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Dispersal and compensatory population dynamics in a harvested mammal

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This thesis is submitted in fulfilment of the requirements for the degree of
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College of Medical, Veterinary and Life Sciences

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Abstract

Populations of wild birds and mammals are often harvested for sport, subsistence or commerce. Sustainable exploitation is an important aspect of environmental management and is critical to human wellbeing. However, our inability to sustainably harvest even well studied populations is often due to poor demographic data and a lack of understanding of critical biological processes. A key component of sustainable harvesting is the density-dependant feedback between vital rates (births, deaths, immigration and emigration) and population density, as this mechanism provides populations with the capacity to compensate for harvest mortality.

The aims of this thesis are to investigate density-dependence, compensation and sustainable harvesting in a traditional Scottish quarry species, the mountain hare, *Lepus timidus scoticus*, using a combination of replicated field experiments, cross-sectional studies and modelling. The mountain hare has been traditionally harvested for centuries and continues to be an important source of revenue for some land owners. Over the past decade the motive for killing hares has switched from predominantly sport shooting, to culling to reduce ticks and the tick-borne disease Louping-ill virus (LIV). Louping-ill virus causes high mortality, and can suppress harvest, in economically important red grouse, *Lagopus lagopus scoticus*. Sustainable management of the mountain hare is further complicated by cyclic, or unstable, population dynamics shown throughout their circumpolar distribution.

The thesis begins with a review of the evidence that culling mountain hares can lead to a reduction in ticks and LIV prevalence, resulting in increased red grouse harvest. The empirical studies follow with the aim of providing evidence for compensatory survival and dispersal, and density-dependent reproduction. Two field study approaches were adopted; the first was a live-capture and radio-telemetry study which compared birth dates, survival probabilities and dispersal distances and rates of different age and sex classes between two populations under different harvesting regimes (harvested and non-harvested). The second empirical study used a cross-sectional design whereby population density of ten independent populations were estimated using Distance sampling, which preceded hare harvesting. Tissue samples of killed hares were collected, enabling the effects of population density on female fecundity and juvenile recruitment to be assessed. Finally, an age-structure, female-only matrix population model was parameterised using data from the empirical studies. Sustainable harvest rates were determined as the maximum harvest that produced a positive population growth rate and an extinction probability of less than 5%. By manipulating age-specific harvest and initial population size, the effects of age-biased harvest and changing population size on population viability could be investigated.

Results of the cross-sectional study revealed evidence for negative density-dependent juvenile recruitment. However, this finding was not translated into compensatory survival in either juveniles or adults, although birth date of leverets was significantly later in the harvested population. Overall, dispersal distances and rates were low. Dispersal distance was greater in the harvested population, although when distance was scaled to account for differences in observation time, to give a dispersal rate, no difference was found. Projections from the matrix model suggest that 40% annual harvest rate is sustainable, although extinction probability

increases with decreasing population size and as harvesting becomes increasingly yearling biased.

Overall, no evidence for compensatory survival or dispersal was found, although density-dependent juvenile recruitment was identified and may be important in population persistence under exploitation. Survival and timing of breeding may be influenced by behavioural and physiological effects of harvesting, or environmental variation, which may have implications for unstable dynamics of mountain hare. I identify and discuss key areas for future research aimed at increasing our understanding of the effects of harvesting on mountain hare population dynamics and demography.

In conclusion, we found little evidence that culling mountain hares can increase red grouse harvest, and therefore, cannot justify culling mountain hares for tick and LIV control. The low dispersal rates and distances, combined with limited evidence for compensatory mechanisms, imply that local blanket culls may succeed in reducing hare numbers with unknown implications for mountain hare population persistence and the wider biodiversity of the Scottish uplands.

Author's Declaration

I declare that the work recorded in this thesis is entirely my own, except where otherwise stated, and that it is also of my own composition. Much of the material included in this thesis has been produced in co-authorship with my supervisors and others, and my personal contribution to each chapter is as follows:

Chapter 2: Published as Harrison, A., Newey, S., Gilbert, L., Haydon, D. T. & Thirgood, S. (2010) Culling wildlife hosts to control disease: mountain hares, red grouse and louping ill virus. *Journal of Applied Ecology* **47**, 926-930. Initial concept developed by ST, SN, LG and AH. Manuscript drafted by AH. Final draft enhanced by ST, SN, LG and DH.

Chapter 3: In preparation for submission as Harrison, A., Newey, S., Thirgood, S., and Haydon, D. T. The effects of harvesting on natal dispersal and the cost for survival in Scottish mountain hare. Data collection by AH. Initial concept developed by AH, SN, ST and DH. Analysis conducted and manuscript drafted by AH. Draft improved by SN and DH.

Chapter 4: In preparation for submission as Harrison, A., Haydon, D. T., Ramsay, S., Thirgood, S and Newey, S. The effects of harvesting on survival and timing of breeding in Scottish mountain hare. Data collection by AH and SR. Initial concept developed by AH, SN and ST. Analysis conducted and manuscript drafted by AH. Draft improved by SN, DH and SR.

Chapter 5: In preparation for submission as Harrison, A, Fowler, P., Ramsay, S., Haydon, D. T., McNeilly, A., Thirgood, S and Newey, S. The effects of population density on the breeding performance of mountain hare in Scotland. Data collection by AH and SR. Initial concept

developed by ST, SN, AH and SR. Analysis conducted and manuscript drafted by AH. Draft improved by SN, DH, PF and SR.

Chapter 6: In preparation for submission as Harrison, A., Newey, S., Thirgood, S., and Haydon, D. T. Sustainable harvest rates of Scottish mountain hare populations. Initial concept developed by AH and DH. Modelling conducted and manuscript drafted by AH. Draft improved by DH and SN.

I further declare that no part of this work has been submitted as part of any other degree.

Annabel Harrison

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March 2011

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Chapter 1

General introduction

1.1. Metapopulation dynamics and dispersal

Populations that dwell in a fragmented landscape are often described as a metapopulation. A metapopulation is defined as a number of subpopulations, with largely independent population dynamics, existing in patches of suitable habitat embedded within a matrix of unoccupied, less suitable habitat which are linked by migration of individuals between them (Hanski 1999).

The metapopulation concept is related to the equilibrium theory of island biogeography, as colonisation and extinction are fundamental processes in both (Begon, Harper & Townsend 1996; Hanski & Gilpin 1991). Mainland-island metapopulations consist of a large 'mainland' population, with smaller 'island' subpopulations linked by dispersal. Causes of extinction of these small island populations include variation in environmental and/or demographic stochasticity (Hanski & Gilpin 1991). However, isolated patches of habitat can vary in quality leading to the source-sink metapopulation concept (Pulliam 1988). At equilibrium, high quality 'source' populations have birth rates exceeding death rates, and more individuals emigrating than immigrating. In contrast, low quality 'sink' populations are characterised by negative population growth rates, where deaths outweigh births, and the number of immigrants exceed the number of emigrants. Sink populations would not be viable in the absence of immigration from source populations (Pulliam 1988). However, identifying sources and sinks can be difficult, with simple comparisons of demographic rates between populations being insufficient. Patches of habitat sufficient to maintain a population may be adjacent to optimal habitat, and therefore, increased immigration from the optimal into the sufficient patch would increase the sufficient population to carrying capacity. If density-dependent processes are present, population growth rate will decrease. This would result in deaths and immigration

exceeding births and emigration making the sufficient patch appear to be a sink population, when it is, in fact, capable of sustaining a population in absence of immigration. These patches have been termed pseudo-sinks (Watkinson & Sutherland 1995).

Metapopulation theory is used to explain dynamics of animal populations, particularly in the conservation of species under pressure from habitat fragmentation and loss (Hanski 1999). However, metapopulation structure can be difficult to identify, and the use of the concept is not always supported by empirical information satisfying the definition of a metapopulation (Hanski 1999; Olivier, van Aarde & Ferreira 2009). This definition outlines that a) habitat patches support local breeding populations with vacant but suitable habitats available for colonisation; b) extinction and colonisation takes place; c) dynamics of subpopulations are asynchronous; and d) dispersal must occur between subpopulations (Hanski 1999).

Dispersal plays an important role in colonisation, population dispersion, dynamics, and ultimately, viability (Gaines & McClenaghan 1980; Greenwood 1980; Hanski 1999; Johnson & Gaines 1990; Sutherland et al. 2000). Although not within the scope of this thesis, dispersal has an important role in maintaining genetic diversity within and between populations by increasing gene flow and reducing homozygosity. This results in an increase in fitness via lower inbreeding depression (Aars & Ims 2000; Hamill, Doyle & Duke 2007).

Dispersal has three main components 1) emigration (leaving), 2) transience (travelling across unfamiliar territory) and 3) immigration (arriving or settling). The costs of dispersal over philopatry are often seen as increased mortality of dispersers (Christian 1970; Greenwood & Harvey 1982; Van Vuran & Armitage 1994), although some studies have failed to find evidence to support this hypothesis (Gillis & Krebs 2000; Lin & Batzli 2004; Van Vuran &

Armitage 1994; Wauters, Matthysen & Dhont 1994). Dispersal can also effect survival and reproduction post dispersal, which can impact lifetime fitness and consequently population dynamics and demography (Ward & Weatherhead 2005). However, no empirical estimate of cost can exist as it is impossible to measure the change in survival or reproductive post emigration compared to the situation had the animal remained in the natal site. In addition, if a juvenile does not breed due to rejection by relatives, then the evolutionary cost of philopatry and not breeding would equal that of dispersing and dying (Wolff 1994).

Dispersal can happen at any stage of an individual's life although there are key times when it would be more beneficial to lifetime fitness. Although breeding dispersal (the subsequent movement of adults after their first reproduction) can be important for lifetime reproductive success (Clutton-Brock 1988), it does not occur as frequently in species, or between populations and individuals, compared to natal dispersal (dispersal from the birth site to that of first reproduction or potential reproduction (Greenwood 1980)) which is often the only long distance movement an individual will make (Dahl & Willebrand 2005).

The cost-benefit ratio of natal dispersal is often sex-dependent and may lead to sex bias in dispersal rate and distance (Sutherland et al. 2000). Male-biased dispersal is common among mammals with polygamous mating systems and is regarded as an inbreeding avoidance strategy (Clutton-Brock 1989; Wolff 1993). For some species where sex-biased dispersal is common (white footed mice *Peromyscus leucopus*; white-tailed deer *Odocoileus virginianus*; yellow bellied marmots *Marmota flaviventris*), removal of parents of the same sex as the offspring resulted in philopatry of offspring where dispersal is normally observed. These results provide evidence that offspring are not forced to disperse but do so 'voluntarily' to

avoid incestuous mating (Wolff 1993). In some species dispersal of both males and females occur. Under these circumstances dispersal distance and rate of dispersal may differ between the sexes (Greenwood 1980; Waser 1985). The distance an individual disperses is dependent, in part, on the importance of different resources to the lifetime fitness of that individual. Males may seek reproductive opportunities, whereas females require space or natal sites to successfully rear their young (Emlen & Oring 1977; Wolff 1993).

1.2. Harvesting and population dynamics

Populations of wild birds and mammals are often harvested for subsistence, recreation or commerce. However, our ability to maintain sustainable exploitation of such populations is often inadequate due to poor demographic data and understanding of critical biological processes (Sutherland 2001). Despite a huge amount of interest in sustainable exploitation theory over the past 50 years (see Sutherland 2001 for review), there are examples of even intensely studied populations collapsing due to overexploitation (e.g. Walters & Maguire 1996). Furthermore, populations can be at greater risk of extinction when exploitation occurs in conjunction with habitat degradation and/or fragmentation (Lande, Engen & Saether 2003b).

However, there are examples of sustained intensive exploitation continuing in seemingly healthy populations (Sutherland 2001). Sustainable exploitation can be achieved if the rate of exploitation occurs at the same rate as population growth or lower (Caughley & Gunn 1995). If reducing a population leads to increased (compensatory) reproduction or survival, then the resulting population increase can be exploited. If, however, there is no effect of increased mortality on natural mortality or reproduction, then this extra mortality is described as

additive. Therefore, density-dependence is essential for sustainable exploitation of harvested populations (Sutherland 2001).

1.2.1 DENSITY DEPENDENCE

Even under optimal conditions, few populations grow without limit. The historic debate over mechanisms of population regulation and population limitation continues today (Sinclair 1989). Here we define population limitation as the process that sets the equilibrium density, and population regulation is the density-dependent process by which a population returns to its equilibrium density, following Sinclair (1989). To understand population regulation and limitation, two paradigms have been developed. The *mechanistic* paradigm is used to explain relationships between the vital rates; births, deaths, immigration and emigration, and factors effecting population density, such as predation, food shortage, disease and territoriality, and seeks to explain population limitation (Krebs 1995; Krebs 2002b; Krebs 2002a; Sinclair 1989). The *density* paradigm, however, is used to explain population regulation and assumes that the vital rates are related to population density, and that there is a stable equilibrium that the population will return to if perturbed (Krebs 1995; Krebs 2002a; Sinclair 1989).

Despite being criticised as ineffective in achieving understanding of population dynamics and preventing progress in population ecology (e.g. Krebs 1995), density-dependent processes are important for sustainable harvesting (Sutherland 2001) and remain a central tenet in population ecology. Indeed, evidence has been found that population density can affect survival (Angerbjorn 1986), dispersal (Matthysen 2005) and reproduction (Both 1998; Coulson, Milner-Gulland & Clutton-Brock 2000; Soutullo et al. 2006) for many terrestrial vertebrate populations.

Density-dependence within populations can occur through a number of mechanisms:

Interference, the short term reversible decline in food intake, is a consequence of the presence of conspecifics (Sutherland, Gill & Norris 2002). Fighting, intraspecific kleptoparasitism (Norris & Johnstone 1998; Triplet, Stillman & Goss-Custard 1999), prey disturbance (Yates, Stillman & Goss-Custard 2000), attraction of interspecific kleptoparasites (Carbone, Toit & Gordon 1997) and the effects of actively avoiding aggressive interactions (Cresswell 1997) are all possible mechanisms leading to interference.

The removal of resources that could be used by others, termed *depletion*, can also lead to density-dependence. As population density increases the availability of resources decreases, altering growth rate (Sutherland, Gill & Norris 2002).

Individuals may exclude others by defending *territories*. Density-dependence due to territoriality can result in two ways; individuals may acquire poor quality territories leading to a lower than expected reproductive output, or a higher proportion of individuals may defer breeding due to poor territory quality and thus reduce mean reproductive output (Sutherland, Gill & Norris 2002).

Although poorly studied, the effects of the *rank* of individuals within a population may lead to density dependence, as dominance hierarchies can affect survival probabilities and reproductive output of individuals (Sutherland, Gill & Norris 2002).

Survival and breeding success can be affected by *predation* and *parasitism* which may increase with population density. Specialisation of predators can lead to density-dependence if an increase in the number of predators specialising on predation of a certain prey species

occurs as density of that prey species increases. Individuals are more likely to become burdened with parasites at high population density than at lower densities, reducing survival and reproduction rates (Hudson, Dobson & Newborn 1998)

1.2.2 DENSITY DEPENDENT DISPERSAL

Studies on the role of density-dependent processes in population dynamics have focused on density-dependence in fecundity and survival (Engen, Lande & Saether 2002; Fowler 1981; Murdoch 1994; Wolff 1997). However, the importance of density-dependent spatial processes (i.e. dispersal, immigration, emigration) in population biology is now receiving greater interest (Hanski 1999). For the effects of dispersal patterns on population dynamics to be apparent, information on both dispersal rate and distance moved is required (Pulliam, Dunning & Liu 1992). Although theoretical work on density-dependent dispersal has been conducted (Haydon & Steen 1997; McCarthy 1999; Saether, Engen & Lande 1999; Travis, Murrell & Dytham 1999), there are little empirical data (Matthysen 2005).

Dispersal rates can be influenced by population density either positively (increased population density causes increased dispersal) or negatively (increased population density causes decreased dispersal rates) (Matthysen 2005). Positive density-dependent dispersal is a result of competition for resources, or increased antagonistic interactions due to overcrowding, increasing the likelihood of dispersal as individuals have better fitness prospects by leaving high density sites (McCarthy 1999; Waser 1985). Negative density-dependent dispersal has been recorded in a number of territorial mammalian species (Wolff 1997) and can also occur from increased aggression between individuals. The “social fence” hypothesis predicts that in high population densities, residents of an area may be more aggressive to immigrants and/or

transient individuals resulting in reducing dispersal of these individuals (Hestbeck 1982). Negative density-dependent dispersal may also be a result of conspecific attraction which is explained by the benefits of aggregation such as anti-predator behaviour or as a cue for resource availability (Danielson & Gaines 1987). Furthermore, an increase in dispersal with decreased population density has also been explained as a strategy to reduce Allee effects, the decrease in population growth rate at low population density (Kuussaari et al. 1998).

1.2.3 COMPENSATORY MECHANISMS

Compensation is the demographic response of populations to additional mortality and is caused by density-dependence of vital population processes (Boyce, Sinclair & White 1999). A reduction in population density reduces the density-dependent feedback on one or more population processes leading to an increase in population growth rate. Therefore, if the population was artificially reduced through harvesting, density-dependent processes would lead to a reduction in natural mortality, which is referred to as compensatory mortality. Similarly, if resource availability for the survivors of harvest is increased, this could result in increased reproductive output, or compensatory reproduction (Boyce, Sinclair & White 1999). However, if harvest mortality increases the overall mortality rate beyond that which would occur by natural processes, then hunting mortality is described as additive.

In addition to compensatory mortality and reproduction, density-dependent immigration can also compensate for additional mortality. Density-dependent immigration can occur by means of increased natal dispersal of individuals into vacant areas (Boutin, Tooze & Price 1993; Tuyttens et al. 2000b), in addition to/or by a shift in range to include the lower density area (Efford, Warburton & Spencer 2000; Verts & Carraway 1986). This 'vacuum' effect refers

specifically to the movement of individuals from an area of high density to an area of low density along a density gradient and is different to dispersal that occurs independently of an induced density gradient (Verts & Carraway 1986). Compensatory immigration is potentially a very important mechanism for resilience of populations to harvesting (Efford, Warburton & Spencer 2000).

1.2.4 HARVESTING STRATEGIES

The major objective in successful management of harvested populations is to find sustainable harvesting strategies that pose minimal risk of extinction or population instability, while producing large annual yield (Aanes et al. 2002). Popular strategies employed to attain sustainable harvesting include the constant yield strategy (where the same numbers of individuals are taken annually), the proportional yield strategy, (where the number of individuals taken is a proportion of the total population size), and the threshold or constant escapement (where all excess individuals above a critical population size are harvested) (Lande, Engen & Saether 1995). Predicting sustainable harvesting levels can be difficult due to uncertainty in, and lack of, biological data used to parameterise harvest models (Sutherland 2001). The problem of uncertainty has been approached by creating no-take areas. While proven successful in some circumstances, the use of no-take areas assumes that protected populations are within their boundaries. Dispersal and migration can span areas much larger than the designated protected area and so limiting the effectiveness of the no-take area (Allison, Lubchenco & Carr 1998).

Despite their problems with data uncertainty, models can be used to study harvesting strategies, by assessing their reliability and robustness. These analyses would not be possible

in real populations, and can be a useful tool for sustainable management of harvested populations (Milner-Gulland et al. 2001).

Using simulation modelling, Milner-Gulland et al. (2001) developed and tested different harvesting strategies for managing populations under uncertainty. It was found that strategies for short-term economic gain often resemble constant or proportional harvest models. However, the proportional yield strategy requires accurate total population size estimates, which is not always possible (Lande, Engen & Saether 1995). In addition, it has been shown that setting a threshold below which harvesting does not occur and above all surplus are harvested, does not provide effective protection against over harvesting (Milner-Gulland et al. 2001) and constant yield strategies are inappropriate for fluctuating or unstable populations (Lande, Engen & Saether 1995).

Overall, strategies that rely on population growth rates, rather than population size, were found to be more robust to biased estimates and that simple harvesting strategies that take a small proportion of the population each year are most robust to uncertainty (Milner-Gulland et al. 2001).

1.3. The mountain hare (*Lepus timidus*)

The mountain hare, *Lepus timidus*, is widely distributed across the northern Palaearctic (Angerbjorn & Flux 1995). The Scottish mountain hare, *L. timidus scoticus*, is a subspecies of *L. timidus* and is native to the highlands of Scotland where it is locally abundant on heather moorland managed for red grouse shooting. Such management involves strict predator control (crows *Corvus corone*, fox *Vulpes vulpes*, weasel *Mustela nivalis*, stoat *Mustela erminea*) and

rotational burning of heather, and is thought to benefit mountain hares as well as grouse (Hewson 1984) though this hypothesis has not been empirically tested (Newey et al 2007). Heather burning creates a mosaic of heather at different ages. Younger heather is a preferred food source and aids mammalian predator avoidance, whereas longer heather provides shelter from adverse weather and avian predation (Hewson 1984; Thirgood & Hewson 1987).

The mountain hare has been traditionally harvested for subsistence and sport across its range, including Scotland, where sport shooting continues to be an important source of revenue for some land owners (Tapper 1992). Mountain hares are sometimes considered a pest and killed to protect forestry, woodland, crops, and increasingly, disease control. Louping-ill virus (LIV) is a tick-borne disease that causes high mortality in infected red grouse chicks, *Lagopus lagopus scoticus*. Although mountain hares do not show clinical symptoms of LIV, they are important hosts to ticks and can lead to persistence and transmission of the virus non-vireamically between co-feeding ticks (Jones et al. 1997; Laurenson et al. 2003). The proposal that culling wildlife hosts, including mountain hares, could be an effective management strategy to control ticks and LIV (e.g. Smith 2009), has led, in recent years, to an increase in management culls of mountain hares for tick and LIV control purposes (Patton et al. 2010).

An apparent decline in mountain hare numbers has been reported in the UK (Battersby 2005). Combined with threats from climate change and a change in upland land use (Robertson, Park & Barton 2001) leading to habitat loss and fragmentation, culling has raised concern amongst conservationists and government agencies about the status of UK mountain hare populations, and the effect of culling on upland ecosystem functioning (Patton et al. 2010). The mountain hare is listed on Annex V of the EC Habitats Directive (1992), which requires Member States

to ensure that their exploitation '*is compatible with their being maintained at a favourable conservation status.*', and has been added to the UK Biodiversity Action Plan list of priority species (UK Biodiversity Action Plan 2008).

In Scotland, breeding begins in late February with gestation lasting around 50 days and post-partum mating. Females can have up to three litters a year, although four is theoretically possible (Hewson 1976), with litter size in litter periods one and two tending to be larger than the third litter period (Iason 1990). Increased food intake by captive females over winter leads to increased birth weight of leverets although has no effect on litter size (Pehrson & Lindlof 1984). Female age does not influence reproduction, although skeletally larger females, as indexed by hind foot length, attempt to reproduce earlier in the year and are able to sustain bigger litter sizes, making larger females more productive annually (Flux 1970; Iason 1990).

Two annual mortality peaks are observed in mountain hares. One occurs between January and April and comprises mostly first year individuals and older hares, with mortality being higher in skeletally smaller animals. The other, which occurs between August and November, coincides with a dietary switch from summer grazing of grasses to winter bulk browsing on woody vegetation (Iason & Waterman 1988) and deteriorating weather, and is largely composed of young animals entering their first winter (Iason 1989a). Leverets born late in the season have a shorter growth period, or may still be growing later in the year, with greater nutritional requirements and are likely to contribute heavily towards this mortality peak (Iason 1989a). Although leverets born in later litters have poorer survival, prenatal mortality is highest in litter period one due to poor weather leading to abortion or reabsorption of embryos (Iason 1989a).

1.3.1 UNSTABLE POPULATION DYNAMICS OF MOUNTAIN HARE

Across their Palearctic distribution, the mountain hare shows cyclic, or unstable, population dynamics (Newey et al. 2007b; Newey et al. 2007a; Reynolds, O'Mahony & Aebischer 2006). Populations that exhibit multi-annual fluctuations in numbers or density, showing a statistically significant periodicity over three or more years, are described as cyclic (Berryman 2002; Newey et al. 2007a; Turchin 2003). Unstable dynamics describe multi-annual fluctuations in numbers or density, but which may or may not be cyclic (i.e. presence or absence of statistical significance in periodicity) (Newey et al. 2007a). Mountain hare populations in Scotland have been shown to fluctuate with a roughly ten year periodicity which sees densities increase to 200 hares km⁻² at peak population phases (Hewson 1976; Newey et al. 2007a; Watson et al. 1973). Time series analysis of game bag records is often used to investigate cyclic population dynamics and it has been demonstrated that, for red grouse at least, bag records reflect population density (Cattadori et al. 2003). With the exception of a strong association between bag records in Scotland and estimates assessed by capture-mark-recapture (Hewson 1976), this assumption has never been tested for mountain hares (Newey et al. 2007b). Time series of mountain hare game bag records from 51 independently managed moors determined the mean cycle periodicity as 9.2 years with a range of 4-15 years (Newey et al. 2007b). However, not all hare populations are cyclic, out of all the moors tested only around 50% exhibited statistically significant cyclic fluctuations (Newey et al. 2007b).

Drivers of these population fluctuations in mountain hares remain unclear. Delayed life-history traits, abiotic factors, food availability, predation and parasites are all possible

explanations for destabilising population dynamics causing population fluctuations (see Newey et al. 2007a for review). Although previous understanding was that food is unlikely to be important in driving Scottish mountain hare cycles (Newey et al. 2007a), results of a more recent food supplementary study showed that food addition had a major effect on survival and reproduction at the individual level. This leads to questions of whether food alone, or in conjunction with other factors, could destabilise mountain hare population dynamics (Newey et al. 2010). High prevalence of the nematode parasite, *Trichostrongylus retortaeformis*, has no effect on survival, but has been shown to reduce female fecundity and has been implicated in the destabilisation of populations leading to cyclic fluctuations (Newey et al. 2005; Newey et al. 2007a; Newey & Thirgood 2004). However, initial modelling studies of the hare-parasite system do not support the hypothesis that parasites alone can drive population dynamics (Townsend et al. 2009). Further modelling suggests that delayed life-history traits have a weakly destabilising effect, increasing the tendency for cyclic dynamics and could be important in the host-parasite system (Townsend et al. 2011). Introducing diffusion (movement, i.e. dispersal, immigration, emigration) of mountain hares, and the corresponding advection of parasites (movement of parasite due to host movement), into simulations of host-parasite models generated periodic travelling waves of both hare and parasite abundance (Townsend 2009). While this hints at a potential explanation for cyclic dynamics, further work is required to determine whether adding spatial parameters to host-parasite models can generate the cycling dynamics seen in Scottish mountain hare populations (Townsend 2009).

1.3.2 DISPERSAL OF MOUNTAIN HARES

The area of heather moorland managed for red grouse shooting has been in decline since the 1940s in Scotland (Robertson, Park & Barton 2001). This has led to fragmentation of the landscape with a decrease in optimal mountain hare habitat and the associated heather moorland management practices (e.g. heather burning, predator control) that benefit mountain hares as they do red grouse. Mountain hare population fluctuations are not spatially synchronised (Newey et al. 2007b), and so their population dynamics can be described as asynchronous. Mountain hares have been described as existing as a metapopulation in Britain (e.g. Anderson et al. 2009). Although a fragmented landscape and asynchronous population dynamics are consistent with the criteria of the metapopulation definition (Olivier, van Aarde & Ferreira 2009; see section 1.1), there is a lack of information on dispersal, colonisation and extinction rates which is required to fulfil the metapopulation definition (Olivier, van Aarde & Ferreira 2009). Dispersal is an important mechanism to link subpopulations and maintain metapopulation viability (Hanski 1999), and so, dispersal, and any factors affecting it, will have important implications for management and conservation of mountain hares in the UK.

Categorising individuals as ‘true’ dispersers can be difficult if maternal information is limited. As dispersal is defined as the movement from one homerange to another homerange with no overlap, individuals are often categorised as dispersers if they travel a distance greater than the mean female homerange diameter between the natal site and site of first breeding (Avril et al. 2010; Bray et al. 2007; Dahl & Willebrand 2005). Only one known study has investigated natal dispersal of mountain hares in Scotland and although no evidence for dispersal was found, conclusions were drawn from results of mark-recapture, showing increased recapture

rate of juveniles (Hewson 1990). However, trapping bias, such as varying susceptibility of individuals to trapping, could cause these differences in recapture rate, and mark-recapture methods may not detect long distance dispersers (Gillis & Krebs 1999).

More recently, a study investigating home ranges and dispersal of mountain hares in the boreal forest of Sweden concluded that natal dispersal was observed in only a limited number of mountain hare individuals (Dahl & Willebrand 2005). Evidence for sex biased dispersal was not found, although this could be due to smaller sample size. Due to a slight sexual dimorphism in body size, with females being the larger sex, it could be expected that dispersal distance and/or probability would be greater in female mountain hares compared to males. It was found that adult mountain hare show strong site fidelity with limited evidence of adult dispersal, although some long distance excursions were recorded particularly in males during the breeding season (Dahl & Willebrand 2005; Hewson & Hinge 1990). When taking into account long distance excursion by adults, even leverets in the Dahl & Willebrand (2005) study that were classed as ‘true’ dispersers, were still within the possible range of their parents. Therefore, it was concluded that neither natal nor breeding dispersal was present in mountain hare in the boreal forest of Sweden (Dahl & Willebrand 2005). The implications of limited dispersal is that some management strategies, such as local blanket culls, could induce a strong local effect on population density (Dahl & Willebrand 2005), with possible negative implications for sustainable management.

1.3.3 DENSITY DEPENDENCE AND COMPENSATORY MECHANISMS OF MOUNTAIN HARE

Despite a wealth of knowledge of mountain hare ecology, the effects of population density and harvesting on vital rates are poorly understood in this species. Harvesting small game through

sport is traditionally assumed to have little effect on harvested populations due to compensatory mechanisms and/or low hunter efficiency to guarantee minimal risks of over-harvesting (Ellison 1991; Willebrand & Hornell 2001). However, a lack of demographic data and knowledge of density-dependent processes for mountain hares means that the effects of exploitation can not be predicted (Sutherland 2001).

In a population study of mountain hares between 1956 and 1969, Hewson (1976) examined differences in breeding success and survival over a course of the population cycle. During this time, fluctuations in hare numbers were assessed from trapping indices, counts and game bag records. Breeding success, estimated as the proportion of leverets caught, was shown to be highest during low and increasing density phases of the cycle. Similarly, adult survival was higher/highest when density was low, although juvenile survival was high during peaks and declines and poor when density was increasing (Hewson 1976). Relative levels of breeding success, adult survival and juvenile survival during different population phases are shown in Table 1.1.

