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The landscape ecology of brown hares and European rabbits in pastures in the north east of England

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Brown hare portrait in North Yorkshire. Photo Silviu Petrovan

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Summary

The declines of the brown hare (Lepus europaeus), a priority species for conservation in the UK, may have been caused by changes in agricultural management. This study aims to identify hare distribution, density, habitat selection and demography in grasslands in order to benefit their future conservation. In addition, this study aims to investigate the impact of current agricultural management on the populations of the European wild rabbit (Oryctolagus cuniculus), a major agricultural pest and potential competitor for hares.

Hare and rabbit populations were surveyed in several large, pasture-dominated, sites in north –east England between 2007 and 2009. Estimated density of brown hares in the studied region was far higher than the published national average density for this species in pastures but with very large variation between superficially similar sites. We explored a new method to survey hares using night-time line transect distance sampling and compared this method with day time surveys. Night-time distance sampling produced improved precision estimates of hares with considerably less survey effort by maximising detectability during surveys.

Hares and rabbits had different habitat requirements in grassland areas and areas dominated by intensive sheep grazing produced the lowest hare densities and in most cases were associated with high rabbit densities. Field size was an important determinant of the distribution of both hares and rabbits but with contrasting effects for the two species. Predator control appeared more important in increasing rabbit numbers than hares in the studied region.

Our results indicate that recent changes in pasture management in the UK might favour high rabbit densities with potentially significant economic impacts for the agricultural sector.

Hare productivity was high but female fertility and survival, in particular juvenile survival, were relatively low. Hares in the studied region were generally in good condition and reached sizes comparable with hares from arable areas. Population modelling suggested the hare population in the area was slowly increasing but was susceptible to decline even at relatively moderate levels of hunting.

Radio-tracking indicated that habitat heterogeneity was important for hares at both between and within field levels. Hares preferentially used field margins during both active and inactive periods and selected woodland edges and unimproved grassland during diurnal periods, suggesting that they might benefit from measures designed to *increase heterogeneity and re-establishment of non-farmed habitat features, particularly field margins. Equally, hares avoided sheep grazed fields with short swards for both foraging and resting indicating that reducing grazing intensity in pastural areas would also be beneficial for hare conservation.*

We suggest that grassland management could be adapted in order to minimize damage by high numbers of rabbits and increase the presence and abundance of the brown hare, a species of conservation concern in Europe and the UK.

Chapter 1 Introduction

1 Species ecology and management; a question of scale

There are few detailed studies of species ecology, including mammals, at large spatial scales yet management and conservation are often more likely to be effective at such scales and local scale studies may be inadequate for understanding the processes determining abundance even within that local study site (Baillie et al. 2000). In this context understanding large scale processes and relating them to local scale ones may be vital for understanding the full impact of habitat changes on species distribution and abundance (Dunning et al. 1992).

Herbivorous mammals dominate the globe being human’s main mammalian competitors for food in productive systems (Olff et al. 2002) as well as a significant source of animal protein. Vertebrate herbivores can also have substantial impacts on the structure and diversity of grassland plant communities (Bakker et al. 2009).

In the UK, where the majority of land is farmed, the study of species that coexist with farming is economically important. In such heavily impacted and modified land use areas loss of heterogeneity and fragmentation are central characteristics, with significant consequences for species composition and abundance. However, in order to adequately manage populations of wild herbivores we need to understand the processes that govern their distribution and abundance at both field and landscape scales.

This thesis examines the ecology of two mammalian herbivores, the European brown hare (*Lepus europaeus*), and the European wild rabbit (*Oryctolagus cuniculus*) at landscape scales and link it to local-scale processes. The main subject of this thesis, the brown hare is an iconic and characteristic species associated with the farmland environment which has suffered extensive declines in recent decades while the European rabbit is an important agricultural pest. To put the study in context this work begins with a review of literature relevant to both species

1.1 Lagomorphs

Until the early 20th century lagomorphs were considered a part of the order Rodentia with which they share several characteristics but from which they are mainly distinguished by the presence of a second pair of incisors located in the back of the upper front incisors (Cowan, 2008). Despite the small number of species (approximately 90) they are an exceptionally important mammal group both economically and ecologically since they occupy, either as native or as introduced species, all continents except Antarctica, in habitats ranging from tropical rainforest, deserts and steppe to arctic tundra and form the base of many predator-prey systems. Some are important game species, food sources or laboratory animals while others are major agricultural or environmental pests. All lagomorphs are herbivorous, have an elongated and fenestrated rostrum of the skull to reduce weight and are adapted for quick movement to escape predators (Chapman & Flux, 2008). Hares and rabbits, which together form the family Leporidae, share a distant common relative and have been separated for more than 50 million years from pikas (family Ochotonidae). The genus *Lepus* includes jackrabbits and hares comprising 32 species and is a notoriously difficult taxonomical group due to low gene pool divergence (Alves et al. 2003), broad phenotypic variation within taxa (Suchentrunk et al. 2008) and complex evolutionary scenarios including phases of secondary contact and introgressive hybridization (Thulin et al. 2006) but also the fact that interspecific recognition is probably chiefly by scent which is not a normal taxonomic character (Chapman & Flux, 2008). Although molecular data support an old ancestry of this genus, fossil evidence suggests that it has experienced its major adaptive radiation only relatively recently, approximately 2-2.5 million years ago, and therefore the overall genetic differentiation between many taxa might be relatively small (Suchentrunk et al. 2008).

1.2 Brown hares

1.2.1 Origins

The brown hare (*Lepus europaeus* Pallas, 1778) was at times regarded as a geographically separated conspecific form of the African cape hare (*Lepus capensis*, Linnaeus, 1758) and reviews of molecular data including new studies of nuclear and mitochondrial gene-pool differentiation suggest that this might indeed be the appropriate nomenclature (Ben Slimen et al. 2006; Suchentrunk et al. 2008). Phenotypic characteristics such as body size, coat colour and ear length appear to be dictated by environmental pressure (Stoner et al. 2003) and are able to modify relatively quickly in order to adapt to new conditions.

