	CV	ChiSq (p)	CvMc (p)	CvMc (p)	K-S (p)
1	1	5%	39	Hn-Cos	29.8 (66)	81.81 (33.89-197.5)	18%	0.36	0.94	0.50	0.70	0.54
	2	18%	33	Hn	30.83 (54)	66.9 (24.4-183.4)		0.37	na	0.50	0.70	0.52
2	1	26%	60	Hn-Cos	54.28 (74)	69.08 (37.11-128.62)	26%	0.25	na	0.90	0.90	0.95
	2	40%	32	Un-Sp	39.37 (55)	50.8 (21.55-119.73)		0.29	na	0.90	0.90	0.95
3*	1	Too few data										
	2	0, 25, 35, …, 85.	31	Hn	0 (82)	42.77 (21.41-85.44)	na	0.29	0.68	na	na	na
4	1	13%	34	Un-Sp	42.43 (58)	50.09 (20.75-120.92)	43%	0.31	na	1.00	1.00	0.89
	2	49%	19	Hn	41.67 (49)	28.5 (11.83-68.65)		0.40	na	1.00	1.00	0.94
5	1	25%	59	Un-Cos	40.21 (58)	91.70 (47.25-177.98)	31%	0.25	na	1.00	1.00	0.97
	2	5%	68	Hn-Cos	67.06 (87)	63.37 (41.24-97.39)		0.19	na	0.90	1.00	0.99
6	1	18%	86	Hn	63.44 (65)	112.9, (69.06-184.79)	26%	0.21	na	0.20	0.30	0.13
	2	10%	85	Un-Cos	46.15 (65)	153.47 (71.36-330.05)		0.32	na	0.60	0.70	0.48
7	1	Too few data	-									
	2	Too few data	-									
8	1	5%	51	Un-Cos	47.98 (78)	73.81 (43.64-124.85)		0.21	na	1.00	1.00	0.90
	2	3%	39	Un-Sp	37.57 (49)	72.09 (41.17-126.24)		0.22	na	1.00	1.00	1.00
	3	32%	30	Un-Sp	35.87	58.08 (35.62-94.68)		0.21	na	1.00	1.00	0.92

					(46)							
	4	5%	62	Hn-Cos	62.27 (97)	69.15 (41.65-114.78)	21%	0.21	na	0.80	0.80	0.69
	5	0, 15, 30, 45, 60, 80	52	Un-Cos	52.18 (77)	69.20 (37.2-128.74)		0.24	0.85	na	na	na
9	1	25%	33	Un-Cos	31.41 (50)	65.66 (36.87-116.91)		0.23	na	0.80	0.90	0.72
	2-5	Too few data										
10	1	25%	23	Hz-Cos	45.81 (55)	31.38 (12.17-80.94)		0.34	na	0.30	0.40	0.47
	2	8%	35	Un-Sp	53.06 (72)	41.22 (18.1-93.91)		0.29	na	1.00	1.00	0.97
	3	Too few data										
	4	10%	30	Un	50 (50)	37.5 (18.71-75.16)		0.22	na	0.70	0.90	0.60
	5	5%	33	Un	66 (66)	31.25 (23.41-41.71)	24%	0.09	na	0.15	0.20	0.15

Truncation/Bins – the level of truncation applied or the distance categories (bins) used, n = number of sightings. Detection Function – Key and Expansion terms used in the detection function; Hn – Halfnormal, Un – Uniform, Hz – Hazard rate, Cos – Cosine, Sp – Simple polynomial, ESW – Effective Strip Width, dMax – Maximum sighting distance from the transect a sighting was recorded, Density – estimated number of hares km^{-2} with 95% confidence limits, %Diff. – Percentage difference between highest and lowest density estimate, CV – coefficient of variation, AIC – Akaike Information Criteria score, ChiSq – p-value from Chi-square goodness of fit test applied to binned data, CvMc\CvMu – p-value associated with the Cramér-von Mises goodness of fit tests with cosine or uniform weighting respectively, K-S – p-value of the Kolmogorov-Smirnov goodness of fit test.

Table A2.2. Site specific density estimates and summary results of distance sampling analyses of lamping data for each study site based on post stratification by replicate using a global detection function. The table shows the best weighted site mean density estimate for each analysis carried out on the same data.

Site	Truncation/Bins	n	Detection Function	ESW (dMax) (m)	Density (95% CL) (Hares km^{-2})	CV	AIC	ChiSq (p)	CvMc (p)	CvMu (p)	K-S (p)
1	5%	75	Hn-Cos	28.89 (68)	81.13 (61.92 - 106.3)	0.14	607.84	na	0.5	0.7	0.53
2	32%	80	Un-Sp	40.29 (55)	62.05 (9.87 - 389.85)	0.21	632.39	na	1	0.9	0.81
3	0, 15, 50, 75	58	Un-Cos	47.87 (75)	42.07 (33.47 - 52.88)	0.11	161.02	0.84	na	na	na
4	5%	66	Un-Cos	53.69 (79)	38.41 (9.79 - 150.75)	0.24	570.79	na	1	1	0.98
5	5%	144	Un-Cos	62.92 (81)	71.52 (54.78 - 93.37)	0.11	1261.35	na	1	1	0.92
6	5%	189	Hz	60.53 (81)	130.1 (110.83 - 152.72)	0.08	1640.49	na	0.4	0.5	0.41
7	no analyses	-	-	-	-	-	-	-	-	-	-
8	5%	260	Un-Cos	54.42 (77)	66.36 (57.22 - 76.96)	0.07	2237.84	na	0.8	0.8	0.63
9	5%	82	Hn	32.81 (40)	31.24 (17.85 - 54.7)	0.24	604.18	na	0.8	0.9	0.59
10	5%	149	Un-Sp	51.19 (69)	36.39 (28.7 - 46.13)	0.10	1244.84	na	0.5	0.6	0.6

Truncation/Bins – the level of truncation applied or the distance categories (bins) used, n = number of sightings. Detection Function – Key and Expansion terms used in the detection function; Hn – Halfnormal, Un – Uniform, Hz – Hazard rate, Cos – Cosine, Sp – Simple polynomial, ESW – Effective Strip Width, dMax – Maximum sighting distance from the transect a sighting was recorded, Density – estimated number of hare km^{-2} with 95% confidence limits, CV –coefficient of variation, AIC – Akaike Information Criteria score, ChiSq – p-value from Chi-square goodness of fit test applied to binned data, CvMc\CvMu – p-value associated with the Cramér-von Mises goodness of fit tests with cosine or uniform weighting respectively, K-S – p-value of the Kolmogorov-Smirnov goodness of fit test.

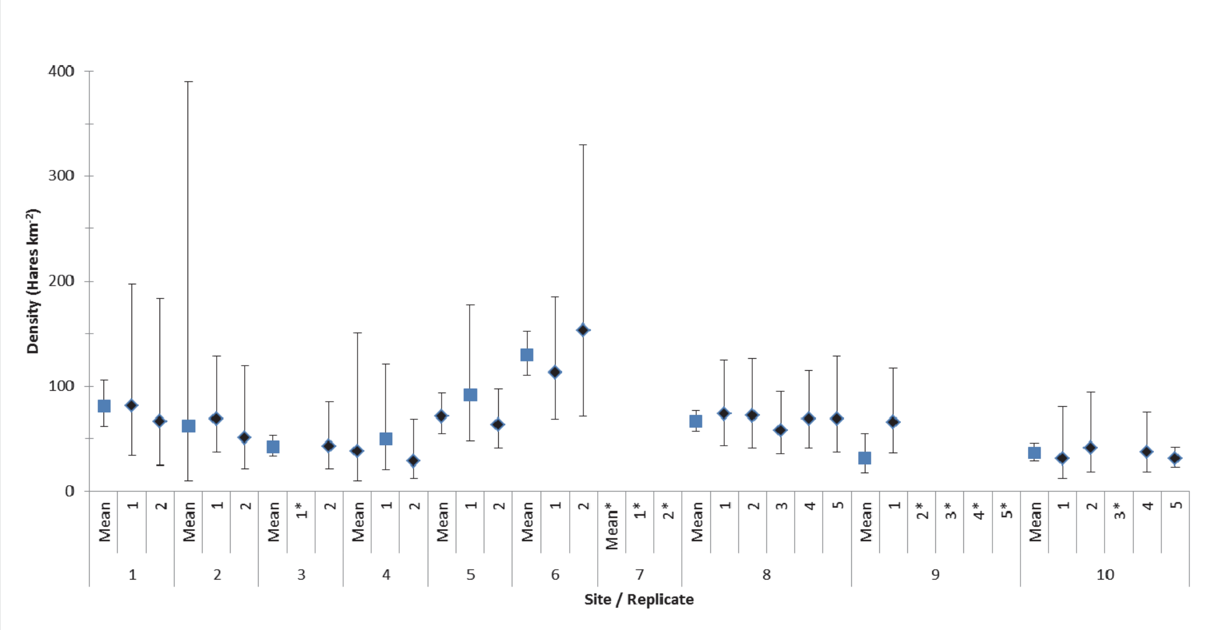


*Figure A2.2. Density estimates from distance sampling analyses for each replicate lamping survey and mean density (hares km^{-2}, with 95% confidence limits). Black diamonds - replicate specific estimates are from a separate analysis of each replicate, blue squares - the mean estimate is from an analysis of replicates for each site pooled and analysed using a global detection function with post-stratification by replicate to get a weighted mean. * - insufficient data, or data were not appropriate for analysis by trying to fit a replicate specific detection function for; site 3-replicate 1, site 7-replicates 1 & 2, site 9-replicates 2-5, and site 10-replicate 3.*

A2.3.2 Comparison with other methods

Comparison of the density estimates from SCR and distance analysis using a global detection function reveals that estimates are similar in four of eight comparisons, differ in two cases, and profoundly differ in two cases where the confidence limits do not overlap (Fig. A2.3). There is only a moderate positive, and not significant, correlation between the density estimates (Table A2.3).

Daylight encounter rates are strongly, positively and in some cases significantly correlated with distance sampling density estimates (Table A2.3, Fig. A2.4). It is unclear why the correlations from first replicates are not significantly correlated when the second replicates, and the means, are so highly significantly correlated (Table A2.3). The correlation between dung standing crop and estimated density is dependent on the replicate survey compared; as with daylight encounter rates, the density estimates from the first replicate are only weakly correlated with standing crop, whereas there is a strong, positive and significant correlation with density estimates from the second replicate, and combined, there is a moderate but not significant positive correlation (Table A2.3, Fig. A2.5). Correlations between density and dung accumulation and dung accumulation rate are all non-significant and negative (Table A2.3). The relationship between measures of dung accumulation and density appear to be strongly influenced by the very high density but low dung accumulation at site 6 (Table A2.3, Fig. A2.5). Removing site 6 from the correlation test for dung accumulation rate to assess its influence, reverses the direction of the correlation in most cases, but the relationships remain non-significant (dung accumulation rate; $r_{(densityreplicate1)} = 0.08$, $t = 0.19$, $p = 0.86$; $r_{(densityreplicate2)} = 0.30$, $t = 0.69$, $p = 0.52$; $r_{(meandensity)} = -0.18$, $t = -0.45$, $p = 0.68$).