Table 1.1: Relative breeding success, adult survival and juvenile survival at different population phases, extracted from Hewson (1976)

Population phase →	Peak	Decline	Trough	Increase
Breeding success	Low	Low	High	High
Adult survival	Low	Low	Highest	High
Juvenile survival	Highest	High	High	Low

Changes in breeding success, adult survival and juvenile survival over the course of the cycle suggest they are influenced by population density. All three parameters are high when population density is low (trough), which could be indicative of negative density-dependence. However, juvenile survival is also high at peak densities, contradicting this idea. Further, these data describe only one population cycle, within one population. Therefore, the results of this study may not be applicable to other populations, or even the same population within a different time period. To investigate density-dependence in vital rates, a more experimental approach with replication (i.e. multiple populations whose dynamics are not synchronised, allowing comparison of different population phases at any one time) is needed to increase reliability of results.

There has been one attempt to follow such a study design which compared three island populations of mountain hare off the west coast of Sweden (Angerbjorn 1986). Angerbjorn (1986) found no relationship between population density and estimated litter size or estimated number of litters. However, a significant relationship between juvenile recruitment (relative number of leverets produced over the breeding season) and population density was found, although there was also a significant difference in juvenile recruitment between islands (Angerbjorn 1986). This suggests that differences in juvenile recruitment could be due to differences between islands rather than a result of population density itself and results of this study should be viewed in light of this limitation. Further, it is unknown whether isolation of these island populations from one another, and the mainland, has intrinsically changed hare demography or dynamics within each population, which may prevent results of this study being representative of the majority of mountain hare populations (Newey et al. 2007a).

These two studies provide the only information currently available concerning density-dependence in mountain hare survival and breeding success. Further, it is currently unknown whether harvest mortality is compensatory or additive to natural mortality, or whether compensatory reproduction occurs in mountain hare demography. Dispersal ecology is poorly understood in mountain hares, and the effects of population density and harvesting are unknown. The effects of population density and hunting on natal dispersal of brown hare have, however, been studied (Avril et al. 2010; Bray et al. 2007).

A higher dispersal rate was observed in a low density hunted area compared to a higher density non-hunted area, although this did not affect the probability of an individual dispersing (Bray et al. 2007). The lack of difference in dispersal probability leads the authors to argue that the higher density in the non-hunted zone is associated with the lower dispersal distance. This negative density-dependence in dispersal could be accounted for by adult home ranges being smaller in the higher density non hunted area. Therefore, escaping from an unsuitable social environment in a high density area would require a shorter distance to be made which may not be classed as a dispersal event (Bray et al. 2007). Alternatively, limited movements of juveniles in high density zones may indicate social stress and avoidance of confrontations with conspecifics (Hestbeck 1982). However, another study investigating the effect of population density alone on dispersal in the brown hare (using the same dispersal criteria) found no relationship between population density and dispersal distance or probability (Avril et al. 2010). It has been shown in the snowshoe hare that predator induced stress can lead to changes in habitat use and foraging patterns (Hik 1995). If hunting is viewed as a form of predation, one could hypothesise that increased dispersal may not be a response to population density,

but to disturbance and stress experienced within the hunted area (Efford, Warburton & Spencer 2000)

However, the hunting methods and strategy used may affect the extent of similarity between hunting and predation. Predation is a background, year-round risk, with peaks associated with predator breeding and alternative prey abundance. Individuals may be pursued but escape, leading to increased levels of stress hormones and the observed stress response. Hunting, however, is more efficient, with most individuals that are pursued being killed, and thus individuals do not survive with the stress increase experience. Further, hunting is often limited to closed seasons, only occurring at certain times of the year, unlike predation that occurs year round.

Mountain hares do not benefit from a closed season in Scotland, although most commercial hare shoots take place in winter. If hare density is high, commercial shoots will involve hare drives, where a line of beaters use dogs to flush hares uphill towards a line of guns. If hare density is lower, hares may be hunted by 'walk-up' drives; hunters with dogs drive hares uphill shooting as they flush. The use of dogs will stimulate a similar stress response by the hare as if it was being predated by a mammalian predator (e.g. Sheriff, Krebs & Boonstra 2009). Further, hares may escape mortality by hiding down burrows, out-running dogs or passing through the guns. So, in these cases the hare's experience of hunting will be analogous to predation.

In addition to commercial shoots, hares are shot year-round to protect forestry and crops, provide food for dogs and bait for traps (Tapper 1992), and as part of culling regimes. In these situations hares may be caught in snares, or killed on a 'shoot on sight' basis. Such hunting

methods would not involve a chase, as with commercial hunting or predation, and the hare has much less chance of surviving. Therefore, hunting will not be similar to predation and populations hunted solely by non-commercial methods are unlikely to illicit the same stress response as predation.

Management of mountain hares is further complicated by the ten year population cycle exhibited by some populations of this species (Lande, Engen & Saether 2003b; Newey et al. 2007b). It is likely that levels of density dependence will differ between population phases due to differing population densities. Harvesting at a given rate may effect populations of different phases to varying extents, and so density-dependent processes at each population phase need to be well understood (Hudson & Dobson 2001). A lack of understanding of these processes could lead to an increased risk of overexploitation of mountain hare in the UK.

1.4 Outline of thesis

The mountain hare has been traditionally harvested in Scotland for centuries and is increasingly culled to control tick-borne disease (Patton et al. 2010). Despite this, there is a paucity of knowledge of density-dependent and compensatory processes in mountain hare demography, despite being vital for predicting sustainable harvesting rates (Sutherland 2001).

The ultimate goal of my PhD research was to fill these gaps in knowledge with the intention of better informing mountain hare management in Scotland. By using a combination of fieldwork and modelling, my research objectives were:

- To critically review the evidence that culling mountain hares can reduce tick-borne disease and increase red grouse harvest (Chapter 2)

- To better understand dispersal patterns and the cost of dispersal in Scottish mountain hare populations (Chapter 3)
- To investigate the effects of harvesting on dispersal patterns and survival rates (Chapters 3 and 4)
- To assess the effects of population density on female fecundity and juvenile recruitment (Chapter 5)
- To develop harvest models to investigate sustainable harvest rates and factors effecting these rates (Chapter 6)

In **Chapter 2**, I review the literature on culling wildlife hosts to reduce disease prevalence in economically important livestock/game species using the mountain hare-LIV-red grouse system as an example. I consider whether culling mountain hares is effective in controlling ticks and LIV and increasing red grouse harvest, or sustainable, in terms of the conservation status of mountain hare in the UK.

Dispersal links subpopulations in fragmented landscapes and can play an important role in population dynamics and persistence under exploitation. However, to what extent depends on the survival of dispersers. In **Chapter 3**, I investigate the effects of harvesting on natal dispersal and assess the cost of dispersal on survival. I used live-capture and radio-telemetry data to compare natal dispersal distance and rate, and the effects on survival probability, of juvenile mountain hares from harvested and non-harvested populations in Scotland.

An important aspect in the sustainable management of harvested populations is that harvesting mortality is partially or fully compensated for by increased survival, breeding performance and/or immigration. Juvenile survival of mountain hare depends on birth date, which also

influences skeletal size, a factor affecting both adult and juvenile survival. Therefore, any factor that affects timing of breeding will also impact survival rates. In **Chapter 4** I use live-capture and radio-telemetry data for both adults and juveniles under different harvesting regimes to investigate the effects of harvesting on survival and timing of breeding.

Density-dependent processes play a central role in driving population dynamics and are a prerequisite for compensatory mechanisms. In **Chapter 5** we use Distance sampling to obtain mountain hare population density estimates for ten independent private hunting estates in the Central Scottish Highlands. *Post mortem* of hares killed on these estates enabled the effects of hare density on female fecundity and juvenile recruitment to be assessed.

Sustainable management of harvested populations involves finding a level of harvest which leads to a maximum yield without compromising population persistence. Using demographic data collected in **Chapters 4 and 5**, an age-structured population matrix model was constructed in **Chapter 6** with the aim of quantifying sustainable harvest rates for Scottish mountain hare populations. Demographic and environmental stochasticity were introduced to the model, and the population growth rate and probability of extinction were assessed under differing harvesting pressures, levels of age-specific harvest bias and initial population sizes.

A key role of applied research is to provide a sound evidence base to direct decisions in sustainable management and policy. In **Chapter 7** I summarise the results of the current study and discuss how these findings can contribute to sustainable management of Scottish mountain hare populations, and also within the wider framework of game management. I then identify gaps in knowledge and highlight key areas for future research necessary to ensure sustainable harvesting of the mountain hare.

Chapter 2

**Culling wildlife hosts to control disease: mountain hares, red grouse and
louping ill virus**

2.1 Abstract

Culling wildlife hosts is often implemented as a management technique to control pathogen transmission from wildlife to domestic or other economically important animals. However, culling may have unexpected consequences, can be expensive and may have wider implications for biodiversity and ecosystem functioning. We assess the evidence that culling mountain hares, *Lepus timidus*, is an effective and practical way to control louping ill virus in red grouse, *Lagopus lagopus scoticus*. Evidence from the available literature is limited, restricting our ability to reliably assess the effectiveness of culling mountain hares to control ticks, louping ill virus, or increase red grouse densities. Furthermore, the information required to assess the cost-benefit of this management strategy is lacking. The population response of mountain hares to culling is not well understood and the possible effects on their conservation status and the upland ecosystem remain unexplored. We conclude that there is no compelling evidence base to suggest culling mountain hares might increase red grouse densities. Overall we found that widespread culling of wildlife is not necessarily effective in reducing disease or improving economic returns. The use of wildlife culls for disease control should be proposed only when: (a) the pathogen transmission cycle is fully understood with all host-vector interactions considered; (b) the response of wildlife populations to culling is known; and (c) cost-benefit analysis shows that increased revenue from reduced disease prevalence exceeds the cost of culling.

2.2 Introduction

The interaction between wild animals and domestic or other managed species, may cause conflict through the effects of predation, competition, or the transmission of epizootic pathogens (Woodroffe, Thirgood & Rabinowitz 2005). The transmission of pathogens from wildlife to domestic animals can create conflict when the resulting disease reduces the economic viability of animal husbandry (Daszak, Cunningham & Hyatt 2000). Although sometimes controversial, a common strategy for disease control has been to cull the wildlife host (Carter *et al.* 2009). However, culling wildlife to manage pathogen transmission from wildlife to domestic animals may be fraught with difficulties, be ineffective and can generate unanticipated results.

For example, in North America, bison, *Bison bison*, and elk, *Cervus canadensis*, are hosts to the bacterium, *Brucella abortus*, that causes brucellosis in cattle. Extensive culling of bison within the Yellowstone National Park between 1996 and 1997 led to the neighbouring American states gaining brucellosis-free status (USDA-APHIS 2009). In the past decade, however, the Yellowstone bison population has more than doubled and now exceeds the original population target size. Future control of the bison population will raise original cost predictions reducing the cost-benefit of the initial cull (Kilpatrick, Gillin & Daszak 2009). Despite the extensive culling of bison, the brucellosis-free status was lost in two states between 2004 and 2006 by infection from elk (Cross *et al.* 2007). Management aimed at reducing contact between elk and cattle, only increased elk aggregation, the prevalence of brucellosis among elk, and the risk of transmission to cattle (Roffe *et al.* 2004).

In the UK there has been an increase of bovine tuberculosis (bTB) in UK cattle herds over the past 30 years. The persistence of and failure to control bTB have been linked to a pathogen reservoir in sympatric badger, *Meles meles*, populations (Donnelly *et al.* 2006). Whilst badger culling has been successful in controlling bTB in Ireland (Eves 1999), culling has not reduced the incidence of bTB in England. Large-scale experimental studies have demonstrated that social perturbations associated with culling badgers may lead to increased immigration of badgers into culled areas increasing the spread of bTB (Woodroffe *et al.* 2006).

In both these cases the response of the wildlife species to culling was unanticipated and reduced the effectiveness of the cull. The increased bison population growth rate led to a reduction in cost benefit, and the increased immigration by badgers resulted in spread rather than control of disease. Furthermore, the failure to consider all potential disease hosts reduced the effectiveness of the cull in the bison-elk-brucellosis-cattle system. In light of these problems we discuss a third system where culling of a wild mammal is implemented to reduce the disease prevalence in economically important game bird populations.

Mountain hares, *Lepus timidus*, and sheep have been implicated in the transmission of the louping ill virus (LIV) to red grouse, *Lagopus lagopus scoticus*. LIV is a flavivirus transmitted by sheep ticks, *Ixodes ricinus*, and can cause high mortality in infected red grouse chicks (Reid 1975) reducing grouse density and the associated revenues from shooting (Laurenson *et al.* 2003). Therefore, controlling LIV is considered to be important for the continued viability of estates managed for grouse shooting (Hudson 1992). Although mountain hares do not show clinical symptoms of LIV, they are hosts for ticks (Laurenson *et al.* 2003) and laboratory trials have shown that non-viraemic tick to tick transmission of LIV can occur when they co-feed on

mountain hares (Jones *et al.* 1997). Promulgation of research findings to moorland managers and the proposal that culling wildlife hosts, including mountain hares, could be an effective management strategy to control ticks and LIV (e.g. Smith 2009), has led to increased culling of mountain hares in some areas of Scotland. Traditionally, mountain hare populations are harvested by land owners and paying clients with the aim of sustainable hunting for sport. However, there is evidence that an increasing proportion and number of hares are now being killed as part of tick control programmes (Patton *et al.* 2010).

Mountain hares are distributed widely across northern Europe and occur at particularly high density on heather, *Calluna vulgaris*,-dominated moors in Scotland. The mountain hare has recently been added to the UK Biodiversity Action Plan list of priority species (UK Biodiversity Action Plan 2008) and is on Annex V of the EC Habitats Directive (1992), which requires Member States to ensure that their exploitation '*is compatible with their being maintained at a favourable conservation status.*' Combined with threats from habitat loss and climate change, culling has sparked concern amongst conservationists and government agencies about the status of UK mountain hare populations, and the effect of culling on upland ecosystem functioning (Patton *et al.* 2010).

Here we assess the published evidence for the effectiveness of culling hares as a management strategy to control ticks and LIV in order to increase grouse density, and consider whether it is either an effective control measure or sustainable given our understanding of this system.

2.3 What are the effects of culling on mountain hare population dynamics?

Whilst mountain hares are an important quarry species in Scotland, little is known about the impact of harvesting or culling on their demography and population dynamics. As their landscape is fragmented (Robertson, Park & Barton 2001), dispersal and any factors affecting it, are likely to be important for metapopulation viability (Hanski & Gilpin 1997). Studies of the movements and natal dispersal of mountain hares in the boreal forest of Sweden demonstrated high adult site fidelity and limited natal dispersal (Dahl & Willebrand 2005) corroborating earlier reports that mountain hares in Scotland show limited dispersal (Hewson 1976). Intensive, localised culling could potentially further fragment populations and if the resulting distance between subpopulations exceeds dispersal distance, or if dispersing individuals are subject to greater mortality risk, dispersal rates and metapopulation persistence may be reduced (Hanski & Gilpin 1997).

A recent comparison of two questionnaire surveys conducted in 1995/96 and 2006/07 found no evidence at the 100 km² scale of major changes in the distribution of mountain hares in Scotland during this time (Patton et al. 2010). Combining questionnaire data on hare management with long-term hunting statistics, Patton et al. (2010) found no evidence of a decline in the numbers of hares recorded in game bags between 1995/96 and 2006/07.

Direct evidence of the effect of hare culling on hare density is limited to one study in the Central Highlands where hares in an area of 130 km² were reduced from a density in excess of 20 km⁻² in the late 1980s to very low density (<1 km⁻²) by 1998 (Laurenson *et al.* 2003). While this study provides evidence that localised culling can significantly reduce hare density

at this spatial scale, neither the efficacy nor effect of culling on densities nationwide can be assessed until long term abundance data are available across Scotland (Patton et al. 2010)

Mountain hare populations in Scotland are shown to have cyclic, or unstable, dynamics (Newey et al. 2007b). Associated changes in demographic parameters seen at different phases of the population cycle may affect any underlying density-dependent mechanisms. Although necessary for understanding the response of mountain hare populations to culling, knowledge of compensatory mechanisms and at what intensity culling becomes additive to natural mortality, is lacking.

2.4 Does culling mountain hares reduce tick abundance and LIV prevalence?

To test the hypothesis that mountain hares can act as a LIV reservoir in the wild, Laurenson et al. (2003) conducted a study where mountain hare density was reduced over a number of years on one sporting estate in the Central Highlands where seroprevalence to LIV antibodies in shot young red grouse was high (80%), red deer, *Cervus elaphus*, were absent and there were very few roe deer, *Capreolus capreolus*. The subsequent changes in tick abundance, LIV prevalence, brood survival and post-breeding densities were compared to grouse moors where mountain hare density was not manipulated. This experiment demonstrated that reducing mountain hare density resulted in fewer ticks, lower LIV seroprevalence in shot young grouse and increased grouse chick survival (Laurenson et al. 2003). However, this did not result in increased post-breeding grouse densities when compared to control areas (Cope, Iason & Gordon 2004; Laurenson et al. 2004). Interpretation and generalisation of these findings, however, requires caution as i) the study area was unusual in having no red deer. Red deer do not display symptoms of LIV or contribute to its transmission (Jones et al. 1997); they are,

however, important hosts for ticks (Gilbert et al. 2000). Modelling studies predict that reducing mountain hare density in areas with red deer will not reduce ticks or LIV because ticks are maintained by the deer population and LIV is maintained by the grouse population (Gilbert et al. 2001). Most Scottish estates have red deer, which means that the results of the Laurensen et al. (2003) study are unlikely to be applicable to most of upland Scotland; and ii) concurrent with the reduction in hare density, sheep on the study area were intensely managed to reduce ticks and LIV through treatment with acaricide three times a year, and vaccination of yearling sheep against LIV. This additional form of tick and LIV control was not implemented on all control sites confounding the effects of mountain hare culling.

The spatial distribution of each species in this system may also be important when considering the effectiveness of mountain hare culling for tick and LIV control. Both mountain hare and red grouse densities tend to increase with altitude between 400-700 m, whilst ticks and red deer show the opposite trend (Gilbert 2010). Ticks are most likely to have impacts on red grouse at lower altitudes where tick density is highest and therefore tick control may be most beneficial in these areas. However, there are fewer mountain hares and more red deer at these lower altitudes (Gilbert 2010) and so culling hares from these areas is unlikely to have a significant impact on red grouse tick burdens as deer will maintain the tick population in the absence of hares.

2.5 Do ticks and LIV affect red grouse demography?

Tick abundance and distribution has increased in the UK (Kirby et al. 2004; Scharlemann et al. 2008), possibly due to increasing host densities (Clutton-Brock, Coulson & Milner 2004),

or a warmer and wetter climate (Barbett et al. 2006), providing a longer season and more favourable conditions for tick development (Lindgren & Polfeldt 2000).

Grouse chicks in areas of high tick abundance tend to have high tick burdens and increased probability of contracting LIV (Reid 1975). Ticks may also directly affect chicks through anaemia, reduced feeding due to ticks aggregating around the eyes, and secondary infections.

Empirical evidence of tick induced morbidity is, however, equivocal. Experimental reduction of tick burdens on breeding female grouse through treatment with acaricide, at one site with very high LIV prevalence (up to 75%) in 1995 and 1996 produced contradictory results; in 1995 acaricide treatment did not reduce LIV infection rates nor increase chick survival at 10 weeks, in 1996 however, LIV prevalence in chicks was significantly reduced at 35 days of age and increased chick survival (Laurenson et al. 1997). A similar study carried out at sites with low LIV seroprevalence (up to 1.4%), found no significant difference in LIV seroprevalence nor brood survival between chicks of treated and control females (Moseley et al. 2007; Mougeot et al. 2008).

LIV prevalence is spatially patchy (Laurenson et al. 2007) and highly variable, with reported seroprevalence in red grouse ranging from low; 1.4% (Moseley et al. 2007), 0% and 7.1-26.1% (Gilbert et al. 2001), to high; 75% (Laurenson et al. 1997), 46% and 81.8% (Gilbert et al. 2001). The high variation in LIV seroprevalence and the patchy nature of its spatial distribution complicate our understanding of the effects of LIV on red grouse demography. With such high variation in LIV prevalence between areas, the ability to assess and reliably recommend control measures for LIV is limited. Furthermore, although LIV can cause 78% mortality in infected red grouse in the laboratory (Reid 1975), the susceptibility of chicks to

LIV in the wild is likely to vary depending on maternal condition, chick health, genetics, weather and stress.

In summary, the evidence that culling mountain hares can reduce tick burdens and LIV seroprevalence of red grouse is provided by Laurenson et al. (2003). This site, however, was unusual with very high LIV seroprevalence levels in grouse, and an absence of red deer. Moreover, the simultaneous management of sheep to act as ‘tick mops’ to reduce tick numbers (Laurenson et al. 2003) is confounding, making it impossible to disentangle the effect of hare culling and sheep management on changes in tick burdens, LIV prevalence and grouse density. In addition, Gilbert et al. (2001) provide evidence that mountain hare culling would not be effective if alternative tick host (such as deer) were present. Laurenson et al. (2003) report that grouse densities increased following hare culling, although the increase was not significant when compared to control sites. Grouse populations in Scotland show cyclic dynamics (Haydon et al. 2002) making it difficult to interpret short-term changes in grouse density. Findings on the effect of ticks on LIV prevalence in grouse chicks and chick survival appear equivocal and dependent on the prevalence of LIV at the study site (Laurenson et al. 1997; Mougeot et al. 2008).

2.6 Discussion

Although widely used, culling of wildlife hosts for disease control can be ineffective and may generate unanticipated results. Failure to take account of the possible effects of perturbation on social behaviour, density-dependent fecundity or survival, and the role of alternative hosts may at best render the approach unsuccessful and at worse may exacerbate the situation.

Heather moorland, red grouse and mountain hares are of significant cultural and conservation concern in the UK. Their future management demands a sound evidence base, and we suggest future work is needed to gain comprehensive knowledge on the effects of high tick burdens on red grouse, individually and at the population level. The role of mountain hares as hosts for ticks and the persistence and transmission of LIV needs greater investigation under a wider variety of circumstances. Research into alternative methods for tick and LIV control, such as treating alternative tick hosts (deer and sheep), with acaricide to act as ‘tick mops’, should be pursued and their efficacy and efficiency investigated. Long term studies are required to assess the effects of mountain hare culling on local and nationwide abundance and to understand the implications of unstable population dynamics shown by many mountain hare populations. Furthermore, information on density-dependent and compensatory mechanisms, in addition to dispersal patterns, is critical in making informed predictions on the demographic response of hare populations to culling. Given the economic importance of grouse moor management in Scotland, there are surprisingly few studies investigating the socio-economics of grouse moors (Redpath & Thirgood 2009; Sotherton, Tapper & Smith 2009; Thompson et al. 2009), prohibiting any meaningful assessment of the cost-benefit of mountain hare culling for tick and LIV control. The way in which economic factors govern and interact with wildlife management and biodiversity are key areas for future research. We conclude that the evidence currently available is insufficient to provide scientific justification for culling of this Annex V species for the purposes of tick and louping ill virus control.

Chapter 3

Natal dispersal and juvenile survival of harvested Scottish mountain hare

3.1 Abstract

Dispersal of individuals link subpopulations in fragmented landscapes and can play an important role in population dynamics, genetics and persistence. However, to what extent depends on fate of dispersers. The cost of dispersal is often seen as increased risk of mortality, but costs can be offset if dispersers immigrate to better quality habitat. Dispersal of individuals into lower density harvested areas can potentially act as a buffer to overexploitation. Mountain hares, *Lepus timidus*, are a traditional small game species and are widely hunted for recreation, subsistence and commerce throughout their circumpolar range. In Scotland, mountain hares have been harvested for centuries with little knowledge of how hunting affects population dynamics and demography. Here we investigate the effects of harvesting on natal dispersal and assess the cost of dispersal on survival by comparing natal dispersal patterns, and survival probability, of juvenile mountain hares of harvested and non-harvested areas in Scotland. We found that natal dispersal distance was significantly greater in the harvested area, although when distance was scaled to give a dispersal rate, no significant effect was found. Harvesting had no effect on juvenile survival probability, although we found that higher natal dispersal rate lead to higher survival probability. We found no evidence for compensatory juvenile survival or natal dispersal suggesting that Scottish mountain hares may show strong local population dynamics. This may leave populations susceptible to overexploitation, and combined with low dispersal distance and dispersal rate, could lead to subpopulation isolation, compromising large scale population viability.

3.2 Introduction

Biological dispersal, the process of leaving a home range and establishing a new home range with no overlap between the two, has important consequences for population dynamics, demography and genetics (Gaines & McClenaghan 1980; Greenwood 1980; Johnson & Gaines 1990; Sutherland et al. 2000). Dispersal is an important mechanism for the persistence of populations that exist in heterogeneous landscapes by linking otherwise isolated subpopulations. Dispersal and immigration of individuals into vacant habitats is necessary for colonisation and recolonisation, as required for source-sink or metapopulation dynamics (Amarasekare 2004; Hanski 1999; Pulliam 1988; Watkinson & Sutherland 1995).

Dispersal can occur at any stage of an individual's life although natal dispersal, the movement of an individual from its birth site to the site of first breeding, is often the only long distance movement an animal will make (Dahl & Willebrand 2005; Greenwood & Harvey 1982). A common assumption in dispersal ecology is that dispersal incurs fitness costs through increased mortality or lower reproductive output (compared to philopatric individuals) due to increased predation pressure, aggression, stress, energy depletion, moving through or settling in unfamiliar habitats, or being unable to find a suitable habitat (Clobert et al. 2003; Greenwood & Harvey 1982; Johnson & Gaines 1990). However, if by dispersing individuals settle in and occupy better quality habitats, they may experience higher survival and/or improved reproductive performance, resulting in the benefits of dispersal exceeding the costs (Van Vuran & Armitage 1994). The relative cost-benefit ratio of dispersal vs. philopatry shapes the degree and extent of dispersal. To understand the genetic and demographic consequences, the fate of dispersers needs to be known (Johnson & Gaines 1990).

Dispersal rates can be influenced by population density either positively, whereby increased population density causes increased dispersal, or negatively, with increased population density causing decreased dispersal rates. The importance of density-dependence in spatial process in population dynamics, and the consequences for conservation and management of wild populations, are becoming increasingly recognised (Clobert et al. 2003; Hanski 1999; Matthysen 2005). Although theoretical work on density-dependent dispersal has been conducted (Haydon & Steen 1997; McCarthy 1999; Saether, Engen & Lande 1999; Travis, Murrell & Dytham 1999) there are few empirical data (Matthysen 2005).

If population density is artificially reduced through harvesting, positive density-dependent dispersal has the potential to buffer local variation in population numbers and could reduce the risk of over harvesting (Willebrand & Hornell 2001). Such movement can be a result of increased natal dispersal of individuals into areas of low density (Boutin, Tooze & Price 1993; Tuytens et al. 2000b), in addition to/or a shift in range of older individuals to include the lower population density area (Efford, Warburton & Spencer 2000; Verts & Carraway 1986). There is also the possibility that harvesting itself influences dispersal patterns independently of population density. Disturbance from predation has been shown to alter habitat use and foraging patterns in the snowshoe hare (Hik 1995). If harvesting is viewed as a form of predation, a similar effect on habitat use and movement patterns could be expected.

The mountain hare, *Lepus timidus*, is distributed across northern Eurasia and is hunted for recreation, subsistence and commerce throughout its range. In Scotland, mountain hares have been harvested for centuries with little knowledge of how hunting affects population dynamics and demography in this species (Tapper 1992). Throughout their circumpolar distribution,

mountain hares show unstable dynamics (Newey et al. 2007b; Newey et al. 2007a), further complicating sustainable management of this species (Lande, Engen & Saether 2003a). British mountain hare populations are thought to be in decline (Battersby 2005), and are increasingly culled in some parts of Scotland as part of tick and tick-borne disease control (Patton et al. 2010). A change in Scottish upland land use in recent years has decreased the extent of heather moorland leading to an increasingly fragmented landscape (Robertson, Park & Barton 2001). This fragmented habitat, combined with population dynamics appearing spatially asynchronous (Newey et al. 2007b), has led mountain hares to be described as existing as a metapopulation in Britain (e.g. Anderson et al. 2009), despite a lack of information on dispersal, colonisation and extinction rates. As dispersal is an important mechanism in linking subpopulations and maintaining metapopulation viability (Hanski 1999), it has the potential to influence mountain hare demography and population persistence in Scotland.

Previous dispersal studies on the snowshoe, *L. americanus*, brown, *L. europaeus*, and mountain hare suggest that most individuals are philopatric although dispersal has been observed (snowshoe hare, (Boutin et al. 1985; Gillis & Krebs 1999; O'Donoghue & Bergman 1992); brown hare, (Avril et al. 2010; Bray et al. 2007); mountain hare (Dahl & Willebrand 2005; Hewson 1990). Male-biased dispersal is often seen in polygamous species (Wolff 1993). Although male-biased dispersal has been reported in the brown hare (Avril et al. 2010; Bray et al. 2007), evidence for male-biased dispersal in mountain and snowshoe hares has yet to be found (Dahl & Willebrand 2005; Gillis & Krebs 1999; Hewson 1990). However, Hewson's (1990) conclusions were drawn from mark-recapture studies which may bias results due to heterogeneity in trapping probability between sexes, cohorts, and individuals, and may fail to detect long distance dispersers (Gillis & Krebs 1999). Dahl and Willebrand (2005) had small

sample sizes, which may have led to failure to detect sex-biased dispersal here. To date, there have been no studies investigating the effects of population density or harvesting on dispersal of mountain hare, and the cost of dispersal on survival is unknown.

This study aims to describe natal dispersal in Scottish mountain hares and investigate how dispersal rate impacts juvenile survival. The effect of harvesting on natal dispersal or juvenile survival will be investigated by comparing individuals from harvested and non-harvested populations.