The brown or European hare is thought to have originated in the open steppes of Eurasia or Africa (Perez-Suarez et al. 1994) and its adaptation to such open grassland habitat is important when considering the true evolutionary nature of this animal. It survived the last glaciation in a refuge around the Black Sea and recent molecular evidence suggests that two lineages, one from the Balkans and the other from Anatolia, have subsequently spread across Europe (Kasapidis et al. 2005). It is genetically more similar to *Lepus capensis* than other European species (*Lepus corsicanus, L. granatensis, L. timidus*) (Perez-Suarez et al. 1994; Suchentrunk et al. 2008). Its current distribution includes most of Europe north of the Alps, northern Scandinavia and the Iberian Peninsula. It extends eastwards into Siberia as far as Lake Baikal and it was successfully introduced to Ireland, south Sweden, south South America, eastern Canada, north-eastern USA, much of western Australia, New Zealand and several small islands in the Mediterranean Sea (Chapman & Flux, 1990; Corbet, 1986; Cowan, 2008; Masseti & De Marinis, 2008).

With an average weight of 3.32kg in males and 3.69kg in females (Cowan, 2008) the brown hare is the largest of the three lagomorph species present in the UK, the other two being the European rabbit (*Oryctolagus cuniculus* Linnaeus, 1758) and the mountain hare (*L. timidus* Linnaeus, 1758). It is now widely accepted that the only native leporid species in the British Isles is the mountain hare and that the brown hare is an introduced species since no archaeological records of fossil bones of *L. europaeus* have been found dating before the time when the English Channel was formed, 7000 - 9500 years ago (Yalden, 1999). Its introduction was assumed to have dated from Roman times 100-400 AD (Corbet, 1986) but since sub-fossils of brown hares have been identified in Neolithic and Bronze age sites its introduction might date as far back as 4000 years, when the clearing of forests to create land for agriculture would have benefited this species. After its introduction to Britain the brown hare most likely displaced the native mountain hare, which is today restricted to high altitudes in the Scottish Highlands, several Scottish islands, the Isle of Man and an isolated population introduced to the Peak District, through exclusive competition (Thulin, 2003).

1.2.2 Population dynamics

The brown hare is described as a polygynous-promiscuous species (Bray et al. 2007) in which breeding can occur throughout the year, with a main breeding season lasting from the end of winter to the beginning of autumn; from late February until August in the Northern Hemisphere, when most of the adult females are pregnant (Lincoln, 1974; Broekhuizen & Maaskamp, 1981). Reproductive success is highly variable in time and space (Broekhuizen, 1979), and it is the result of female fecundity and leveret survival (Pepin, 1989; Marboutin et al. 2003). European hares can reach puberty at an early age (4-6 months) (Marboutin & Peroux, 1995) and produce well developed neonates, whose high postnatal growth rate permits a short nursing period and a high weight at weaning (Broekhuizen & Maaskamp, 1981). Annual productivity of females varies widely in different areas (Pepin, 1989), with a peak in productivity in the middle of the birth season (Raczynski, 1974, Hewson & Taylor 1975, Broekhuizen & Maaskamp, 1981). The number of litters produced in a year is positively correlated with body weight in reproductive females (Marboutin et al. 2003) while three-year old females tend to have the highest fertility (Frylestam, 1980). Mean litter size varies inversely with mean annual temperature and is around 2.7 in the UK, peaking in the middle of the breeding season in late spring (Hewson & Taylor, 1975; Pepin, 1981). Annual numbers of litters are reported to be 4.5 per female and total number of young produced per female was 11.3 in an area in the Paris Basin for all fertile females, or 9.4 for all the females present (Pepin, 1989). Marboutin et al. (2003) estimated higher fecundity rates in central France, with 13.4 leverets produced in an area of lowland agriculture, but much smaller numbers were reported in Northern Europe with 6.8-8.9 in Sweden (Frylestam, 1980) and only 5 per annum in a study in Denmark (Hansen, 1992).

Survival in leverets, and individuals in their first year is significantly lower than in adults, influenced by climate, disease, predators and agricultural mechanisation, with 85-95% reported mortality between birth and autumn in Poland (Wasiliewski, 1991) and 70.5-84.2% in another Polish study (Pielowski, 1971); 73-84% losses in mainland Denmark compared to 68-91% on an island (Frylestam, 1980). In the UK White et al. (2000) used annual mortality figures of 50-60% for young born in January and February, 90% for those born between April and July and 40-50% for October and November. Leveret survival was found to decrease with increasing litter size due to lighter weight at birth and lower milk supply per leveret (Hackländer et al. 2002b). Leveret mortality is thus highest for young born during the period when productivity is also at its peak, in terms of both litter production and litter size (Cowan, 2004). Major variations in annual survival rates of the leverets, extracted by hunting bag data obtained in France (Pepin, 1989) seem to show good survival rates for hares born early in the season in areas where winter cereals and lucerne are grown, and lower values in areas where spring cereals, maize and potatoes are produced. However, the harvesting of lucerne in the summer has proved to have a drastic impact on the leverets, killing about 50% (Kaluzinski & Pielowski, 1976).

The mean lifespan varies from 2.5 to 5 years among different regions and habitats (Marboutin & Peroux, 1995, Smith et al. 2005a), with hares in pastural areas generally living shorter lives (Smith et al. 2005a).

Survival of yearlings is lower than that of adults and seems to be sex-dependent: male yearlings survived better than female yearlings in a declining hare population in France (Marboutin & Peroux, 1995). There are few data however on hare juvenile survival in pastural areas and, more importantly, on ways to reduce juvenile mortality.

1.2.3 Abundance and surveys

Understanding the environmental and anthropogenic factors affecting the distribution and abundance of wildlife is a major goal of ecological studies. For conservation purposes, this question is particularly important in the case of declining species, such as the brown hare. Because of their wide distribution and high environmental and economic importance lagomorphs have been surveyed using a diversity of techniques including total clearances, wide belt, line transect counts, circular spotlighting, twilight counts and dung pellet counts, all based on three main approaches: counts of inactive hares, counts of active hares and indirect methods (Langbein et al. 1999).

The brown hare is one of the most abundant and widespread medium-sized mammals in Britain, with an over-winter population size estimated at 817,520 ±137,251 hares in 1992-1993 (Hutchings & Harris, 1996). The exact number of hares in Britain has been a subject of debate and numerous methods have been employed to create an accurate estimation of the total population size including spotlighting (Barnes & Tapper, 1985), drag line counts (Barnes et al. 1983), day-time line transect distance sampling

(Hutchings & Harris, 1996) and the use of records from game bags (Tapper & Stoate, 1992).