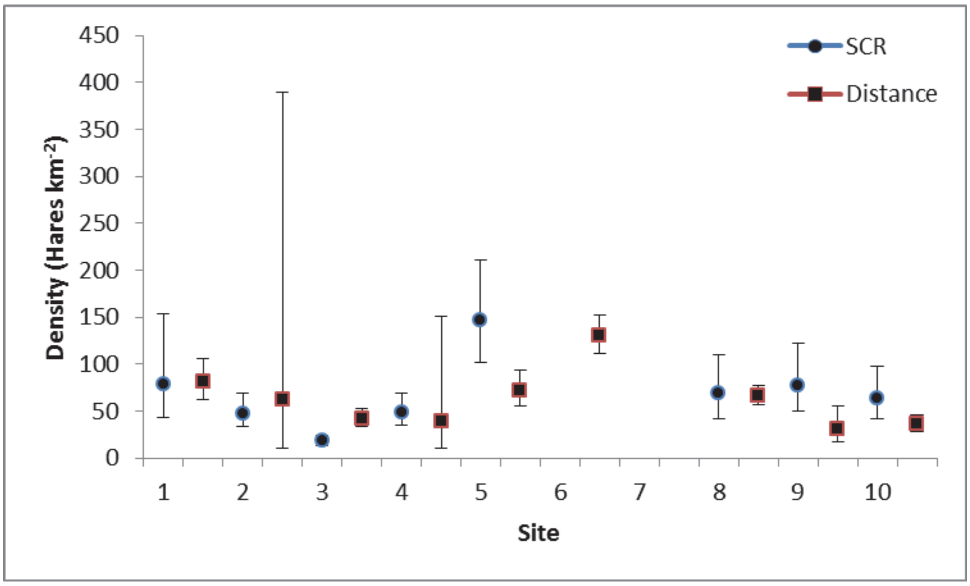


Figure A2.3. Comparison of density estimates from model averaged Spatial Capture-Recapture (SCR) analysis and distance sampling (Distance) analysis of night time lamping surveys. Estimated density shown with 95% confidence limits.

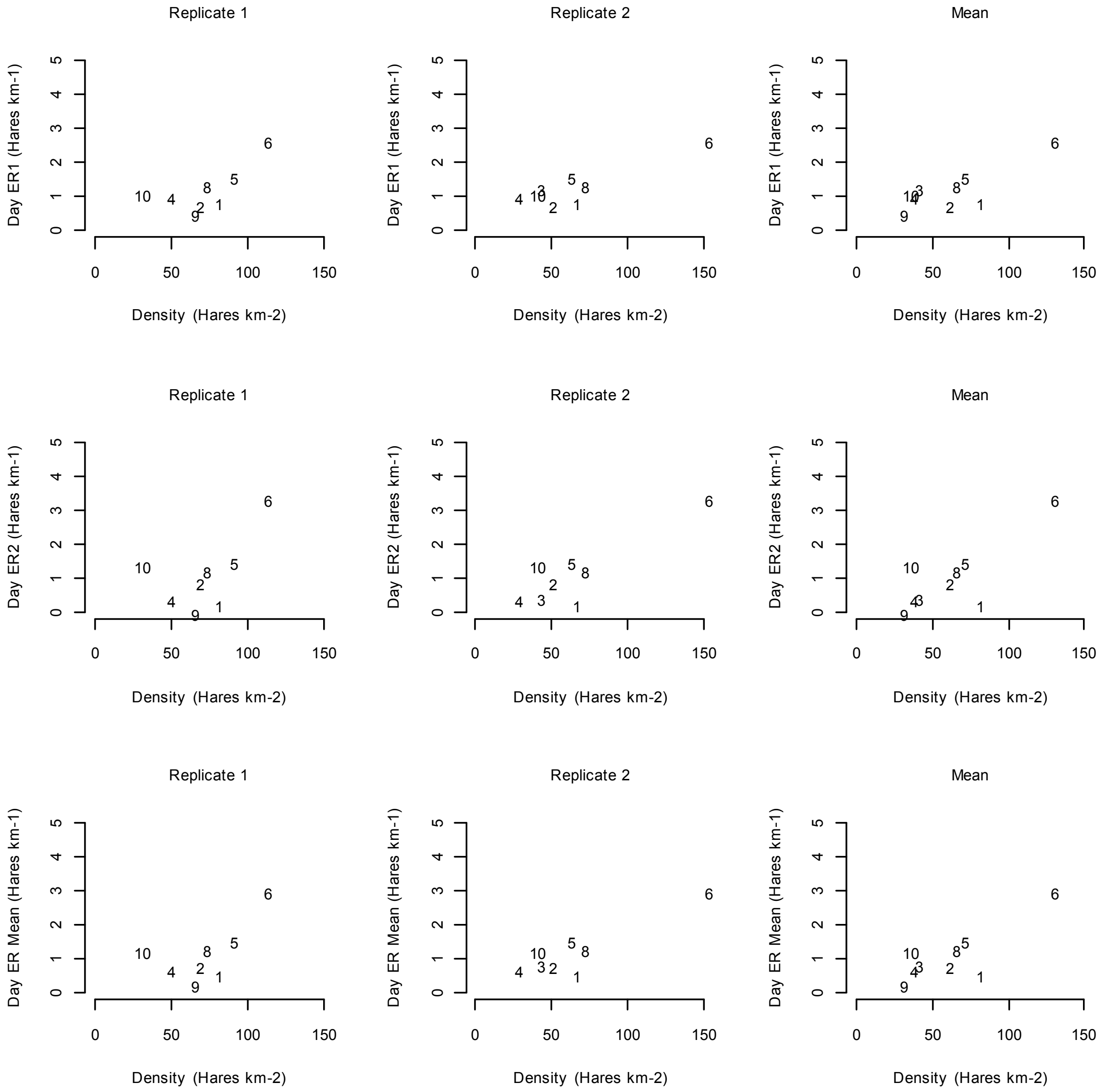


Figure A2.4 Scatter plots showing the relationship between densities estimated by distance sampling night time lamp surveys (x axis) and daylight surveys for each replicate and pooled estimate (y axis).

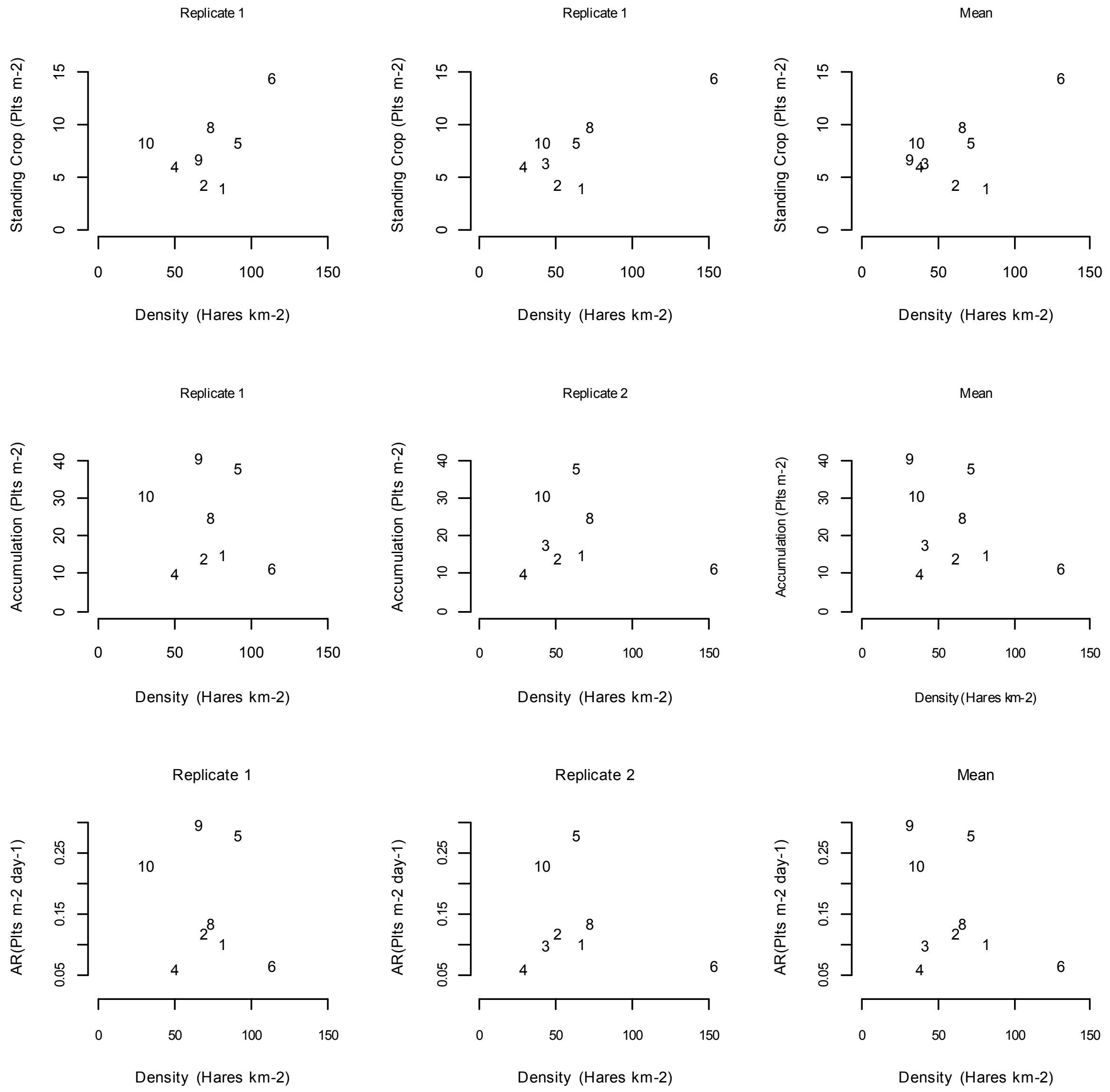


Figure A2.5 Scatter plots showing the relationship between densities estimated by distance sampling night time lamp surveys (x axis) and dung standing crop, dung accumulation, and dung accumulation rate (y axis) for each replicate and pooled estimate. Dung standing crop and dung accumulation are presented as mean number of pellets per m^2, and dung accumulation rate as the mean number of pellets per m^2 per day.

Table A2.3. Pearson correlations between density estimates from distance analysis of lamping data and the other methods.