3.3 Methods

3.3.1 STUDY SITE

The study was carried out on one sporting estate managed for red grouse shooting in the Central Scottish Highlands. Management of the estate and study areas was typical of grouse moors in Scotland, including rotational burning of heather and legal predator control (crow, red fox, stoat and weasel). For the purpose of this study, the estate is split into three areas, each between 2000 and 2500ha in size and subjected to the same habitat and predator management by game keepers. In one area, mountain hares were subject to ongoing, legal traditional harvest (treatment = harvested), while in the second, hares were not hunted (treatment = control), and the third was not used in this study. Each management area was *Calluna*-dominated with heather moorland extending to around 700m. Above 550m the vegetation became more arctic/alpine in character with shorter heather and lichens *Cladonia* spp. The proximity of the two management areas, and the similarities in altitude and vegetation, allows confidence that both areas are alike. Prior to the start of the study, both

areas were harvested at similar intensities and population densities were thought to be comparable. Within the harvested management area, hares were hunted by ‘walked up’ shooting; hunters with guns walk up the hillside flushing hares and shooting them on sight. Harvesting rates in the harvested population are believed to be approximately 20% of the total population. Hunters were able to identify study animals but were advised not to select against them. Within each management area were two trapping sites placed on traditional hare drives. The management areas are defined by natural boundaries shown in Figure 3.1. These boundaries do not prevent movement of hares between management areas.

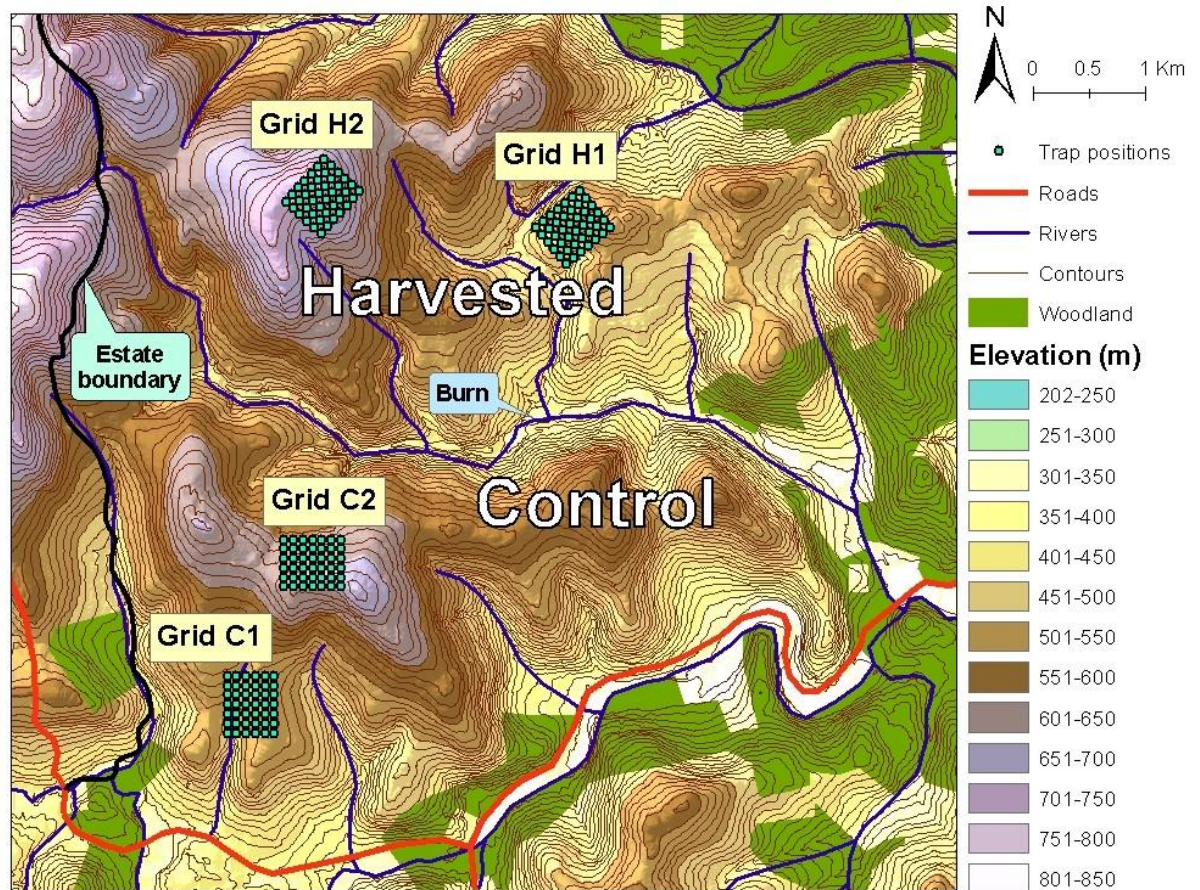


Figure 3.1: Map of the study site showing trapping areas (labelled grid) and management areas. The stream labelled “Burn”, the “Estate boundary” and the main road represent hare management boundaries. Hares are not shot within the control area, although these boundaries do not obstruct hare movement.

3.3.2 LIVE TRAPPING AND RADIOTELEMETRY

The study was carried out over three years from October 2007 until July 2010. Live trapping was carried out October-December and April-July from October 2007 to December 2009 using Tomahawk model 107 double-door cage traps (Tomahawk Livetraps, Wisconsin, USA)

and Tomahawk clones (Jeremy Dewhurst Ltd, Bankfoot, Scotland). In winter 2007 and summer 2008, a mean (\pm SE) of 57 (\pm 1.96) traps per trapping site, with a mean (\pm SE) inter-trap spacing of 71m (\pm 1.02), were placed within the trapping site to maximise use of a limited number of traps. In winter 2008, summer 2009 and winter 2009, 42 traps per trapping site were placed on a six by seven grid with 85 m spacings (Figure 3.1). The traps were pre-baited with apple and locked open for one night prior to trapping, after which traps were set, baited at dusk and checked at dawn. All captures were sexed, weighed, and the right hind foot length (excluding claws) measured. Young leverets can be difficult to sex and so the sex of individuals was only included in the analysis if it could be verified at six months of age. Leverets, up to 6 months old, are easily distinguished from adults by their smaller body size and colour. Juveniles up to 9 months can be distinguished from adults by the presence of the epiphyseal notch (Broekhuizen & Maaskamp 1979). New captures were fitted with a uniquely numbered metal ear tag (National Band and Tag Company, Newport, USA.) in each ear and recaptured hares were identified by these tags. Tag loss was extremely low and having both ears being tagged allowed 100% positive identification of each recapture. All adult hares were fitted with a TW3 (Biotrack Ltd, Dorset, UK) collar mounted radio transmitter. Leverets weighing less than 700g were fitted with a TW41 (Biotrack Ltd, Dorset, UK) tag glued to a clipped area of skin between the shoulder blades. Larger leverets, more than 700g, were fitted with a TW4 (Biotrack Ltd, Dorset, UK) nylon collar modified with 2.5cm foam fixed on the internal circumference of the collar to allow for hare growth. No individual was fitted with a radio collar or tag that was greater than 2% of its total body weight. Each radio tagged leveret was tracked one to four times per week from the date of capture up to the age of six months, until the tag dropped off, or the leveret died. Adults and leverets over six months were tracked

fortnightly until the individual died or radio collar battery failed. Radio tracking fixes were obtained from homing-in on tagged individuals and recording each location with a handheld GPS (Garmin GPS 60™). This meant that the accuracy of each fix was very high, being within the accuracy of a GPS (~10m). Radio tag loss was minimal, none of the adult tags were lost, but around 3% of leverets lost their tag before recapture was possible. Radio tracking was carried out between October 2007 and July 2010.

3.3.3 LEVERET BIRTH DATE

Leveret birth date was estimated by incorporating weight at first capture and an estimated birth weight of 90g (Flux 1970) into regression equations (Iason 1989b).

3.3.4 POPULATION DENSITY

Trapping seasons spanned two to four consecutive months, therefore, it is not possible to make the assumption that the hare populations were closed over this time, as required for closed-population density estimation methods. Therefore, adult only data from one, four-week sub-sample, end of October/beginning of November representing winter and end of April/beginning of May representing spring, were used for capture-recapture analysis to estimate population density (Table 3.1). Trapping effort (represented by the number of trap nights) varies between management area and season depending on capture and recapture rate. Where rates were lower, trapping effort was increased to maximise the number of animals caught. Low capture rates were linked with inclement weather which affected both management areas and so is not thought to bias density estimates.

Table 3.1: The number of occasions (number of nights traps were set), the number of traps set (for the time period used in density estimate analysis only), number of trap-nights (number of occasions \times number of traps), the number of captures and recaptures (with capture and recapture rate, calculated as number of captures or recaptures/trap-nights, shown in brackets) for the harvested (H) and non-harvested (C) populations for each season (W=winter, S=spring) in each year of the study. All values are summed across the two trapping sites in each management area, giving a total for the each respective management area.

Season	Year	Site	Number of traps	Occasions	Trap nights	Captures (Rate)	Recaptures (Rate)
W	2007	C	102	5	510	16 (0.03)	1 (0.01)
S	2008	C	39	7	273	36 (0.13)	11 (0.28)
W	2008	C	84	12	1008	46 (0.05)	16 (0.19)
S	2009	C	84	6	504	41 (0.08)	7 (0.08)
W	2009	C	84	5	420	29 (0.07)	6 (0.07)
W	2007	H	115	6	690	43 (0.06)	11 (0.10)
S	2008	H	56	6	336	40 (0.12)	9 (0.16)
W	2008	H	84	6	504	104 (0.21)	42 (0.50)
S	2009	H	84	6	504	65 (0.13)	20 (0.24)
W	2009	H	84	8	672	47 (0.07)	12 (0.14)

Capture-recapture data were analysed using Density 4.4 (Efford 2007). Due to a low number of recaptures in some seasons, data from trapping sites within the same management area were

pooled. The low number of recaptures also meant that spatially explicit methods that use recapture data to estimate effective trapping area were not appropriate and so conventional capture-recapture methods were used. Following Boulanger & Krebs (1994; 1996) and Newey et al. (2003), a Jack-knife estimator of $M_{(h)}$ (closed capture model with heterogeneity) was used for all estimates. The effective trapping area (ETA) (the total area that the traps will cover after taking into account the possibility that individuals caught in traps on the edge of the trapping area may not have their entire home range overlapping with the actual trapping area) was obtained by adding a boundary strip of width W to the sides of the trapping grid. As a consequence of the low number of recaptures in some seasons, it was not possible to use ARL (setting W equal to half the Asymptotic trap-revealed Range Length) methods of estimating W . Therefore, the conventional estimator of W , $MMDM/2$ (half the mean maximum distance moved), was employed. The mean density of each management area (harvest, control) in each season were compared with a Student's t -test in Excel, followed by a comparison of each season with every other season within each management area.

3.3.5 ESTIMATING DISPERSAL DISTANCE

We defined natal dispersal distance (NDD) as the linear distance between the natal site (the site of first capture) and the first adult breeding site (the mean of the last three radio-tracking locations in February, when breeding begins (Angerbjorn & Flux 1995), or, if the individual died before February, the last three locations prior to death) following methods of Bray et al. (2007). Indeed, dispersal distances of individuals that died before February were similar to dispersal distances of individuals that did not die, validating this assumption. Data from nine pre-weaning leverets (caught less than 20 days in age) showed that distance moved from site

of first capture was not greater than 255m before they reached 100 days in age (Figure 3.2). This indicates that captured juveniles that were less than 100 days in age, and used in the dispersal analysis, were highly likely to have been captured close to the natal site and had not yet dispersed (Bray et al. 2007)

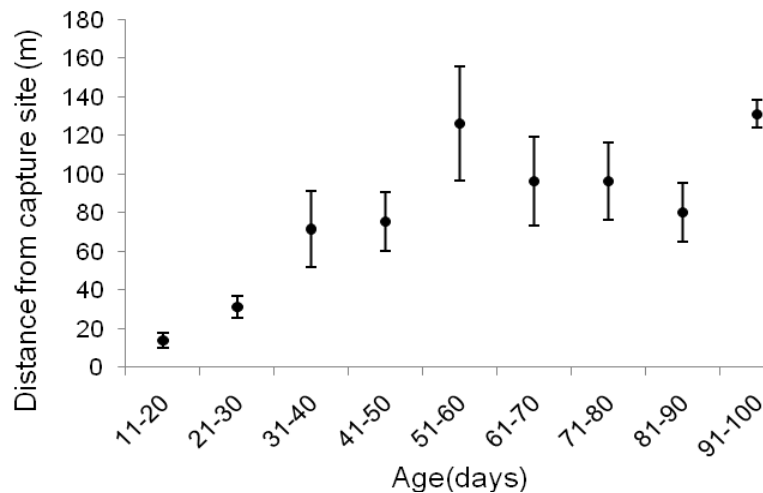


Figure 3.2: Distances (\pm SE) (m) between site of first capture and successive locations of nine pre-weaned leverets with age (days).

Natal dispersal distance was calculated using Geospatial Modelling Environment v0.3.3 Beta (Beyer 2009) in ArcMap v9.3.1 (ESRI 2009) and R v2.12.0 (R Development Core Team 2010). Individuals were classed as ‘true’ dispersers if NDD exceeded the diameter of the average annual adult female home range (Dahl & Willebrand 2005). Annual adult female home range was estimated for 57 (harvested=28, control=29) adult females with >10 locations over 12 months using 90% Kernel methods (Borger et al. 2006), in the adehabitat package

(Calenge 2006) in R. The diameter of the home range was calculated as $2\sqrt{\text{area}/\pi}$, assuming a circular shaped home range.

Individuals died at different points throughout the study, meaning that the age that the adult breeding site was calculated, and so the observation time (time elapsed between estimation of natal site and estimation of adult breeding site), varied between individuals. To account for this difference in observation time, and any consequence it may have when comparing populations, we derived a natal dispersal rate (NDR) as NDD (m) divided by t^γ , where t is time (days from birth to age that adult breeding site was calculated) and γ is a scaling parameter. Displacement for a simple diffusion model scales linearly with the square root of time ($\gamma=0.5$), although with our data $\gamma=1.2$ was found to be a better fit of the linear relationship between NDD and time (Haydon et al. 2008).

3.3.6 STATISTICAL ANALYSIS

The effect of management (harvest, control; see methods), birth month, sex, year and the age that the adult breeding site was calculated on NDD; and treatment, birth month and sex on NDR, were assessed using General Linear Mixed Models with normal errors and identity link function with trapping site included as a random effect. Analyses were performed in R v2.12.0 using the lme4 package (Bates & Maechler 2010). We first specified the full model including all terms and second order interactions, and then sequentially removed terms through a process of stepwise deletion of the least significant term, until no non-significant terms remained. Candidate models were compared, and the best fit model chosen, using Log-Likelihood Ratio Tests (LRT).

3.3.7 SURVIVAL ESTIMATES

Survival was estimated using Known-Fate models in RMark 1.9.7 (Laake 2010), which allows mark recapture models from program MARK v5.1 (White 2000) to be run in R v2.12.0. Known-Fate models are based on the Kaplan-Meier estimator and enabled a staggered entry design, and right-censoring of individuals to accommodate the fact that at the end of the study an individual could be alive, dead or unknown. Unknown fates were due to radio tag failure or loss, probability of which was not thought to differ between individuals or areas and therefore censoring is not thought to bias survival estimates. Management (harvested, control), birth month (March, April, May, June), sex (male, female) and year (2008, 2009) were used as factors, and NDR included as an individual covariate. Individuals that were shot were excluded from the analysis so that survival estimates represent natural mortality only. Natal dispersal rate was chosen over NDD to account for individual variation in observation time. Model selection was based on AICc scores, model weight and deviance.

3.4 Results

3.4.1 POPULATION DENSITY

Over the entire study period the mean (\pm SE) population density for the control area was 0.46 ± 0.08 , and for the harvested area, 0.36 ± 0.02 . Although population density appeared to be higher in the control area, in no season was the population density significantly greater in the control area compared to the harvested area when a Student's t-test was performed on the population density estimates ($p > 0.1$ in all cases). That population density of the control area seems lower in winter 2007 compared to other seasons is due to low recapture rate making

computation of standard errors impossible for winter 2007. Population density of neither the control nor the harvested area was significantly different in any comparison of each season with any other season ($p > 0.1$ in all cases), showing that population density did not fluctuate with time. Population density estimates for both control and harvested areas in each season can be seen in Figure 3.3.

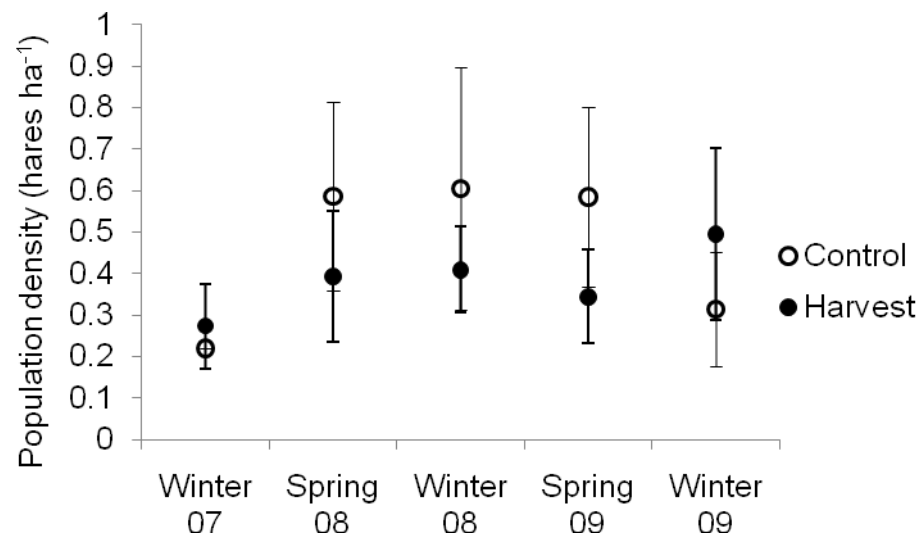


Figure 3.3: Population density estimates ($\pm 2SE$) (hares ha^{-1}) of the control (open circle) and harvested (full circle) areas for each season of the study period calculated using closed population methods with $M(h)$ jack-knife estimator and MMDM/2 strip method.

3.4.2 NATAL DISPERSAL DISTANCE

The mean annual adult female home range ($\pm SE$) for the control area was 78.34 (± 15.14) ($n=33$), and 83.34 (± 13.01) ($n=31$) for the harvested area. Since mean home range size between the two areas were similar, all home ranges were pooled to give a mean annual adult

female home range size (\pm SE) of 81.15 (\pm 10.75) ha. To account for the variation in home range size, home range diameter was calculated for the mean home range size plus one standard error, which equates to a home range diameter of 1.04km. Only four out of 44 hares (9%) had a NDD greater than this distance and hence, could be classed as true dispersers (Figure 3.4). Of these four hares, two were from the harvested area, two from the control area, each were born in different months and were evenly spread over 2008 and 2009.

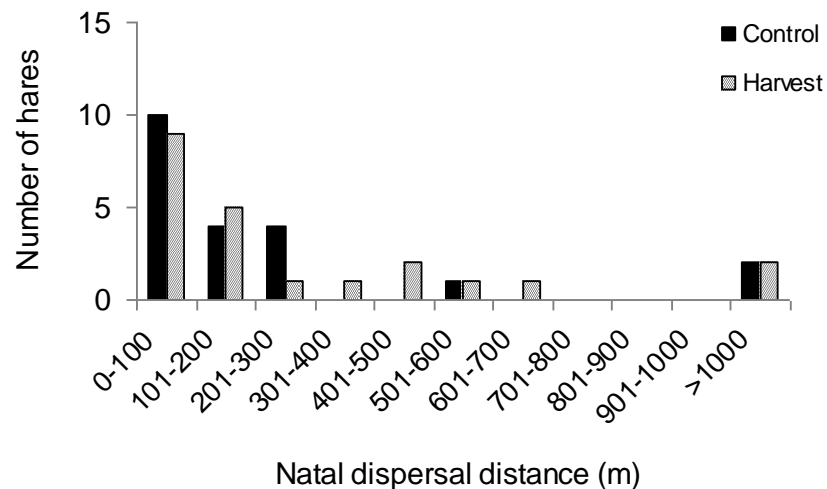


Figure 3.4: Distribution of natal dispersal distances (NDD) for harvest (hatched) and control (solid) populations. Only individuals with NDD greater than 1000m are defined as ‘true’ dispersers.

Natal dispersal distance was greater in the harvested area compared to the control area (median natal dispersal distance (interquartile range) for the harvested area was 137.94 (54.90-

420.95) m, and 125.16 (46.61-247.93) m for the control area). Natal dispersal distance increased significantly with age that the breeding site was estimated (management: estimate=1.14, se= 0.51, t=2.23, and age: estimate=0.01, se=0.001, t=7.35) (Figure 3.6). Dispersal distance did not significantly differ between leverets born in different birth months or in different years as shown by the LRT (birth month; $\chi^2=3.95$, d.f.=3, p=0.27, and year; $\chi^2=0.62$, d.f.=1, p=0.43). Females appeared to disperse greater distances compared to males (Figure 3.5), and although sex itself was not significant (estimate=-0.15, se=0.25, t=-0.60) the LRT showed that it improved model fit compared to when it was removed ($\chi^2=51.87$, d.f.=1, p<0.001). No interactions between any variable effected NDD with none of the second order interactions significantly reducing the LRT when compared to the full additive model (p>0.06 in all cases).

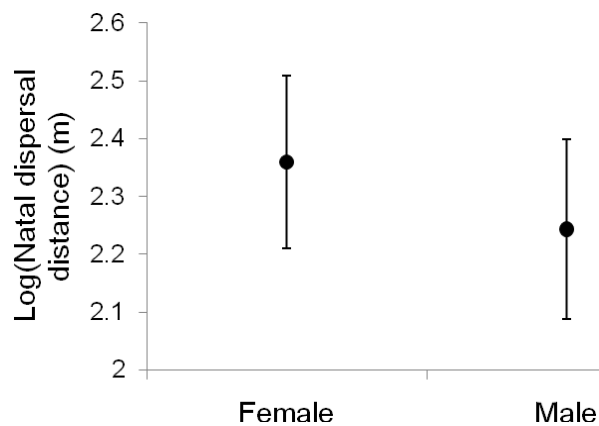


Figure 3.5: The mean (\pm SE) log of natal dispersal distance (NDD) (meters) for males and females.

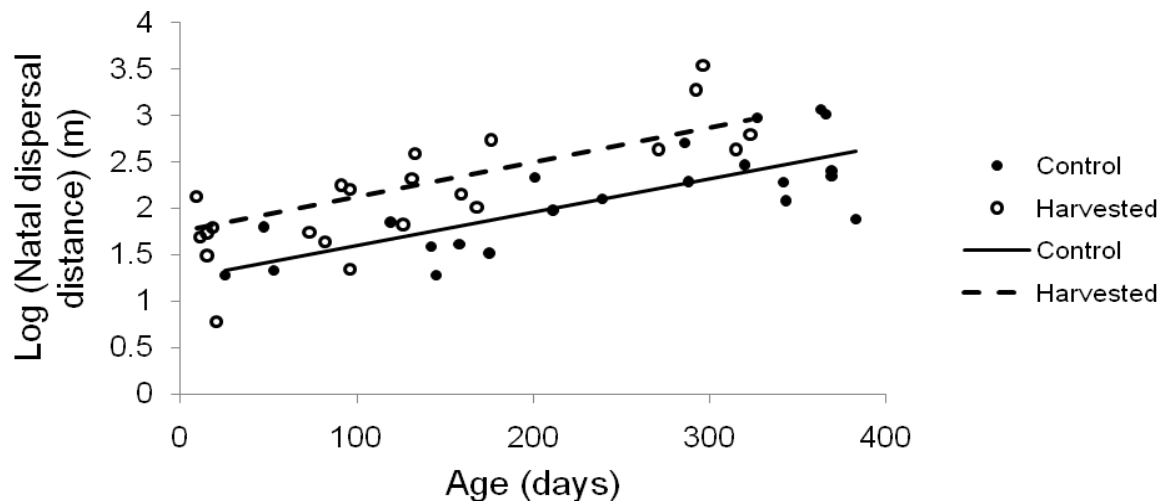


Figure 3.6: Log of Natal dispersal distance (NDD) (meters) with age in days, for control area (solid circle, solid line) and harvested area (open circle, dashed line).

3.4.3 NATAL DISPERSAL RATE

Neither birth month, year, management or sex, nor any secondary interactions between them, had any significant effect on natal dispersal rate. None of the second order interactions significantly reduced the LRT compared to the full additive model ($p > 0.5$ in all cases) and deletion of each term from the model was supported by the LRT (birth month, $\chi^2 = 2.56$, d.f. = 3, $p = 0.47$; year, $\chi^2 = 0.44$, d.f. = 1, $p = 0.51$; management, $\chi^2 = 1.8$, d.f. = 1, $p = 0.18$, sex = $\chi^2 = 0.39$, d.f. = 1, $p = 0.53$).

3.4.4 COST OF DISPERSAL ON SURVIVAL

In total, 49 models were tested, details of the best ten are given in Table 3.2.

Table 3.2: Details of the top ten Known-Fate models estimated by RMark for juvenile survival. Model = model structure; #parm = number of parameters; AICc = Akaike's Information Criteria, adjusted for small sample sizes; Δ AICc = difference between AICc scores; S = survival; Management (harvested, control); BM=birth month; NDR= natal dispersal rate; Time=age in days; Year=year of study.

	Model	#parm	AICc	Δ AICc	Weight	Deviance
1	S~BM+Year+NDR	6	103.35	0.00	0.20	90.90
2	S~BM+Year+Time+NDR	7	104.65	1.30	0.10	90.05
3	S~NDR	2	105.15	1.80	0.08	101.09
4	S~Management +NDR	3	105.41	2.06	0.07	99.29
5	S~Year+NDR	3	105.71	2.36	0.06	99.58
6	S~Year+Management +NDR	4	105.94	2.60	0.05	97.73
7	S~Management *NDR	4	106.11	2.76	0.05	97.90
8	S~Year+Sex+NDR	5	106.47	3.12	0.04	96.15
9	S~BM+NDR	5	106.97	3.62	0.03	96.66
10	S~Sex+NDR	4	107.02	3.67	0.03	98.81

The top three models all had relatively close AICc scores and similar model weight. Therefore it is not possible to confidently select one best fit model. A model averaging approach was used to combine the top three models, giving a mean (\pm SE) estimated survival rate of 0.91 (\pm 0.07). Overall, survival probability was lower in 2009 compared to 2008 and was lower in

leverets born later with lowest survival probability seen in birth month June. Survival probability decreased slightly over time indicating that survival probability decreases with age. The effect of time on survival probability can be seen in Figure 3.7a and the effect of birth month and year on survival probability can be seen in Figure 3.7b. Management did not feature in the top three models and so was not included in the model averaged estimate. The mean (\pm SE) survival estimate for the harvested area was 0.92 ± 0.03 and the control area was 0.94 ± 0.03 , which, combined with the delta AICc of the model including management (model 4) being greater than 2, indicates that harvesting populations may not significantly affect survival probability of individual juvenile mountain hares.

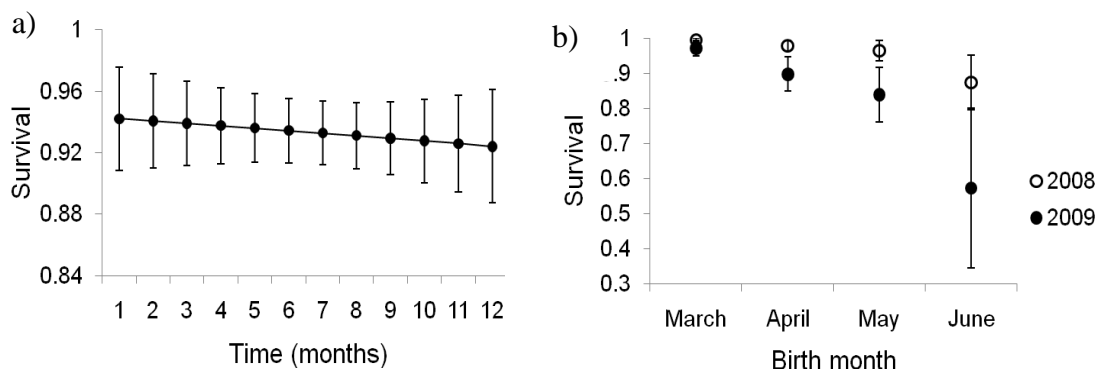


Figure 3.7: Survival probability for juveniles a) with time (age in months) and b) for each birth month (March, April, May, June) in 2008 (open circle) and 2009 (closed circle).

All of the top ten models include NDR, indicating that survival probability increases with increasing NDR (Figure 3.8). The poor fit of the model including the interaction between NDR and management (Table 3.2, model 7) indicates that harvesting does not influence the effect of NDR on survival probability.

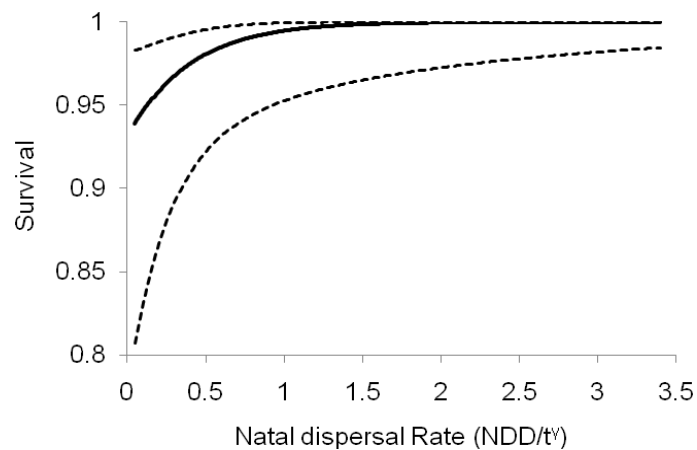


Figure 3.8: Significant positive effect of natal dispersal rate (m/day^{-2}) on survival probability.

Estimates are the solid line, with 95% confidence intervals shown in dashed lines.

3.5 Discussion

We found that Scottish mountain hare natal dispersal distances were greater in the harvested population, although when dispersal was scaled to give a natal dispersal rate, subsequently no effect of harvesting was found. Although there was no effect of harvesting on survival probability of juveniles, our results suggest that increased natal dispersal rates increased survival probability in the mountain hare.