A comprehensive review and comparison of different techniques used for brown hares is provided by Langbein et al. (1999) who concluded that day-time line transect distance sampling provides the best reliability-efficiency solution. Of the counts of inactive hares, total clearances are very useful as they give an absolute figure of density but are labour intensive and can only be applied in small areas. Furthermore there is no robust way of defining confidence limits of estimates from such clearances. Of indirect methods, faecal pellet counts are problematic as hare droppings are difficult to find in a complex substrate such as grassland and the rate of decomposition varies widely with region and season (Murray et al. 2005). Because hares are mainly a nocturnal species counts of active animals require the use of spotlights or other more expensive equipment such as infrared or thermal imaging. Additionally, night time surveys can be logistically difficult and potentially hazardous which makes them less suitable for large scale studies that rely on volunteers for data collection. Because visibility and detectability are strongly correlated with vegetation height, surveys can only be conducted during late autumn and early spring when crops have been harvested and grass is generally short (Hutchings & Harris, 1996). This coincides with the end of the breeding season before the autumn rest period and the onset of the following reproductive cycle with mating usually starting in January (Lincoln, 1974).

Distance sampling is a method of abundance estimation developed from transect sampling and which has become a widely used tool for monitoring terrestrial and marine species in recent years due to the ability to cover large areas relatively quickly while using less labour intensive or intrusive techniques than other methods, such as total clearances or mark recapture. The method allows animal population densities to be estimated by knowledge of animal distribution with respect to the transect and it is considered to be more robust than other methods because it does not assume that all animals present will be observed. It has been used to produce accurate abundance estimates in a variety of mammalian species including deer, fox, brown hare, mountain hare and Irish hare (*Lepus timidus hibernicus*) (Hutchings & Harris, 1996; Newey et al. 2003; Rouette et al. 2003; Ward et al. 2003; Reid et al, 2007). However, distance sampling requires that a number of assumptions are met by the surveyor to ensure accuracy of the technique; 1) all individuals at 0 distance (i.e. on the transect line) are detected; 2) individuals are detected before substantial movement away from the observer; 3) measurements of distance from the transect line are accurate and 4) the transects are randomly distributed with respect to the density of the animal population being surveyed. Violation of any of these assumptions can seriously compromise the accuracy and precision of density estimates. If these assumptions are met and if good estimates are to be obtained, the histogram of perpendicular sighting distances should possess a shoulder near the transect line, i.e. detection is certain near the transect line and stays nearly certain for some distance (Buckland et al., 2001).

1.2.4 Status

The brown hare has a wide distribution in the UK, occupying all favourable areas, usually below 500m, comprising mainly farmland, but also woodland, marshes and uplands (Vaughan et al. 2003). However, since Victorian times hare populations seem to have retracted to islands of high densities creating “a very clumped distribution” (Hutchings & Harris, 1996). Density appears greatly influenced by the presence of arable land, where it is able to attain high mean population densities of up to 65 hares km^{-2} in areas with predator control (Brockless, 1995). Densities in pastural landscapes are considered to be much smaller, from 9-16 hares km^{-2} across Europe (Smith et al. 2005a) and an average of only 3.3 hares km^{-2} in Britain (Hutchings & Harris, 1996).

Pastural areas, mainly in the western parts of England, have experienced an ongoing decline in hare numbers, especially in the south west, even though at a national level hare numbers seem to have stabilised since the 1980s (McLaren et al. 1997; University of Bristol, 2003; Battersby, 2005). They are absent from the north-west and western Highlands of Scotland where they are replaced by the mountain hare (Harris et al. 1995; Cowan 2008), which seems better adapted to these upland habitats.

The brown hare is believed to have declined over most of its Western and Central European range since the 1960s (Fig.1.1) (Pielowski & Pucek, 1976; Tapper & Parsons, 1986; Harris et al, 1995; Marboutin & Peroux 1995; Mitchell-Jones et al, 1999; Smith et al. 2005a). Reasons for this decline are likely to vary across its range and remain a complex issue involving several processes; those that have been proposed are: agricultural intensification and habitat destruction (Tapper & Barnes, 1986; Smith et al 2004, 2005a), increased predation, disease (Duff et al. 1994, 1997, Frolich et al. 1996), heavy hunting (Pepin, 1987), changes in climate (Hackländer et al. 2002) and reduction in suitable habitat and food resources following land conversion and land abandonment (Genghini & Capizzi, 2005). The hare decline in the UK appears dramatic if current estimates are compared to those for 1880 (4 million in mid-winter), before the introduction of the Ground Game Act (Hutchings & Harris, 1996). As a consequence, and given their economic importance as a game animal, many studies have been undertaken that address hare habitat preferences and abundance (Tapper & Barnes, 1986; Edwards et al, 2000; Smith et al, 2004; 2005a) as well as the causes of its decline and possible ways to increase its numbers.

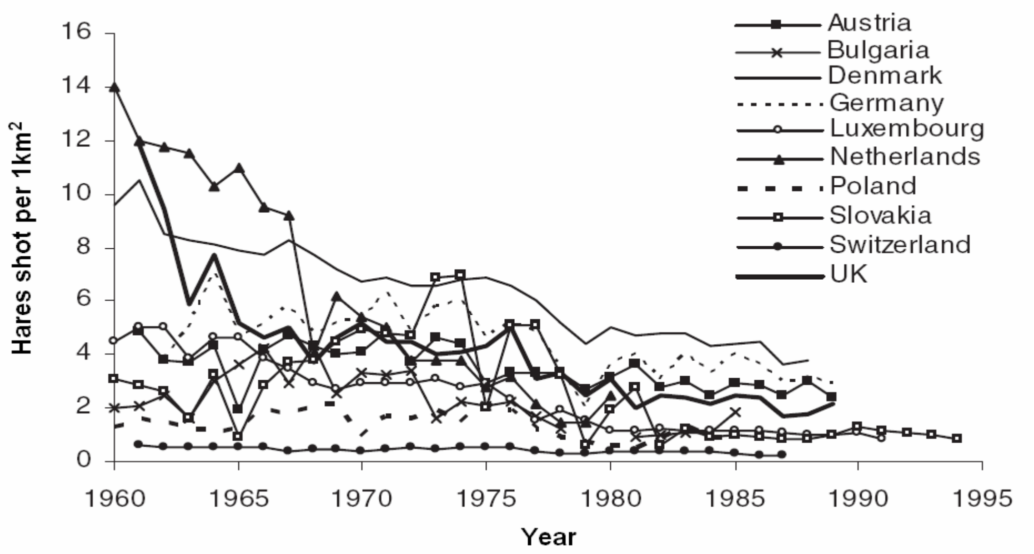

Fig. 1.1 Decline in Brown hare (*Lepus europaeus*) hunting gamebags across Europe post-1960 (extracted from Smith *et al*. 2005a).