	Density estimate from distance analysis of lamping surveys		
	Replicate 1	Replicate 2	Pooled*
Estimated Density from SCR	0.64 (t_5 = 1.80, p = 0.12)	0.54 (t_5 = 1.44, p = 0.21)	0.47 (t_6 = 1.29, p = 0.24)
Daylight Encounter Rate			
Replicate 1	0.67 (t_6 = 2.20, p = 0.07)	0.88 (t_6 = 4.49, p = 0.004)	0.80 (t_7 = 3.56, p = 0.01)
Replicate 2	0.56 (t_6 = 1.68, p = 0.14)	0.87 (t_6 = 4.30, p = 0.004)	0.79 (t_7 = 3.40, p = 0.01)
Mean	0.61 (t_6 = 1.90, p = 0.11)	0.89 (t_6 = 4.80, p = 0.003)	0.81 (t_7 = 3.64, p = 0.01)
Thermal Imaging Encounter Rate			
Replicate 1	0.60 (t_4 = 1.50, p = 0.21)	0.32 (t_4 = 0.68, p = 0.53)	0.54 (t_5 = 1.43, p = 0.21)
Replicate 2	0.27 (t_4 = 0.57, p = 0.60)	-0.09 (t_4 = -0.19. p = 0.86)	0.25 (t_5 = 0.58, p = 0.56)
Mean	0.42 (t_4 = 0.94, p = 0.40)	0.06 (t_4 = 0.13, p = 0.90)	0.39 (t_5 = 0.94, p = 0.39)
Dung			
Standing crop	0.48 (t_6 = 1.35, p = 0.22)	0.79 (t_6 = 3.18, p = 0.019)	0.61 (t_7 = 2.06, p = 0.078)
Accumulation	-0.18 (t_6 = -0.44, p = 0.68)	-0.20 (t_6 = -0.49, p = 0.64)	-0.40 (t_7 = -1.14, p = 0.29)
Accumulation rate	-0.21 (t_6 = -0.54, p = 0.61)	-0.23 (t_6 = -0.59, p = 0.58)	-0.40 (t_7 = -1.14, p = 0.29)

The table shows the Pearson correlation coefficient, t-value with degrees of freedom, and estimated p-value. We do not show the correlation between encounter rates from night time lamping surveys and density estimates from night time lamping surveys because they are based on the same survey data. * - the mean density for sites 8-10 based on five replicate surveys.

A2.4 Discussion

Histograms of the perpendicular distance of hare sightings from the transect line often show spikes or heaping suggesting that more hares than expected are being recorded in particular distance categories. Spikes and heaping can occur due to rounding errors of sighting distance or angle measurements. Sighting distances in this study were recorded using a laser range finder and are likely to be accurate. Sighting angles were measured using a sighting compass which may not always be accurate for measuring the angle to a small animal at long range. Measurement of sighting distance and angle can be biased if an observer records the distance or angle after the animal has moved – most likely increasing the sighting distance or angle relative to the direction of travel. However, heaps and spikes can also indicate that animals moved away from the transect line prior to detection. Both measurement error and movement away from the transect line have both been noted in other distance sampling studies of mountain hares (Newey *et al.*, 2003; Shewry *et al.*, 2002). Irrespective of the cause, heaping and spikes in the perpendicular distances can pose problems to model fitting, and can lead to negative bias in density estimates (Buckland *et al.*, 2001). Some histograms also show that sightings of hares fall away rapidly with distance from the transect line. This suggests that either, as already noted above, hares are moving away from the transect line before being detected, or that a high proportion of hares just off the transect line are going undetected. The rapid fall off in the number of sightings is a documented feature of other distance sampling studies of mountain hares (Newey *et al*., 2003; Shewry *et al*., 2002). However, in these studies surveys were carried out in daylight when hares are generally inactive and often concealed sheltering in tall, dense vegetation (Hewson & Hinge, 1990; Thirgood & Hewson, 1987). Shewry *et al.* (2002) and Newey *et al.* (2003) suggest that the rapid fall off in sightings may be due to hares sheltering in tall vegetation just off the transect line going undetected. Here though, surveys were carried out during the night when hares are usually actively feeding and moving around and it seems unlikely that hares would be sheltering. We therefore suggest that the steep decline in number of hares seen with increasing distance is more consistent with hares moving away from the transect line prior to detection.

Histograms of perpendicular distance also appear to vary markedly between sites and replicate surveys within sites, suggesting that site specific features (e.g. vegetation, terrain) or survey (replicate) specific characteristics (e.g. weather, observer), either influence the distribution of hares relative to the transects or the behaviour and sighting distances of hares.

The coefficients of variation associated with each replicate specific density estimate and the variability between replicates vary considerably by site. Estimates for some sites show both low replicate specific variability – indicating that a relatively consistent number of hares were seen along each transect within a replicate survey, and low variability between different replicates – suggesting better repeatability. The coefficients of variation for the site level density estimates from fitting a global detection function are lower as a result of data from all the site replicate surveys. The lower coefficients of variation are reflected in much narrower confidence limits. Whereas the confidence limits from the replicate specific estimates overlap suggesting that there is likely little if any real difference in estimated density between sites, the confidence limits for site specific estimates indicate that hare densities are likely to differ between some sites.

Compared to density estimates from SCR, distance estimates are similar in six of eight cases. The two cases where the confidence limits for the two methods do not overlap are from; site 3 – where the SCR density estimate is low compared to the distance based estimate, and evidence from other survey methods indicate that numbers may be higher than the model averaged densities estimate suggests, and site 5; where the SCR density estimate is higher than the distance based estimate. Carrying out distance sampling surveys can be difficult when hare numbers are high because many hares can be detected at the same time and it is difficult to take accurate measurements, and disturbed hares tend to disturb other hares causing a ‘cascade’ of fleeing hares (Newey *et al*., 2003; Shewry *et al*., 2002). Despite giving similar density estimates in most cases, there is only a moderate positive and non-significant correlation between SCR density and distance sampling based density estimates.

Except for two cases, both from the first distance sampling replicate, daylight encounter rates are strongly, positively and significantly correlated with distance sampling density estimates. Daylight and night time surveys were carried out along the same transects so perhaps the strong and significant correlation is to be expected. However, the correlation between thermal encounter rates, also undertaken along the same transect, and distance sampling density estimates are variably weak or moderate and all non-significant.

There is mixed evidence as to the relationship between dung standing crop and distance based density estimates. Any potential relationship between density and dung accumulation is likely to be obscured by the very high density estimates at site 6, but very low dung accumulation rate.

Distance based density estimates based on pooling replicates, fitting a global detection function and then post-stratifying by replicate to obtain a weighted mean density, appear to provide precise and repeatable density estimates. The significant correlation between density estimates and daylight encounter rate warrants further investigation. However, the low numbers of hares seen during daylight surveys and the high coefficient of variation associated with each replicate, raises concern regarding the suitability of daylight surveys. The absence of significant correlations between encounter rates from night time thermal imaging surveys is intriguing. Similarly the absence of any significant correlation between SCR density estimates is puzzling – maybe some sites are more suited to different methods.

Despite the lack of a clear correlation between distance sampling and SCR density estimates, and some practical issues in applying distance sampling to survey mountain hares on heather moorland, our results show that distance sampling can provide reasonable density estimates. Field surveys and data collection are relatively simple, though distance surveys do require more equipment than a simple count of hare seen, namely a sighting compass and range finder. However, data analysis is more involved, requires specialist (but freely available) software and knowledge.

Table A2.4 Density estimates for each replicate lamping survey.

Density estimates and model summaries of replicate specific distance analyses of lamping surveys. Each replicate (of four transects) is analysed separately; truncation/binning, and detection function are all determined at the replicate level.

Site	Replicate	Truncation/Bins	n	DetFunc.	ESW (dMax) (m)	Density (SE, 95% CL) (Hares km^{-2})	CV	AIC	ChiSq. (p)	CvMc (p)	CvMu (p)	K-S (p)
1	1	5%	39	Un-Cos	33.91 (66)	71.88 (29.71-173.89)	0.36	318.11	na	0.40	0.50	0.54
1	1	5%	39	Un-Sp	34.89 (66)	69.87 (28.8-169.49)	0.35	320.38	na	0.30	0.50	0.54
1	1	5%	39	Hn-Cos	29.80 (66)	81.81 (33.89-197.5)	0.36	318.03	na	0.50	0.70	0.54
1	1	12%	36	Un-Cos	33.90 (55)	66.37 (28.33-155.48)	0.31	281.59	na	0.20	0.30	0.49
1	1	12%	36	Un-Sp	34.01 (55)	66.16 (28.87-151.62)	0.33	283.52	na	0.20	0.30	0.49
1	1	12%	36	Hn-Cos	26.16 (55)	86.02 (37.71-196.25)	0.35	282.13	na	0.50	0.70	0.49
1	2	5%	36	Un-Cos	39.07 (68)	57.59 (20.06-165.29)	0.37	293.07	na	0.30	0.40	0.26
1	2	5%	36	Un-Sp	39.15 (68)	57.47 (20.41-161.82)	0.37	295.01	na	0.30	0.40	0.26
1	2	5%	36	Hn-Cos	28.93 (68)	77.77 (28.64-211.14)	0.40	293.04	na	0.90	1.00	0.80
1	2	15%	35	Un-Cos	36.50 (58)	59.94 (21.93-163.83)	0.35	280.81	na	0.30	0.40	0.32
1	2	15%	35	Un-Sp	42.10 (58)	51.96 (18.79-143.64)	0.35	282.17	na	0.10	0.15	0.13
1	2	15%	35	Hn	34.56 (58)	63.30 (23.7-169.08)	0.36	280.39	na	0.50	0.60	0.44
1	2	18%	33	Un-Cos	31.60 (54)	65.27 (23.3-182.87)	0.36	255.46	na	0.50	0.60	0.48
1	2	18%	33	Un-Sp	31.07 (54)	65.06 (23.75-178.19)	0.37	257.40	na	0.50	0.60	0.48
1	2	18%	33	Hn	30.83 (54)	66.90 (24.4-183.4)	0.37	255.68	na	0.50	0.70	0.52
2	1	5%	61	Un-Cos	50.88 (95)	74.94 (40.45-138.81)	0.21	533.87	na	0.80	0.80	0.62

2	1	5%	61	Un-SP	58.92 (95)	64.71 (35.38-118.34)	0.27	534.90	na	0.80	0.80	0.87
2	1	5%	61	Hn-Cos	51.22 (95)	74.43 (41.24-134.33)	0.23	534.62	na	0.90	0.90	0.75
2	1	5%	61	Hz-Cos	51.71 (95)	73.73 (40.31-134.86)	0.27	536.88	na	0.90	1.00	0.96
2	1	26%	60	Un-Cos	52.60 (74)	71.30 (38.28-132.78)	0.25	514.54	na	0.90	1.00	0.94
2	1	26%	60	Un-SP	56.85 (74)	65.96 (34.96-124.46)	0.23	514.53	na	0.80	0.90	0.89
2	1	26%	60	Hn-Cos	54.28 (74)	69.08 (37.11-128.62)	0.25	514.41	na	0.90	0.90	0.95
2	1	56%	48	Un-Cos	38.78 (55)	77.35 (46.07-129.89)	0.23	382.83	na	0.80	0.80	0.82
2	1	56%	48	Un-SP	41.32 (55)	72.60 (43.47-121.24)	0.20	382.01	na	0.80	0.80	0.78
2	1	56%	48	Hn-Cos	39.94 (55)	75.11 (44.75-126.05)	0.23	382.25	na	0.80	0.80	0.79
2	1	56%	48	Hz-Cos	45.85 (55)	65.42 (39.15-109.34)	0.20	383.11	na	0.70	0.80	0.78
2	2	5%	51	Un-Cos	71.19 (95)	44.78 (19.21-104.37)	0.32	463.31	na	0.70	0.70	0.80
2	2	5%	51	Un-Sp	95.00 (95)	33.55 (13.42-83.91)	0.29	464.50	na	0.05	0.10	0.08
2	2	5%	51	Hn	75.68 (95)	42.12 (17.98-98.64)	0.32	464.19	na	0.50	0.50	0.61
2	2	40%	32	Un-Cos	32.50 (55)	61.54 (27.1-139.76)	0.31	251.61	na	0.60	0.60	0.55
2	2	40%	32	Un-Sp	39.37 (55)	50.80 (21.55-119.73)	0.29	252.20	na	0.90	0.90	0.95
2	2	40%	32	Hn	34.29 (55)	58.33 (25.97-131)	0.33	251.68	na	0.80	0.80	0.76
2	2	40%	32	Hz-Cos	38.42 (55)	52.05 (23.08-117.39)	0.32	252.82	na	1.00	1.00	0.94
3	1	No analysis										
3	2	No analysis										
3	2	0, 25, 35, 45, 55, 65, 75, 85.	31	Un-Cos	50.08 (82)	42.99 (21.39-86.42)	0.27	97.33	0.67	na	na	na
3	2	0, 25, 35, 45, 55, 65, 75, 85.	31	Un-Sp	57.80 (82)	37.25 (18.22-76.13)	0.26	97.96	0.63	na	na	na
3	2	0, 25, 35, 45, 55, 65, 75, 85.	31	Hn	0.00 (82)	42.77 (21.41-85.44)	0.29	97.30	0.68	na	na	na