3.5.1 NATAL DISPERSAL DISTANCE, PROBABILITY AND RATE

Natal dispersal distances were small and the probability of a juvenile dispersing a distance greater than the mean diameter (+1 SE) of a female's home range was low. Home range sizes we report here are much larger than those of Rao et al. (2003) and Hulbert et al (1996) but are

comparable to those found by Hewson & Hinge (1990). Differences in home range size found between these studies could be due to differences in food availability (Boutin 1984), amount of cover (Hulbert et al. 1996) or sampling regime and analytical technique (Borger et al. 2006). The study sites of Hulbert et al. (1996) and Rao et al. (2003) were a mixture of heather moorland, forestry and grassland, compared to the more moorland habitat managed specifically for red grouse shooting of Hewson & Hinge (1990) and the present study. Even hares categorised as 'moorland' hares in the Hulbert et al. (1996) study were located in forest habitat more often than the moorland habitat. The altitude of Hulbert et al. (1996) and Rao et al. (2003) study sites was also lower than that of Hewson & Hinge (1990). In addition, Hulbert et al. (1996) and Rao et al. (2003) used Multinuclear Probability Polygon (MPP) method of home range estimation which uses cluster analysis of nearest neighbour distances to distinguish home ranges with multiple cores. This technique would be useful for estimating home ranges for individuals in fragmented habitats (Kenward et al. 2001). Hewson & Hinge (1990) use Minimum Convex Polygon (MCP) methods which can overestimate home range size (Borger et al. 2006). We use 90% Kernel methods which should reduce overestimation of home range size compared to MCP, but do not consider multiple cores like MPP. We use fewer locations to calculate home range size compared to Hewson & Hinge (1990) (>20 fixes), Hulbert et al. (1996) (>30 fixes) and Rao et al. (2003) (>30 fixes), although it has been shown that 10 fixes give efficient, robust and unbiased estimates using Kernel methods (Borger et al. 2006). Our study sites are more comparable, in terms of vegetation and altitude, with that of Hewson & Hinge (1990) than those of Rao et al. (2003) and Hulbert et al. (1996), which, combined with differences in analytical technique, could explain the large home range size we report here.

Unlike most polygamous mammalian species (e.g. Wolff 1993), sex did not significantly effect dispersal distance or rate in mountain hare, which is not surprising given the low dispersal probabilities reported. However, model selection favoured inclusion of sex in the dispersal distance analysis. This suggests that the sex of hares explains some of the variation in natal dispersal distance, and with a larger data set, a significant result may occur. Female mountain hares appeared to disperse greater distances compared to males, a result also reported for the brown hare (Bray et al. 2007). There was no effect of birth month on dispersal distance or probability, and therefore, factors affecting birth date are unlikely to influence dispersal potential. Dispersal distance was greater for individuals in the harvested area, and none of the hares from the control area dispersed into the harvested area indicating a lack of immigration into the harvested area. This is a similar results found in the Bray et al. (2007) study on harvesting and natal dispersal of brown hares. However, population density of the hunted zone in the Bray et al. (2007) study was lower and so it is possible the changes in dispersal distance were due to density-dependence rather than harvesting. As both areas in the current study had similar population densities, the difference in dispersal distance observed in the harvested area cannot be attributed to density-dependence, unlike Bray et al. (2007) but more likely harvesting itself. Predator induced stress has been shown to effect foraging patterns and habitat use in the snowshoe hare (Hik 1995). If harvesting is viewed as a form of predation, increased movements in response to predator induced stress within a harvested population of mountain hares could be expected.

Although natal dispersal distances were greater in the harvested area, when we scaled NDD to control for variation in observation time, to give the NDR ($NDR = NDD / \text{time}^\gamma$, where γ is a scaling parameter), there was no difference in NDR between the two management areas. At

1.2 our estimation of the scaling parameter γ is unusually high. However, this is likely due to leverets diffusing (i.e. dispersing) at a faster rate than the units of a classic diffusion model where $\gamma=0.5$. Repeating the analysis when NDD is scaled with $\gamma=0.5$ made no difference to the overall results. Therefore, the significant difference in NDD between the harvested and non-harvested populations is confounded by varying periods of observation between individuals. This stresses that dispersal distances need to be scaled, if observation times for individuals within the study vary, and suggests that harvesting does not significantly affect natal dispersal of mountain hares.

3.5.2 JUVENILE SURVIVAL AND THE COST OF DISPERSAL

There was no difference in survival probability between the harvested and control areas and so we found no evidence of compensatory juvenile survival. However, juveniles were only captured from seven days of age onwards. It is possible that some neonatal mortality would occur in the first few days after birth, which went undetected in our study. Inclusion of neonatal mortality could provide different results. In studies on natal dispersal of the snowshoe hare, pregnant females were kept in captivity while they gave birth, ensuring that data was collected on leverets from the moment they were born (Gillis & Krebs 1999; O'Donoghue & Bergman 1992). Although this was not possible in the current study, capture methods that also include newborn leverets to allow quantification of neonatal dispersal and mortality should be pursued in future studies. Contrary to predictions based on theory and empirical observation (Christian 1970; Greenwood & Harvey 1982; Johnson & Gaines 1990; Van Vuran & Armitage 1994), we found a positive effect of dispersal rate on survival probability. Our results concur with other studies that have also failed to find reduced survival among

dispersers (Gillis & Krebs 2000; Lin & Batzli 2004; Van Vuran & Armitage 1994; Wauters, Matthysen & Dhont 1994). Dispersers may be in better condition prior to dispersal, which is why they are able to travel the distance and survive. Also, by dispersing, individuals may find better quality habitats which can impact lifetime fitness by increasing survival, the number of offspring successfully raised, or both, with consequences for population dynamics and demography (Ward & Weatherhead 2005). Unfortunately, with the data available it is not possible to assess post-dispersal survival or reproductive output. Long term studies are required for this information to be collected, which should be a future research priority.

3.6 Management implications and conclusion

Results of the present study concur with previous studies (Dahl & Willebrand 2005; Hewson 1990) that mountain hares disperse infrequently and when they do, they don't disperse far. This may result in some management strategies, such as strict predator control or local blanket culls, inducing a strong local effect on population density (Dahl & Willebrand 2005). This suggests that local, intensive culls of mountain hares for tick and LIV control may drastically reduce local mountain hare density (Harrison et al. 2010). Furthermore, this strong potential of culling in reducing mountain hare densities may have implications for their long term status. Local density reduction could lead to a decrease in overall population density and increase fragmentation, adding to the already fragmented habitat as a result of land use change (Robertson, Park & Barton 2001). If distance between subpopulations exceeds dispersal distance, recolonisation of vacant habitats or recruitment from source populations into sinks, could decrease with negative implications for large scale population viability (Hanski 1999; Watkinson & Sutherland 1995).

Source-sink and metapopulation theory is often used in the conservation of species (Hanski 1999). For such a framework to be implemented for Scottish mountain hare populations, knowledge of immigration rates, into suitable, but unoccupied, habitat, and dispersal between subpopulations, are required. The effect of habitat fragmentation on dispersal and immigration may be significant for population persistence and demography of the mountain hare, and are key areas for future research.

Chapter 4

Harvesting of Scottish mountain hares has no effect on survival but can delay breeding.

4.1 Abstract

Compensation of harvest mortality is important in the sustainable management of small game species. If hunting mortality is additive, or the number killed exceeds the number that can be compensated for, overexploitation can occur. The mountain hare, *Lepus timidus*, has been harvested traditionally in Scotland for centuries although knowledge of compensatory mechanisms is lacking. Juvenile survival of mountain hares is related to birth date, which also influences skeletal size, a factor affecting both adult and juvenile survival. Therefore, any factor that affects timing of breeding will also impact survival rates. The aims of this study were to assess the effects of harvesting on survival and timing of breeding. We used live-capture data to estimate birth date of mountain hare leverets and radio-telemetry to estimate survival rates using known-fate models in RMark. We found no evidence of compensatory survival in mountain hares. Juvenile survival was lower in the harvested area where leverets were born significantly later. Survival of both juveniles and adults differed between years, as did the timing of breeding, suggesting both these parameters are affected by environmental variation. Environmental variability and hunting-induced stress have the potential to affect female body condition. Female mountain hares may maintain body condition at a cost to reproduction, such as delaying the start of breeding and/or investing less in gestation and lactation. This would result in smaller leverets born later in the breeding season leading to potentially lower leveret survival and recruitment. This final result suggests that current conditions (either environmental variation or harvesting) could influence both current survival, and survival of future generations via the effects on timing of breeding and offspring size. We conclude that until the effects of environmental variation and harvesting at the individual and

population level are better understood, harvesting of mountain hare in Scotland should remain conservative.

4.2 Introduction

Populations of wild birds and mammals are often harvested for subsistence, recreation or commerce. Our ability to sustainably exploit populations is, however, often inadequate due to limitations in our understanding of critical biological processes, and poor demographic data (Sutherland 2001). The challenge of managing a population is even more difficult for species that dwell in fragmented landscapes (Hanski & Gilpin 1997) or exhibit cyclic or regular, high amplitude changes in density (Lande, Engen & Saether 2003a). The compatibility of harvesting with long-term conservation status of exploited species is dependent on the interaction between natural and human caused mortality and, given the increasingly fragmented habitat in which many species exist, the linkage (immigration and emigration) of populations.

Harvesting small game is traditionally assumed to have little effect on population abundance or density as a result of compensatory effects (Ellison 1991). Compensation is the demographic response of populations to additional mortality and is caused by changes in density-dependent processes, specifically, per capita reproduction and survival. Density-dependence is thought to occur when a reduction in population density leads to reduced competition for resources that might otherwise limit or regulate population growth. Hunting mortality may be additive if it increases the overall mortality rate above and beyond that which would occur by natural processes. Density-dependent processes are seen as a prerequisite to sustainable harvesting of wild bird and mammal populations and therefore, quantifying density-dependent and compensatory mechanisms are recommended for small game management (Sutherland 2001).

Harvesting may also reduce survival indirectly through stress if hunting is considered a form of predation. It has been shown in the snowshoe hare, *Lepus americanus*, that increased predation leads to reduced body condition by affecting behaviour and foraging patterns (Hik 1995) and increasing levels of stress, which directly influences body mass (Boonstra et al. 1998). A reduction in body condition may also have a negative effect on reproductive output (e.g. Hodges, Stefan & Gillis 1999; Rogowitz 1996). As predation risk increased, snowshoe hares attempted to maintain condition rather than maximise survival (Hik 1995). If hunting induces similar behavioural or physiological reactions, such as reducing body condition in response to harvesting, hunting mortality may surpass simply the number of individuals directly harvested.

The mountain hare, *Lepus timidus*, is distributed across Eurasia and is hunted for recreation, subsistence and commerce throughout this Palaearctic range. In Scotland, mountain hares have been harvested for centuries with little knowledge of how hunting affects population dynamics and demography in this species (Tapper 1992). British mountain hare populations are thought to be in decline (Battersby 2005) but are increasingly culled in some parts of Scotland to control tick-borne disease (Patton et al. 2010). Throughout their circumpolar distribution, mountain hares show unstable dynamics (Newey et al. 2007b; Newey et al. 2007a). In Scotland, mountain hare populations show high amplitude cyclic, or unstable, dynamics with a mean periodicity of 9.5 years (Newey et al. 2007b), further complicating sustainable management of this species (Lande, Engen & Saether 2003a).

Leveret mortality peaks in September when vegetation growth is low, weather is deteriorating and hares undergo a seasonal dietary switch (Iason & Waterman 1988). Although leverets

born earlier in the year are exposed to mortality risk for a longer period of time, leverets born later in the breeding season have a shorter growth period, leading to failure to meet nutritional demands of growth, so suffering higher winter mortality and contributing less to the breeding population (Iason 1989a). Further, later born leverets that survive to adulthood tend to attain smaller skeletal size (Hewson 1968; Iason 1989a). As adult survival is positively influenced by skeletal size (Iason 1989b), any factor that effects the timing of breeding would tend to influence survival too.

Although many studies have investigated survival patterns in Scottish mountain hare (Flux 1970; Hewson 1976; Iason 1989a; Iason 1989b), the effects of harvesting on survival have yet to be studied. The aims of this study were to investigate the effect of harvesting on timing of breeding and survival rates in mountain hare in Scotland by comparing two populations under differing harvest regimes.

4.3 Methods

4.3.1 STUDY SITE

The study was carried out on a sporting estate managed for red grouse shooting in the Central Scottish Highlands. For detailed description of the study site see Chapter 3 section 3.3.1.

4.3.2 LIVE TRAPPING

For details of methodology of the live trapping and radio-telemetry, see Chapter 3 section 3.3.2.

4.3.3 LEVERET BIRTH DATE

Birth date of leverets was estimated by incorporating weight at first capture and an estimated birth weight of 90g (Flux 1970) into regression equations formulated by Iason (1989a). The growth curves were calculated over two years and comparison of the growth curves were almost identical suggesting very little variation in growth rates between individuals (Iason 1989a). However, with very few recaptures of leverets in the present study, it was impossible to verify the accuracy of using previously calculated growth curves to predict birth date. Further, male leverets have a shorter, quicker growth rate compared to females, which may lead to birth dates of males being estimated consistently earlier. Results of this analysis should be interpreted in light of these limitations. The effects of management (harvest, control), year and sex were tested using a General Linear Mixed Model (GLMM) with normal errors, identity link function and trapping grid as a random effect using the lme4 package (Bates & Maechler 2010) for R v2.12.0 (R Development Core Team 2010).

4.3.4 BODY CONDITION INDEX

We used the residuals of a linear regression of hind foot length and mass as an index of body condition (BCI). Regressions were carried out in R in accordance with regression assumptions. Although there has been criticism of this method (e.g. Green 2001), assumptions of these methods have been verified in five species of small mammal (Schulte-Hostedde et al. 2005). Due to differences in growth rate between leverets and adults, and due to the slight sexual dimorphism in body size in adult mountain hares, BCI were calculated separately for three groups; leverets of both sexes, female adults and male adults, following Hodges, Stefan & Gillis (1999). Leveret BCI was estimated from mass and hind foot length at first capture. Body

condition index was estimated for adult male hares trapped in the two trapping seasons, winter and spring. However, as we cannot account for the effects of pregnancy and gestation on female body condition, female body condition index was estimated for winter only.

The effect of management (harvested, control) and study year on BCI were assessed independently for leverets and adult females using a GLMM with normal errors, identity link function and trapping grid included as a random effect. Using the same GLMM structure, the effect of management, study year and season on BCIs of adult males was assessed. Data analysis was performed in R v2.12.0 using the lme4 package. We first specified the full model including all terms and interactions, and then sequentially removed terms through a process of stepwise deletion of the least significant term. Candidate models were compared and the best fit model chosen using Log-Likelihood Ratio Tests (LRT).

4.3.5 POPULATION DENSITY

See Chapter 3 section 3.3.5 for methods for estimating population density using closed population models from trapping data.

4.3.6 SURVIVAL ESTIMATES

Survival was estimated using Known-Fate models in RMark 1.9.7 (Laake 2010), which allows mark-recapture models from program MARK v5.1 (White 2000) to be run in R v2.10.1. Known-Fate models are based on the Kaplan-Meier estimator and enabled a staggered entry design and right-censoring of individuals, which was necessary due to individuals at the end of the study could be classed as alive, dead or unknown. Unknown fates were due to radio tag loss or failure, probability of which is not thought to differ between individuals, and therefore,

censoring does not bias survival estimates. RMark adopts a design matrix development scheme that enabled time and age dependent models to be constructed. We used a staggered entry design within different study year cohorts, which allowed individuals to change age class (from juvenile to adult) at different times relative to other cohorts. We split the year into four seasons: 1) early breeding; February – April, onset of breeding with mating and first litters born, 2) late breeding; May – July, mating and later litters born, 3) post breeding; August – October, no mating, females still nursing last litter, and 4) winter; November to January, no breeding, partial snow cover and period of weight gain. In addition, management (harvested, control), sex and year were used as groups and BCI included as an individual covariate. In total, data from 44 leverets and 189 adults were used in the survival models. Individuals that were shot were excluded from the survival analysis and therefore mortality estimates represent natural mortality only. For model simplification, all leverets were transferred to the adult age class in the “early breeding” season the year following their year of birth, even if they were born later in the breeding season. Due to the inability to reliably distinguish between juveniles and adults past 9 months in age (Flux 1970), new adult captures only entered the model at “early breeding”, even if first captured in the “winter”, to ensure they were not juveniles misclassified as adults.

Juvenile survival was then investigated more thoroughly to compare survival probability between leverets born in different months. In a separate analysis using the same Known-Fate model design, we used leveret only data to estimate survival rates between the following four groups; treatment, sex, years and birth month, and with BCI as an individual covariate. Model selection was based on AICc scores, model weight and deviance.

4.4 Results

4.4.1 POPULATION DENSITY

There were no significant differences in population density estimates between the control and harvested areas, details of the results of the analysis can be seen in Chapter 3, section 3.4.1.

4.4.2 LEVERET BIRTH DATE

Leverets were born $19.74 (\pm 7.73)$ days later in the harvested area compared to the control area ($t=2.55$) and $26.44 (\pm 7.77)$ days later in 2008 compared to 2009 ($t=3.40$) (Figure 4.3a). The LRT indicated that the additive model was a better fit than the full model ($\chi^2=2.15$, $df=4$, $p=0.71$). Although birth dates were not significantly different for male and female leverets (estimate= 14.03 , $se=7.77$, $t=1.81$) results of the LRT showed improved model fit when sex was included in the final model ($\chi^2=178.89$, $df=1$, $p<0.001$) indicating that overall, males were born later than females (Figure 4.3b).

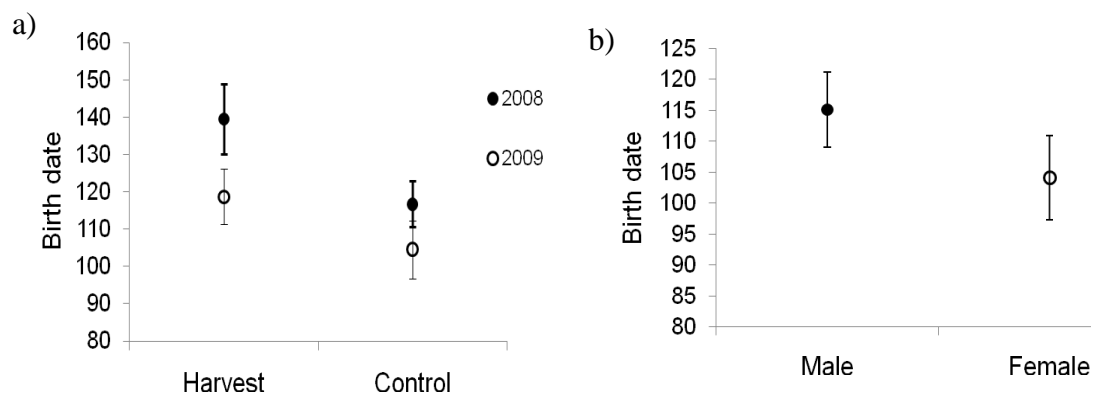


Figure 4.1: The significant effect of year and management on birth date (a), and difference in birth date between the sexes (b). Birth date is numbered from 1st January =1.

4.4.3 BODY CONDITION

Body condition index in leverets did not differ between the harvested and control areas, sexes or study years. Results of the LRT for the leveret BCI GLMM indicated that neither sex, management, year, nor any second or third order interaction improved model fit over the null model ($p > 0.46$ in all cases). Likewise, for adult females, BCI differed between neither year nor management area. The LRT revealed that neither year or treatment, nor the interaction between the two terms, significantly improved model fit compared to the null model ($p > 0.5$ in all cases). In males however, BCI was higher in 2009 compared to 2008 (estimate=0.04 se=0.02, $t=2.27$) (Figure 4.4), although there was no effect of season or management. The LRT showed that the full male BCI model, including all interactions, was a poorer fit compared to the additive model ($\chi^2=3.7$, $df=4$, $p=0.45$) and inclusion of season or management, or an interaction between the two, did not improve model fit ($p > 0.2$ in all cases),

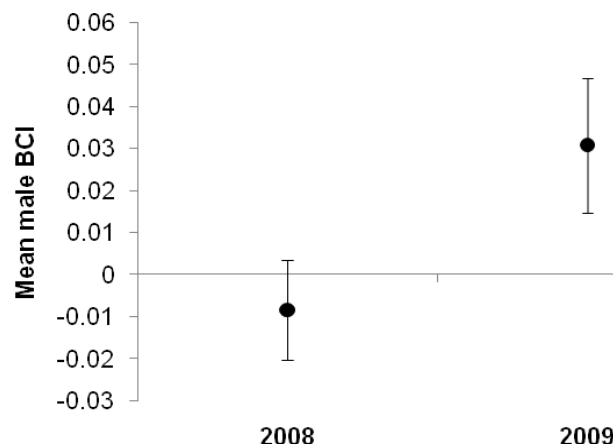


Figure 4.2: The significant difference in mean male BCI between 2008 and 2009, estimated by GLMM with normal errors and identity link function.

4.4.4 SEASONAL SURVIVAL

In total, 109 models were tested with details of the best ten given in Table 4.2. Delta AICc was less than 2 between the top four models, therefore, it is not possible to confirm a best fit model and so a model averaging approach was employed. Survival estimates of the top four models were averaged to give a mean (\pm SE) survival estimate of 0.38 (\pm 0.09) across season, age, sex, and treatment.

Table 4.1: Details of the top ten Known Fate models estimated by RMark. Model = model structure; #parm = number of parameters; AICc = Akaike's Information Criteria, adjusted for small sample sizes; Δ AICc = difference between AICc scores; S = survival; Age=adult, juvenile; Year = study year; Management = control, harvest; Sex = male, female; BCI = body condition index; Season = Early breeding = February – April; Late breeding = May – July; Post breeding = August – October; Winter = November – January.

Model	#parm	AICc	Δ AICc	Weight	Deviance
1 S~Age+Season+Year	7	612.76	0.00	0.24	257.09
2 S~Age+Season+Sex+Year	8	614.30	1.54	0.11	256.59
3 S~Age+Season+Management+Year	8	614.44	1.69	0.10	256.73
4 S~Age+Season+Year+BCI	8	614.58	1.82	0.10	598.37
5 S~Age+Year	4	614.80	2.04	0.09	265.23
6 S~Age+Season+Sex+Management +Year	9	615.88	3.13	0.05	256.12
7 S~Age+Season+Sex+Management +Year	9	615.88	3.13	0.05	256.12
8 S~Age+Season+Sex+Year+BCI	9	616.14	3.39	0.04	597.89
9 S~Age+Season+Management +Year+BCI	9	616.30	3.54	0.04	598.04
10 S~Age+Year+BCI	5	616.53	3.77	0.04	606.44

Survival differed between years with the lowest survival probability in adults in 2010 (no leverets were caught in 2010 so no juvenile survival data are available). Survival was higher overall in juveniles compared to adults and each age class exhibited different seasonal mortality peaks. Juveniles had greatest mortality in post breeding. Although in this season both adults and juveniles had similar survival probabilities, mortality was comparatively low for adults. Adults suffered greatest mortality in late breeding which was a season of relatively high survival for juveniles. Juveniles which survived late- and post-breeding went on to have high survival probability over winter (Figure 4.5). However, the model with the interaction between age and season was not listed in the top two models and so these differences are unlikely to be significant.

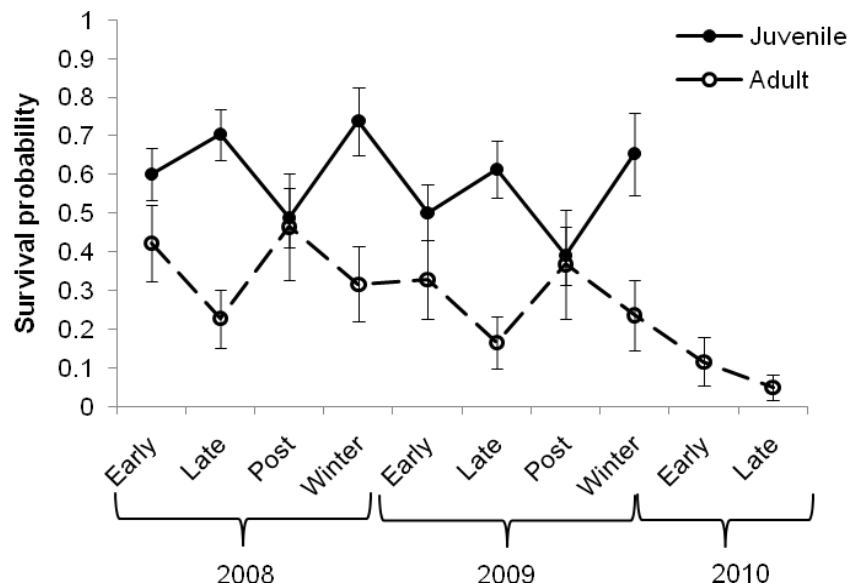


Figure 4.5: Survival probability for juveniles (full circle) and adults (empty circle) in each season over the entire length of study, estimated using Known Fate models in RMark. Early breeding = February – April; Late breeding = May – July; Post breeding = August – October; Winter = November – January.

Sex was included in Model 2 and was included in the model averaging estimate. Mean survival probability was higher overall in females compared to males, with the same trend within adults and juveniles. Management was also included in Model 3 and the model averaged estimate. Overall survival was slightly higher in the control area compared to the harvested area, and was greater in juveniles compared to adults (Table 4.2). As individuals that were killed by hunting were excluded from the analysis, our results suggest that harvesting populations does not lead to higher survival of individuals within the population subjected to harvesting.

Table 4.2 Mean (\pm SE) annual survival estimates for juvenile and adult mountain hares for the control and harvested areas, and for males and females, estimated using Known Fate models in RMark.

	Mean survival (SE)	
	Juvenile	Adult
<i>Management</i>		
Control	0.54 (0.05)	0.34 (0.08)
Harvested	0.52 (0.05)	0.32 (0.08)
<i>Sex</i>		
Female	0.56 (0.05)	0.35(0.09)
Male	0.50 (0.05)	0.30 (0.08)

Body condition index (BCI) featured in Model 4 and was included in the model averaged estimate. Survival probability increased with increasing BCI as shown in Figure 4.6 and the low delta AICc of Model 4 indicates that the effect of BCI on survival probability could be significant.

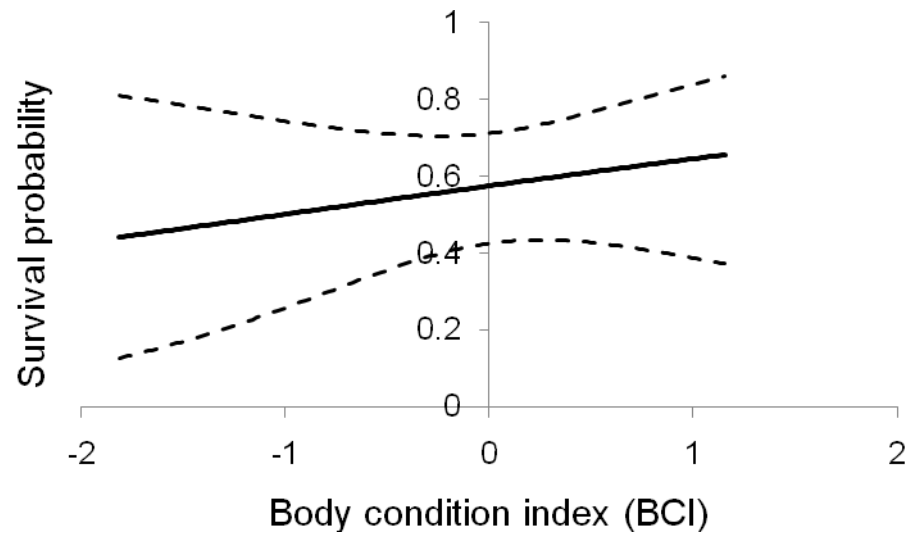


Figure 4.4: The effects of Body Condition Index (BCI) on estimated survival probability (solid lines) with upper and lower confidence intervals (dashed lines), estimated using Known Fate models in RMark.

4.4.5 JUVENILE SURVIVAL

In total 56 models were tested, details of the best ten are given in Table 4.3. The delta AICc values between the top seven models were small and so a model averaging approach was used. The mean (\pm SE) survival estimates across study year, season, treatment, sex and birth month was 0.60 ± 0.20 .

Table 4.3: Details of the top ten Known Fate models estimated by RMark for juvenile survival. Model = model structure; #parm = number of parameters; AICc = Akaike's Information Criteria, adjusted for small sample sizes; Δ AICc = difference between AICc scores; S = survival; Year = study year; Management = control, harvest; Sex = male, female; BCI = body condition index; Birth Month = March, April, May, June; Season = Early breeding = February – April; Late breeding = May – July; Post breeding = August – October; Winter = November – January.

Model	#parm	AICc	Δ AICc	weight	Deviance
1 S~Season+Management+Year+Birth Month	9	109.94	0	0.09	57.47
2 S~Season+Sex+ Birth Month	8	110.26	0.32	0.08	60.10
3 S~Season+ Birth Month	7	110.35	0.41	0.07	62.47
4 S~Season+ Birth Month +BCI	8	110.56	0.62	0.07	93.36
5 S~Season+ Management +Year+ Birth Month +BCI	10	110.64	0.70	0.06	88.78
6 S~Season+Sex+ Birth Month +BCI	9	111.02	1.08	0.05	91.51
7 S~Year+Sex+ Birth Month	6	111.67	1.73	0.04	66.03
8 S~ Management +Season+ Birth Month +BCI	9	112.20	2.26	0.03	92.69
9 S~ Management +Season+ Birth Month	8	112.28	2.34	0.03	62.12
10 S~Season+Sex+ Treatment + Birth Month	9	112.43	2.49	0.03	59.96

Overall, survival was lower in 2009 compared to 2008 and lower in the harvested area compared to the control. Leverets born in June had lower survival probability than earlier born leverets. There were similar seasonal patterns in survival in both years and between leverets

born from different birth months, although the post breeding mortality peak was larger in 2009 compared to 2008. The significant difference in survival probability between birth month, year and management can be seen in Figure 4.5. To aid interpretation, the effect of management and year, without the effects of season or birth month, are shown in Figure 4.6.