Because of this recent decline the brown hare is protected under Appendix III of the Convention of the Conservation of European Wildlife and Natural Habitats (Bern Convention, 2002) and is classed as a “priority species of conservation concern” and as such it has a Species Action Plan in the UK. This plan’s objective is “to maintain and expand existing populations, doubling spring numbers in Britain by 2010” (Anonymous, 1995).

Despite being a priority species included in the UK BAP, current legislation does not offer brown hares any special protection and hares are less protected formally in the UK than almost anywhere else in Europe (Cowan, 2004). The provisions of the Hare Act 1848 which allowed the possibility of culling hares as a pest without the need for a game licence were strengthened under the Ground Game Act 1880 which gave tenant farmers the right to kill hares on their land at any time of the year to protect crops (Cowan, 2004). However, following a massive decline in brown hare game bags and pressure from naturalists and hunters the Hare Preservation Act was introduced in 1892 which forbids the sale (not the hunting) of hares during what was perceived as the main breeding season, between 1 March and 31 July inclusive. This is contrary to most

European countries where hares are typically shot only from October to December (Cowan, 2004).

It has been suggested recently that the main way to increase numbers of hares is through increasing recruitment and adult survival (McLaren et al. 1997; University of Bristol, 2003) or by increasing the survival of both adults and leverets (Cowan, 2004) but the objective of doubling the hare numbers in spring by 2010 in the pastural areas seems “highly unlikely” to have been attainable (University of Bristol, 2003).

1.2.5 Habitat associations and food selection

The primary habitat of the Brown hare is considered to be farmland (Harris et al. 1995 Baldi & Farago 2006) but with major discrepancies between arable and pastural fields (McLaren et al. 1997; University of Bristol, 2003; Smith et al, 2005a). Hares in pastural landscapes have lower population densities, poorer body condition and participate less in breeding than in arable habitats (Smith et al. 2005b; Jennings et al. 2006). They are also smaller in length and weight and have less fat reserves around the kidney (University of Bristol, 2003, Smith et al. 2005b). However this appears to be a recent phenomenon as Harris et al. (1995) quotes Thorburn (1920) who describes hares as being “plentiful in cultivated areas, especially grasslands”. Hare populations and percentage of grasslands have decreased and acreage of winter cereals has increased in several European arable regions in recent decades (Ruhe & Hoffmann, 2003). Suggested reasons for the hare decline in pastures include seasonal food shortage due to the shift in cultivation of grass for silage rather than hay (Harris et al. 1995), loss of habitat heterogeneity and suitable cover (Smith et al. 2004), high stress levels from increased disturbance by predators, grazing domestic stock, humans and mechanical equipment as well as changes in vegetation due to the use of pesticides that reduce the diversity and abundance of weeds that can form an important part of the diet (Reichlin et al. 2004). The increase in the density of livestock in pastures is likely to have had an impact on populations of hares since they have been shown to prefer stock-free pastures and avoid stocked pastures and other crops (Barnes et al, 1983), though this is contradicted by a more recent study (Smith et al. 2004) which found that hares actually preferred cattle pastures over arable fields for most of the year but avoided sheep pastures for most of the year.

Despite a wealth of studies, optimal habitat requirements for the brown hare remain unclear (Cowan, 2004). Hares seem to favour diverse and small to medium-size fields (Meriggi & Alieri 1989, Lewandowski & Nowakowski 1993), comprising different crops, and move daily and seasonally to take advantage of the food resources available as crops develop (Tapper & Barnes, 1986; Ruhe & Hofmann, 2003), although large fields and relatively low habitat diversity can also be beneficial for the hares (Vaughan et al. 2003). It has been suggested that hares do better in large, open fields with short vegetation because these allow them to spot approaching dangers and to use their escape strategy, which involves outrunning predators at high speed with sudden changes in direction. However, Smith et al. (2005a) reviewing 77 papers on hare declines throughout Europe, found field size to be negatively associated or neutral to hare abundance and no effect of field size on hare density once data was reanalysed. As expected, large monocultures are negatively associated with hare abundance, as crops reach maturity simultaneously and no food resources are available after harvesting due to the long distances and loss of diversity in the form of hedgerows and fallow land (Frylestam 1980, 1986; McLaren et al. 1997; Smith et al. 2005a). The fact that hares have declined significantly post 1960 even in what was considered to be optimal habitat for them, large areas of arable habitats dominated by a variety of crops including cereals and root vegetables, seems linked with the general trend of farmland biodiversity decline in most northern European countries as a consequence of increased mechanisation and farm size, simplification of crop rotations and loss of non-crop features such as hedgerows, field boundaries and vegetation along ditches (Stoate et al. 2001; Benton et al. 2003). The decline of species associated with farmland has been well documented for birds such as the grey partridge (*Perdix perdix*), lapwing (*Vanellus vanellus*) and skylark (*Alauda arvensis*) and they are usually more severe then for species not associated with such habitats (Donald et al. 2001, Gregory et al. 2004).

One major aspect in the hare selection of favourable habitat seems to be the trade-off between food presence and cover. Hares are mainly active during the night and at dusk and dawn periods (Pepin & Cargnelutti 1994, Hansen 1996, Holley 2001; Ruhe & Hofmann, 2003), though activity is reduced on cold nights (Tapper & Barnes, 1986). Hares use forms, shallow depressions in the soil surface, to take cover from predators, especially avian predators (Holley, 2001), during the day and in pastural areas hares were found to prefer areas with tall vegetation such as improved grass or fallow land, stubble or other crops while avoiding broadleaved plantation, mixed or coniferous woodland, semi-improved grassland and tall scrub (Hutchings & Harris, 1996). The importance of diversity in habitats populated by hares is viewed in different and sometimes contradictory ways by different authors, but it is generally accepted that hares require a degree of diversity throughout the year to use as food resources and cover from predators. At the European level, a comparison of farmland differing substantially in landscape structure indicates that, up to a mean field size of 20 ha, hares tend to extend their home ranges with increasing mean field size but they may reduce their home-range size if field size exceeds this value considerably (Ruhe & Hofmann, 2003). Home ranges also expanded significantly in large, uniform fields, where hares had to move frequently to gain access to food and cover, while they remained small in areas where field diversity was larger and both food and cover were available (Tapper & Barnes, 1986; Smith et al. 2004).