4	1	5%	43	Un-Cos	61.48 (85)	43.71 (16.19-118.03)	0.37	380.15	na	0.70	0.60	0.68
4	1	5%	43	Un	85.00 (85)	31.62 (10.95-91.27)	0.34	382.07	na	0.03	0.05	0.03
4	1	5%	43	Hn-Cos	52.67 (85)	51.02 (19.48-133.65)	0.42	382.03	na	0.80	0.70	0.80
4	1	13%	34	Un-Cos	38.87 (58)	54.67 (23.27-128.4)	0.33	275.68	na	0.80	0.90	0.76
4	1	13%	34	Un-Sp	42.43 (58)	50.09 (20.75-120.92)	0.31	275.10	na	1.00	1.00	0.89
4	1	13%	34	Hn-Cos	40.22 (58)	52.83 (22.62-123.39)	0.34	275.36	na	0.90	1.00	0.81
4	1	13%	34	Hz	44.68 (58)	47.56 (20.32-111.35)	0.34	276.97	na	1.00	1.00	0.94
4	2	5%	25	Un	70.00 (70)	22.32 (9.1-54.73)	0.29	212.42	na	0.60	0.50	0.50
4	2	5%	25	Hn	55.37 (70)	28.22 (12.43-64.06)	0.35	213.22	na	1.00	1.00	0.97
4	2	5%	25	Hz	59.42 (70)	26.30 (11.6-59.58)	0.34	215.04	na	1.00	1.00	0.99
4	2	49%	19	Un	49.00 (49)	24.23 (9.46-62.12)	0.30	147.89	na	0.90	0.90	0.72
4	2	49%	19	Hn	41.67 (49)	28.5 (11.83-68.65)	0.40	149.46	na	1.00	1.00	0.94
4	2	49%	19	Hz	45.55 (49)	26.07 (11.01-61.7)	0.35	150.07	na	1.00	1.00	0.96
5	1	5%	75	Un-Cos	58.69 (79)	79.87 (49.6-128.61)	0.20	652.28	na	0.60	0.60	0.63
5	1	5%	75	Un-Sp	63.94 (79)	73.31 (45.44-118.27)	0.19	653.48	na	0.30	0.30	0.35
5	1	5%	75	Hn-Cos	47.59 (79)	98.50 (58.83-164.93)	0.24	651.68	na	1.00	1.00	0.95
5	1	25%	59	Un-Cos	40.21 (58)	91.7 (47.25-177.98)	0.25	476.10	na	1.00	1.00	0.97
5	1	25%	59	Un-Sp	40.12 (58)	91.92 (47.71-177.06)	0.27	477.85	na	1.00	1.00	0.97
5	1	25%	59	Hn-Cos	42.37 (58)	87.02 (44.88-168.75)	0.25	477.27	na	0.90	0.90	0.83
5	1	25%	59	Hz-Cos	37.93 (58)	97.23 (47.36-199.61)	0.35	478.19	na	1.00	1.00	1.00
5	2	5%	68	Un-Cos	64.45 (87)	65.95 (42.77-101.67)	0.19	605.46	na	0.80	0.90	0.93
5	2	5%	68	Un-Sp	69.19 (87)	61.42 (40.25-93.73)	0.17	605.33	na	1.00	1.00	1.00
5	2	5%	68	Hn-Cos	67.06 (87)	63.37 (41.24-97.39)	0.19	605.28	na	0.90	1.00	0.99

5	2	5%	68	Hz-Cos	70.78 (87)	60.05 (38.92-92.64)	0.19	606.82	na	1.00	1.00	1.00
5	2	12%	64	Un-Cos	59.81 (80)	66.88 (41.79-107.05)	0.21	559.64	na	0.70	0.80	0.88
5	2	12%	64	Un-Sp	63.29 (80)	63.20 (39.86-100.21)	0.18	559.02	na	0.90	1.00	0.98
5	2	12%	64	Hn-Cos	61.84 (80)	64.68 (40.57-103.11)	0.20	559.14	na	0.80	0.90	0.95
5	2	12%	64	Hz-Cos	66.79 (80)	59.89 (37.77-94.96)	0.19	560.37	na	1.00	1.00	1.00
5	2	16%	61	Un-Cos	70.00 (69)	54.46 (33.39-88.84)	0.15	518.32	na	0.70	0.60	0.75
5	2	16%	61	Un-Sp	70.00 (69)	54.46 (33.39-88.84)	0.15	518.32	na	0.70	0.60	0.75
5	2	16%	61	Hn-Cos	61.67 (69)	61.82 (39.00-97.98)	0.21	519.49	na	1.00	1.00	0.99
5	2	16%	61	Hz-Cos	64.02 (69)	59.55 (37.99-93.34)	0.19	521.22	na	1.00	1.00	1.00
6	1	5%	100	Un-Cos	67.73 (87)	123.05 (79.64-190.1)	0.22	889.53	na	0.10	0.20	0.05
6	1	5%	100	Un-Sp	67.16 (87)	124.08 (88.81-173.37)	0.14	888.09	na	0.15	0.20	0.05
6	1	5%	100	Hn-Cos	66.58 (87)	125.16 (88.52-176.97)	0.16	888.82	na	0.15	0.20	0.05
6	1	5%	100	Hz-Cos	70.10 (87)	118.88 (84.63-167)	0.15	888.60	na	0.20	0.30	0.08
6	1	18%	86	Un	65.00 (65)	110.26 (64.49-188.5)	0.17	717.99	na	0.20	0.30	0.19
6	1	18%	86	Hn	63.44 (65)	112.97 (69.06-184.79)	0.21	719.95	na	0.20	0.30	0.13
6	1	18%	86	Hz	63.44 (65)	112.97 (69.06-184.79)	0.21	719.95	na	0.20	0.30	0.13
6	1	0, 20, 30, 40, 50, 60, 70	92	Un	70.00 (70)	109.52 (70.63-169.84)	0.14	331.71	0.05	na	na	na
6	1	0, 20, 30, 40, 50, 60, 70	92	Hn-Cos	67.26 (70)	113.99 (75.76-171.52)	0.18	333.59	0.03	na	na	na
6	1	0, 20, 30, 40, 50, 60, 70	92	Hz-Cos	65.86 (70)	116.41 (77.72-174.35)	0.17	335.09	0.02	na	na	na
6	1	0, 25, 35, 45, 55, 65	86	Un	65.00 (65)	110.26 (64.49-188.5)	0.17	268.81	0.09	na	na	na
6	1	0, 25, 35, 45, 55, 65	86	Hn-Cos	58.79 (65)	121.91 (74.65-199.1)	0.20	270.89	0.06	na	na	na

6	1	0, 25, 35, 45, 55, 65	86	Hz-Cos	58.79 (65)	121.91 (74.65-199.1)	0.20	270.89	0.06	na	na	na
6	1	0, 30, 40, 50, 60, 70	92	Un	70.00 (70)	109.52 (70.63-169.84)	0.14	276.75	0.12	na	na	na
6	1	0, 30, 40, 50, 60, 70	92	Hn-Cos	65.58 (70)	116.90 (77.72-175.82)	0.18	278.45	0.07	na	na	na
6	1	0, 30, 40, 50, 60, 70	92	Hz-Cos	65.80 (70)	116.51 (77.74-174.61)	0.17	280.13	0.04	na	na	na
6	2	5%	90	Un-Cos	45.94 (75)	163.25 (79.12-336.86)	0.25	760.34	na	0.50	0.60	0.39
6	2	5%	90	Un-Sp	45.70 (75)	164.10 (80.94-332.69)	0.26	761.53	na	0.50	0.60	0.38
6	2	5%	90	Hn-Cos	47.65 (75)	157.40 (77.05-321.55)	0.26	761.63	na	0.60	0.70	0.47
6	2	5%	90	Hz-Cos	49.97 (75)	150.09 (74.45-302.58)	0.27	762.12	na	0.70	0.80	0.58
6	2	10%	85	Un-Cos	46.15 (65)	153.47 (71.36-330.05)	0.32	698.77	na	0.60	0.70	0.48
6	2	10%	85	Un-Sp	47.05 (65)	149.11 (65.51-339.39)	0.27	699.12	na	0.60	0.70	0.57
6	2	10%	85	Hn-Cos	43.28 (65)	163.67 (74.27-360.7)	0.29	698.53	na	0.40	0.60	0.35
6	2	10%	85	Hz-Cos	48.33 (65)	146.56 (66.03-325.27)	0.28	699.32	na	0.70	0.80	0.60
7	1	No analysis										
7	2	No analysis										
8	1	5%	51	Un-Cos	47.98 (78)	73.81 (43.64-124.85)	0.21	433.74	na	1.00	1.00	0.90
8	1	5%	51	Un-Sp	54.43 (78)	65.07 (37.97-111.51)	0.20	434.58	na	0.70	0.70	0.45
8	1	5%	51	Hn-Cos	49.12 (78)	72.11 (42.62-121.98)	0.22	433.82	na	1.00	1.00	0.85
8	1	5%	51	Hz-Cos	49.52 (78)	71.52 (41.01-124.72)	0.26	435.17	na	1.00	1.00	0.97
8	1	22%	42	Un-Cos	34.11 (52)	85.52 (51.35-142.42)	0.22	331.74	na	0.40	0.50	0.62
8	1	22%	42	Un-Sp	37.82 (52)	77.11 (46.00-129.29)	0.19	330.54	na	0.80	0.90	0.86
8	1	22%	42	Hn-Cos	35.71 (52)	81.67 (48.5-137.53)	0.23	331.26	na	0.60	0.70	0.74