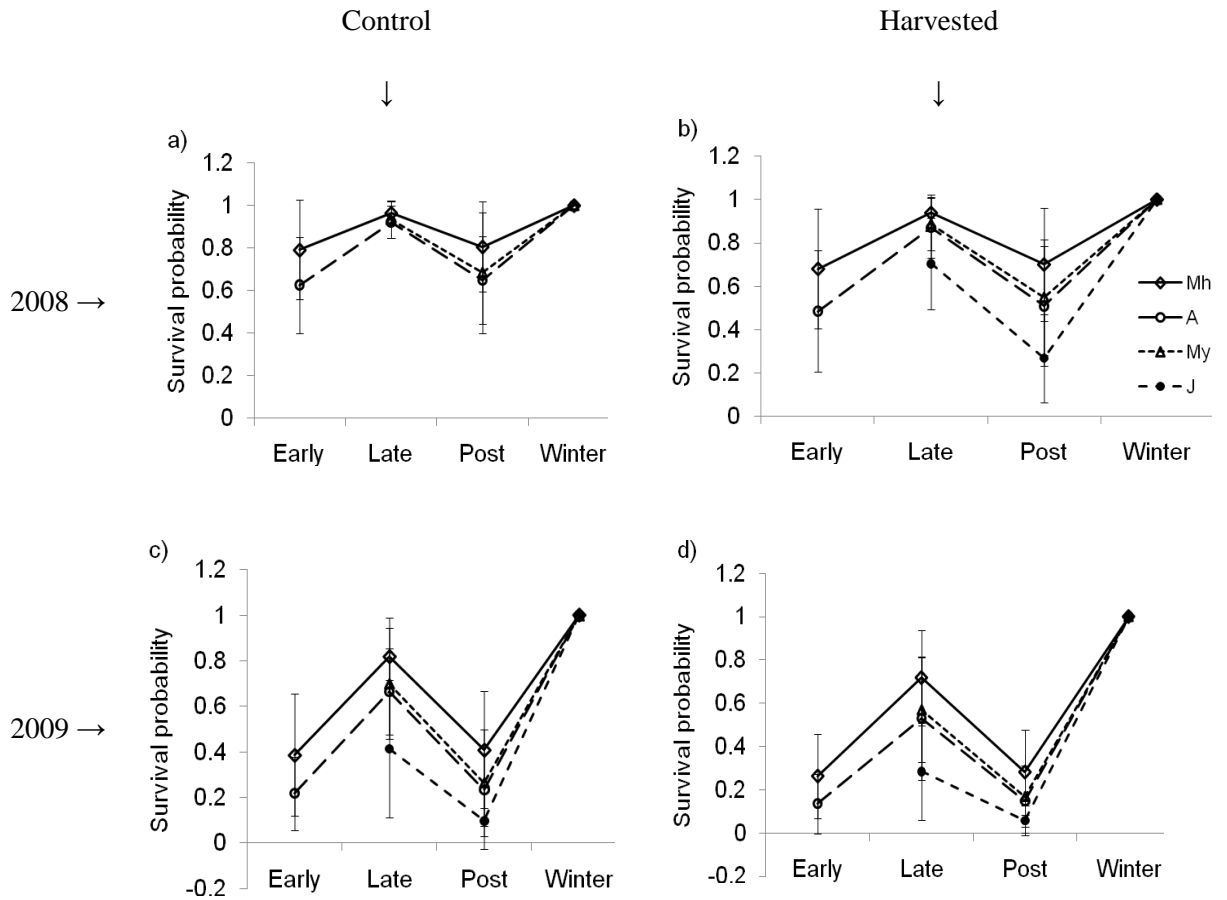


Figure 4.5: Survival probability for juveniles born in March (Mh) (diamond, solid line), April (A) (empty circle, large dash line), May (My) (triangle, dotted line) and June (J) (full circle, small dashed line) for a) control area in 2008, b) harvested area in 2008, c) control area in 2009, and d) harvested area in 2009, estimated using Known Fate models in RMark. Early breeding = February – April; Late breeding = May – July; Post breeding = August – October; Winter = November – January.

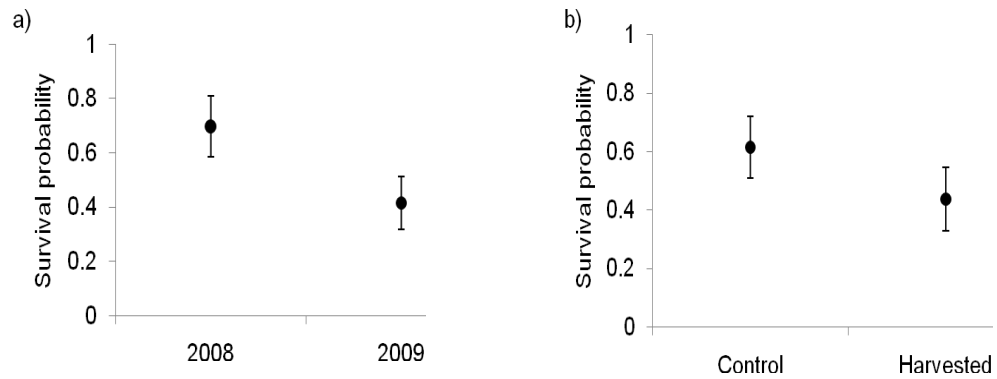


Figure 4.6: Differences in survival probability for all juveniles between a) years, and b) management, over the first 12 month in age, estimated using Known-Fate models in RMark.

Sex featured in Models 2, 6 and 7 and was included in the model averaged survival estimate. Overall, the mean (\pm SE) survival estimate was higher in females (0.62 ± 0.10) compared to males (0.40 ± 0.12). Body condition index (BCI) also appeared in Models 4, 5 and 6 and was included in the model averaged estimate. Survival probability appeared to decrease with increasing BCI, although the amount of variance around this estimate increased greatly with increasing BCI index (Figure 4.7)

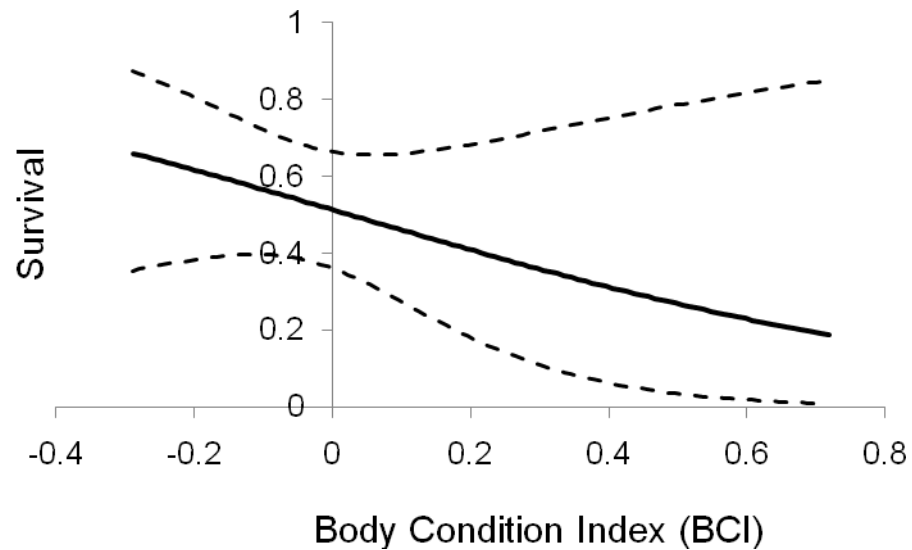


Figure 4.7: The decreasing survival probability estimates (solid line) and upper and lower confidence intervals (dashed line) with increasing body condition index (BCI), estimated using Known Fate models in RMark.

4.5 Discussion

Sustainable management of harvested small game populations relies on knowledge of compensatory mechanisms, such as survival. Here, we compared survival probabilities between harvested and non-harvested areas in Scotland in an attempt to find evidence of compensatory survival. Survival of mountain hare leverets is influenced by birth date which also dictates skeletal size in adulthood, another factor influencing survival probability. Therefore, any factor effecting birth date will also have implications for both juvenile and adult survival. Overall we found no evidence that individuals from the harvested area had greater survival probability compared to those from non-harvested area, and therefore there is no evidence of compensatory survival, However, survival differed between years suggesting

an environmental effect. That we didn't find evidence of compensatory survival could be due to either i) harvest pressure is negligible, or ii) harvest mortality is not compensated for by an increase in natural survival. We found that birth date was significantly later in the harvested area compared to the control, and also differed significantly between years. Within juveniles, survival was poorest in leverets born later in the breeding season, and was lower overall in the harvested area. Birth date was significantly later in 2008, when survival probability of juveniles was higher suggesting that the effect of the environment on survival overrides the effect of birth date.

4.5.1 BIRTH DATE AND BODY CONDITION

We observed a difference in birth date between year and management, indicating differences in the timing of breeding, and also that male leverets were born later than females. The difference in birth date between the sexes is likely to be an artefact of the aging method. Male leverets grow at a greater rate than females, yet males reach a smaller mass than females (Iason 1989a). This may result in males being consistently estimated as younger than females. The number of males and females was even across management area and year, and therefore, the significant difference in birth date between treatment and year are unlikely to be biased by the effect of sex on birth date estimation. Differences between years can be attributed to differences in environmental conditions. The effects of weather have been shown to affect the timing of breeding in rodents (Fichet-Calvet et al. 1999) and lagomorphs (Flux 1970; Hamilton 1940; Hewson 1970; Rodel et al. 2005; Wright & Conoway 1961). Adverse weather can affect vegetation quality and availability resulting in poorer body condition. In cotton rats, *Sigmodon hispidus*, lactating females under different energetic demands maintained body

mass but varied the amount and quality of milk to offspring (Rogowitz 1996). Hodges, Stefan & Gillis (1999) suggest that in times of nutritional deficit, female snowshoe hares may maintain mass during gestation and lactation, but reduce investment in reproduction.

The difference in birth date between the harvested and control area is more difficult to explain. Although we cannot exclude the possibility of an area effect caused by differences in some inherent quality of the two management areas, the two areas are managed by the same owner and land managers and therefore levels of habitat management and predator control should be consistent. Population density was shown not to differ and the proximity of the two areas to one another means that photoperiod and climate should not differ greatly. Although there are no *a priori* reason to believe growth rate would differ between leverets of the control and harvested areas, it is possible that differences in growth rate between the two areas could lead to the observed differences in birth date. It has been shown in the snowshoe hare that increased predation can lead to reduced body condition by affecting behaviour and foraging patterns (Hik 1995) and increasing levels of stress, which directly influences body mass (Boonstra et al. 1998). If hunting is considered a form of predation, female body condition could be affected by harvesting. We did not find a significant difference in body condition between the two areas in either sex. However, the effect of stress on body condition may not be detectable as, in times of poor nutrition, female hares may maintain body condition with costs to reproduction (Hodges, Stefan & Gillis 1999), such as timing of breeding (Rodel et al. 2005). In our study the mean birth date was significantly later in the harvested area than the control. However, the effects of hunting on foraging behaviour or stress levels have yet to be investigated in any hare species.

4.5.2 SURVIVAL

Population density did not differ between the harvested or control areas, or between seasons. This means that either the effect of harvesting at our study site is negligible, or that density-dependence in one or a combination of vital rates is compensating for increased mortality due to hunting in the harvested area. Although a large number of hares were taken from the harvested area, very few of them were radio collared hares. We therefore excluded shot hares from any of the survival models and so mortality rates reported here are of natural (i.e. not hunting) mortality alone. There was no difference in natural mortality rates between the harvested and control areas. If density-dependent survival was evident, natural mortality would be lower in the harvested area in order for increased survival to compensate for the increased mortality from hunting. That we found no evidence for compensatory survival in either adults or juveniles suggests that the level of harvesting within the harvested area was negligible. Indeed, harvest rates in the harvested area were low (between 15% and 23%), based on the number of individuals shot/population density.

In the overall survival model we found that survival probability increased with increasing BCI. This result would be expected as individuals in better condition with greater fat reserves will be more resilient to periods of poor weather or low food resources. However, in the juvenile study survival probability appeared to decrease with increasing BCI. This could be due to the residual index being an ineffective measure of body condition in young animals that are still undergoing growth. Body condition was estimated for each hare at first capture and this estimate may not truly represent the individual's body condition at any given time in the study

period. Repeated measures of body condition would enable changes in individual condition between seasons to be calculated and may prove a more accurate measure of relative body condition, particularly for leverets and juveniles (Hodges, Stefan & Gillis 1999) and could be included in the survival models as a time-varying individual covariate. Such data, however, may be logistically difficult to collect in species with low recapture rates, such as mountain hare.

Survival probability differed between and within years. Between year differences suggest environmental factors affecting survival probability either directly or indirectly through reduced body condition. The lowest survival occurred in the first half of 2010 which coincided with heavy snowfall, persistent snow cover and lowest recorded temperatures since 1985 in Scotland (Met Office 2010). Cold weather will increase energy requirements of thermoregulation and heavy snow cover will reduce available forage, and increase the amount of time spent foraging. Within years, survival followed seasonal patterns which differed between adults and juveniles. Adult peak mortality occurred in the late breeding season, May to July, similar to results of Iason (1989b), when energy reserves of both males and females will be low from high energy expenditure during breeding. In leverets, highest mortality occurred in the post breeding season, August to October, which again is similar to previous studies (Iason 1989a). This mortality coincides with declining vegetation growth and quality, and an associated dietary switch (Iason & Waterman 1988). Within leverets, survival was affected by birth date with later born leverets having the poorest survival. Leverets born later in the breeding season have a shorter growth period before the onset of declining vegetation quality and the dietary switch resulting in higher mortality (Iason 1989b). However, in 2009 leverets were born earlier than in 2008 but juvenile survival overall was lower for 2009. This

could be due to leverets being exposed to mortality risk for a greater period of time (Iason 1989a), or to harsher weather in 2009.

Leveret survival was lower in the harvested area overall. This could be directly linked to the timing of breeding, with a higher proportion of later born leverets with predisposed lower survival probability. Alternatively, increased stress levels amongst adults caused by hunting could affect maternal body condition, which is maintained by compromising lactation or gestation (Hodges, Stefan & Gillis 1999). It was shown that captive hares fed on higher quality feed produced heavier leverets at birth than females fed poorer quality feed (Pehrson & Lindlof 1984). It could be that adults invest less in gestation when trying to maintain body condition resulting in smaller offspring, or invest less in lactation leading to slower growth rate and smaller offspring (Rogowitz 1996). The implication is that smaller leverets are prone to higher mortality than larger leverets (Hewson 1968; Iason 1989a).

4.6 Management implications and conclusion

Timing of breeding differed between years and management areas. Although the causes of these observations remain speculative, the results have important management implications. Leverets born later have lower survival probability and those that do survive grow to become smaller adults than leverets born earlier (Iason 1989b). Smaller adults are then subjected to higher mortality rates (Iason 1989a). Reproduction is also related to size, with larger adults attempting reproduction earlier and sustaining a higher level of reproductive activity longer than smaller individuals. The result is more offspring being produced over the entire breeding season by larger adults (Iason 1990).

We found no evidence for compensatory survival in Scottish mountain hare. In fact, juvenile survival was lower in the harvested area than the control. This could be linked to later birth dates on average, or an indirect effect of harvesting effecting maternal condition (Boonstra et al. 1998; Hik 1995) which is maintained at a compromise of reproduction (Hodges, Stefan & Gillis 1999). This results in smaller and/or later born leverets, with the consequence of a predisposed lower survival probability (Iason 1989b). Survival also differed between years suggesting survival is influenced by environmental factors. Therefore, both direct effects of current conditions (either environmental or management) on survival, and indirect effects of current conditions on survival of future generations via the effects on timing of breeding and offspring size, could be expected.

Mountain hares show unstable population dynamics and drivers of these dynamics remain inconclusive (Newey et al. 2007b; Newey et al. 2007a). There is increasing awareness that multiple factors may regulate populations and that the causes of cycles may include complex interactions between trophic interactions, individual variability and environmental variation (Bjornstad & Grenfell 2001; Lundberg et al. 2000). Until the effects of environmental variation and harvesting at the individual (physiological) and population level become more clearly resolved, and their ability to effect mountain hare population cycles is better understood, harvesting rates of mountain hare in Scotland should remain conservative.

Chapter 5

Population density and breeding performance of mountain hare in Scotland

5.1 Abstract

Density-dependent processes, specifically feedback between population density and demographic parameters, play a central role in driving population dynamics, and are particularly important in managing exploited or harvested populations. The mountain hare, *Lepus timidus*, is a traditional game species and killed in Scotland for sport and, increasingly, for disease control. However, information about how reproductive parameters respond to changes in population density is lacking. We collected a sample of killed hares from ten independent private hunting estates and assessed the effects of hare density on female fecundity and juvenile recruitment into the breeding population. We found no evidence of density-dependent fecundity, but found a significant negative correlation between population density and the proportion of juveniles, indicating negative density-dependence acting on juvenile recruitment. The results suggest the potential for compensatory juvenile recruitment, which may increase the resilience of populations to hunting. Compensatory juvenile recruitment may also act to reduce efficacy or cost-benefit of culling mountain hares as part of disease control measures. We conclude that the effect of population density on the age-structure of mountain hare populations has the potential to influence population dynamics, and consequently, viability and persistence.

5.2 Introduction

The role and relative importance of the interaction between population density and the basic demographic parameter rates; births, deaths, immigration and emigration, are fundamental questions in ecology. Despite the historic and ongoing debate over the mechanism of population regulation and population limitation (Sinclair 1989), density-dependence; the feedback between population density and demographic rates, remains a central principle in population ecology. Population density has been demonstrated to affect survival (Angerbjorn 1986), dispersal (Matthysen 2005) and reproduction (Both 1998; Coulson, Milner-Gulland & Clutton-Brock 2000; Soutullo et al. 2006) for many terrestrial vertebrate populations. Negative density-dependent reproduction (whereby an increase in population density leads to a decrease in reproductive rates) has been detected in both birds (Both 1998; Dhont, Kempnaers & Adiaensen 1992) and mammals (Coulson, Milner-Gulland & Clutton-Brock 2000).

If, as a result of density-dependence, reducing a population by harvesting leads to increased survival or reproduction, resulting in a relative increase in population growth, the effect can be described as compensatory (Boyce, Sinclair & White 1999). Therefore, density-dependence is an essential pre-requisite for compensatory mechanisms and sustainable harvesting and if harvesting occurs at the same rate as population growth, sustainable harvesting can be achieved (Caughley & Gunn 1995; Sutherland 2001).

To understand the effects of population density on effective annual reproduction, and implications on population dynamics, it is important to consider both fecundity (the numbers of live offspring a female gives birth to) and recruitment (the numbers of young born that subsequently survive to enter the population and breed themselves). A reduction in fecundity

or juvenile recruitment can occur at high population density via decreased access to resources, through increased competition or environmental degradation (Kruger & Lindstrom 2001; Rodenhouse, Sherry & Holmes 1997; Sillett, Rodenhouse & Holmes 2004; Sutherland & Norris 2002). The effects of population density on juvenile recruitment can lead to changes in the age structure of populations. Those composed of older individuals may have different population growth potential than those composed of younger individuals, influencing the population response to harvesting (Sinclair, Fryxell & Caughley 2006).

Throughout their circumpolar distribution, mountain hares, *Lepus timidus*, show unstable population dynamics (Newey et al. 2007b; Newey et al. 2007a; Reynolds, O'Mahony & Aebischer 2006). In Scotland, mountain hare populations show high amplitude cyclic, or unstable, population dynamics with a mean periodicity of 9.5 years (Newey et al. 2007b), further complicating sustainable management of this species (Lande, Engen & Saether 2003a). Drivers of mountain hare population dynamics remain unclear (Newey et al. 2007a; Townsend et al. 2009; Townsend et al. 2011). Although the nematode parasite *Trichostrongylus retortaeformis*, has been implicated as a driver of mountain hare population cycles (Newey et al. 2005; Newey et al. 2007a; Newey & Thirgood 2004), modelling studies of the hare-parasite system do not support the hypothesis that parasites alone can drive population dynamics (Townsend et al. 2009). Further modelling studies have shown that juvenile survival is potentially an important determinant of parasite infection in adult hares and may be an important factor in destabilising mountain hare population dynamics (Townsend et al. 2011). Knowledge of the relationships between population density and female fecundity, juvenile recruitment, and population age and sex structure are important in understanding the dynamics

of Scottish mountain hare populations. However, few studies to date have investigated the effects of population density on reproduction in mountain hare.

Following population density, survival and fecundity of a Scottish mountain hare population over one 10-year cycle, Hewson (1976) found higher rates of reproduction during the low and increasing phases of the cycle, and higher juvenile survival rates during the increase phase of the cycle. However, breeding success in this study was estimated as the proportion of leverets snared in autumn, which may not be a very precise measure of reproductive performance (Hewson 1976). Angerbjorn (1986) compared island populations of different population densities and found that although litter size was unaffected by density, juvenile recruitment was higher on islands and in years with lower density populations (Angerbjorn 1986). However, findings of this study should be treated with caution as it is unknown whether isolation of these island populations from one another, and the mainland, over the time period since the last ice age has intrinsically changed hare demography or dynamics within each population (Newey et al. 2007a).

Mountain hares have been traditionally harvested in Scotland for centuries. Despite this, there is a paucity of knowledge about how demographic parameters respond to changes in population density or harvesting (Tapper 1992). Furthermore, mountain hares are increasingly culled to control tick-borne disease (Patton et al. 2010). In addition to climate change, hybridisation with the brown hare, *L. europaeus*, (Thulin, Jaarola & Tegelstrom 1997) and changes in land use (Robertson, Park & Barton 2001), overexploitation has raised concern over the long term status of this species in Britain (Battersby 2005). The aim of this study is to investigate whether population density affects fecundity and recruitment in Scottish mountain

hare populations. Specifically, we tested the following non-exclusive null hypotheses: H₀1) There will be no relationship between population density and the proportion of juveniles in the population, H₀2) There will be no relationship between population density and litter size, and H₀3) There will be no relationship between population density and prenatal mortality.

5.3 Methods

5.3.1 STUDY SPECIES AND SITES

The study was carried out on ten independently managed grouse moors (labelled A-L) across the Central Scottish Highlands. Mountain hares were shot or snared as part of routine estate management or sporting activities between January and April 2009. In Scotland, mountain hares begin mating in late January, with leverets being born from March onwards, although they do not breed in the year of their birth (Flux 1970; Hewson 1976). Therefore, hares collected in this study were either breeding for the first time (juvenile), or had survived at least one previous breeding season (adult). With a 50 day gestation, and post-partum mating within hours of giving birth, female mountain hares typically produce up to three litters a year, although four is theoretically possible (Hewson 1976). Mountain hares are usually hunted from December to April, therefore measures of fecundity used for this study only apply to the first litter. Samples collected from two study sites (Sites E and G) where hares were shot in January (i.e. prior to the breeding season) are omitted from the fecundity analysis. Harvest pressure for each estate was assigned to a harvest pressure category (high, medium, low) based on numbers shot ha⁻¹/density and the opinion of gamekeepers. Estates H, J and L confirmed that the primary purpose for hare shooting was for disease control. Estate code, the date hares were shot and the total number of females (for fecundity analysis), all hares (for age structure

analysis) and harvest pressure of each estate are shown in Table 5.1. All hares that were shot were included in the study and so the total numbers of hares represents the total number of hares shot on each estate.

Table 5.1: The estate code, date that hares were killed and the total number of females (for fecundity analysis, * = sites excluded from fecundity analysis) total number of hares of both sexes (age structure analysis) and harvest pressure.

Estate Code	Date samples collected	Number of females	Total number of hares	Harvesting pressure
A	01/04/2009	10	29	Low
B	23/03/2009	10	19	Low
C	24/03/2009	9	20	Medium
D	26/03/2009	16	27	Medium
E	08/01/2009	12	23	High
G	02/02/2009	10	16	Low
H*	05/03/2009	8	15	Medium
J*	05/04/2009	16	27	High
K	09/03/2009	17	37	Medium
L*	24/03/2009	7	20	High

*Hares shot for disease control

5.3.2 POPULATION DENSITY ESTIMATES

Population assessment of small, nocturnal and cryptic species, like mountain hares, is difficult. Distance sampling (Buckland et al. 2001; Thomas et al. 2010) has been shown to be effective at estimating mountain hares in the Scottish uplands (Newey et al 2003). Here we use Distance sampling to estimate population density prior to any hunting of the hares. Four to twelve parallel transect lines spaced 500 m apart, were placed over each study area. Each transect line varied between 0.5 - 4.5 km long, depending on the size and shape of the area over which hares were to be killed. Transects were orientated parallel to the altitude gradient in order to account for changes in vegetation or hare density with altitude. Transect lines were traversed on foot by a single observer. Adjacent transect lines were not sampled on the same day to minimise repeated counting of hares flushed from one transect line to the next. Hares are generally crepuscular, with increased activity at dusk and dawn (Angerbjorn & Flux 1995). Therefore, to reduce bias in detection probability caused by diurnal changes in activity rates, surveys were not carried out within an hour of sunrise or sunset. When hares were sighted, the time and distance, estimated using a laser range finder (Bushnell YardagePro, Bushnell, Denver Co, USA), and the bearing to the hare, measured with a sighting compass, were recorded. The sighting angle and distance were used to estimate the perpendicular distances used in Distance analysis, data were analysed using DISTANCE 5.0 (Thomas et al. 2010).

Due to a low number of hare sightings at some sites, we pooled distance data from all sites, used a global detection function and estimated mountain hare density for each study area by post-stratification. The greatest 5% of perpendicular distances in the data were truncated to remove outliers and increase precision (Buckland et al. 2001). We identified the best fit

detection function by comparing the distribution of perpendicular distances with a range of candidate models. Model fit was first visually assessed by examining histograms and q-q plots, where special attention was paid to the crucial model fit close to the transect line. The best fit model was selected as the model with the lowest AIC score, χ^2 goodness of fit tests and results of the Kolmogorov–Smirnov test for normality for the distribution of perpendicular distances.

5.3.3 TISSUE SAMPLE COLLECTION

Tissue samples were collected within 48 hours of the hares being killed. Body mass and hind leg length (from the talocrural joint to the base of the longest toe, excluding the claws) were recorded prior to post mortem. Both jaw mandibles were extracted, and the right kidney and associated kidney fat (fat that came away with the kidney) were removed and frozen within 12 hours and stored at -20°C until processing. Animals were sexed by internal examination and for each female the uterus was removed and examined. If present, foetuses were counted and length (crown to rump) recorded. Uteri were stored in 70% alcohol. Both ovaries were removed and placed immediately in 4% formalin for 24 hours, before being transferred and stored in 70% alcohol.

5.3.4 BODY CONDITION AND SKELETAL SIZE

The kidney and its kidney fat were weighed separately. We derived an index of body condition calculated as mass of kidney fat divided by mass of kidney (Finger et al. 1981). Hind leg length was used as a measure of skeletal size (Iason 1990). Although sexual dimorphism in

body size is apparent, with females being the larger sex, body size was only used in the female fecundity analysis and so will not bias our results.

5.3.5 FECUNDITY ESTIMATES

A total of 93 females were killed across eight sites; details of sample sizes and date of sample collection are shown in Table 5.1. The majority of post-implantation loss of litters occurs before half-term, when foetuses are 1-2cm in length (Flux 1970). With the exception of three foetuses, all from different study sites, all foetuses were >3cm in length, therefore, we assume that embryo loss is low and the number of foetuses represents the number of young born. Post-implantation losses may have occurred prior to sampling that we were unable to detect, therefore we derived an ovulation rate for each female. Both ovaries from 50 females from five sites, two high density (Site A and B) and three low density (Site H, J and L) were cut laterally, and the four halves embedded into four wax blocks and each block cross-sectioned at 5 μ m. For each block, the 5th, 10th and 15th section were mounted onto a microscope slide, and stained with hematoxylin and eosin (H&E) (VWR International, Pennsylvania, USA; TAAB Laboratories Equipment Ltd, Berks, UK) to give a total of 12 sections per ovary. This enabled mature Graafian follicles and corpora lutea (CL), the structure that remains after follicles that have shed ova, to be counted. Both ovaries from the remaining 42 females from three medium density sites (Site C, D and K) were cross-sectioned by hand every 1mm and CL counted under a 10x stereomicroscope. Cross sectioning by hand does not allow follicle health to be assessed. However, the large size of CL during gestation (7 - 11mm in diameter (Angerbjorn & Flux 1995; Harrison et al. Unpublished data)) means that the CL can be counted as reliably in hand sectioned ovaries as in the stained ovary sections. Therefore, the CL counts of the

different methods are comparable. The appearance of the CL in both stained and hand-sectioned ovary sections can be seen in Figure 5.1. Corpora lutea counts can be used to give an estimate of the number of ovulations (Iason 1990; Newey et al. 2010; Newey & Thirgood 2004) and when numbers of foetuses are subtracted, prenatal mortality (Iason 1990).

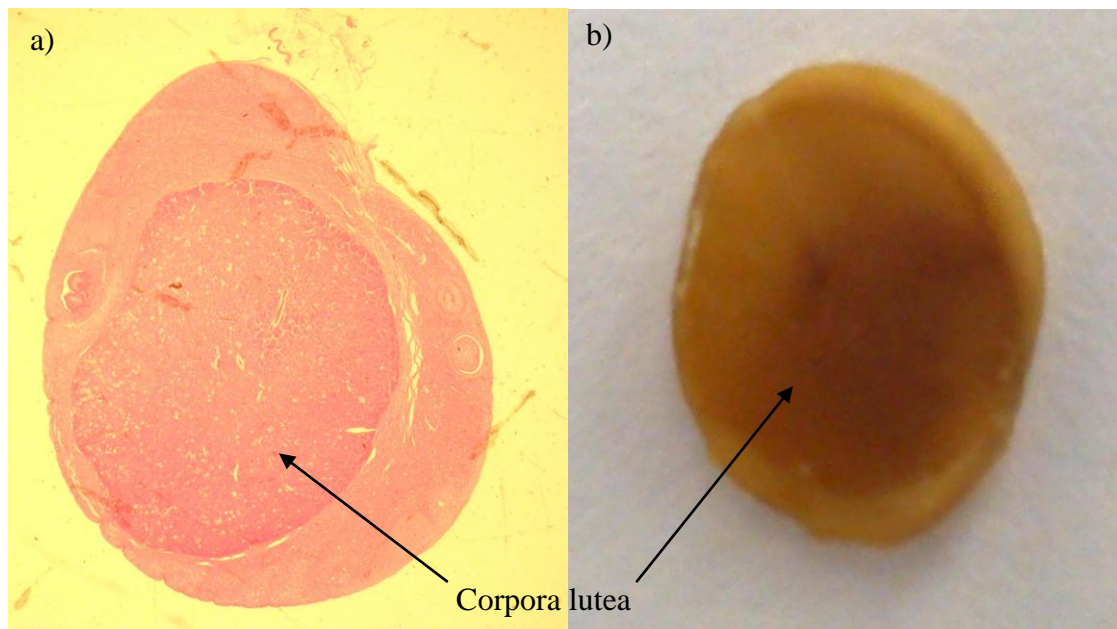


Figure 5.1: Corpora lutea of mountain hare ovaries a) cross-sectioned and stained with H&E, and b) cross-sectioned by hand.

5.3.6 AGE DETERMINATION

We estimated the age of shot hares by counting adhesion lines in the lower mandible. These lines are formed by differing bone density produced by seasonal changes in growth, giving rise to annual ‘rings’ in the periosteal zone of the jaw bone (Frylestam & Schantz 1977; Henderson & Bowen 1979; Iason 1988; Morris 1972; Ohtaishi, Hachiya & Shibata 1976). Jaw

bones were cut using a circular saw and polished with a fine grade emery paper to create a smooth bone surface allowing the adherence lines to be counted using a 10x stereomicroscope (Figure 5.2).