Predator avoidance could make hares tend to avoid woodland margins and hedgerows where predators such as foxes (*Vulpes vulpes*) and buzzards (*Buteo buteo*) often hunt (Hewson, 1977) but this is in apparent contradiction with Tapper & Barnes (1986) who observed that radio-tracked hares in a mixed farmland area abandoned cropped areas after harvesting and relied on other habitats for cover during daytime, sometimes using woodland for most of the rest of the year (Tapper & Barnes, 1986). Foxes have been shown to be the major predators of hares (Pielowski 1976, Erlinge et al. 1984, Goszczynski & Wasilewski 1992, Reynolds & Tapper 1995; Reynolds et al. 2010) and are considered by several authors to impact significantly on hare populations, causing up to 40% of all juvenile hare mortality (Erlinge et al. 1984). However, juvenile mortality due to predation remains poorly explained due to the difficulties in studying this age group in a field setting. Frequent sightings of foxes were negatively associated with hare abundance in a large scale questionnaire (Vaughan et al. 2003).

As the area occupied by arable land has remained stable through most parts of Europe since the 1960s and the area of fallow land has remained stable or has increased, the hare’s decline cannot be associated with the conversion of arable land, considered to be optimal habitat for hares, to less suitable, pastural areas as these areas have remained stable or actually decreased in large parts of the UK and Germany (Smith et al. 2005a). Instead the decline of hares seems to be caused by the intensification of agricultural practices, including changes in yields and increased stocking density, especially of sheep, and a consequent loss of field level diversity that could make hares more vulnerable to predators and changes in climate (Smith et al. 2005a). However, the nature of their association with pastural habitats is unclear as even in mainly arable or mixed areas, pastures are negatively associated with hare density (Pepin, 1987, Vaughan et al. 2003).

Recently, it has been suggested that weed reduction, following the intensification of agricultural practices in Europe, might have played a major role in the decline of the hare by depriving them of an important source of food during periods of high energy requirements (Hackländer et al. 2002a). According to some authors brown hares actually avoid arable crops in their diet (Frylestam 1980; Tapper & Barnes 1986) and particularly seem to prefer parts of weeds and grasses rich in fat (Frylestam, 1986, Reichlin et al. 2006) or select a combination of cereal crops, grasses and weeds (Katona et al. 2010). Reasons given for this are that a diet that includes an abundance of plants with a high fat content would both enhance energy assimilation and allow the animals to reduce foraging activity and hence predation risk. The selection of such plants would minimize the weight load of ingested food which should be particularly advantageous for hares, which rely on high running speeds to escape predators. Also, leverets are fed with milk only once a day (Broekhuizen & Maaskamp 1980) and most of the fat content (20% of the milk) originates from food intake rather than own synthesis (Hackländer et al. 2002a). Hackländer et al. (2002a) suggested that low milk production by female hares, as a consequence of low weed diversity and abundance in intensively managed farmland, combined with low temperatures and/or increased precipitation might reduce leveret growth rates, increase the mortality, and therefore facilitate, if not cause, the decline of this species across Europe. However, a study designed to investigate the importance of weeds as a possible cause for the hare decline in Austria concluded that brown hares most frequently used arable crops for food throughout the year although they did select for weeds in spring and summer and preferred arable crops and food items provided by hunters in autumn and winter (Reichlin et al. 2006). As summer months provide low food resources after the harvesting of cereal crops, the hares have to be able to shift to a diet based on other available crops or weeds and as such habitat diversity may become a “crucial factor” (Reichlin et al. 2006).

Winter diet of the brown hare was found to expand at sites in Germany where winter conditions were severe and access to ground vegetation was limited by snow cover and it was dominated by terminal twigs of Blackthorn (*Prunus spinosa)* and Hawthorn (*Crataegus monogyna)* but included other woody plants while other available plant species were rarely or never selected (Rodel et al. 2004). This supports the idea that hares are capable of broadening their diet and selectively include a range of low quality food items following food restrictions, in response to a reduction in food availability, as would be predicted for a generalist herbivore species.

Investigating food selection on cereal and turnip crops Hewson (1977) showed that three factors seem to influence the selection of food by brown hares: nutrient content, vegetation structure, especially the height of the plants or the open spaces and the palatability. The preference for cereals or turnips, regardless of nutrient content, in open spaces or of short height is attributed to the advantage for hares in detecting predators. Brown hares in Sweden were found to prefer feeding on the edges of meadows where grass was shorter and in the middle of the fields after the grass was cut for hay (Frylestam, 1976).

Considerable variation of the diet among different areas and individuals seems typical for hare populations but grasses represented a large proportion of the diet (Katona & Altbacker, 2002; Katona et al. 2010). Schmidt et al, (2004) found a significant positive association between root crops and brown hare abudance and a negative association between winter cereals and hares. Surprisingly, the same study found no effect of the grasses or green fodder areas on hare numbers.

These findings may play an important role in understanding food-based microhabitat selection in different agricultural landscapes as an adaptation to heavy predation.

1.2.6 Interspecific competition

Competition between rabbits and hares has received significant attention in the past but underlying mechanisms remain unknown. The perceived increase in hare abundance in the middle of the 20th century was dismissed as being a direct result following the rabbit myxomatosis epidemic in the 1950s in Britain (Barnes & Tapper, 1986). In another natural experiment, in a juniper scrubland habitat in Hungary, where the same epidemic occurred and wiped out most of the rabbit population, there was no increase in hare abundance and the moderate dietary overlap seemed to indicate no significant competition for food between the two species (Katona et al. 2004). However, other studies show evidence of significant dietary overlap and competition between the two species (Chapuis, 1990; Kuijper et al. 2004) and hares were very efficient in outcompeting rabbits from small islands; equally, in most situations they are able to occupy most of the habitat of the other species in its absence (Flux, 2008). Rabbits, in particular bucks, are known to be more aggressive towards other species such as hares and it was hypothesised that this behaviour would force hares out of the area shared by the two species but more recent direct observations of the two species feeding together dismissed this idea as antagonism is very rare (Barnes & Tapper, 1986; Flux 2008).

High rabbit densities could impact on hare populations in several ways, including direct competition for food, shared diseases, attraction of increased numbers of predators to the area and habitat modification through intense grazing.

1.3 European rabbit

The European wild rabbit (*Oryctolagus cuniculus*, Linnaeus, 1758) is the only extant representative of a monospecific genus in the family Leporidae which probably originated in the Iberian Peninsula and survived the last glaciation in two refugia, one in southern Spain and the other in southern France and north-eastern Spain (Ferrand, 2008). These two refugia were the origins for the two main recognised subspecies, *Oryctolagus cuniculus algirus* and *O.c. cuniculus*, of which the latter was introduced widely around the world including in Europe (Branco et al. 2002) and probably also formed the basis for domestication.