8	1	22%	42	Hz-Cos	40.93 (52)	71.26 (42.87-118.47)	0.21	331.48	na	1.00	1.00	0.96
8	2	5%	53	Un	65.00 (65)	56.62 (29.25-109.62)	0.21	442.49	na	0.40	0.50	0.63
8	2	5%	53	Hn	60.76 (65)	60.58 (33.15-110.69)	0.25	444.29	na	0.70	0.70	0.85
8	2	30%	39	Un-Cos	34.75 (49)	77.94 (44.3-137.14)	0.25	303.61	na	1.00	1.00	0.96
8	2	30%	39	Un-Sp	37.57 (49)	72.09 (41.17-126.24)	0.22	303.23	na	1.00	1.00	1.00
8	2	30%	39	Hn-Cos	35.98 (49)	75.28 (42.76-132.53)	0.25	303.30	na	1.00	1.00	0.98
8	2	30%	39	Hz-Cos	40.27 (49)	67.25 (38.45-117.63)	0.24	305.24	na	1.00	1.00	0.99
8	3	5%	43	Un	70.00 (70)	42.66 (25.86-70.38)	0.16	365.37	na	0.30	0.40	0.35
8	3	5%	43	Hn-Cos	61.86 (70)	48.28 (29.95-77.81)	0.22	366.82	na	0.60	0.70	0.72
8	3	32%	30	Un-Cos	34.16 (46)	60.98 (36.6-101.61)	0.23	233.34	na	1.00	1.00	1.00
8	3	32%	30	Un-Sp	35.87 (46)	58.08 (35.62-94.68)	0.21	232.92	na	1.00	1.00	0.92
8	3	32%	30	Hn-Cos	34.80 (46)	59.87 (35.68-100.45)	0.24	233.10	na	1.00	1.00	0.98
8	4	5%	62	Un-Cos	60.77 (97)	70.85 (42.63-117.75)	0.20	557.81	na	0.80	0.90	0.79
8	4	5%	62	Un-Sp	69.73 (97)	61.74 (36.52-104.39)	0.19	558.78	na	0.40	0.50	0.25
8	4	5%	62	Hn-Cos	62.27 (97)	69.15 (41.65-114.78)	0.21	557.78	na	0.80	0.80	0.69
8	4	5%	62	Hz-Cos	56.20 (97)	76.61 (41.41-141.73)	0.30	559.61	na	0.80	0.90	0.83
8	4	28%	47	Un-Cos	41.06 (59)	79.48 (34.92-180.92)	0.31	381.90	na	0.60	0.70	0.62
8	4	28%	47	Un-Sp	45.49 (59)	71.75 (30.85-166.9)	0.30	382.23	na	0.70	0.80	0.69
8	4	28%	47	Hn-Cos	42.78 (59)	76.30 (33.60-173.26)	0.32	381.97	na	0.70	0.80	0.71
8	4	28%	47	Hz-Cos	44.75 (59)	72.94 (32.43-164.08)	0.33	383.39	na	0.80	0.90	0.79
8	5	5%	52	Un-Cos	57.10 (77)	63.24 (34.09-117.33)	0.25	449.58	na	0.40	0.50	0.50
8	5	5%	52	Un-Sp	59.35 (77)	60.84 (32.75-113.04)	0.26	450.33	na	0.50	0.60	0.57
8	5	5%	52	Hn-Cos	54.50 (77)	66.26 (35.71-122.93)	0.26	449.78	na	0.30	0.40	0.41

8	5	5%	52	Hz-Cos	59.57 (77)	60.62 (32.31-113.72)	0.23	449.61	na	0.50	0.50	0.59
8	5	0, 15, 30, 45, 60, 80	52	Un-Cos	52.18 (77)	69.20 (37.20-128.74)	0.24	164.78	0.85	na	na	na
8	5	0, 15, 30, 45, 60, 80	52	Un-Sp	57.60 (77)	62.69 (33.42-117.61)	0.23	165.16	0.77	na	na	na
8	5	0, 15, 30, 45, 60, 80	52	Hn-Cos	53.83 (77)	67.09 (36.15-124.50)	0.25	164.86	0.83	na	na	na
8	5	0, 15, 30, 45, 60, 80	52	Hz-Cos	56.78 (77)	63.60 (34.15-118.43)	0.27	166.50	0.77	na	na	na
9	1	5%	41	Un-Cos	46.24 (76)	55.42 (38.48-79.81)	0.16	347.28	na	0.50	0.60	0.68
9	1	5%	41	Un-Sp	46.48 (76)	55.13 (37.64-80.76)	0.18	349.33	na	0.50	0.60	0.68
9	1	5%	41	Hn-Cos	34.86 (76)	73.51 (45.95-117.59)	0.23	347.25	na	0.90	1.00	0.83
9	1	5%	41	Hz-Cos	36.13 (76)	70.93 (36.28-138.67)	0.34	347.95	na	0.90	1.00	0.83
9	1	25%	33	Un-Cos	31.41 (50)	65.66 (36.87-116.91)	0.23	253.45	na	0.80	0.90	0.72
9	1	25%	33	Un-Sp	31.19 (50)	66.13 (36.29-120.5)	0.27	255.12	na	0.90	0.90	0.72
9	1	25%	33	Hn-Cos	32.51 (50)	63.45 (35.60-113.08)	0.24	254.45	na	0.80	0.80	0.72
9	1	25%	33	Hz-Cos	29.11 (50)	70.86 (34.28-146.47)	0.36	255.78	na	0.80	0.90	0.72
9	1	31%	30	Un-Cos	25.25 (42)	74.24 (45.38-121.46)	0.21	219.87	na	0.70	0.80	0.66
9	1	31%	30	Un-Sp	30.33 (42)	61.82 (37.83-101.03)	0.18	220.76	na	0.70	0.80	0.66
9	1	31%	30	Hn-Cos	26.29 (42)	71.31 (42.81-118.78)	0.23	220.01	na	0.80	0.90	0.66
9	1	31%	30	Hz-Cos	29.96 (42)	62.58 (37.79-103.64)	0.23	221.87	na	0.80	0.90	0.66
9	2	No analysis										
9	3	No analysis										
9	4	No analysis										
9	5	No analysis										

10	1	25%	23	Un	55.00 (55)	26.14 (9.66-70.70)	0.32	184.34	na	0.30	0.30	0.43
10	1	25%	23	Un-Sp	40.71 (55)	35.31 (13.92-89.60)	0.43	182.89	na	0.10	0.15	0.17
10	1	25%	23	Hn-Cos	41.66 (55)	34.51 (13.67-87.13)	0.42	184.75	na	0.20	0.30	0.32
10	1	25%	23	Hz-Cos	45.81 (55)	31.38 (12.17-80.94)	0.34	181.55	na	0.30	0.40	0.47
10	1	0, 25, 35, 45, 55	23	Un-Cos	35.21 (55)	40.82 (16.41-101.57)	0.36	56.03	0.20	na	na	na
10	1	0, 25, 35, 45, 55	23	Un-Sp	34.50 (55)	41.67 (16.05-108.19)	0.33	53.06	0.13	na	na	na
10	1	0, 25, 35, 45, 55	23	Hn-Cos	36.86 (55)	39.00 (15.75-96.55)	0.38	55.19	0.26	na	na	na
10	1	0, 25, 35, 45, 55	23	Hz-Cos	42.89 (55)	33.52 (12.98-86.52)	0.34	51.95	0.39	na	na	na
10	2	8%	35	Un-Cos	47.05 (72)	46.49 (21.05-102.69)	0.32	297.09	na	0.70	0.80	0.78
10	2	8%	35	Un-Sp	53.06 (72)	41.22 (18.1-93.91)	0.29	296.80	na	1.00	1.00	0.97
10	2	8%	35	Hn-Cos	49.46 (72)	44.23 (20.07-97.48)	0.32	296.81	na	0.90	0.90	0.91
10	2	8%	35	Hz-Cos	56.36 (72)	38.81 (17.34-86.89)	0.30	297.80	na	1.00	1.00	1.00
10	3	No analysis										
10	4	10%	30	Un	50.00 (50)	37.5 (18.71-75.16)	0.22	234.72	na	0.70	0.90	0.60
10	4	10%	30	Hn	48.37 (50)	38.76 (19.93-75.40)	0.31	236.70	na	0.70	0.80	0.56
10	4	10%	30	Hz	48.44 (50)	38.71 (20.16-74.32)	0.24	238.51	na	0.70	0.80	0.56
10	4	0, 15, 25, 35, 45, 55	31	Un	55.00 (51)	35.23 (18.01-68.90)	0.21	99.21	0.50	na	na	na
10	4	0, 15, 25, 35, 45, 55	31	Hn-Cos	44.55 (51)	43.49 (23.2-81.53)	0.28	100.06	0.42	na	na	na
10	4	0, 25, 35, 45	31	Un-Cos	55.00 (45)	35.23 (18.01-68.90)	0.21	78.21	0.38	na	na	na
10	4	0, 25, 35, 45	31	Un-Sp	55.00 (45)	35.23 (18.01-68.90)	0.21	78.21	0.38	na	na	na
10	4	0, 25, 35, 45	31	Hn-Cos	43.79 (45)	44.25 (23.6-82.97)	0.28	78.87	0.30	na	na	na
10	5	5%	33	Un	66.00 (66)	31.25 (23.41-41.71)	0.09	276.52	na	0.15	0.20	0.15

10	5	5%	33	Hn	65.99 (66)	31.25 (18.95-51.53)	0.25	278.52	na	0.15	0.20	0.15
10	5	5%	33	Hz	60.93 (66)	33.85 (24.95-45.92)	0.14	279.72	na	0.10	0.10	0.09

Truncation/Bins – the level of truncation applied or the distance categories (bins) used, n = number of sightings. DetFunc. – Key and Expansion terms used in the detection function; Hn – Halfnormal, Un – Uniform, Hz – Hazard rate, Cos – Cosine, Sp – Simple polynomial, ESW – Effective Strip Width, dMax – Maximum sighting distance from the transect a sighting was recorded, Density – estimated number of hare km^{-2} *with standard error and 95% confidence limits, CV – coefficient of variation, AIC – Akaike Information Criteria score, ChiSq – p-value from Chi-square goodness of fit test applied to binned data, CvMc\CvMu – p-value associated with the Cramér-von Mises goodness of fit tests with cosine or uniform weighting respectively, K-S – p-value of the Kolmogorov-Smirnov goodness of fit test. na – no appropriate entry.*

Table A2.5 Site specific density estimates using a replicate specific detection function.

Density estimates and model summaries from distance analysis of replicate lamping surveys using a replicate specific detection function and post-stratification by replicate to obtain site specific weighted mean density.