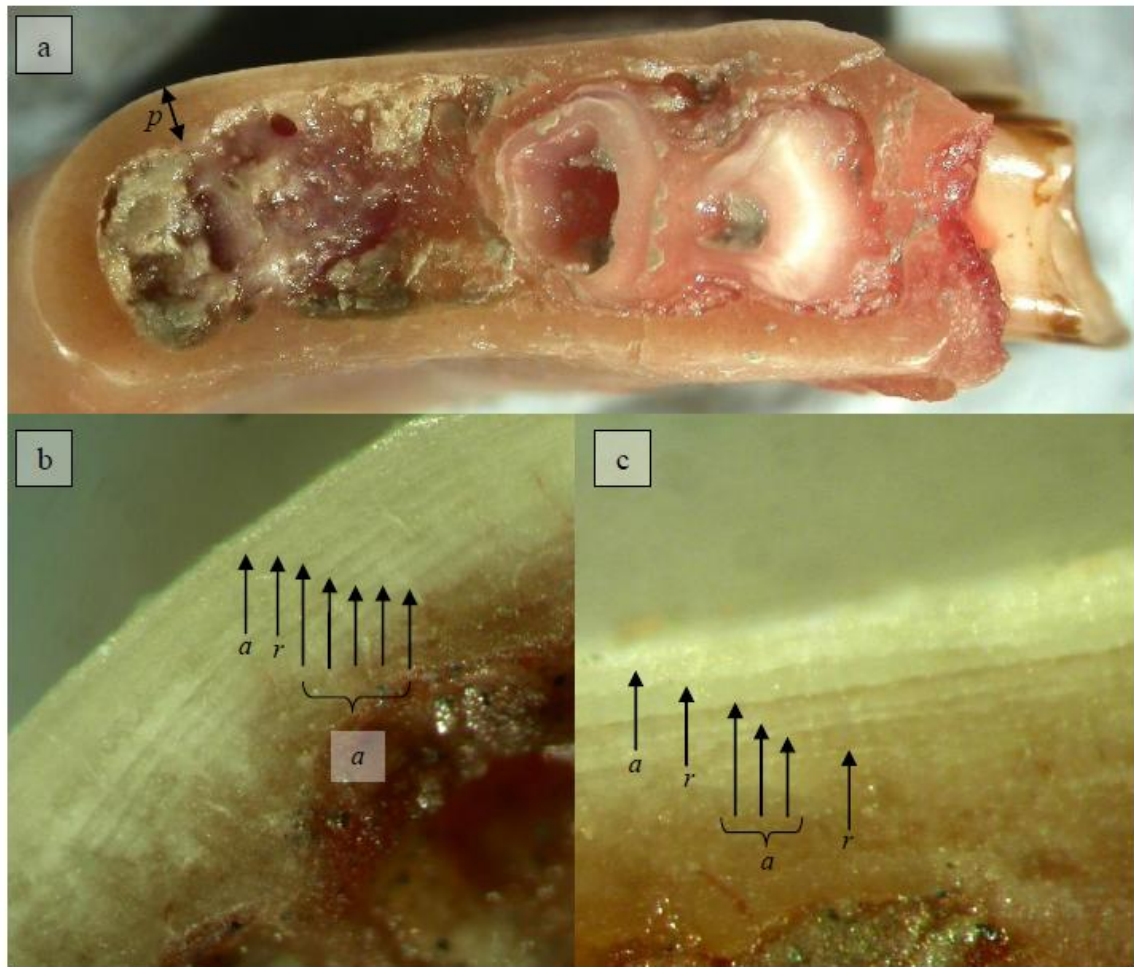


Figure 5.2: a) cross section of the lower mountain hare mandible prepared for interpretation showing periosteal zone (*p*); b) annual (*a*) and reabsorbed (*r*) growth lines of a six year old mountain hare; c) annual (*a*) and reabsorbed (*r*) growth lines of a four year old mountain hare.

Due to a low number of individuals with an age greater than two years (Table 5.2), actual age was not used in any analyses. Instead individuals were categorised as juvenile (1 year of age) and adult (2 years of age or more).

Table 5.2: Frequency of individuals in each age group for all 233 shot hares across all ten sites.

Age (years)	Total number of individuals at each age
1	127
2	74
3	24
4	6
5	1
6	1

5.3.7 STATISTICAL ANALYSIS

Analyses were performed using the lme4 package (Bates & Maechler 2010) for R v2.12.0 software (R Development Core Team 2010). The effect of population density, body condition (kidney fat index), skeletal size (hind foot length), previous breeding experience (juvenile or adult) and hunting method (shot or snared) on litter size and prenatal mortality of litter one were assessed using a Generalised Linear Mixed Model (GLMM) with Poisson errors and log link function. To account for uncontrollable differences between sites, such as climate and vegetation quality, we include site in the model as a random effect. As all females included in

the fecundity analysis were shot within a month of each other (Table 5.1), date of sample collection is unlikely to confound reproductive status of females between sites and so was not included in the model. The effect of population density, method of hunting and sex on the proportion of juvenile animals in the killed sample were assessed using a GLMM with binomial errors and logit link function with site included in the model as a random effect. We first specified the full model including all terms and second order interactions, and then sequentially removed terms through a process of stepwise deletion of the least significant term, determined by the t value closest to zero. Candidate models were compared, and the best fit model chosen, using Log-Likelihood Ratio Tests (LRT).

5.4 Results

5.4.1 POPULATION DENSITY ESTIMATES

Model selection suggested that the half-normal cosine model fitted the histogram of perpendicular distances best, indicated by the visually good fit of the half-normal cosine model to the histogram of perpendicular distances (Figure 5.3) and by the highest p values of the Kolmogorov–Smirnov and χ^2 tests (Table 5.3).

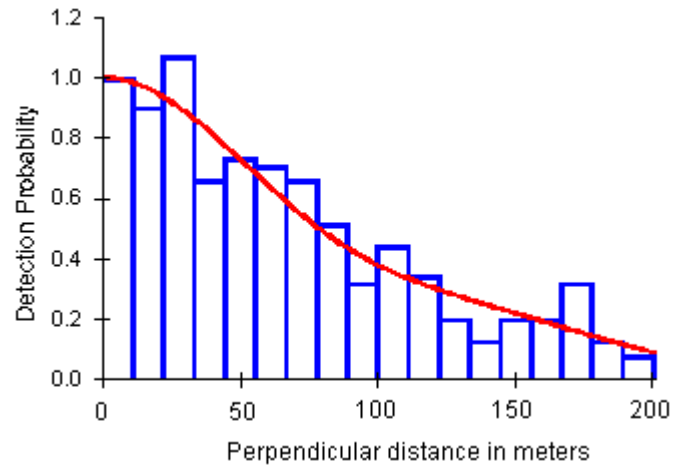


Figure 5.3: The probability of detecting mountain hares decreases with increasing perpendicular distance. The red line is the detection function as fitted by the half-normal cosine model while the blue histograms indicate the detection probability of individuals sampled at different perpendicular distances.

Table 5.3: Details of distance analysis using a global detection function. Abbreviations are as follows: Key=key term with HN= half-normal and HR=hazard rate; E=expansion term with C=cosine, SP=simple polynomial and HP=hermite polynomial; AIC=Akaike's Information Criteria; ESW=effective strip width (the distance from the line for which as many individuals are detected passed this distance as are missed within this distance); D=density hares ha^{-1} (global density); LCL= lower 95% confidence limit; UCL= upper 95% confidence limit; CV= coefficient of variation; K-S p= probability (Kolmogorov–Smirnov); and χ^2 p=probability (χ_2)

Key	E	AIC	ESW	D	LCL	UCL	%CV	K-S p	χ^2 p
HN	C	3590.5	95	0.131	0.09	0.18	16	0.956	0.103
HN	SP	3591.1	102	0.121	0.09	0.167	16	0.858	0.090
HN	HP	3593.9	109	0.113	0.07	0.168	20	0.172	0.013
HR	C	3591.1	102	0.121	0.09	0.167	16	0.858	0.090
HR	SP	3591.6	102	0.121	0.09	0.167	16	0.858	0.08
HR	HP	3591.1	102	0.121	0.08	0.181	21	0.858	0.090

Taking the half-normal cosine model, global population density was estimated at 0.13 hares ha^{-1} , with post-stratification of data allowing estimation of population density for each site shown in Figure 5.4.

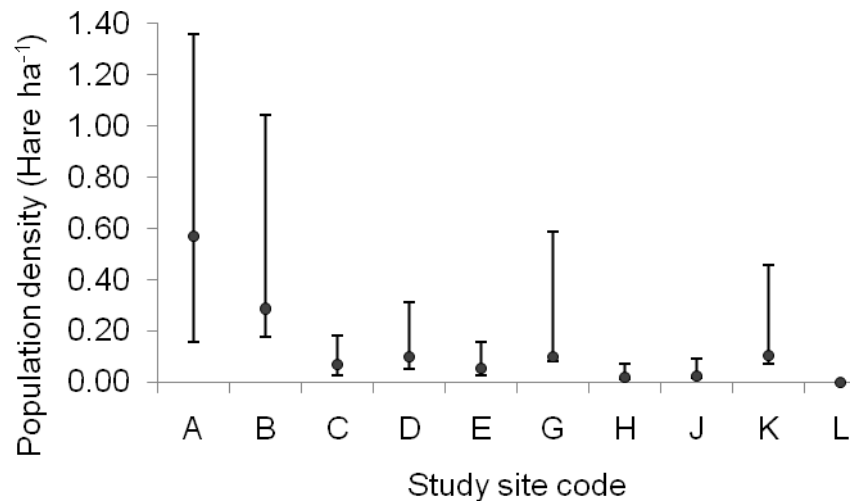


Figure 5.4: Population density (hares ha⁻¹) estimates for each site (coded A – L for anonymity) following post-stratification of global population density. Error bars show upper and lower 95% confidence limits.

Pre-harvest population density varied from 0 to 0.56 hares ha⁻¹. However, only 3 out of the 10 sites had a population density higher than 0.1 hares ha⁻¹, resulting in the low global density shown in Table 5.2. Due to the amount of error estimated for each point estimate, confidence limits of each site overlapped with the site immediately higher or lower. However, the two highest density sites (A and B) had confidence limits that did not overlap with the three lowest density sites (H, J and L) and so population density of sites A and B were significantly greater than of sites H, L and J (Figure 5.4).

5.4.2 FEMALE FECUNDITY

The mean litter size across all sites was 1.35 (± 0.08) and mean prenatal mortality was 0.59 (± 0.09) ova per female. Overall, 29.3% of ova shed did not result in a developed foetus. Both litter size and prenatal mortality appear to be slightly greater than those of a previous study on Scottish mountain hare reproductive biology. Iason (1990) found between 19% and 23% mortality of embryos or ova and litter sizes of 0.56 in the first litter period. Differences are likely due to variation in factors such as population density, climate and land use, that may have occurred between data collection of the current study (2009) and data collection of Iason's (1990) study (1984). Five females out of a total of 93 (5.4%) showed signs of neither pregnancy nor ovulation. These five individuals came from different sites and were of different ages.

None of the second order interactions significantly reduced the log-likelihood ratio compared to the full additive model ($p > 0.2$ in all cases). Population density, skeletal size, body condition and hunting method had no significant effect on litter size or prenatal mortality of the first litter period, and in both cases the null model (no explanatory variables) was the best fit model (Table 5.4). Although results of the LRT suggest that keeping previous breeding experience in the litter size analysis would almost significantly improve model fit, there appeared to be no difference in mean (\pm SE) litter size between juveniles (1.41 ± 0.17) and adults (1.41 ± 0.20).

Table 5.4: The χ^2 values, degrees of freedom (d.f.), and p values of the LRT, and order of deletion of each explanatory variable from the full additive GLMM for both litter size and prenatal mortality of the first litter period.

Explanatory Variable	Litter Size				Prenatal Mortality			
	χ^2	d.f.	p	Order	χ^2	d.f.	p	Order
Skeletal size	0.36	1	0.55	1	5x10 ⁻⁵	1	0.9	1
Method	0.59	1	0.44	2	0.68	1	0.41	4
Density	1.80	1	0.18	3	1.08	1	0.30	5
Body condition	2.34	1	0.13	4	1.97	1	0.16	3
Previous breeding experience	3.63	1	0.06	5	0.35	1	0.55	2

5.4.3 JUVENILE RECRUITMENT

The proportion of juvenile individuals in the samples of killed hares significantly decreased with increasing population density (Estimate=-6.36, se=2.23, z=-2.85, d.f.=5, p=0.004). Further, there was a significant interaction between population density and sex (Estimate=5.40, se=2.45, z=2.21, d.f.=5, p=0.03), with model selection supported by the LRT ($\chi^2=6.55$, d.f.=1, p= 0.01). This result indicates that the proportion of male juveniles is higher than female juveniles and that the effect of increasing population density on the proportion of juveniles differs between the sexes showing that juvenile recruitment becomes increasingly male biased with increasing population density. The slope describing the relationship between

the proportion of male juveniles and population density is less steep than the slope for the proportion of female juveniles with population density (Figure 5.5). There was no significant effect of hunting method (i.e. snaring vs shooting) on the proportion of juveniles (Estimate=-0.78, se=0.51, z=-1.5, p=0.13), with deletion from the model supported by the LRT ($\chi^2=2.31$, d.f.=1, p=0.13).

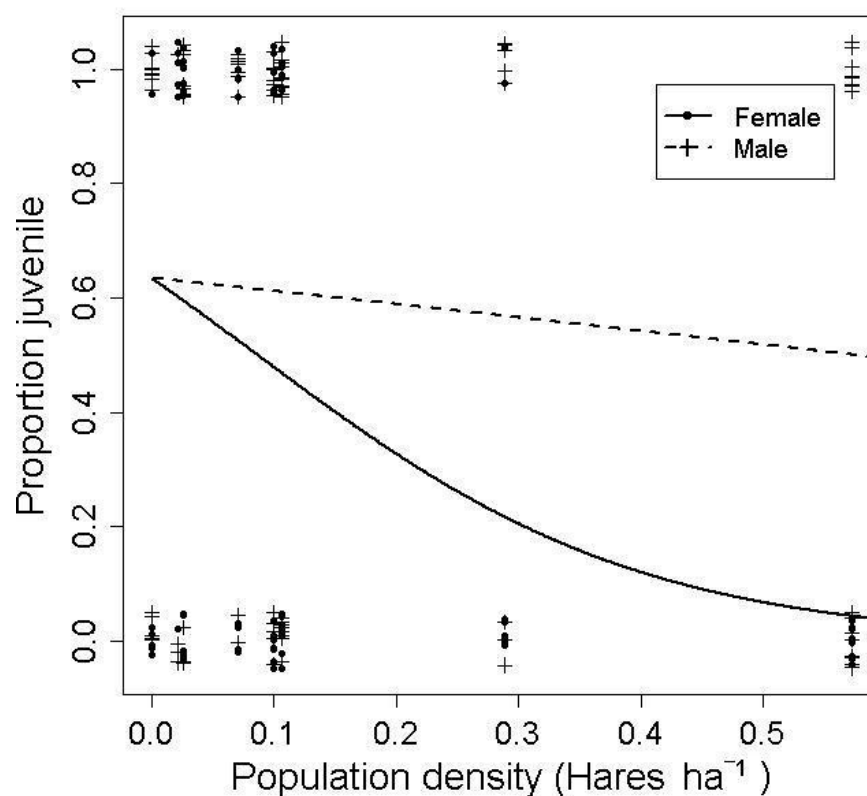


Figure 5.5: The proportion of female juveniles (solid line) declines more steeply with increasing population density (hares ha⁻¹) than the proportion of juvenile males (dashed line). Observed data for individual hares is also shown for both females (solid circle) and males (cross); points are jittered around 0 (adult) and 1 (juvenile) to aid interpretation.

5.5 Discussion

Although the mountain hare has been traditionally harvested in Scotland for centuries, little is known about how harvesting, or changes in population density, effect population dynamics or demography in this species (Tapper 1992). Here we have investigated the effect of population density on fecundity and recruitment of ten mountain hare populations. We found evidence of negative density-dependent juvenile recruitment with juvenile recruitment becoming male biased with increasing population density. However, no relationship between population density and either litter size or prenatal mortality were found, and therefore, we found no evidence of density dependence in either litter size or prenatal mortality.

5.5.1 FEMALE FECUNDITY

In mountain hares, the number of leverets produced in the first and second litters in any one year negatively affect the number in the third litter of the year (Iason 1990). This complex relationship between litter sizes of different litter groups makes it difficult to infer, from information on litter size one alone, how population density affects annual fecundity. We found no evidence for density-dependent female fecundity in either litter size or prenatal mortality. That we did not identify a significant affect may be due to focusing on the first litter group, repeating the study with annual fecundity rates would produce more comprehensive results. However, unless mountain hares are killed at the end of the breeding season, annual fecundity rates cannot be obtained until reliable non-destructive methods of fecundity assessment are available. Microclimate and other environmental conditions, such as habitat quality and quantity, are likely to differ between sites, years and between successive litters. These uncontrolled, indeed uncontrollable, variables could lead to differences in carrying

capacity between the different sites, confounding the effects of population density on vital rates, including fecundity. Across the sites and population densities sampled here, there was a low variability in both litter size (1.35 ± 0.08) and prenatal mortality (0.59 ± 0.09) which may suggest that fecundity is limited more by physiological factors than environmental factors (Hodges, Stefan & Gillis 1999).

5.5.2 JUVENILE RECRUITMENT

The proportion of juveniles found in the sample of killed hares was significantly higher at lower density sites. As female fecundity is unaffected by population density, the higher proportion of juveniles at low density will be the result of increased juvenile survival or immigration, and not of increased number of offspring born per female. Our results concur with Angerbjorn's (1986) study, where a significant negative correlation of juvenile recruitment with population density was observed, but no relationship between density and litter size or number of litters was found. This suggests that higher juvenile recruitment, rather than greater female fecundity, increases the proportion of juveniles at low population density. Negative density-dependent juvenile recruitment could be a result of improved habitat quality at low density reducing resource competition with the result of increased survival or immigration of juveniles (Rodenhouse, Sherry & Holmes 1997; Sutherland & Norris 2002).

There were higher proportions of juvenile males compared to juvenile females across all sites and population densities. A significant interaction between sex and population density shows that with increasing population density, the proportion of juvenile females decreased more steeply than the proportion of juvenile males. This could be indicative of different survival rates between the sexes, with lower juvenile survival in females at high density than males.

Life-history theory predicts that on the basis of sexual dimorphism in body size, mortality should be higher in the larger sex due to a faster growth rate and higher nutritional demands (Clutton-Brock, Albon & Guinness 1985). Although previous studies have failed to find male biased survival (Iason 1989a), this could be due to absence of nutritional limitation in the productive heather moorland of this study.

The higher proportion of male juveniles at high population density we report here could be due to higher competition for resources at high population density leading to higher mortality in the larger sex (i.e. female mountain hares) at high population density. Alternatively, female-biased density-dependent dispersal at high population densities may also lead to fewer juvenile females being observed in the high density breeding populations when our samples were collected. Density-dependent dispersal has been documented in many species. However, in polygamous species, such as mountain hares, dispersal is usually male-biased (see Matthysen 2005 for review). Although a study on natal dispersal of mountain hare in Sweden found no evidence for sex-biased dispersal (Dahl & Willebrand 2005), sample sizes in that study were small. In Chapter 3, I found that although dispersal distances did not significantly differ between the sexes, females tended to disperse greater distances. Model selection favoured the inclusion of sex, indicating that a larger sample size may produce significant results. Further, in the brown hare, males dispersed more frequently but females on average moved longer distances (Bray et al. 2007). This sex difference however was not affected by population density (Bray et al. 2007), which runs contrary to the idea of female-biased dispersal leading to low proportions of juvenile females at high density. The effect of harvesting and changing population density on survival rates and dispersal in Scottish mountain hare populations are key areas for future research.

It is possible that population density effects the sex ratio of offspring produced as seen in the red deer, *Cervus elaphus*, (Kruuk et al. 1999). Under nutritional stress, *in utero* mortality of male calves is higher than female calves. At high population density, competition for resources is higher and so hinds bias production of young towards females, which have a greater chance of survival, and so increase lifetime fitness of the mother (Kruuk et al. 1999). In mountain hares, prenatal mortality is higher in litter period one when conditions, such as weather, are harsher (Iason 1989a). Therefore it is likely that prenatal mortality will be affected by nutrition. However, there is no evidence of a link between population density and nutritional stress, nor is it known if *in utero* mortality differs between the sexes.

In high density red grouse populations, more young were shot than were expected from pre-shooting grouse counts, demonstrating an unintentional harvest bias towards juveniles (Bunnefeld et al. 2009). Unintentional hunting bias in mountain hares could result in more juvenile males being shot at high densities, although this has yet to be tested. A comparison of individuals captured by live traps and individuals flushed into nets, found heterogeneity in capture probability between capture methods (Bisi et al. Submitted). However, this study found that adults were more likely to be caught than juveniles, and females more than males (Bisi et al. Submitted), a trend also reported by Flux (1970), which goes against the idea of male and/or juvenile bias in shooting. Juvenile mountain hares were more likely to be caught in traps than in nets (Bisi et al. Submitted), with the same observation recorded for brown hare (Smith et al. 2004). It has been suggested that juveniles use burrows more often than adults to escape while being chased during long-netting (Flux 1970), a tactic that could also be employed during hare drives, resulting in adult-biased harvesting. Nevertheless, the presence of sex and age bias in the probability of mountain hares being captured, shot or snared,

stresses that the assumption that harvest records reflect age and sex ratio of populations accurately cannot be made and conclusions of this study should be viewed in light of this limitation (Bunnefeld et al. 2009).

If vital rates change with individual age, changing population age structure can affect population dynamics by creating multiple time delays destabilising population dynamics (Lande, Engen & Saether 2003a). Drivers of unstable population dynamics in Scottish mountain hares are not fully understood (Newey et al. 2007a). Although evidence of parasite-mediated reduction in female fecundity (Newey & Thirgood 2004) suggests that parasites may play a role, recent modelling studies suggest that parasites alone cannot drive population fluctuations (Townsend et al. 2009). However, further models suggest that parasite intensity in adults may be determined by the rate of juvenile survival. Consequently, the host age-structure may be an important aspect of the host-parasite system and driving population cycles (Townsend et al. 2011). Therefore, the effect of population density on age structure reported here, has the potential to contribute to unstable population dynamics of mountain hare in Scotland.

5.6 Management implications and conclusion

We found evidence for negative density-dependent juvenile recruitment. Therefore, compensatory juvenile recruitment may be an important factor in the resilience and persistence of harvested mountain hare populations in Scotland. However, if the number of hares harvested exceeds the upper limits of increased juvenile recruitment, overexploitation and population decline could occur (Caughley & Gunn 1995). Future work should aim to quantify harvesting pressure of populations in order to assess if current harvest rates are sustainable.

The increasing numbers of ticks and associated tick-borne disease, Louping ill virus (LIV), are of increasing concern to Scottish grouse moor managers (Laurenson et al. 2003). Culling tick hosts, including mountain hares, has been proposed as a tick control strategy (e.g. Smith 2009). Although conclusive evidence that mountain hare culling is an effective method to reduce LIV prevalence in red grouse is lacking (Harrison et al. 2010), it continues in some parts of Scotland (Patton et al. 2010). The response of the host to culling, including any density-dependent processes, needs to be understood in order to assess the efficacy of culling for disease control (Harrison et al. 2010). Increased juvenile recruitment reported here could be indicative of increased immigration into low density sites, which would reduce efficacy of culling by spreading, rather than controlling, ticks and LIV, an effect shown in the culling of badger to reduce bTB prevalence in cattle (Tuytens et al. 2000a). In addition, if higher juvenile survival contributes to increased juvenile recruitment, the result could be a greater rate of population growth in low density sites. Such a scenario would require a higher number of hares to be killed to maintain the low population density necessary to reduce disease persistence and transmission (Harrison et al. 2010). The role of density-dependent dispersal and juvenile survival in unstable population dynamics of mountain hares needs to be investigated in order to improve our understanding of their population dynamics and better inform mountain hare management in Scotland.

Chapter 6

Sustainable harvest rates for Scottish mountain hare populations

6.1 Abstract

Throughout history, overexploitation of natural resources has led to population decline, and even extinction, in many populations and species. Sustainable management of harvested populations involves finding a level of harvest which leads to sufficient off-take, without compromising population persistence. Sustainable harvest rates can be difficult to quantify due to uncertainty and bias in demographic data. However, harvest models can provide a useful tool for investigating harvest rates on populations. Throughout much of its circumpolar distribution, the mountain hare, *Lepus timidus*, is harvested for sport, subsistence and commerce. In Scotland, mountain hares have been harvested for centuries and are increasingly culled to control tick-borne disease. Harvesting strategies for Scottish mountain hare populations are absent, and the numbers of hares killed is unmonitored, despite concerns over their UK status. Here we develop a stochastic, density-independent matrix population model, parameterised from results of field based studies, to investigate sustainable harvest rates in Scottish mountain hare populations. We explore the effect of parameter variability on population growth rate (λ), the effects of different levels of non-biased and age-biased harvest rates on the deterministic model output, population growth rate and extinction probability in a stochastic formulation of the model measured over a 50 year time horizon, and finally, the effect of changing initial population size on this extinction probability. Sustainable harvest rates were derived as the maximum harvest that gave a positive growth rate ($\lambda \geq 1$) and an extinction probability less than 5%. We found that female fecundity was the most sensitive parameter in mountain hare demography. Increasing harvesting pressure decreased population growth rate and increased extinction probability. The maximum sustainable harvest rate was 40% of individuals each year. This sustainable harvest rate decreased as harvesting became

more juvenile biased or as population size became smaller. Results of the matrix model suggest that Scottish mountain hares can be harvested at low intensity with low risk of overexploitation. However, if harvesting is age-biased, or if habitat fragmentation leads to smaller populations, there is a greater chance of over harvesting. Quantifying density dependence in demographic parameters and rates of colonisation and recolonisation, are priorities for future research. Such information is needed to better understand the effects of harvesting on mountain hare population dynamics and better inform management of Scottish populations.

6.2 Introduction

Sustainable exploitation of natural resources is recognised by the Convention on Biological Diversity (CBD) as an important goal of environmental management, critical to human wellbeing (United Nations 1992). A major goal for successful management of harvested populations is to find a harvesting strategy that is sustainable, and that results in large annual yields (Aanes et al. 2002). Optimal harvesting strategies are a trade-off between taking high numbers to meet demands, against leaving high numbers extant to ensure population persistence. Popular strategies often employed to achieve optimal harvesting include the constant yield strategy (where the same numbers of individuals are taken annually), the proportional yield strategy (where the number of individuals taken is a proportion of the total population size) and the threshold or constant escapement (where all excess individuals above a critical population size are harvested) (Lande, Engen & Saether 1995).

Despite numerous studies over the past 50 years exploring sustainable harvesting, overexploitation has occurred, even in the most intensely studied populations (Ludwig, Hilborn & Walters 1993; Milner-Gulland & Akcakaya 2002; Sutherland 2001). Uncertainties in the biology, difficulties in estimating parameters, stochastic and deterministic population fluctuations, and market forces often lead to the risk of population collapse despite harvesting at a level predicted as sustainable (Milner-Gulland & Akcakaya 2002; Sutherland 2001). One key component of exploitation that is difficult to quantify is the scope for population compensation as a result of density-dependent feedback (Caughley & Gunn 1995; Sibly & Hone 2002; Sutherland 2001). For example, reducing the number of breeding individuals in a population may improve breeding success of the remaining breeding individuals through

reduced competition (Boyce, Sinclair & White 1999). Estimates of sustainable yield are also sensitive to population growth rate, which is either obtained from unexploited populations, leading to underestimated yield, or as the maximum possible growth rate (under ideal conditions, r_{\max} , or in absence of competition, r) which can lead to yield being overestimated (Sutherland 2001). Further, quantitative models for population viability analysis are often unreliable due to poor quality data, difficulties in measuring variance and a lack of information on dispersal (Beissinger & Westphal 1998). Although results of modelling studies should be interpreted cautiously in light of these limitations, developing models of virtual populations allows management strategies to be tested and robustness investigated (Milner-Gulland et al. 2001).

The mountain hare, *Lepus timidus*, is a traditional small game species and is widely hunted for recreation, subsistence and commerce across its Palaearctic distribution. In Scotland, the mountain hare is locally abundant on heather moorland managed for red grouse, *Lapogus lapogus scoticus*. Mountain hares have been harvested here for centuries, but with little in the way of a management strategy (Tapper 1992). Throughout their circumpolar distribution, mountain hares show unstable dynamics (Newey et al. 2007b; Newey et al. 2007a) further complicating sustainable management of this species (Lande, Engen & Saether 2003a).

Although the presence of mountain hares in Scotland under sustained harvesting suggests that sustainable exploitation can be achieved (Sutherland 2001), an apparent decline in numbers has raised concern about their population status (Battersby 2005). Possible causes for this decline include habitat fragmentation, climate change, hybridisation with the brown hare, *Lepus europaeus* (Thulin, Jaarola & Tegelstrom 1997), and overexploitation. In recent years

the motivation for hunting mountain hares has switched from mainly harvesting for recreation, to culling for disease control (Patton et al. 2010). Whilst the success of harvesting for recreation and subsistence relies on sustainable exploitation, the aim of culling is to reduce numbers. Therefore, in areas where hare culling is employed as a disease control strategy, exploitation of mountain hare may no longer be sustainable in terms of population persistence,

Here we use data from current research on density-dependent and compensatory population dynamics of a harvested mammal to parameterise a population matrix model in order to estimate sustainable harvest rates and help inform sustainable management of this species. We simulate the proportional harvest strategy which is most commonly used in small game management and is the strategy most robust to uncertainty (Milner-Gulland et al. 2001). The aims are to i) study the effects of parameter variation on population growth rate using elasticities (Caswell 2001); ii) determine sustainable harvest rates for both unbiased and age-biased harvesting; iii) investigate how changing initial population size affects sustainable harvest rates.

6.3 Methods

6.3.1 STUDY SITES AND DATA COLLECTION

Data were collected from 10 independently managed sport shooting estates located in the Central Scottish Highlands. All sites were, to a greater or lesser extent, managed for red grouse shooting, which includes rotational burning of heather, legal predator control (crow, fox, stoat and weasel) and, on some estates, tick control strategies. Population density for each site was estimated prior to hare shooting using Distance sampling methods (Buckland et al.