The current status of the wild rabbit has been described as "paradoxical" given that it is largely threatened within its native range but extremely successful elsewhere as an introduced species (Lees & Bell, 2008) and is present in most of Europe, North Africa, parts of South America, Australia, New Zealand and hundreds of islands (Flux, 1994) including the UK, where the rabbit is probably the most important vertebrate pest species (Smith et al. 2007).

Fossil records show that the rabbit was formerly present as a native species in the UK but became extirpated during one of the later glaciations and was apparently not reintroduced until 700-800 years ago by the Normans (Flux, 1994; Yalden, 1999). However, for a long time following reintroduction rabbit populations were mostly restricted to managed warrens and numbers in the wild only began to rise significantly in the 18th century following changes in agricultural landscape and the introduction of widespread predator control (Cowan, 2008). Populations reached a peak in the early 1950s when the species was considered a major agricultural pest but suffered a catastrophic decline following the introduction of myxomatosis as a biological controlling agent in 1953 and which in its early stages, killed at least 99% of the exposed population (Lloyd, 1970; Trout et al. 2000).

Since the post-myxomatosis crash there has been a strong recovery of rabbit numbers concomitant with attenuation of the disease and increased genetic resistance in rabbits and although populations are probably still at low levels compared to pre-1953 numbers rabbits are reaching pest status again in some areas of the UK (Trout et al. 2000; Smith et al. 2007). However, more recent monitoring reports suggest local declines following the spread of Rabbit Haemorrhagic Disease in both England and Scotland (Battersby 2005).

In common with most successful colonisers, rabbits display an extreme environmental plasticity which allows them to adapt to new areas and conditions by including new plant species in their diets (Lees & Bell, 2008) or quick transitions between preferred and unpreferred food resources (Ferreira & Alves, 2009). Equally, rabbits are capable of highly efficient food conversion through re-ingestion of soft faeces (Kuijper et al. 2004) making them adaptable and resistant to adverse conditions (Stott, 2008). However, rabbits are typically selective grazers feeding on a variety of gramineous species (Williams et al. 1974) including cereal crops. Experimental studies suggest that rabbits selected the shortest sward during summer for foraging irrespective of biomass intake, probably as an anti-predator strategy (Iason et al. 2002).

The proverbial rabbit reproduction means that this r-selected species reaches sexual maturity at a very early stage, has a short gestation and post-partum oestrus, with ovulation induced by copulation and females usually pregnant within 24 hrs of parturition (Cowan, 2008; Tablado et al. 2009). Litter size, breeding season and pre-natal mortality are all influenced by population density (Lloyd, 1963), climate and environmental conditions, allowing great plasticity (Tablado et al. 2009) but expanding populations can reach annual productivity of 30 juveniles per female (Lloyd, 1970).

In contrast to brown hares rabbits produce altricial young commonly known as kittens, which are born with no fur and are raised in blind tunnels within the purposefully excavated burrow system (Kolb, 1994). Although a proportion of the rabbit population can live above ground for much of the year (Kolb, 1991), most rabbit populations depend on the warren density and quality and consequently on the soil characteristics (Barrio et al. 2009), with intense competition for access to the best sites (Cowan & Garson, 1984).

The drastic population declines of the wild rabbits in the Iberian Peninsula, where they are a keystone species, and their impact on native predators have been well documented, particularly in relation to the world's rarest cat species, the Iberian lynx *Lynx pardinus* (Delibes-Mateos et al. 2007; Lees & Bell, 2008). More surprisingly though, rabbits can have an important conservation role even in areas where they have been introduced, including the UK, both as a prey species and for their role in creating and maintaining particular plant communities and habitats (Manchester & Bullock, 2000; Lees & Bell, 2008). However, despite the importance for conservation and as a game species, rabbits are still largely viewed as a major agricultural pest in Britain due to their capacity to produce important economic damage and this situation is likely to worsen as populations increase (Trout et al. 2000).

Due to their particular ecology rabbit damages extends beyond direct and indirect effects of plant overgrazing, competition with domestic stock and pasture impoverishment (Bell et al. 1999; Trout 2002; Dendy et al. 2003) and include damage caused by burrowing, including erosion and degradation (Eldridge & Myers, 2001). Damage to crop species by rabbits generally relates to cereal crops (Bell et al. 1998; Dendy et al. 2004) but impacts can also be substantial in grasslands, especially at high densities, and are usually more easily overlooked by farmers (Dendy et al. 2003). For these reasons an array of measures has been designed to control rabbit populations and to reduce rabbit-inflicted damage in forestry, horticulture and agriculture. These include the destruction of warrens, wide-scale poisoning and gassing (Cooke, 2008) as well as non-lethal methods which are considered more humane and socially acceptable, such as fencing, chemical repellents and diversionary feeding (Barrio et al. 2010).

1.4 Conclusions

The brown hare is a widely distributed species in Europe and one of the most common medium-sized mammals in the UK. They are a typical farmland species and an important game animal but despite this population declines may have reduced their number to about 20% of that in 1880 and this trend appears to have accelerated since the 1960s but stabilised since the 1980s. While most authors agree that the brown hare declines have been caused by changes in land management practices and agricultural intensification during the 20th century it is still unclear why they have become so rare in pastures where they had been previously abundant. The SAP for the hare aims to double the spring population by 2010 and even though this objective now seems very unlikely to have been attained there is no real scope for increasing their numbers in arable areas where they generally still maintain good numbers and where major increases would probably result in stronger hunting pressure in response to increased damage to crops.

So far, most of the studies conducted on brown hares in the UK have been performed on small scale areas of less than 1000ha and even at a European level there are few studies that focus entirely on pastures (Smith et al. 2005a). This is probably due to the fact that in many pastural areas hare numbers are so low that it becomes difficult to quantify their density or habitat preferences but these are precisely the habitats where hares would have the potential to increase their population significantly should adequate conservation measures be put in place.

Brown hare breeding and population dynamics have been well investigated in the past but the influence of habitat, and in particular of pastures, on reproductive parameters and on juvenile and adult survival remains poorly understood.

In large areas dominated by sheep pastures competition for food and destruction of resting sites for adults and shelter for leverets through intense grazing might play a major part in habitat selection for brown hares. Sheep grazing, especially at high density, produces a short and uniform sward which was shown to be avoided by hares at the field scale during most seasons in an area of mixed farming (Smith et al. 2004).