Site	Replicate	Truncation/Bins	n	DetFunc.	ESW (dMax) (m)	Density (SE, 95% CL) (Hares km^{-2})	CV	AIC	ChiSq. (p)	CvMc (p)	CvMu (p)	K-S (p)
1	1	5%	39	Hn-Cos	29.44 (68)	82.78 (34.27 - 199.99)	0.36	318.69	na	0.54	0.7	0.6
1	2	5%	36	Hn-Cos	28.93 (68)	77.77 (28.64 - 211.14)	0.4	293.04	na	0.9	1	0.8
1	Pooled	5%	75	na	na	80.28 (53.96 - 119.43)	0.03	611.73	na	na	na	na
1	1	7%	38	Hn-Cos	28.13 (62)	84.43 (35.54 - 35.54)	0.36	307.20	na	0.5	0.7	0.53
1	2	7%	35	Hn	34.56 (62)	63.3 (23.70 - 169.08)	0.36	280.39	na	0.5	0.6	0.44
1	Pooled	7%	73	na	na	73.87 (12.11 - 450.53)	0.14	587.59	na	na	na	na
1	1	13%	36	Un-Cos	33.9 (54)	66.37 (28.33 - 155.48)	0.31	281.59	na	0.2	0.3	0.49
1	2	13%	33	Un-Cos	31.6 (54)	65.27 (23.30 - 182.87)	0.36	255.46	na	0.5	0.6	0.48
1	Pooled	13%	69	na	na	65.82 (59.20 - 73.19)	0.01	537.05	na	na	na	na
2	1	5%	61	Un-Cos	50.88 (95)	74.94 (40.32 - 138.81)	0.21	533.87	na	0.8	0.8	0.62
2	2	5%	51	Un-Cos	71.19 (95)	44.78 (19.21 - 104.37)	0.32	463.31	na	0.7	0.7	0.8
2	Pooled	5%	112	na	na	59.86 (2.56 – 1,399.7)	0.25	997.18	na	na	na	na
2	1	21%	60	Hn	54.28 (74)	69.09 (37.11 - 128.62)	0.25	514.41	na	0.9	0.9	0.95
2	2	21%	46	Un	75.00 (74)	38.33 (15.75 - 93.32)	0.29	397.21	na	0.2	0.3	0.29
2	Pooled	21%	106	na	na	53.71 (1.52 – 1,900.1)	0.29	911.62	na	na	na	na
2	1	32%	48	Un-Cos	41.33 (55)	72.6 (43.47 - 121.24)	0.2	382.01	na	0.8	0.8	0.78
2	2	32%	32	Un-Cos	32.50 (55)	61.54 (27.1 - 139.76)	0.31	251.61	na	0.6	0.6	0.55
2	Pooled	32%	80	na	na	67.07 (23.59 - 190.72)	0.25	633.62	na	na	na	na

3	1	too few data	0	-	-	-	-	-	-	-	-	-
3	2	too few data	0	-	-	-	-	-	-	-	-	-
3	Pooled	too few data	0	-	-	-	-	-	-	-	-	-
4	1	5%	40	Un-Cos	53.70 (79)	46.56 (17.36 - 124.87)	0.36	346.24	na	1	0.8	0.86
4	2	5%	26	Un-Sp	56.59 (73)	28.72 (11.67 - 70.68)	0.34	225.87	na	1	1	0.92
4	Pooled	5%	66	na	na	37.64 (1.93 - 734.06)	0.24	572.11	na	na	na	na
4	1	19%	34	Un-Sp	42.43 (57)	50.09 (20.75 - 120.92)	0.31	275.10	na	1	1	0.89
4	2	19%	23	Un	60.00 (60)	23.96 (11.3 - 50.79)	0.24	188.34	na	0.9	0.8	0.76
4	Pooled	19%	57	na	na	37.02 (0.48 - 2875.90)	0.35	463.44	na	na	na	na
4	1	23%	32	Un	50.00 (50)	40.00 (15.24 - 105.02)	0.31	250.37	na	1	0.9	0.81
4	2	23%	22	U	50.00 (50)	27.50 (13.92 - 54.33)	0.22	172.13	na	0	0	0
4	Pooled	23%	54	na	0.00 (50)	33.75 (3.27 - 347.99)	0.19	422.50	na	na	na	na
5	1	5%	77	Hn-Cos	49.73 (80)	96.77 (56.41 - 166.01)	0.22	673.47	na	1	1	0.93
5	2	5%	67	Un	na	51.70 (32.67 - 32.67)	0.15	588.86	na	0.4	0.3	0.37
5	Pooled	5%	144	na	na	74.23 (1.71 – 3,229.36)	0.3	1262.32	na	na	na	na
5	1	13%	71	Un-Cos	55.05 (69)	80.61 (46.27 - 140.47)	0.23	600.53	na	0.6	0.5	0.63
5	2	13%	61	Un	69.00 (69)	55.25 (33.87 - 90.13)	0.15	516.56	na	0.8	0.8	0.86
5	Pooled	13%	132	na	na	67.93 (6.47 - 713.34)	0.19	1117.09	na	na	na	na
5	1	25%	59	Un-Cos	40.29 (58)	91.52 (47.22 - 177.4)	0.26	474.91	na	1	1	0.96
5	2	25%	54	Un	58.00 (57)	58.19 (34.33 - 98.65)	0.17	438.53	na	1	1	0.99
5	Pooled	25%	113	na	na	74.86 (4.58 – 1,224.69)	0.22	913.43	na	na	na	na
6	1	no analyses	0	-	-	-	-	-	-	-	-	-

6	2	no analyses	0	-	-	-	-	-	-	-	-	-
6	Pooled	no analyses	0	-	-	-	-	-	-	-	-	-
7	1	no analyses	0	-	-	-	-	-	-	-	-	-
7	2	no analyses	0	-	-	-	-	-	-	-	-	-
7	Pooled	no analyses	0	-	-	-	-	-	-	-	-	-
8	1	5%	52	Un-Cos	49.70 (77)	72.66 (41.25 - 127.98)	0.22	445.25	na	1	1	0.86
8	2	5%	54	Un-Sp	56.31 (77)	66.59 (36.83 - 120.41)	0.22	464.80	na	1	0.9	0.8
8	3	5%	44	Un-Sp	60.58 (77)	50.44 (30.82 - 82.53)	0.21	381.55	na	0.7	0.8	0.72
8	4	5%	58	Un-Cos	57.67 (77)	69.85 (41.36 - 117.94)	0.22	502.25	na	0.8	0.8	0.66
8	5	5%	52	Hn	57.10 (77)	63.24 (34.09 - 117.33)	0.25	449.58	na	0.4	0.5	0.5
8	Pooled	5%	260	na	na	64.55 (54.68 - 76.22)	0.06	2243.43	na	na	na	na
8	1	29%	41	Un-Sp	36.75 (50)	77.48 (46.62 - 128.79)	0.2	318.04	na	0.8	0.9	0.84
8	2	29%	39	Un-Sp	37.57 (50)	72.09 (41.17 - 126.24)	0.22	303.23	na	1	1	1
8	3	29%	30	Un-Sp	35.87 (50)	58.08 (35.63 - 94.68)	0.21	232.92	na	1	1	0.92
8	4	29%	42	Un-Sp	38.13 (50)	76.49 (34.01 - 172.01)	0.30	326.91	na	0.6	0.7	0.63
8	5	29%	42	Un	50.00 (50)	58.33 (29.06 - 117.11)	0.22	328.61	na	0.4	0.5	0.53
8	Pooled	29%	194	na	0.00 (50)	68.49 (57.55 - 81.51)	0.06	1509.71	na	na	na	na
9	1	no analyses	0	-	-	-	-	-	-	-	-	-
9	2	no analyses	0	-	-	-	-	-	-	-	-	-
9	3	no analyses	0	-	-	-	-	-	-	-	-	-
9	4	no analyses	0	-	-	-	-	-	-	-	-	-
9	5	no analyses	0	-	-	-	-	-	-	-	-	-
9	Pooled	no analyses	0	-	-	-	-	-	-	-	-	-
10	1	no analyses	0	-	-	-	-	-	-	-	-	-
10	2	no analyses	0	-	-	-	-	-	-	-	-	-

10	3	no analyses	0	-	-	-	-	-	-	-	-	-
10	4	no analyses	0	-	-	-	-	-	-	-	-	-
10	5	no analyses	0	-	-	-	-	-	-	-	-	-
10	Pooled	no analyses data	0	-	-	-	-	-	-	-	-	-

Truncation/Bins – the level of truncation applied or the distance categories (bins) used, n = number of sightings, DetFunc. – Key and Expansion terms used in the detection function; Hn – Halfnormal, Un – Uniform, Hz – Hazard rate, Cos – Cosine, Sp – Simple polynomial, ESW – Effective Strip Width, dMax – Maximum sighting distance from the transect a sighting was recorded, Density – estimated number of hares km^{-2} with standard error and 95% confidence limits, CV – coefficient of variation, AIC – Akaike Information Criteria score, ChiSq – p-value from Chi-square goodness of fit test applied to binned data, CvMc\CvMu – p-value associated with the Cramér-von Mises goodness of fit tests with cosine or uniform weighting respectively, K-S – p-value of the Kolmogorov-Smirnov goodness of fit test. na – no appropriate entry. '-' – no analysis.

Table A2.6 *Site specific density estimates using a global detection function.*

Site specific density estimates and model summaries of distance analysis of lamping surveys with a common/global detection function using post-stratification by replicate to obtain site specific weighted mean density.

Site	Replicate	Truncation/Bins	n	DetFunc.	ESW (dMax) (m)	Density (SE, 95% CL) (hares km^{-2})	CV	AIC	ChiSq. (p)	CvMc (p)	CvMu (p)	K-S (p)
1	1	5%	39	Hn-Cos	na	84.37 (34.26 - 207.81)	0.34	207.81	na	na	na	na
1	2	5%	36	Hn-Cos	na	77.88 (27.85 - 217.79)	0.38	217.79	na	na	na	na
1	Pooled	5%	75	Hn-Cos	28.89 (68)	81.13 (61.92 - 106.3)	0.14	607.84	na	0.5	0.7	0.53
1	1	7%	38	Hn-Cos	na	85.01 (35.22 - 205.16)	0.33	205.16	na	na	na	na
1	2	7%	35	Hn-Cos	na	78.30 (29.48 - 207.97)	0.36	207.97	na	na	na	na
1	Pooled	7%	73	Hn-Cos	27.94 (62)	81.65 (61.87 - 107.77)	0.14	584.37	na	0.5	0.7	0.51
1	1	13%	36	Un-Cos	na	81.20 (35.07 - 188.01)	0.32	188.01	na	na	na	na
1	2	13%	33	Un-Cos	na	74.43 (27.1 - 204.44)	0.37	204.44	na	na	na	na
1	Pooled	13%	69	Un-Cos	27.71 (54)	77.81 (59.44 - 101.87)	0.13	534.50	na	0.4	0.5	0.48
2	1	5%	61	na	na	64.20 (34.92 - 118.03)	0.22	118.03	na	na	na	na
2	2	5%	51	na	na	53.68 (22.11 - 130.33)	0.30	130.33	na	na	na	na
2	Pooled	5%	112	Un-Cos	59.38 (95)	58.94 (39.96 - 86.94)	0.11	1000.90	na	0.9	0.9	0.69
2	1	21%	60	na	na	66.18 (35.26 - 124.24)	0.24	124.24	na	na	na	na
2	2	21%	45	na	na	49.64 (21.75 - 113.27)	0.30	113.27	na	na	na	na
2	Pooled	21%	105	Un-Cos	56.66 (74)	57.91 (28.84 - 116.29)	0.17	900.04	0	0.8	0.7	0.67
2	1	32%	48	na	na	74.45 (43.84 - 126.44)	0.19	126.44	na	na	na	na
2	2	32%	32	na	na	49.64 (20.9 - 117.87)	0.29	117.87	na	na	na	na
2	Pooled	32%	80	Un-Sp	40.29 (55)	62.05 (9.87 - 389.85)	0.21	632.39	na	1	0.9	0.81