2001; Thomas et al. 2010; Chapter 5). Mountain hares were shot between December and April 2009, and fecundity and age determined by *post-mortem* (Chapter 5). The shooting sample is considered a random population sample.

6.3.2 PARAMETERISATION OF FECUNDITY AND BREEDING PROPORTION

In Scotland, mountain hare begin breeding in February and do not breed in the year of their birth (Flux 1970; Hewson 1976). Therefore, hares collected in this study were either breeding for the first time (yearling), or had survived at least one previous breeding season (adult). The uteri of 93 female hares, killed across eight sites, were removed and the number and length (crown to rump) of any foetuses were recorded (Chapter 5). The mean and standard error of the proportion of pregnant yearling (P_Y) and adult (P_A) female hares was calculated across the eight sites. Female mountain hares have a 50 day gestation period, and post partum mating, which enables production of typically three litters a year, with four litters being theoretically possible (Hewson 1976). As the data available only offer female fecundity estimates of the first litter period, we parameterised annual female fecundity from estimates in the literature (Newey, Thirgood & Hudson 2004).

6.3.3 PARAMETERISATION OF SURVIVAL

On one site, an intensive live-capture and radio-telemetry study was also conducted. Live trapping was carried out from October-December and from April-July in the period of October 2007 to December 2009. All captures were sexed, weighed, and the right hind foot length (excluding claws) measured. Leverets, up to 6 months old, are easily distinguished from adults by their smaller body size and colour. Juveniles up to 9 months can be distinguished from

adults by the presence of the epiphyseal notch (Broekhuizen & Maaskamp 1979). Individuals were fitted with radio collars and radio-tracked year round between October 2007 and July 2010 (Chapter 3 and 4). Survival was estimated using Known-Fate models in RMark v1.9.7 (Laake 2010; Chapter 4). Survival of adults over winter (October to March) (S_W) and annual adult survival (October – September) (S_A) were estimated from 189 adults. S_W and S_A were estimated separately to distinguish between survival averaged over the whole year (S_A) and survival between October and March (S_W) which specifically covers the time period between the beginning of the model (population size, N_t) and breeding, as required for the matrix model (Figure 6.1). Leveret survival (S_L), the survival probability up to 6 months in age (April to September), juvenile survival (S_J), the survival probability between 6 and 12 months of age (October to March), and breeding yearling survival (S_B), survival probability from 12 to 18 months in age, when breeding for the first time (April to September), were obtained from 51 individuals captured from 100 days old (Chapter 4).

6.3.4 MATRIX POPULATION MODEL

Parameters, description and data source are provided in Table 6.1. The mountain hare life cycle, and how the matrix model is constructed and parameterised, is detailed in Figure 6.1.

Table 6.1: Description, notation, values with standard error, and data source of demographic parameters.

Description	Parameter	Value (\pm SE)	Data source
Annual adult survival (Oct-Sept)	S_A	0.51 ± 0.14	Chapter 4
Adult winter survival (Oct-March)	S_W	0.54 ± 0.07	Chapter 4
Breeding yearling survival (April-Sept)	S_B	0.57 ± 0.2	Chapter 4
Juvenile survival (6 – 12 months)	S_J	0.64 ± 0.10	Chapter 4
Leveret survival (<6months)	S_L	0.79 ± 0.09	Chapter 4
Annual female fecundity	Fe	3.1 ± 2.1	(Newey, Thirgood & Hudson 2004)
Proportion of yearling females breeding	P_y	0.96 ± 0.02	Chapter 5
Proportion of adult females breeding	P_A	0.75 ± 0.07	Chapter 5
Yearling harvest pressure	h_y	Manipulated	Manipulated
Adult harvest pressure	h_a	Manipulated	Manipulated

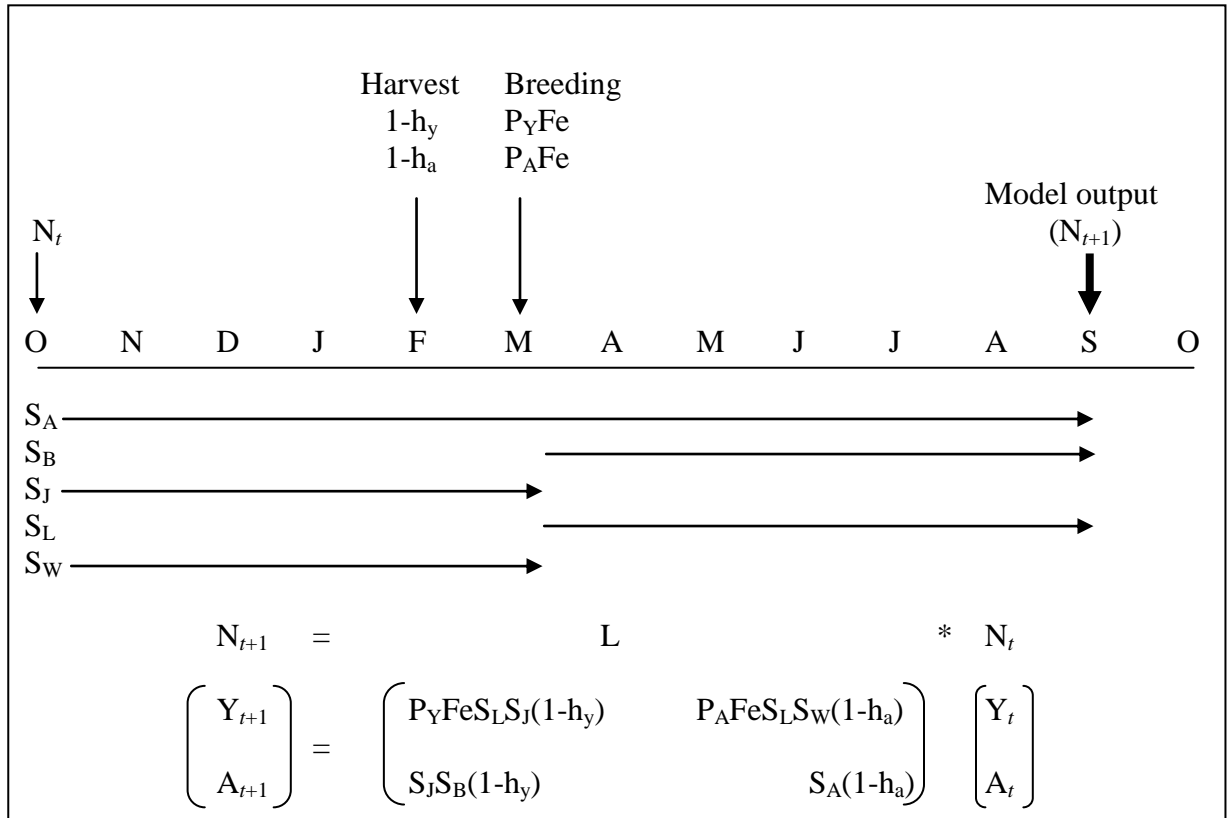


Figure 6.1: Mountain hare life cycle, parameterisation and Leslie matrix (L). Population size N at time t is the total number of adults (A_t) and yearlings (Y_t). Using estimates of annual adult survival (S_A), winter adult survival (S_W), breeding yearling survival (S_B), juvenile survival (Poysa et al. 2004), leveret survival (S_L), annual female fecundity (Fe), the proportion of breeding yearlings (P_Y) and the proportion of breeding adults (P_A), total population size the next year (N_{t+1}) is estimated via the matrix model. Harvest mortality is manipulated and applied to adults and juveniles separately prior to breeding.

Since we were limited by the availability of robust biological data, a simple, female only, age structured, density-independent model was chosen. A 1:1 sex ratio was observed overall (Harrison et al. unpublished data), hence the output from a female only model will be indicative of total population. The species life cycle was simplified based on two age classes;

yearlings (0-18 months, includes first breeding season) and adults (>18 months, individuals have previous breeding experience). Births occurred post-harvest. A simple deterministic projection matrix model was then constructed with corresponding transition probabilities and reproductive parameters outlined in (Table 6.1).

Environmental stochasticity was modelled by sampling survival and proportion of breeding females from a beta distribution (so that values are bound between 0 and 1) and female fecundity from a gamma distribution (so that negative fecundity cannot occur), with the same mean and standard deviation as estimated from the data (Table 6.1). Details of the parameters for the beta and gamma distributions for each demographic parameter are found in Table 6.2. Demographic stochasticity was incorporated by using a binomial distribution for survival probability and proportion of females breeding (giving individuals a fixed probability of surviving or breeding), and a Poisson distribution for the fecundity of each female (giving a fixed number of offspring each year) from the estimates under environmental stochasticity. The model was run over 50 years (the maximum amount of time that an estate is likely to be under consistent management) and simulated 1,000 times to account for stochasticity.

Table 6.2: Demographic parameters and the associated distribution parameters for beta (α , β) and gamma (k , θ) distributions used in the stochastic model.

Demographic parameter	Distribution parameters	
<i>Beta distribution</i>	α	β
S_A	2	1.8
S_B	3.5	2.6
S_J	3.4	2.1
S_L	8	2.3
S_W	2	1.2
P_Y	20	1.5
P_A	6	2.5
<i>Gamma distribution</i>	k	θ
Fe	4.4	0.7

The mean population growth rate (λ) over 50 years is projected as the arithmetic mean of the dominant eigenvalue over 50 years, which was determined using the popbio package (Stubben & Milligam 2007) for R v2.12.0 (R Development Core Team 2010). This resulted in 1,000 eigenvalues, one from each repetition, from which a mean and standard deviation could be calculated. The mean reproductive value (a measure of potential reproductive output taking into account both fecundity and survival) over 50 years and the mean stable age structure (the stable ratio of juveniles to adults) over 50 years, are the corresponding left and right

eigenvectors respectively (Caswell 2001). The reproductive values are scaled so that the reproductive value of the first stage (i.e. yearlings) is equal to 1, and all others are a proportion of this value. The damping ratio (ρ), measures the rate of convergence to the stable age structure and is calculated as the ratio of the dominant eigenvalue to the second largest eigenvalue (Stubben & Milligam 2007). The lower the damping ratio, the longer it takes for the population structure to stabilise (Caswell 2001). The effect of unbiased and age-biased harvesting on the damping ratio, stable age structure and reproductive value was also investigated.

We used elasticity, the proportional change in population growth rate (λ) due to proportional changes in each parameter, to assess the effects of parameter variation on λ . So, for parameter p_i elasticity, e_i , is the slope of $\log \lambda$ plotted against $\log p_i$ (Caswell 2001). Elasticity values were then rescaled with a coefficient of variation (CV_i), which is calculated as standard deviation/mean for each parameter. The resulting actual elasticity coefficient (AE) was then calculated as $AE_i = e_i \times CV_i$, which combines ‘the proportional sensitivity of the growth rate to the parameter with the observed empirical variation in that parameter’ (Haydon et al. 1999).

Harvest mortality was considered additive to natural mortality and was manipulated to determine indices of sustainable harvest rates under a proportional harvest strategy, the largest rate of harvest that gave a stable or increasing mean population growth rate ($\lambda \geq 1$), and a probability of extinction (probability that a population will be reduced to zero over a specified time span) <5% (Beissinger & Westphal 1998; Marboutin et al. 2003). The extinction probability at differing levels of harvest was determined for different time spans. The effects of age-biased harvest pressure were investigated by manipulating juvenile and adult harvest

pressure, so that harvest pressure differed between the age categories, while maintaining a constant overall average harvest pressure.

Population density of the study sites varied from 0.02 to 0.57 hares ha^{-1} , and the area over which hares were harvested was 400 to 800ha. When population size over the harvested areas was estimated as density \times area, the mean population size (\pm SE) was 72 (\pm 26.47) with a range of 15 to 250 individuals. Sustainable harvest rates for unbiased and age-biased harvesting mortality were therefore obtained for a population with an initial size of 72. As the matrix model is density-independent, changing initial population size would not affect the model outputs (e.g. λ), however, changing the initial population size will effect whether different levels of harvesting lead to population extinction within a specified time span. We tested the effect of different harvesting rates on extinction probability after 50 years for different initial population sizes using the stochastic model.

6.4 Results

6.4.1 ELASTICITY

The elasticity analysis suggests that population growth rate (λ) is most sensitive to changes in female fecundity, and juvenile and leveret survival (Table 6.3). Adult winter survival and the proportion of adults breeding were shown to be the least important. The elasticity values for juvenile and leveret survival were more than four times greater than that of annual adult survival indicating that the population growth rate is three times more sensitive to survival of first year individuals compared to survival in adulthood. However, the coefficient of variation (CV) was almost eight times greater for annual adult survival compared to either leveret or

juvenile survival, and the AE values suggest that variation in adult survival is almost three times more influential in mountain hare demography than variation in survival during the first year of life. Adult winter survival had the lowest AE of all the survival parameters and so is the least likely to affect hare demography. The elasticity analysis illustrated that the population growth rate is more sensitive to the number of offspring produced per female (fecundity), than the proportion of females breeding. Within the proportion of females breeding, λ is more than three times more sensitive to the proportion of breeding yearlings than breeding adults. The AE, however, shows that variation in the proportion of breeding adults has more effect on demography compared to the proportion of breeding yearlings. Fecundity has over ten times more influence than either breeding proportion parameters, and overall is the most sensitive parameter in mountain hare demography as shown by the AE value (Table 6.3).

Table 6.3: Demographic parameters ranked according to their actual elasticity coefficient.

Parameter	Elasticity	CV	AE coefficient
Female fecundity (i.e litter size)	0.77	2.95	2.27
Annual adult survival	0.23	8.38	1.92
Juvenile survival	0.77	1.12	0.86
Leveret survival	0.77	0.81	0.63
Juvenile breeding survival	0.13	1.39	0.19
Adult winter survival	0.17	0.27	0.05
Proportion of adult breeding females	0.17	0.27	0.05
Proportion of yearling breeding females	0.60	0.04	0.03

6.4.2 EFFECT OF HARVESTING ON STABLE AGE AND REPRODUCTIVE VALUE

In a non-harvested population, growth rate was positive ($\lambda=1.76$). The damping ratio (ρ) was 7.54, stable age structure was 0.77:0.23 (yearling:adult) and the reproductive values are 1, for yearlings and 0.76 for adults, indicating that adults have 0.76 (or 76%) the reproductive value of yearlings. Unbiased harvesting had no effect on the stable age structure or reproductive value, and only very small changes in damping ratio. When overall harvest pressure averaged 0.4, but the proportion of yearlings and adults harvested differed simulating age-specific harvest bias, the damping ratio decreased as harvesting become more yearling biased (Figure 6.2a), although the ratio of yearlings to adults in the stable age structure changed very little (Figure 6.2b). As harvesting became more yearling biased, the reproductive value of adults increased relative to yearling reproductive value. The reproductive value of adults increased from 0.76 of yearling reproductive value, when adult and yearling harvest pressure are equal at 0.4, to 2.81 when harvesting was highly yearling biased (yearling and adult harvest pressures at 0.7 and 0.1, respectively) (Figure 6.2c).

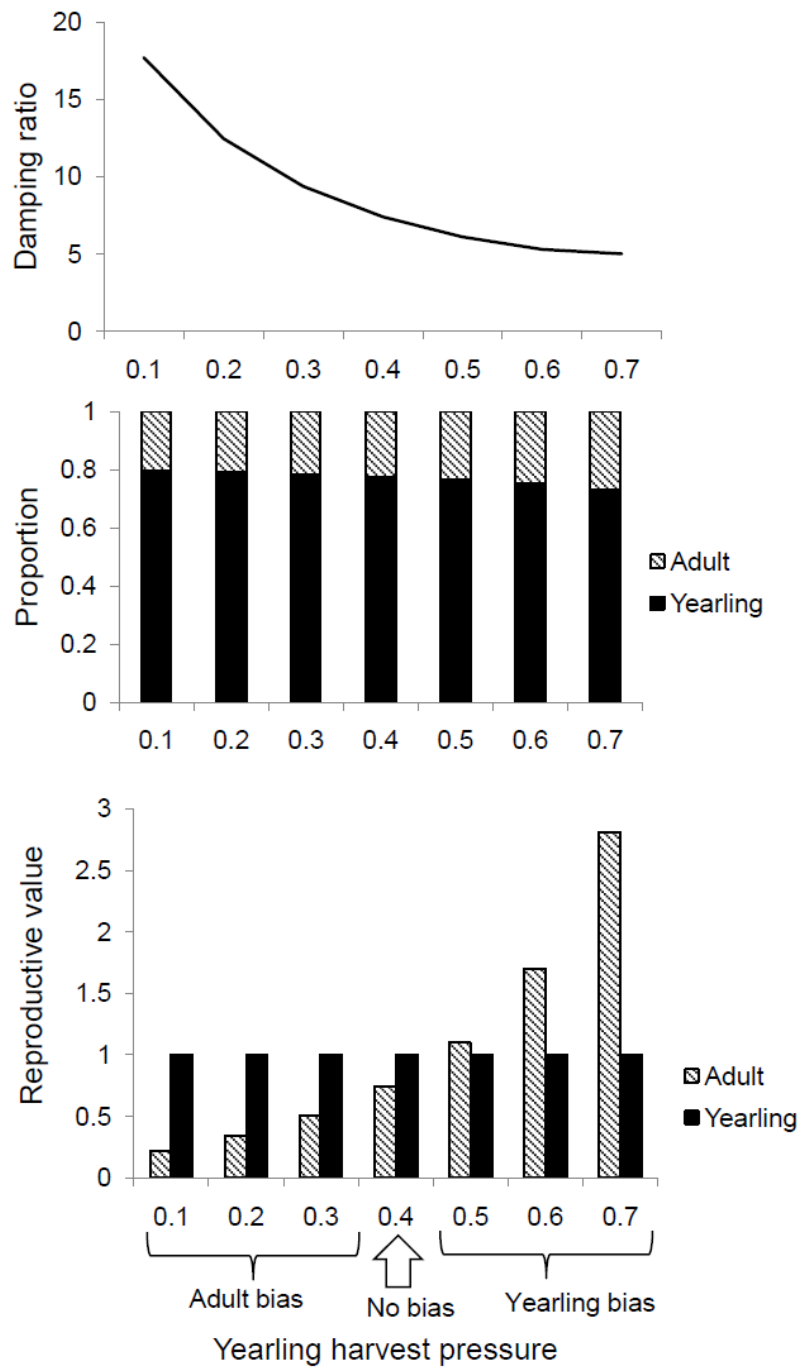


Figure 6.2: The effects of harvesting bias on a) damping ratio (ρ), b) stable age structure, and c) reproductive value. Mean harvest pressure (proportion of population harvested) equals 0.4 in all cases.

6.4.3 EFFECT OF HARVESTING ON POPULATION GROWTH RATE AND EXTINCTION PROBABILITY

Increasing harvest pressure on an initial population size of 72 led to a decrease in mean estimate and reduced variation of population growth rate (λ) (Figure 6.3). The mean estimate of population growth rate did not fall below 1 until harvest pressure was 0.5. At this harvest pressure, the probability of extinction after 50 years was 0.98; too high to be considered sustainable. Probability of extinction was lower after shorter periods of time and higher levels of harvesting could be sustained over shorter periods of time (Figure 6.4). These estimated extinction probabilities combined with a mean population growth rate <1 , suggests that a harvesting press of 0.5 could not be sustainable for any longer than 10 years (Figure 6.4). However, harvesting at high intensities would drastically reduce population size leaving such populations vulnerable to stochastic events and the negative effects of inbreeding. Therefore, the maximum possible sustainable harvest over 50 years would be 0.4 with extinction probability $<5\%$ and with the mean population growth >1 (Figure 6.3).

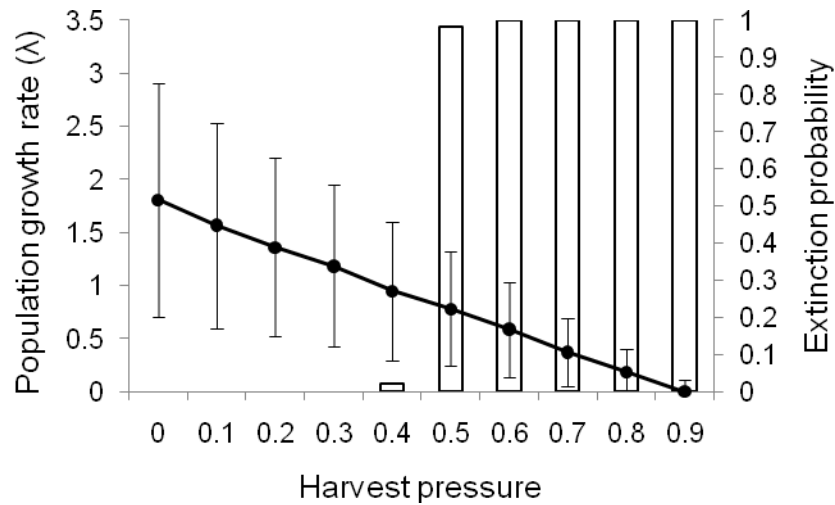


Figure 6.3: Effects of changing harvest pressure (proportion of population harvested) on mean population growth rate (λ) \pm s.d. (solid line), and extinction probability (bars) of a population with initial size of 72.

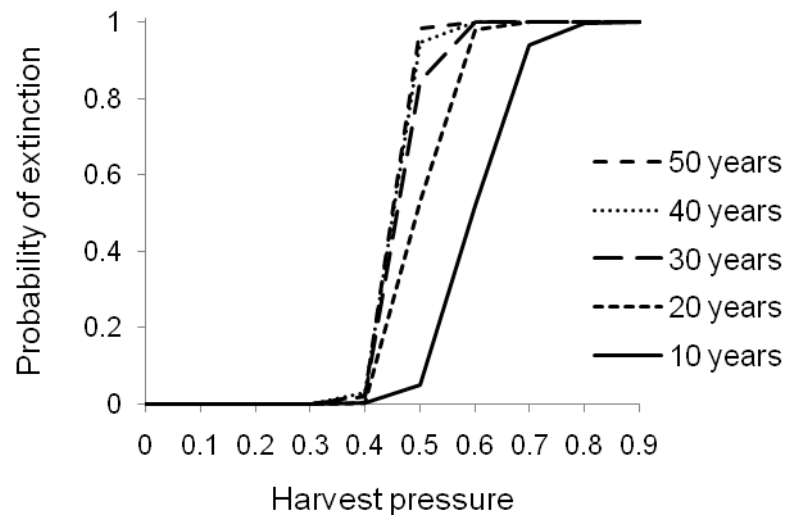


Figure 6.4: Probability of population of 72 going extinct at differing harvest pressures over different time spans

6.4.4 EFFECTS OF AGE BIASED HARVESTING

Using 0.4 as a common rate of harvest mortality, the effect of changing age-specific harvest bias is shown in Figure 6.5. As harvesting became increasingly yearling biased, the mean population growth rate decreased and extinction probability increased. Whereas an unbiased harvest pressure of 0.4 is sustainable, if a higher proportion of the harvest is of yearlings, a harvest pressure of 0.4 becomes unsustainable.

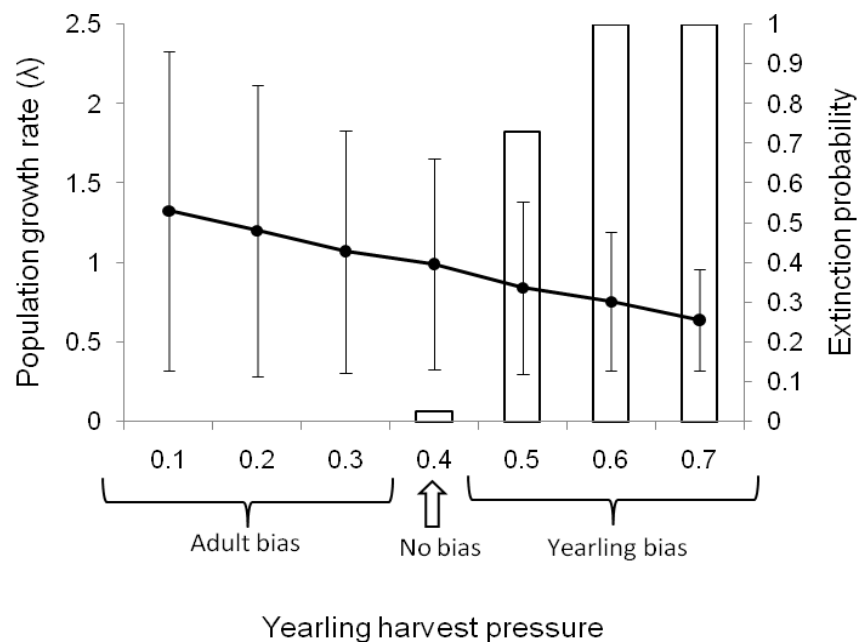


Figure 6.5: Mean population growth rate (λ) \pm s.d. (solid line) and probability of extinction (bars) at different levels of harvest bias in a population of initial size of 72. Mean harvest pressure equals 0.4 in all cases.

6.4.5 EFFECTS OF CHANGING INITIAL POPULATION SIZE

Smaller populations have higher extinction probability, which increases with increasing harvesting pressure (Figure 6.6). Whilst a harvest pressure 0.4 was sustainable at population size 72, at lower population sizes this level of harvesting results in an extinction probability too great to be classed as sustainable. However, even the largest populations cannot be harvested at levels greater than 0.4 without an unacceptable (>5%) risk of extinction (Figure 6.6).

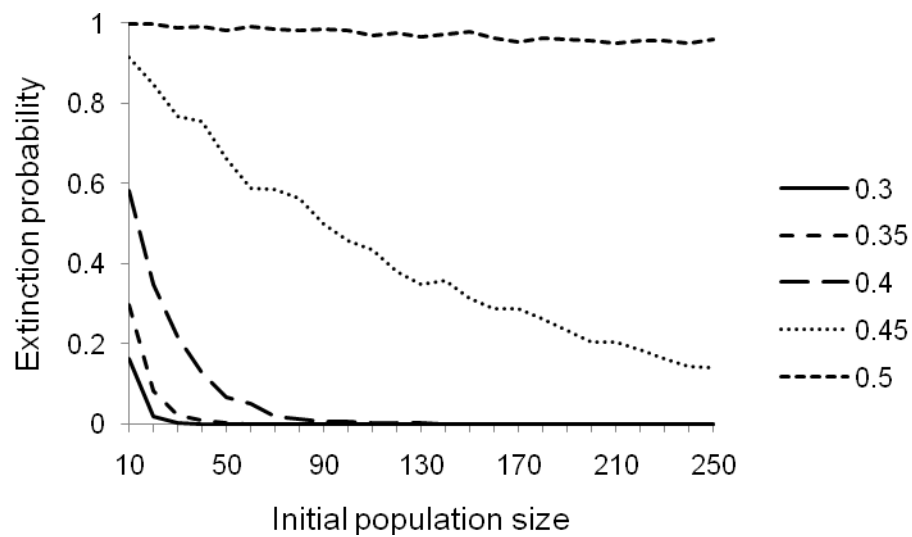


Figure 6.6: Extinction probability of populations (probability of population decreasing to 0) of different initial size (number of individuals) with changing levels of harvest pressure (proportion of population harvested) shown in legend.

6.5 Discussion

We use a matrix population model to demonstrate that harvesting mountain hare in Scotland at rates of greater than 40% of the population is unsustainable even for very large populations,

and that harvesting at 40% becomes unsustainable when the harvesting is yearling biased. Successful management of exploited populations can be achieved through adopting harvesting strategies that are sustainable, in terms of minimal risk of extinction, and by maintaining economic gain (Aanes et al. 2002). Models can be used to test harvesting strategies and assess their reliability and robustness which would not be possible in real populations (Milner-Gulland et al. 2001) and can be a useful tool for sustainable management of harvested populations.

6.5.1 MODEL PROJECTIONS AND STOCHASTICITY

Female fecundity was shown to be the most sensitive parameter overall in mountain hare demography. This means that changes in female fecundity have great potential to perturb population growth rate, and hence, any factors effecting female fecundity rates have implications for mountain hare demography. In the non-harvested population the population growth rate was 1.76 indicating an increasing population. The stable age structure revealed that 77% of the population were yearling, with the remaining 23% comprising of all other age groups. These proportions are more yearling biased than those in the literature (Flux 1970; Hewson 1976) but are similar to our observed data (Chapter 5). In a population study examining demographic parameters over a ten year hare cycle, the proportion of yearlings was higher in the increasing population phase compared to decline, peak or trough (Hewson 1976). The high proportion of yearlings we report here and in Chapter 5 may indicate that the population(s) we sampled, and used to obtain parameter estimates, were under going growth, or were more heavily harvested leading to density-dependent juvenile recruitment (Chapter 5), over the course of the study.

The reproductive value of yearlings was greater than that for adults. Female fecundity is unaffected by age (Iason 1990; Chapter 5) and the higher survival rates of juveniles and leverets compared to adults, leads to yearlings having greater reproductive potential than adults and contributing more to population growth rate. There was a large amount of variation around the female fecundity estimate (Newey, Thirgood & Hudson 2004), suggesting that female fecundity can strongly influence mountain hare demography. In short-lived species it is common that proportional changes in fecundity have a greater effect on population growth rate than proportional changes in survival (Sibly & Hone 2002). The addition of environmental and demographic stochasticity to the model resulted in a similar mean population growth rate, but resulted in high variation around this mean. Even at the very low harvest pressure of 0.1, taking into account the lower limit of a standard deviation, λ was less than 1, suggesting that even less intensely harvested populations are at risk of population decline due to stochasticity and variation in vital rates.

6.5.2 EFFECT OF HARVESTING AND SUSTAINABLE HARVEST RATES

The maximum sustainable harvest rate for an average sized population of 72 was 0.4. However, extinction probability increases dramatically between harvest pressures of 0.4 and 0.5, indicating that even a very small increase of harvest pressure over 0.4 would leave the population very vulnerable to overexploitation. As proportional harvest rates rely on good estimates of population size, which are renownedly difficult to obtain, aiming for a harvest pressure of 0.4 leaves very little room for error and we suggest a more conservative harvest pressure be sought. However, the time span over which the harvesting strategy is to be applied is also an important consideration. Probability of extinction increased the longer the harvesting

was applied and populations could withstand higher harvest rates over shorter periods of time. However, harvesting will decrease population size, at least in the short term. As extinction probability is higher in smaller populations, the effect of current management needs to be considered when considering future management of populations. The sustainable harvest rate of 0.4 identified above is only sustainable for populations of 70 individuals or more. Conversely, larger populations are more resilient to larger harvests, although extinction probability exceeds 5%, and is therefore unsustainable, at 0.45 harvest pressure, even for the largest populations. As we use a female-only matrix model, the initial population sizes used in the model will be for females only and half the total population size. Therefore, an initial population size of 72 females would be equivalent to a total population size of 144, leading to our sustainable harvest rates being over estimated. Further, as population sizes are difficult to estimate and we observed a high level of variation in population size, the strong effect of population size on extinction probability reiterates the need for a more conservative harvest pressure.