European wild rabbits are far more abundant than hares in the UK and are generally perceived to be pests, although this is usually the case in arable areas. Changes in agricultural management have been shown to be potentially beneficial for common, generalist or invasive species (Henein et al. 1998; Tscharntke et al. 2005) including the European rabbit (Reid et al. 2007). Although the evidence remains unclear and contradictory there are several strong suggestions of competition for resources or otherwise between rabbits and hares and this competition might be exacerbated in a simplified environment such as grassland fields in farmland. Understanding how land use and agricultural management factors influence rabbit populations in grasslands will allow for a better targeted management of this species and a clearer understanding of the ecological relationships between hares and rabbits in such habitats.

1.5 Aims, objectives and study description

The main aim of this study was to examine aspects of the ecology of the brown hare in grasslands that directly relate to its conservation including current status, habitat associations, population dynamics and hunting levels as well as the role of specific habitat structures linked with agri-environment schemes. In addition, this project aimed to get a better understanding of the impact of current pasture management by investigating its effect on the distribution and abundance of the European wild rabbit, a major agricultural pest and a potential competitor of the brown hare in such areas.

Specific objectives and actions were:

1. Estimate the current distribution and abundance of brown hares in pastures in the north-east of England and evaluate survey methodologies for brown hares at varying densities. Large grassland-dominated sites were selected and surveyed

intensively during autumn 2007-spring 2009 during both day time and night time (**Chapter 2**).

2. Identify the habitat and management factors associated with hare distribution and abundance in grasslands in order to understand the possible causes of their recent declines. Data on habitat and grazing management were collected and analysed in relation to hare distribution and density at different scales. (**Chapter 3**).

3. Investigate the factors influencing rabbit distribution and abundance in grasslands in order to fully explain the impact of grazing and habitat management in such areas. Data collected on habitat management and grazing regimes in the sites were analysed in relation to rabbit density at both local (field) and landscape (site) scales. (**Chapter 4**).

4. Identify the age and sex structure, demographic parameters and sustainable hunting rates in pastural sites in order to provide solutions for a better management of this species. Hare carcasses were collected between 2007 and 2009 and were investigated including jaw sections, placental scar counting, body size and condition. The data was used to compare hares from grasslands in the study area with hare carcasses obtained at a national level (**Chapter 5**).

5. Investigate habitat use and range selection of hares in relation to farmed and non farmed habitat structures and relate these to the effects of agricultural intensification and agri-environment schemes on hare populations. Brown hares were radio-collared and tracked continuously for 13 months in a mixed area of farmland where both agri-environment and game bird shooting measures had been put into place (**Chapter 6**).

Chapter 2 Brown hares in UK pastures; rare or under-detected?

A manuscript based on this chapter has been submitted for publication as:

Petrovan, S.O, Ward, A.I. & Wheeler, P.M. -Detectability counts when assessing populations for biodiversity targets.

Summary

Efficient and accurate estimates of population parameters are a necessary basis for effective conservation action to meet biodiversity targets. The brown hare is representative of many European farmland species: historically widespread and abundant but having undergone rapid declines as a result of agricultural intensification. As a priority species in the UK Biodiversity Action Plan, it has national targets for population increase that are part of wider national environmental indicators.

Previous research has indicated that hare declines have been greatest in pastural landscapes and that gains might be made by focussing conservation effort there. We therefore used hares in pastural landscapes to examine how basic changes in survey methodology can affect the precision of population density estimates and related these to national targets for biodiversity conservation in the UK. We compared the method used for a previous national survey for brown hares; day time distance sampling, with distance sampling at night and carried out an extensive survey of brown hares in pastural landscapes in north east England. Line transects for hares carried out at night resulted in higher numbers of detections, had better-fitting detection functions and provided more robust density estimates with lower effort than those during the day, due primarily to the increased probability of detection of hares at night and the nature of hare responses to the observer. The high number of encounters allowed us to resolve hare densities at site, season and year scales.

This study demonstrates how survey conduct can impact on data quantity and quality with implications for setting and monitoring biodiversity targets. The case study of the brown hare provides evidence that for wildlife species with low detectability, large scale volunteer-based monitoring programmes, either species specific or generalist, might be more successfully and efficiently carried out by a small number of trained personnel able to employ methods that maximise detectability.

2.1 Introduction:

In many countries, including the UK, the government employs headline indicators to assess progress in sustainable development as a basis of informing and shaping policy (http://www.defra.gov.uk/sustainable/government/). One such indicator of 'Biodiversity Conservation' is based partly on an assessment of changes in population trends of priority species under the UK Biodiversity Action Plan (UK BAP). Adequate assessments of changes in priority species are therefore a key component of national biodiversity policy and a wider governmental sustainable development agenda.

The brown hare *Lepus europaeus* is an iconic species of European farmland regarded as indicator for the habitat quality of lowland agricultural landscapes (Cowan 2004), a popular game species and a "priority species of conservation concern" in the UK BAP with a target of doubling 1996 numbers by 2010 (UK BAP 1995). The 1996 assessment of the population size of hares was based on the 'national hare survey', a country-wide survey using volunteers to carry out line-transect distance sampling of resting hares during the daytime (Hutchings & Harris 1996). This survey was a landmark in wildlife monitoring in Britain as it was the first attempt to provide a country-wide population estimate of a terrestrial mammal based on a properly stratified sample of survey sites and designed as part of a programme to measure performance against a defined policy objective (UKBAP 1995; Hutchings & Harris 1996). The methods for the survey were selected on the basis of practicality, robustness, ability to incorporate wide spatial coverage and to allow participation by volunteers (Hutchings & Harris 1996, Langbein et al. 1999). The survey's results indicated that hares occurred at low densities in marginal upland and identified significant opportunities for increasing the British hare population through improving the quality of hare habitat in such landscapes (Hutchings & Harris 1996). However, because relatively few hares (400) were seen in pastural and marginal upland areas, despite over 3,000 km of survey effort, the survey was unable to resolve hare densities at a ‘habitat within region’ scale. The methods employed in this first survey were therefore not able to deal with the key management questions that the results of the survey raised.

Brown hares are largely crepuscular and nocturnal, resting in a ‘form’ during the day (Holley 2001). Night time surveys were rejected as a method in the national survey for reasons of logistical feasibility and to avoid the possibility that active animals would move prior to observation or remain concealed in tall vegetation. However, attempting to count inactive animals is much more challenging as their detectability is likely to be significantly lower than active individuals. We considered *a priori* that a hypothesised increased detectability of hares at night would increase encounter rates and facilitate greater spatial and temporal resolution of population density estimates from distance sampling with consequences for the spatial and temporal scale of monitoring and, by implication, target-setting. This study therefore had three aims:

1. To carry out a regional scale survey of brown hares in a pasture-dominated region.
2. To carry out a quantitative assessment of differences between daytime and night time line-transect distance sampling surveys of brown hares.
3. To attempt to resolve densities of hares at seasonal and sub-regional scales.