3	1	0, 15, 50, 75	28	Un-Cos	na	40.62 (13.26 - 124.44)	0.4	124.44	na	na	na	na
3	2	0, 15, 50, 75	30	Un-Cos	na	43.52 (22.25 - 85.14)	0.26	85.136	na	na	na	na
3	Pooled	0, 15, 50, 75	58	Un-Cos	47.87 (75)	42.07 (33.47 - 52.88)	0.11	161.02	0.84	na	na	na
4	1	5%	40	na	na	46.56 (17.11 - 126.73)	0.35	126.73	na	na	na	na
4	2	5%	26	na	na	30.27 (12.11 - 75.65)	0.33	75.65	na	na	na	na
4	Pooled	5%	66	Un-Cos	53.69 (79)	38.41 (9.79 - 150.75)	0.24	570.79	na	1	1	0.98
4	1	19%	34	na	na	46.28 (19.10 - 112.15)	0.31	112.15	na	na	na	na
4	2	19%	23	na	na	31.31 (15.47 - 63.37)	0.26	63.37	na	na	na	na
4	Pooled	19%	57	Un-Sp	45.92 (60)	38.80 (10.84 - 138.81)	0.21	464.04	na	1	1	0.95
4	1	23%	32	na	na	40.00 (15.24 - 105.02)	0.31	105.02	na	na	na	na
4	2	23%	22	na	na	27.50 (13.92 - 54.33)	0.22	54.37	na	na	na	na
4	Pooled	23%	54	Un	50.00 (50)	33.75 (3.27 - 347.99)	0.19	422.50	na	0.8	0.7	0.8
5	1	5%	77	na	na	76.49 (45.75 - 127.86)	0.2	127.86	na	na	na	na
5	2	5%	67	na	na	66.55 (43.76 - 101.22)	0.17	101.22	na	na	na	na
5	Pooled	5%	144	Un-Cos	62.92 (81)	71.52 (54.78 - 93.37)	0.11	1261.35	na	1	1	0.92
5	1	13%	71	na	na	77.04 (44.05 - 134.75)	0.22	134.75	na	na	na	na
5	2	13%	61	na	na	66.19 (42.34 - 103.46)	0.18	103.46	na	na	na	na
5	Pooled	13%	132	Un-Cos	57.60 (69)	71.61 (53.49 - 95.88)	0.12	1117.05	na	1	0.9	0.91
5	1	25%	59	na	na	78.98 (40.61 - 153.6)	0.25	153.60	na	na	na	na
5	2	25%	54	na	na	72.28 (44.65 - 117.03)	0.20	117.03	na	na	na	na
5	Pooled	25%	113	Un-Cos	46.69 (58)	75.63 (60.1 - 95.17)	0.11	916.32	na	1	1	0.98
6	1	5%	97	Hz	na	133.54 (91.67 - 194.54)	0.15	194.54	na	na	na	na

6	2	5%	92	Hz	na	126.66 (61.01 - 262.95)	0.26	262.95	na	na	na	na
6	Pooled	5%	189	Hz	60.53 (81)	130.10 (110.83 - 152.72)	0.08	1640.49	na	0.4	0.5	0.41
6	1	14%	86	Hz	na	130.82 (79.33 - 215.73)	0.18	215.73	na	na	na	na
6	2	14%	85	Hz	na	129.30 (57.43 - 291.09)	0.28	291.09	na	na	na	na
6	Pooled	14%	171	Hz	54.78 (65)	130.06 (113.14 - 149.51)	0.07	1421.76	na	0.3	0.4	0.35
6	1	0, 20, 30, …, 80	96	Hz	na	133.86 (90.41 - 198.18)	0.15	198.18	na	na	na	na
6	2	0, 20, 30, …,80	92	Hz	na	128.28 (61.63 - 267.01)	0.25	267.01	na	na	na	na
6	Pooled	0, 20, 30, …, 80	188	Hz	59.77 (79)	131.07 (112.91 - 152.14)	0.08	681.6	0.21	na	na	na
6	1	0, 25, 35, …, 85	99	Hz	na	137.08 (98.16 - 191.43)	0.13	191.43	na	na	na	na
6	2	0, 25, 35, …, 85	92	Hz	na	127.39 (61.04 - 265.86)	0.25	265.86	na	na	na	na
6	Pooled	0, 25, 35, …, 85	191	Hz	60.18 (85)	132.23 (112.44 - 155.50)	0.08	645.38	0.76	na	na	na
6	1	0, 30, 40, …, 70	92	Hz	na	135.39 (90.44 - 202.69)	0.16	202.69	na	na	na	na
6	2	0, 30, 40, …, 70	86	Hz	na	126.56 (55.56 - 288.31)	0.28	288.31	na	na	na	na
6	Pooled	0, 30, 40, …, 70	178	Hz	56.63 (70)	130.98 (111.58 - 153.75)	0.08	486.89	0.06	na	na	na
7	1	too few data	0	-	-	-	-	-	-	-	-	-
7	2	too few data	0	-	-	-	-	-	-	-	-	-
7	Pooled	too few data	0	-	-	-	-	-	-	-	-	-
8	1	5%	52	Un-Cos	na	66.36 (36.73 - 119.91)	0.20	119.91	na	na	na	na
8	2	5%	54	Un-Cos	na	68.91 (37.47 - 126.75)	0.21	126.75	na	na	na	na
8	3	5%	44	Un-Cos	na	56.15 (33.75 - 93.43)	0.18	93.425	na	na	na	na
8	4	5%	58	Un-Cos	na	74.02 (42.92 - 127.64)	0.19	127.64	na	na	na	na
8	5	5%	52	Un-Cos	na	66.36 (34.57 - 127.38)	0.22	127.38	na	na	na	na
8	Pooled	5%	260	Un-Cos	54.42 (77)	66.36 (57.22 - 76.96)	0.07	2237.84	na	0.8	0.8	0.63

8	1	29%	41	Hz	na	68.19 (40.4 - 115.09)	0.19	115.09	na	na	na	na
8	2	29%	39	Hz	na	64.86 (36.27 - 115.99)	0.02	115.99	na	na	na	na
8	3	29%	30	Hz	na	49.89 (30.27 - 82.23)	0.18	82.23	na	na	na	na
8	4	29%	42	Hz	na	69.85 (30.17 - 161.71)	0.28	161.71	na	na	na	na
8	5	29%	42	Hz	na	69.85 (35.75 - 136.46)	0.23	136.46	na	na	na	na
8	Pooled	29%	194	Hz	41.76 (50)	64.53 (54.01 - 77.10)	0.08	1507.72	na	0.7	0.8	0.54
9	1	8%	43	Hz	na	35.22 (24.30 - 51.06)	0.13	51.06	na	na	na	na
9	2	8%	30	Hz	na	24.57 (19.04 - 31.71)	0.09	31.71	na	na	na	na
9	3	8%	14	Hz	na	11.47 (7.41 - 17.76)	0.15	17.76	na	na	na	na
9	4	8%	22	Hz	na	18.02 (10.54 - 30.82)	0.17	30.82	na	na	na	na
9	5	8%	45	Hz	na	36.86 (29.49 - 46.07)	0.08	46.068	na	na	na	na
9	Pooled	8%	154	Hz	76.3 (90)	25.23 (14.88 - 42.76)	0.20	1368.15	na	0.4	0.6	0.47
9	1	5%	29	Hn	na	55.25 (35.44 - 86.12)	0.02	86.12	na	na	na	na
9	2	5%	12	Hn	na	22.86 (15.32 - 34.12)	0.18	34.12	na	na	na	na
9	3	5%	9	Hn	na	17.15 (9.28 - 31.69)	0.24	31.69	na	na	na	na
9	4	5%	15	Hn	na	28.58 (12.82 - 63.7)	0.30	63.70	na	na	na	na
9	5	5%	17	Hn	na	32.39 (18.15 - 57.81)	0.23	57.81	na	na	na	na
9	Pooled	5%	82	Hn	32.81 (40)	31.24 (17.85 - 54.7)	0.24	604.18	na	0.8	0.9	0.59
9	1	0, 5, 10, …, 90	43	Un-Sp	na	42.19 (29.26 - 60.82)	0.13	60.82	na	na	na	na
9	2	0, 5, 10, …, 90	30	Un-Sp	na	29.43 (22.89 - 37.85)	0.10	37.85	na	na	na	na
9	3	0, 5, 10, …, 90	14	Un-Sp	na	13.74 (8.92 - 21.15)	0.15	21.15	na	na	na	na
9	4	0, 5, 10, …, 90	22	Un-Sp	na	21.58 (12.69 - 36.71)	0.18	36.71	na	na	na	na
9	5	0, 5, 10, …, 90	45	Un-Sp	na	44.15 (35.40 - 55.06)	0.09	55.06	na	na	na	na
9	Pooled	0, 5, 10, …, 90	154	Un-Sp	63.71 (90)	30.22 (17.86 - 51.12)	0.20	871.15	0.79	na	na	na
9	1	0, 5, 10, …, 40	29	Hn	na	57.57 (36.94 - 89.71)	0.19	89.71	na	na	na	na
9	2	0, 5, 10, …, 40	12	Hn	na	23.82 (15.97 - 35.53)	0.18	35.53	na	na	na	na

9	3	0, 5, 10, …, 40	9	Hn	na	17.87 (9.66 - 33.03)	0.24	33.031	na	na	na	na
9	4	0, 5, 10, …, 40	15	Hn	na	29.78 (13.35 - 66.41)	0.30	66.41	na	na	na	na
9	5	0, 5, 10, …, 40	17	Hn	na	33.75 (18.90 - 60.24)	0.23	60.24	na	na	na	na
9	Pooled	0, 5, 10, …, 40	82	Hn	31.49 (40)	32.55 (18.60 - 56.99)	0.24	338.97	1.00	na	na	na
10	1	0, 25, 35, …65	27	Un-Sp	na	35.15 (15.28 - 80.84)	0.28	80.84	na	na	na	na
10	2	0, 25, 35, …65	34	Un-Sp	na	44.26 (18.72 - 104.68)	0.29	104.68	na	na	na	na
10	3	0, 25, 35, …65	20	Un-Sp	na	26.04 (10.60 - 63.93)	0.30	63.93	na	na	na	na
10	4	0, 25, 35, …65	33	Un-Sp	na	42.96 (25.46 - 72.5)	0.18	72. 50	na	na	na	na
10	5	0, 25, 35, …65	32	Un-Sp	na	41.66 (29.83 - 58.17)	0.13	58.17	na	na	na	na
10	Pooled	0, 25, 35, …65	146	Un-Sp	48.01 (64)	38.01 (29.82 - 48.46)	0.10	411.03	0.15	na	na	na
10	1	5%	29	Un-Sp	na	35.41 (14.87 - 84.29)	0.29	84.293	na	na	na	na
10	2	5%	34	Un-Sp	na	41.51 (17.52 - 98.36)	0.29	98.36	na	na	na	na
10	3	5%	20	Un-Sp	na	24.42 (9.93 - 60.07)	0.30	60.07	na	na	na	na
10	4	5%	33	Un-Sp	na	40.29 (23.83 - 68.13)	0.18	68.13	na	na	na	na
10	5	5%	33	Un-Sp	na	40.29 (30.94 - 52.48)	0.11	52.48	na	na	na	na
10	Pooled	5%	149	Un-Sp	51.19 (69)	36.39 (28.70 - 46.13)	0.10	1244.84	na	0.5	0.6	0.6

Truncation/Bins – the level of truncation applied or the distance categories (bins) used, n = number of sightings, DetFunc. – Key and Expansion terms used in the detection function; Hn – Halfnormal, Un – Uniform, Hz – Hazard rate, Cos – Cosine, Sp – Simple polynomial, ESW – Effective Strip Width, dMax – Maximum sighting distance from the transect a sighting was recorded, Density – estimated number of hares km^{-2} with standard error and 95% confidence limits, CV – coefficient of variation, AIC – Akaike Information Criteria score, ChiSq – p-value from Chi-square goodness of fit test applied to binned data, CvMc\CvMu – p-value associated with the Cramér-von Mises goodness of fit tests with cosine or uniform weighting respectively, K-S – p-value of the Kolmogorov-Smirnov goodness of fit test. na – no appropriate entry.