Harvesting mortality was additive in the model and therefore it is unsurprising that increasing harvesting pressure lead to decrease in population growth rate and an increase in extinction probability. However, increasing harvesting pressure had no effect on the damping ratio, stable age structure or reproductive value. Therefore, unbiased harvesting is likely to change neither the age structure of populations, nor the relative contribution of individuals of different age classes to population growth. The fact that the damping ratio was not greatly affected by unbiased harvesting suggests that unbiased harvesting does not cause instability of populations.

6.5.3 AGE-SPECIFIC HARVESTING BIAS

As harvesting became more yearling biased, population growth rate decreased and extinction probability increased. Although a harvest pressure of 0.4 was shown to be sustainable for unbiased harvesting, if harvesting is biased towards yearlings, even slightly, an overall harvest pressure of 0.4 reduces λ and increased extinction probability passed the 5% threshold, and is no longer sustainable. The decrease in damping ratio with increasingly yearling-biased harvesting suggests that populations take longer to reach stable age structure and are therefore less stable under yearling-biased harvesting. As the reproductive value of the deterministic model indicated that yearlings contributed more to population growth, it is unsurprising that yearling-biased harvest pressure affected population growth rate and extinction probability differently to unbiased harvesting. Although yearling-biased harvesting had little effect on the stable age structure, the reproductive value of adults increased with increasing yearling-biased harvesting. This suggests that as proportionally more yearlings are harvested, the contribution of adult reproduction to overall population growth rate increases, making the importance of adult fitness greater for continued population growth.

6.5.4 MODEL ASSUMPTIONS

It is important to note that simulations of a population matrix model produce trajectories, not predictions, as they rely on the quality of both model structure and demographic data (Caswell 2001). Therefore, validation of trajectories is necessary. Due to a lack of biological data, we were unable to validate our model with real data. However, the stable age structure produced by the model was similar to the mean 3:2 juvenile to adult ratio seen across our 10 study sites (Chapter 5). Further, the population growth rate of 1.76 would indicate that the mountain hare

populations are increasing on the estates we sampled, which matches anecdotal evidence. However, this does not reflect national population trends which appear to show populations declining (Battersby 2005). To increase our confidence in the model, long term demographic data should be collected and applied to the model, and population growth compared with observed population growth rates.

Other assumptions also need to be considered, particularly concerning the population extinction estimates (Beissinger & Westphal 1998). Firstly, males were not included in the model. As fecundity is limited by the number of offspring that can be successfully gestated and lactated by females, it is possible that males can be harvested at a greater rate than females without compromising sustainability. The absence of males in the model also prevents the investigation of the effects of sex-biased harvesting on sustainable harvest rates. Secondly, harvesting mortality was assumed to be additive. There is limited evidence of compensatory mechanisms in mountain hare (Harrison et al. 2010) and such mechanisms are notoriously difficult to quantify (Berryman 2002; Turchin 2003). Although no evidence for compensatory survival or dispersal in mountain hare was found in recent studies (Chapters 3 and 4), further work is required to better quantify compensatory population dynamics. For compensatory mechanisms to be present, density-dependent processes are required. This is another area poorly understood in mountain hare population dynamics, although time series analysis suggests both direct and delayed density-dependence in Scottish populations (Newey et al. 2007b). Further, in a recent study we found evidence of negative density-dependent juvenile recruitment via a greater proportion of juveniles in low density sites (Chapter 5). However, due to a lack of knowledge of density-dependence in other vital rates, it was not possible to set a carrying capacity limit to our model. Models without carrying capacity limits often over-

estimate population persistence (Ginzberg, Ferson & Akcakaya 1990), and as a result, our estimates of sustainable harvesting rates are likely to be higher than the actual sustainable rates. Model parameters were estimated from across several populations for which harvest intensity, population density and phase of the population cycle are likely to vary. Variation in model parameters is likely to effect model output by influencing the projected population growth rate, which should be considered when interpreting results of this model. The elasticity analysis indicates that population growth rate was influenced most by female fecundity, which was shown in Chapter 5 to have little individual variation and was unaffected by population size. However, juvenile and leveret survival also had high elasticity values. Evidence of density-dependent juvenile recruitment suggests that juvenile survival may vary between populations depending on density or management. Finally, the model assumes that hares were equally harvestable regardless of population size. In reality, hunter efficiency will decrease with smaller population sizes which may help buffer small populations from overexploitation (Marboutin et al. 2003). However, the legal use of wire snares in Scotland for capturing hares in low density populations will be likely to maintain hunter efficiency, exposing small populations to constant harvest, with an associated risk of over-exploitation.

6.6 Management implications and conclusion

The mountain hare show cyclic, or unstable, dynamics (Newey et al. 2007b; Newey et al. 2007a). Although the causes of these cycles are unclear, large fluctuations in populations density are evident (Newey et al. 2007a). This means that the relative population growth rate at different phases of the cycle will differ which needs to be taken into account. In a declining population, population size is smaller in the next year than the present year. If harvesting in

the present year exceeds the sustainable rate, this could accelerate the decline, leaving the populations vulnerable to extinction. Developing harvest models to include unstable dynamics is a priority for understanding the effects of harvesting on mountain hare population dynamics.

Fragmentation of the optimal mountain hare habitat (Robertson, Park & Barton 2001) or of the populations themselves, caused by local blanket culling, could lead to smaller, isolated subpopulations. As dispersal rates have been shown to be low (Dahl & Willebrand 2005; Chapter 3), recruitment into these populations will mainly come from births within the population, rather than from immigration. This means that reducing population growth rate via harvesting could leave small, isolated subpopulations more vulnerable to extinction, compared to larger subpopulations of comparable population growth rate. There are many examples where overexploitation combined with habitat destruction has caused extinction or serious depletion (Hutchings 2000; e.g. Redford 1992). If habitat fragmentation continues, harvest rates should be more conservative to take into account effects of habitat degradation on population growth rate.

The mountain hare is increasingly culled for disease control in Scotland (Patton et al. 2010). The model presented here indicates that only conservative levels of harvesting can ensure that overexploitation does not occur. It is likely that culled populations are being subjected to higher off-take rates. Indeed, of the three populations that were carrying out hare culling for disease control, all had harvest pressures greater than 0.7. Out of the seven populations that were harvesting hares for sport, only three had harvest rates that were less than 0.4 and could be described as sustainable under our model estimates. Such high harvest rates combined with apparently low dispersal rates of mountain hare, could lead to successful local eradication in

some areas. Therefore, widespread and intensive culling of mountain hares could dramatically reduce numbers and with no current knowledge on recolonisation rates, could be detrimental for the conservation status of this species in the UK. Colonisation and recolonisation of vacant areas by mountain hares is a key area for future research and is vital for directing mountain hare management in Scotland.

Chapter 7

General discussion

Populations of wild birds and mammals are often harvested for sport, subsistence or commerce. Sustainable exploitation of natural resources is recognised by the Convention on Biological Diversity (CBD) as an important aspect of environmental management critical to human wellbeing (United Nations 1992). However, sustainable management represents one of the most challenging areas of ecology, which is reflected in our inability to sustainably harvest even well studied populations (e.g. Walters & Maguire 1996). This inability is often due to poor demographic data and a lack of understanding of critical biological processes (Sutherland 2001). A key component of sustainable exploitation is density-dependent feed back. Density-dependent feedback provides mechanisms by which population dynamics change in response to changes in population density (Caughley & Gunn 1995; Sibly & Hone 2002; Sutherland 2001). If a population is reduced through harvesting or predation and density-dependence leads to a relative increase in population growth, the effect can be described as compensatory (Boyce, Sinclair & White 1999).

We use the Scottish mountain hare, *Lepus timidus scoticus*, as a model game species to investigate density-dependent and compensatory mechanisms, and sustainable harvesting strategies. The mountain hare has been traditionally harvested for subsistence and sport in Scotland, and continues to be an important source of revenue for some land owners (Tapper 1992). Mountain hares are also killed to protect forestry, woodland, crops, and increasingly, to control sheep ticks and the tick-borne disease Louping-ill virus (LIV) (MacDonald & Burnham 2007). Although mountain hares do not show clinical symptoms of LIV, they are important hosts to ticks, can act as a disease reservoir and can transmit the virus non-vireamically between co-feeding ticks (Jones et al. 1997; Laurenson et al. 2003). The proposal that culling mountain hares, and other tick hosts, could be an effective management strategy to

control ticks and LIV (e.g. Smith 2009), has led to an increase in management culls of mountain hares over the past 10 years (Patton et al. 2010). Between 1995/96 and 2006/07 the total number of hares killed in Scotland increased by 32%. Further, in 1995/96 60% of hares killed were done so for sport. This proportion decreased to 40% by 2006/07 with the majority (50%) being killed for the sole purpose of tick control (Patton et al. 2010).

Combined with threats from climate change, hybridisation with the brown hare (Thulin, Jaarola & Tegelstrom 1997) and a change in upland land use (Robertson, Park & Barton 2001), leading to habitat loss and fragmentation, culling has raised concern amongst conservationists and government agencies about the status of UK mountain hare populations, and the effect of culling on upland ecosystem functioning (Harrison et al. 2010; Patton et al. 2010). Further, the mountain hare is listed on Annex V of the EC Habitats Directive (1992) and has been added to the UK Biodiversity Action Plan list of priority species (UK Biodiversity Action Plan 2008).

7.1. Culling mountain hares for disease control

A review of the literature revealed that culling wildlife to control disease in economically important livestock or game species can have unexpected consequences, be ineffective and expensive, and may have wider implications for biodiversity (Harrison et al. 2010; Chapter 2). We determined that for widespread culling of wildlife to be proposed as an effective method of disease control, the following criteria should be met:

- “(i) the pathogen transmission cycle is fully understood with all host-vector interactions considered; (ii) the response of wildlife populations to culling is known; and (Green & Evans 1940)

cost benefit analysis shows that increased revenue from reduced disease prevalence exceeds the cost of culling.”

The mountain hare-red grouse-LIV system is well understood (Gilbert et al. 2000; Gilbert et al. 2001; Jones et al. 1997; Laurenson et al. 2003) and modelling studies show that removing mountain hares will be ineffective in decreasing LIV if alternative tick hosts (such as deer) are present (Gilbert et al. 2001). Although Laurenson et al. (2003) provide evidence that culling mountain hares reduced tick burdens and LIV seroprevalence in red grouse chicks, the absence of red deer, and low density of roe deer, on this study site means that results from this quasi-experiment are unlikely to be applicable to the majority of Scottish grouse moors where red and roe deer are generally ubiquitous and numerous (Clutton-Brock, Coulson & Milner 2004). Further, there is a lack of information on density-dependence, compensatory mechanisms and dispersal patterns, which are necessary to predict how mountain hare populations might respond to culling. Finally, there are few studies investigating the socio-economics of grouse moors (Redpath & Thirgood 2009; Sotherton, Tapper & Smith 2009; Thompson et al. 2009) which prevents any cost-benefit analyses of mountain hare culling for tick control to be performed. In light of these gaps in knowledge, combined with the unknown implications of hare culling on upland ecosystem functioning, we concluded that there is insufficient evidence currently available to justify culling mountain hares for the purpose of tick and LIV control (Harrison et al. 2010; Chapter 2).

7.2 Identifying density-dependent and compensatory mechanisms

Evidence for density-dependent and compensatory mechanisms is notoriously difficult to detect (Berryman 2002; Turchin 2003) despite being important in sustainable management of exploited populations (Sutherland 2001).

To identify compensatory survival and dispersal (Chapters 3 and 4) we compared survival and dispersal between a population subjected to traditional harvest, and a non-harvested (control) population. Harvesting can decrease population density in the short term. However, population density could not be shown to differ between the two populations or between seasons within the same population. That there was no difference in population density between the two populations suggests that either the survey methods were too insensitive to detect any changes, the level of harvest is negligible or density-dependent processes within the harvested population are leading to compensation of harvest mortality. Compensation could be in either survival (adult or juvenile), reproductive success (number of individuals born or number that survive to recruit into the breeding population), dispersal of individuals into the lower density harvested population, or a combination of these factors.

A comparison of survival rates between the two populations did not find a statistically significant increase in adult or juvenile survival within the harvested population. However, when we sampled ten independent populations of different population density (Chapter 5), we found evidence for negative density-dependent juvenile recruitment via an increase in the proportion of juveniles with increasing population density. However, this negative density-dependent juvenile recruitment does not appear to translate into compensatory juvenile survival (Chapter 4). That we did not find evidence for compensatory juvenile recruitment

could be due to a lack of information on neonatal survival, highlighting the need for this information when assessing impacts of harvesting on populations.

The proportion of juveniles across the ten sites of different population density decreased more steeply in females than it did in males. This could be due to differing juvenile survival rates between the sexes. In Chapter 4 we found that survival rates were higher in females compared to males in both juveniles and adults. If female survival was effected by population density, one would expect a significant interaction between sex and treatment (harvested, control) on survival rates. This was not the case with similar survival rates of males and females across the two populations. However, sex differences in neonatal survival remain unknown. Alternative hypotheses could include 1) a population density induced skewed sex ratio; 2) sex-biased density-dependent dispersal; or 3) sex- and/or age-biased harvesting.

7.3 Population density and sex ratio

Increasing population density can be associated with increased resource competition, which in turn can increase nutritional stress of females during pregnancy. Clutton-Brock, Albon and Guinness (1986) found that high ranking, good condition red deer hinds, *Cervus elaphus*, produce offspring biased towards males, but this trend disappeared if winter rainfall was high and as population density increased (Kruuk et al. 1999). As male red deer suffer high *in utero* mortality, producing females instead of males in years of high nutritional stress increases lifetime reproductive fitness of red deer mothers (Kruuk et al. 1999). Although we found the opposite trend, with a higher proportion of males with increasing population density, there could still be a role of nutritional stress in pregnant mountain hares. Larger females attempt to breed earlier and sustain a higher level of reproductive activity longer during the breeding

season, resulting in higher annual reproductive output compared to smaller females (Iason 1990). Increased food intake by females over winter, although had no effect on litter size, led to increased birth weight of leverets (Pehrson & Lindlof 1984). Therefore, females with higher food intake have larger offspring, which if female, go on to produce more and larger offspring, increasing reproductive fitness of the mother. Conversely, at high density when resource competition is high, food intake could be lower resulting in smaller leverets, which if female would have lower reproductive potential. Therefore, at high density it would be more beneficial to bias offspring towards males where size may not influence reproductive potential.

7.4 Dispersal of mountain hares

The steeper decline in juvenile females with increasing population density could be explained by female-biased negative density-dependent dispersal, whereby juvenile females disperse at high density. Although statistically insignificant, sex improved model fit in the dispersal distance analyses (Chapter 3). This suggests that the difference between male and female mountain hares accounts for some of the variation in dispersal distance. A larger data set may show females dispersing significantly greater distances compared to males (Chapter 3). Although previous studies failed to find evidence of sex-biased dispersal in mountain hares (Dahl & Willebrand 2005; Hewson 1990), likely as a result of small sample sizes, female brown hares have also been shown to disperse greater distances, although at a lower rate, compared to males (Bray et al. 2007). As with the brown hare (Bray et al. 2007), we did not find a significant interaction between sex and treatment (harvested, non-harvested) (Chapter

3). However, as population density did not significantly differ between the two treatment sites, it is not possible to assess the effect of population density on sex-biased dispersal.

Although we found that individuals of the harvested population dispersed greater distances than individuals of the non-harvested population, this result was confounded by differing lengths of observation period and a significant positive correlation between age and dispersal distance. When we scaled natal dispersal distance with observation time to give a dispersal rate, we found no statistically significant difference in dispersal rate between the two populations, highlighting the need to account for observation time when comparing dispersal distances of different populations. The lack of difference in natal dispersal rate between the two populations could be due to the spatial scale on which the comparison is made. Our study site is relatively homogenous compared to much of the Scottish uplands. In a more heterogeneous landscape, dispersal distances, rates or probability could differ to our results. Smith & Willebrand (1999) found no difference in population density between a harvested and non-harvested population of willow grouse, *Lapogus lapogus lapogus*, in Sweden and no evidence for compensatory survival or increased immigration into the harvested area. They suggested that movements at a much larger spatial scale may have a role in maintaining populations with locally high mortality (Smith & Willebrand 1999).

Spatial scale is also important when considering the implications of dispersal as a means of population persistence under exploitation. Traditional hare harvest takes place over relatively small (~200-400 ha) areas of heather moorland, compared to the area of mountain hare habitat (> 5,000 ha) found on many Scottish estates. This means that individuals do not need to disperse far from a 'source' population into harvested areas of low density (sinks) to sustain

the harvested area. Hare culling, however, takes place over much larger areas, entire estates in some cases, which will result in a reduced source population from which individuals emigrate and recolonise culled, low density areas of moorland. Low dispersal rate and distances combined with widespread culling could reduce population density over large areas, further fragmenting populations. If the distance between subpopulations increases beyond the maximum dispersal distance, local extinction due to stochastic processes or overexploitation is possible, with detrimental impacts on overall population persistence. Furthermore, if, due to increased fragmentation, a higher proportion of individuals are forced to disperse greater distances, these individuals may be exposed to greater risk of mortality, and thus higher mortality across the population may be observed. However, we found no evidence that increased dispersal rates reduce survival probability, suggesting that increased dispersal may not necessarily result in greater mortality risks.

7.4.1 METAPOPOPULATION THEORY AND MOUNTAIN HARES

Metapopulation theory is used for management of species under threat from habitat fragmentation and loss (Hanski 1999). However, use of the metapopulation concept is not always supported by empirical information fulfilling the definition: 1) habitat patches support local breeding populations with vacant but suitable habitats available for colonisation; 2) extinction and colonisation takes place; 3) dynamics of subpopulations are asynchronous; and 4) dispersal must occur between subpopulations) (Hanski 1999; section 1.1; Olivier, van Aarde & Ferreira 2009).

The mountain hare has been described as existing as a metapopulation in Britain (e.g. Anderson et al. 2009). While two of the above criteria are met; 1) mountain hares exist in a

fragmented habitat (Robertson, Park & Barton 2001) with patches of optimal habitat supporting local breeding populations, and 2) the dynamics of different populations are not synchronised (Newey et al. 2007b), the low dispersal distance, rate and probability found in our study and others (Dahl & Willebrand 2005; Hewson 1990) suggests that mountain hares in Britain fail to meet this requirement. Further, colonisation and recolonisation rates remain unknown and, therefore, with the information available, it is not possible to define the mountain hare as existing in a metapopulation in Britain, and may not be an appropriate concept to describe or manage for mountain hares in Scotland.

7.5 Harvesting bias

Selective harvesting based on phenotypic characteristics occurs in many species (e.g. trophy hunting) but in species with no obvious morphological differences between age and sex classes, hunters cannot consciously select for a specific age or sex class. However, differences in behaviour could lead to certain classes being more susceptible to hunting than others, resulting in a biased representation of the population. For example, in high density red grouse populations, more young were shot than were expected from pre-shooting grouse counts (Bunnfeld et al. 2009). Unintentional harvest bias in mountain hares could result in more juvenile males being shot at high densities resulting in the high proportion of juvenile males at high density sites. This stresses that the assumption that harvest records reflect age and sex ratio of populations accurately cannot be made and conclusions of this study should be viewed in light of this limitation (Bunnfeld et al. 2009).

Harvesting bias, whether intentional or not, can effect the phenotype and life-history of vertebrates (Garel et al. 2007; Hutchings 2005) and also demographic structure, and therefore,

population growth rate (Cameron & Benton 2004; Hutchings 2005; Milner, Nilsen & Andreassen 2007). It was not possible, with the data available, to test whether a harvest bias exists in mountain hares. However, using estimates from our empirical work we parameterised a stochastic population matrix model to investigate sustainable harvesting (Chapter 6). We manipulated harvest pressure so that overall harvest pressures were equal, yet the proportion of adults and yearlings varied. Sustainable harvest indices were based on the largest harvest pressure that produced a positive growth rate, and a less than 5% chance of extinction (Beissinger & Westphal 1998; Marboutin et al. 2003). We found that harvesting at a common rate became less sustainable the more yearling (<18 months old) biased harvesting became. As the reproductive value of yearlings was greater than adults, suggesting that yearlings contribute more to population growth, it follows that yearling bias harvesting would be more detrimental to population growth rate. If adults had contributed more to population growth, as observed in longer lived species for example, adult biased harvesting would be less sustainable (Milner, Nilsen & Andreassen 2007). This stresses the importance of understanding the life-history of harvested species in order to predict how harvested populations will respond to different levels of harvesting with and without the presence of sex or age bias.

7.6 Physiological and behavioural effects of harvesting

While several studies have investigated the effects of predator-induced stress on snowshoe hare population dynamics (Boonstra et al. 1998; Hik 1995; Sheriff, Krebs & Boonstra 2009), no such studies exist for the mountain hare. If hunting is viewed as a form of predation, one could hypothesise that the effects of predator induced stress could also be caused by hunting. Although key differences between predation and hunting exist (predation is a continuous

background risk with more individuals escaping predation, and therefore, surviving through the stress response), there are some circumstances where hunting may be comparable to predation. Flushing hares with dogs, combined with escaping harvest mortality by out running dogs, hiding down burrows or running through the line hunters, will stimulate a similar stress response by the hare as if it was being pursued by a predator, making the hare's experience of hunting analogous to predation. If hares are shot for other purposes (bait for traps, food for dogs, protection of forestry or crops, or disease control) hares may be caught in snares, or killed on a 'shoot on sight' basis. Individuals killed this way will rarely escape, and therefore it is unlikely to result in the same response as predation. Hares in the harvested population of our study site are hunted by flushing with dogs and driving hares uphill towards a line of hunters who attempt to shoot the hares as they run past. Although harvesting of hares only occurred in late January, and predation occurs year-round, it is possible that harvesting on our study site elicited similar physiological and behavioural stress responses as predation.

We found that birth date was significantly later, and that dispersal distances were significantly greater, in the harvested population. As population density and environmental factors were the same between the harvested and non-harvested populations, we hypothesise that these results were caused by physiological and behavioural responses of individuals to harvesting induced stress (Chapters 3 and 4). An increase in stress in the harvested population could lead individuals to change habitat use and foraging behaviour (Hik 1995) leading to increased distances moved (Chapter 3). Further, increased movement, decreased foraging (Hik 1995) or an increase in stress hormones (Boonstra et al. 1998), can lead to lower body condition. It has been suggested that female snowshoe hares will invest less in reproduction (e.g. timing of breeding (Rodel et al. 2005)) in order to maintain body condition (Hodges, Stefan & Gillis

1999), which may explain why birth dates were significantly later in our harvested population. Leverets born later have lower survival (Hewson 1968; Chapter 4; Iason 1989a), and grow to become smaller adults, which also lowers survival in adulthood (Iason 1989a; Iason 1989b). Smaller adult females also attempt to breed later and sustain a lower level of reproductive activity compared to larger females, resulting in fewer offspring produced overall (Iason 1990). This could lead to a negative feedback loop whereby harvest-induced stress leads to leverets being born later (and so have lower survival), which if survive become smaller adults (with lower survival), and if female, breed later (so young have poorer survival) and have lower reproductive outputs overall. The implication of this feedback loop is that harvesting has the potential to affect demography, and that harvest mortality can extend past simply the number of individuals harvested directly.

7.7 Implications for unstable population dynamics of mountain hare

Mountain hares show unstable population dynamics and drivers of these dynamics remain inconclusive (Newey et al. 2007b; Newey et al. 2007a; Townsend et al. 2009; Townsend et al. 2011; Section 1.3.1). Although identifying drivers of unstable or cyclic population dynamics in mountain hares is not a major aim of this thesis, some of the results may be of relevance. Evidence of parasite-mediated reduction in female fecundity (Newey & Thirgood 2004) suggests that parasites may be a factor in limiting and regulating mountain hare populations, although classical models suggest that parasites alone can not drive population fluctuations (Townsend et al. 2009). Further individual-based modelling (IBM) studies suggest that juvenile survival can potentially determine parasite intensity in adult hares (Townsend et al. 2011). Therefore, the host age-structure may be important in the host-parasite system. We

found a significantly higher proportion of juveniles at high density (Chapter 5), and therefore, the effect of population density on age-structure may contribute to unstable population dynamics.

In addition, we found that adult and juvenile survival varied greatly between years which could be a result of environmental variation (Chapter 4). Further, the possible effects of harvesting on behaviour and physiology of individuals may lead to variation in breeding performance with implications for leveret and adult survival. It has been suggested that multiple factors regulate populations, which may include complex interactions between trophic interactions, individual variability and environmental variation (Bjornstad & Grenfell 2001; Lundberg et al. 2000). Therefore, the effects of environmental variation and harvesting at the population and individual level have potential to contribute to unstable dynamics.

7.8 Suggestions for future research

An important aim of applied research is to provide evidence to inform decisions in sustainable management and policy. Management of mountain hares in Scotland has continued on an *ad hoc* basis for centuries. However, an apparent decline in numbers (Battersby 2005), changes in upland land use (Robertson, Park & Barton 2001) and a greater number and proportion of hares now being killed for disease control over sport shooting (Patton et al. 2010), means that existing management may no longer be sustainable. Although there have been impressive advances in the understanding of cyclic, or unstable, population dynamics of mountain hare in recent years (Newey et al. 2010; Newey et al. 2007b; Newey et al. 2005; Newey & Thirgood 2004; Townsend et al. 2009; Townsend 2009; Townsend et al. 2011), drivers of these cycles remain ambiguous, complicating their sustainable management (Lande, Engen & Saether

2003b; Newey et al. 2007b). Here, I identify key areas for future research within three broad topics:

1) To better understand mountain hare population dynamics and demography

Understanding the effects of habitat fragmentation, either through changes in land use or widespread blanket culls, requires more information on dispersal distance, rates and probabilities within fragmented landscapes, including colonisation and recolonisation rates. To fully understand the implications of dispersal on population persistence, the effects of dispersal on survival and reproductive performance post-dispersal are required. In addition, the effects of environmental variation on vital rates may be one of a number of factors contributing to population instability. While our results hint at a possible effect of environmental stochasticity on survival and timing of breeding, long term studies are required to fully understand the effects of environmental variation on vital rates and the implication for demography.

2) To assess the effects of harvesting on mountain hare population dynamics and demography

The physiological and behavioural response of mountain hares to harvesting may lead to changes in body condition with subsequent affects on survival and reproduction. Experimental studies are required to understand the stress responses under different levels of harvesting, and between different hunting methods, and how stress responses affect population growth, and therefore, demography. Harvesting bias can affect the phenotypic and demographic structure of populations, and therefore, population growth rate. Identifying age or sex classes that are

more susceptible to harvest mortality would improve our understanding of how harvesting effects demography.

3) To better inform mountain hare management in Scotland

Our knowledge of mountain hare population dynamics, the drivers of population cycles and the implications for population persistence, would be improved by incorporating information on dispersal, density-dependence and harvesting into population models. This would enable more informed decisions to be made on the management of mountain hares. At present, the numbers of mountain hares being killed is neither monitored nor regulated in the UK. Monitoring the number of mountain hares taken, the location from where they are taken and at what time of year, would enable realistic harvest rates to be quantified. From this information it would be possible to estimate whether current harvest rates are sustainable, or whether a change in legislation to increase protection of the mountain hare is needed to maintain their favourable conservation status in the UK.

7.9 Final conclusion

Harvesting for sport and culling for disease control have very separate aims. Sustainable harvesting strives to take maximum yield without compromising population viability (Aanes et al. 2002). Whereas the efficiency of culling for disease control depends on the ability to significantly reduce population density within a desired area.

The mountain hare has been traditionally harvested for centuries. That harvest has occurred over this time span is evidence in itself that sustainable harvesting of mountain hare in Scotland can be achieved (Sutherland 2001). However, we found little evidence of

compensatory mechanisms, although negative density-dependent juvenile recruitment was observed (Chapter 5). When sustainable harvest rates were estimated using a matrix population model, a harvest rate of 40% was deemed sustainable as it resulted in a positive growth rate and a less than 5% chance of extinction (Chapter 6). However, of the ten populations sampled in Chapter 5, only three had harvest pressures less than 40% suggesting that unsustainable harvesting of mountain hares is occurring in Scotland. Further, the model estimates that if harvesting was yearling biased, or the initial population size was reduced, a 40% harvesting rate ceased to be sustainable. It remains unknown whether harvesting of mountain hares is unintentionally biased. Mountain hare optimal habitat is becoming increasingly fragmented due to changes in land use in the uplands and further fragmentation from widespread culling is also a possibility. This could result in smaller, more isolated subpopulations, in which harvest levels of 40% may not be sustained. Further, we suggested that until evidence that proves that harvesting is not biased towards a specific age or sex classes is found, harvest rates should remain conservative.

Mountain hare population density over an area of 130 km² was successfully reduced from 20 hare km⁻² to almost zero (Laurenson et al. 2003). The lack of compensatory mechanisms we report here, and low dispersal rate, distance and probability, suggest that population growth rate in the culled population will not increase in response to culling, and an influx of individuals into the culled area is unlikely. Whilst this means that culling can successfully reduce mountain hare numbers, it does not necessarily mean that a reduction in ticks or LIV will also occur. Even in absence of mountain hare, LIV will persist if red deer are also present. Further, the amount of time that would need to be invested in culling mountain hares could lead to the costs being greater than the benefits of reducing the disease. It is likely that estates

using mountain hare culling as a tick control strategy will be taking more than 40% of the population annually. Therefore, not only is it doubtful that culling mountain hares for tick and LIV control is effective in reducing disease prevalence (Harrison et al. 2010), but it also unlikely to be sustainable in terms of mountain hare population persistence.

The mountain hare is the UK's only native lagomorph and has potential to act as an indicator species for the upland environment, influencing the habitat through grazing and browsing pressures and providing a food source for raptors (Watson 1997). Until mountain hare population dynamics, including how populations respond to harvesting and culling, are better understood, it is not possible to predict if current management strategies are sustainable. Unsustainable exploitation could lead to a significant reduction in numbers of this iconic upland species, with currently unknown consequences for the wider biodiversity and ecosystem functioning of the Scottish uplands.

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