ANNEX 3: SUGGESTED METHODS FOR SURVEY

A3.1 Background

Managers need to have reliable information about the status of wildlife populations and their response to management actions to make informed decisions. A key tool in successful management of wildlife for a range of goals is the estimation of population size (abundance or density). Changes in population size can tell us about species' responses to land and wildlife management, and help to set and implement thresholds for conservation or control action.

The research project presented in this report has tested how to estimate mountain hare population densities, comparing practical field methods with results from a live-trapping programme. The study found that the density indices provided by; a) counting mountain hares at night by walking transects using a spotlight, and b) measurement of dung accumulation over a longer period (four to six months) during the winter were both positively, but not statistically significantly, correlated with the number of hares estimated by trapping in autumn on the same ground. At this stage these indices cannot be accurately converted to hare density (hares per km²), but may provide trends for individual sites which can be compared between years.

These guidance notes are based on our current best understanding and the personal experience of the authors. The advice and guidelines may change as further research is carried out and so it is important that practitioners refer to the latest information. Here we provide some 'rules of thumb' to aid in setting up and carrying out surveys for mountain hares that should be suitable for a wide range of conditions/circumstances, but will not be suitable for all occasions. Practitioners are advised to seek expert advice if there is any doubt.

A3.2 Mountain hare lamping surveys

Aim – to provide a post-breeding density index, which can be used to assist with management decisions within the same winter period, and provide data for longer term monitoring.

<u>Overall approach</u>
The number of hares seen when walking across moorland with a lamp is related to the actual number of hares in the population; more hares seen in the lamp means more hares in the population. However, the relationship between the number of hares seen and the actual number present is not statistically significant. In open terrain and habitats, however, counts along transects of known length can be used to provide an '*encounter rate*' which represents a reasonable index of hare density. The '*encounter rate*' is simply the number of hares encountered by walking along transects at night with a spotlight divided by the total length of the transects. Much the same approach would apply to carrying out surveys using thermal imaging equipment.

1. **Identify area to be surveyed:**
   a. It should include areas where hares are known (or suspected) to feed at night, but should also represent the variation in habitats within the site (i.e. areas dominated by heather, grass or rushes), including less used areas.
   b. If hares are known to move between areas, e.g. in response to changes in wind direction then the survey area should include both areas (or two survey areas may be needed).

2. **Mark the area on a map and identify transect lines:**
   a. For a 4 km square (400 ha) area we recommend a minimum of four transects, each of around 2 km in length (minimum 8 km of transects), however more transects will give better, more precise, results, especially where habitats are variable.
   b. Transects should run uphill-downhill and should be between 250 and 500 m apart.
   c. The start of each transect should be approached without disturbing the area to be surveyed.
   d. Transects should **not** follow tracks, walls, rivers, or habitat edges such as forest or woodland boundaries as this will bias the number of hares seen.
   e. The same survey area / transects should be used in future years.

3. **Survey timing:**
   a. We recommend surveys are undertaken late September to November.
   b. Surveys should start 1-2 hours after sunset when hares are most active.
   c. Surveys should only be carried out only when visibility is good (avoiding fog / rain / strong winds).
   d. Multiple transects can be covered in one night (2 km length of transect should take about 1.5 hours, plus the time needed to walk between transects).
   e. The area should not be disturbed for 1-2 days prior to the survey.

4. **Equipment needed:**
   a. Map / GPS to aid navigation and define the start / end locations.
   b. Hand held spot light and battery (e.g. 50 watt, Tracer Sport Light 140). A lamp / torch with the same beam size / brightness should be used for all surveys to avoid variation in the number of hares detected.
   c. Notebook.

5. **Survey Method:**
   a. To aid comparison between years, we recommend recording survey dates, times, observer and the start / end location of each transect.
   b. Walk at a steady pace along each transect moving the lamp beam side to side, in a 180^{o} arc recording all hares seen.
   c. When disturbed, hares often move uphill, so bare this in mind to avoid double counting.
   d. Each transect can be surveyed again on a different night to obtain a better estimate of precision, though adding new transects is usually better.
   e. Calculate the encounter rate as total number of hares / length of transect:

Transect id (length)	Date of Survey	Number of hares seen
1 (2 km)	29.9.2017	10
	05.10.2017	8
2 (2.2 km)	30.9.2017	5
	07.10.2017	6
3 (1.8 km)	29.9.2017	13
	05.10.2017	9
4 (2 km)	30.9.2017	2
	07.10.2017	4

In this example each of four transects was surveyed twice on different nights, giving a total transect length of 16 km, during which a total number of 57 hares were seen giving an encounter rate of 3.6 hares / km.

Further explanation of the spot-lamping survey method:

Transects should be marked on a map for planning and reference, with the start and end points of each transect logged in a GPS for navigation in the field. Only a very small proportion of the hares are seen and recorded during night time surveys beyond 100 m distance from the transect line. We advise parallel transects 250-500 m apart. The number and length of transects will depend on the size of the area to be surveyed. However, more short transects is usually better than fewer long transects, provided transect length is sufficient to encompass the underlying variation in environmental conditions and distribution of hares. We recommend that monitoring of mountain hares should take place over an area no smaller than 4 km^2 (400 ha). Within this area we recommend a minimum of four transects of not less than 8 km in total length. The precision of estimates will be improved if there are more transects, or by repeat surveys of the same transects. However, survey effort has not been formally investigated and these figures should be treated as guidelines only. Each transect should accurately reflect the overall proportion and types of habitat in the survey area. The reason for this is that the accuracy of estimation of the number of hares encountered is determined by the variability in the number of hares encountered between transects. For example, many areas occupied by mountain hares in the Scottish uplands are likely to include hills. The distribution of hares is known to be affected by elevation, therefore transects should be orientated up and down the hill, and not along the contour. Similarly, where there are patches of contrasting habitats that are suitable or unsuitable for mountain hares, transects should, as far as is practicable, pass through both. Ideally, transect placement should be random relative to the animals, so it is advisable to avoid placing transects along tracks/roads, streams, fence lines, or along habitat or landscape boundaries. A systematic regular layout of parallel transects is probably easiest to implement.

Mountain hares are usually most active just after sunset, and surveys should aim to start within one to two hours of sunset. When disturbed mountain hares will usually run uphill, and where possible we advise walking transects downhill. If hares are known, or suspected of moving from one area to another, as appears to be the case in winter, e.g. from one side of a hill to the other, or between areas seasonally, in response to weather, then transects should cover both areas. Alternatively the two areas may be surveyed separately but concurrently (i.e. over a short enough period of time that the same conditions apply). Multiple transects can be surveyed in one night though we recommend that surveying adjacent transects in the same night is avoided. Rather, we suggest walking alternate, rather than adjacent transects, in any one night. With other transects completed on a different date, as soon after the first transect was completed as is practical.

It is important to standardise surveys as much as possible in terms of weather conditions, equipment, and time of year. We recommend that night surveys are best conducted in the early winter in clear, dry weather avoiding very windy conditions, rain, snow and fog. October-November is likely to be the most practical in terms of weather, access to survey areas, and surveys will provide an index of the post-breeding population. All surveys in this study were undertaken on foot and so we cannot offer any recommendation on the use of vehicles for surveys.

This methodology has been tested on upland areas of heather moorland in Perthshire, Strathspey and Deeside and not in other areas or habitats. The limits of application of this methodology are determined by restrictions to the visibility of hares afforded by the habitat.

A3.3 Mountain hare dung accumulation rate surveys

Aim – to provide an over winter abundance index.

Overall approach

The rate at which mountain hare dung accumulates on cleared sites is associated with the number of hares; more hares, the faster the accumulation of dung. Dung accumulation rate is therefore useful as an index of mountain hare density when access to an area may be difficult, or disturbance undesirable. The method involves clearing dung from circular plots marked with a single peg, and revisiting them after a period of four to six months to count the pellets deposited during the known time period. Implementing the method from autumn, over winter, reduces the effect of decomposition of pellets, and spans a period of relative population stability in comparison to the summer period of rapid pellet decomposition and population growth.

1. **Identify area to be surveyed:**
    a. We recommend the area surveyed should cover at least 4km^2 (400 ha), as for the lamping survey method. We further recommend that the survey area includes the entire area that will be used by hares over the winter period; if hares are known to move between areas in response to prolonged bad weather then the survey area should include both areas (or two survey areas may be needed).
    b. It should include areas where hares are known to feed at night, but should also represent the variation in habitats within the site (i.e. areas dominated by heather, grass or rushes), including areas used to a lesser degree by hares, due to short term or seasonal variation in weather conditions.

2. **Mark the area on a map and identify dung plot locations:**
    a. We recommend a minimum of 50 dung plots per 1 km^2 (100 ha) of the survey area (a total of 200 plots in a 4 km^2 area).
    b. These should be randomly located.
    c. The same survey area should be used in future years, although plot locations can vary.

3. **Survey timing:**
    a. The plots should be cleared in October to November (but before snow lies on the study area).
    b. A second visit should be undertaken in early spring (after snow melt, but before the weather warms up) in March to April, allowing four to six months between visits.

4. **Equipment needed:**
    a. Map / GPS to aid navigation.
    b. Wooden stakes (20 cm length) to mark plot centre, and mallet.
    c. Bamboo cane (1 m) to aid finding each plot.
    d. Plot measuring: String marked with 69 cm (radius of circular plot) and 79 cm (radius plus 10 cm buffer) with loop to place over the end of the cane and wooden stake.
    e. Notebook.

5. **Survey Method:**
    a. Record survey dates and GPS location of each plot (if available we recommend using the ‘averaging function’ of the GPS to obtain a more accurate location record); about eight plots can be done in an hour depending on distance between plots on the amount of dung that needs to be counted, so multiple observers or multiple days may be needed.

b. Mark the centre of the plot with a wooden stake (hammered into the ground leaving approximately 5 cm above ground) and a long bamboo cane to aid relocation of the plot.
c. Remove all animal dung from the plot area, a radius of 69 cm (equivalent to a 1.5 m^2 plot) and a buffer area of a further 10 cm extension to the radius.
d. Re-visit each plot recording the number of mountain hare pellets within the plot area (radius 69 cm).
e. Calculate the total area of plots (radius of 69 cm equates to area of 1.5 m^2, so 200 plots = 300 m^2).
f. Calculate the median (middle) date for the first and second visit and therefore the number of days between visits. (If plots are set up and then revisited over more than one week it is best to use the actual date that the plot was revisited, rather than a median which is acceptable if plots were initially set up over less than a week, and then cleared over less than a week).
g. For each plot calculate the pellets collected on the second visit, divide this by 1.5, and then divide by the number of days between initially setting up the dung plot and when it was revisited to calculate the mean of these rates of accumulation.

Further explanation of the dung accumulation method:

We suggest that plots should be left for four to six months between initial set up and clearance. Plots should be set up in October-November, but can be set up later if there is no snow. Plots should be revisited as soon as any snow had been cleared. Any plots which were burnt or the habitat or terrain altered prior to the second visit will need to be discarded. This method has not been tested at other times of the year and so cannot currently be recommended for outside this period. This dung accumulation provides an index of the over winter population, with the values being calculate in March / April.

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ISBN: 978-1-78391-510-1

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