2.2 Methods:

2.2.1 Study site

Line transect distance sampling was carried out at seven study sites (named A-G) located in a lowland/marginal upland (30-250m above sea level) pastural landscape in North Yorkshire, England (Figure 2.1). A detailed description of the site selection is given in Chapter 4 and in Petrovan et al. (2011). All sites were dominated by pastures and six of the seven were surrounded by more pastures and/or moorland; one, site G, was surrounded by a mixed arable-pastural landscape. Some form of shooting (mainly of pheasants *Phasanius colchicus*) took place at most sites but only sites B, C, D and G included a permanent gamekeeper and even in these sites there were farms where no form of hunting or predator control was permitted. Hares were actively hunted with relatively low intensity in sites C, F and G.

2.2.2 Sampling design

Sites were selected through inspection of remotely sensed images in Google Earth (http://earth.google.com) searching for large areas of grasslands, supported by ground truthing. Field transects were established along 'transect routes' composed of consecutive fields; each route incorporated between 6 and 22 fields (mean 9). Each site had between two and six routes, each 2-3 km long. Transects followed the length of the entire field and were surveyed by walking a straight line through the middle of the field. Routes were designed to cover as much of each site as possible given the constraints of accessibility and access permission. Less than 5% of >60 landowners refused permission, hence coverage was reasonably comprehensive and representative of the landscape with no obvious geographical or land use bias. In order to ensure independence of detections transect routes were a minimum of 300 m apart or separated by substantial natural or artificial barriers such as streams or robust fences. Routes did not deliberately follow landscape or manmade features, such as streams, valleys, roads or foot paths.

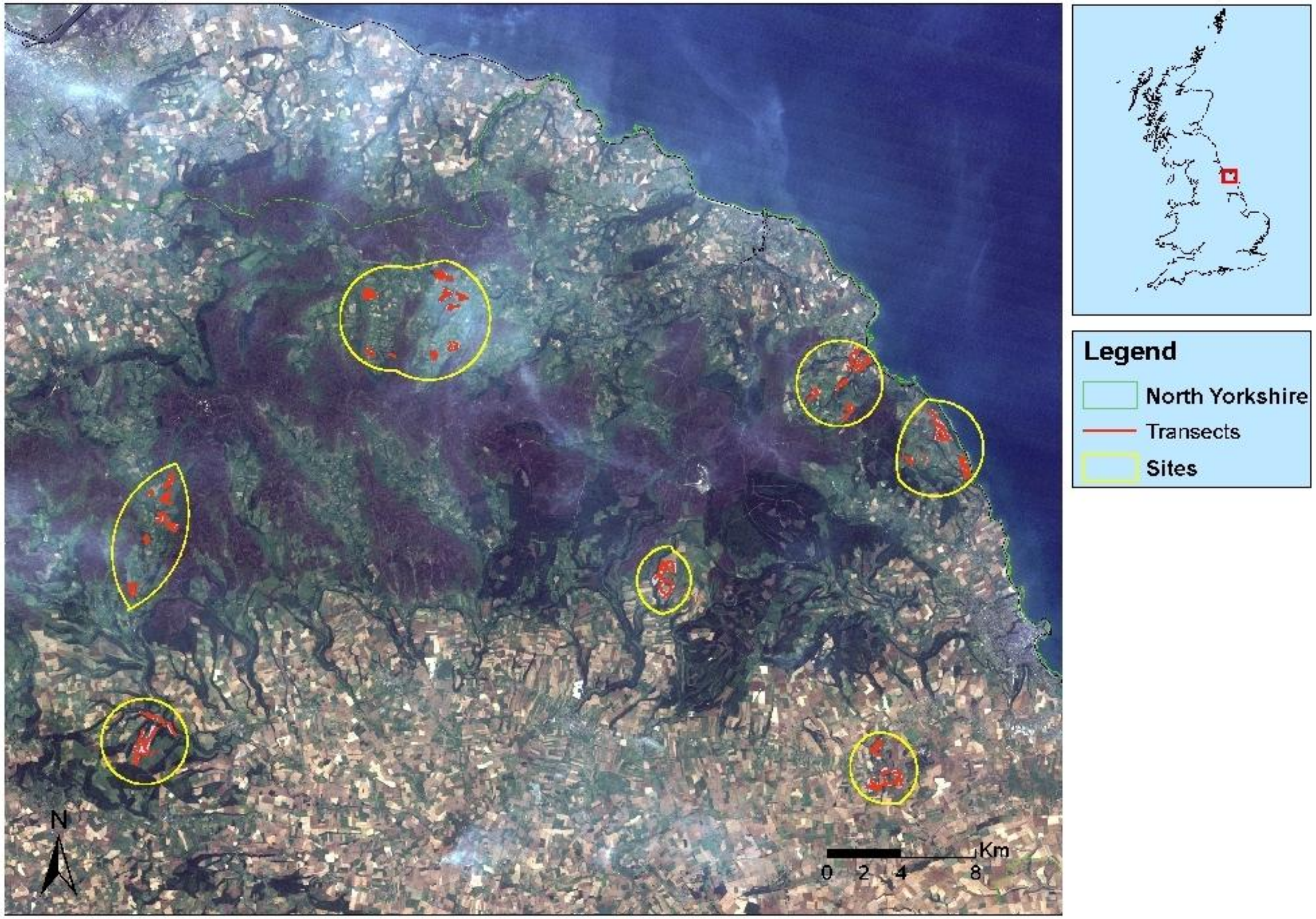

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Figure 2.1 Location of individual sites and corresponding transects used in this study

2.2.3 Data collection

2.2.3.1 **Population density estimates**

From autumn 2007 to spring 2008 we set out to survey all transects at all seven sites twice during the night; once between October and December 2007 (hereafter ‘autumn surveys’) corresponding with the end of the hare breeding season when population levels should be at their maximum (Hutchings & Harris 1996) and the second time between January and March 2008 (hereafter ‘spring surveys’), after peak winter mortality when the adult population should be at a minimum. However, due to the difficult weather conditions, with extensive rain and fog in spring 2008, surveys had to be extended into April and early May for a small number of transect routes (<7% of total transect length).

All night-time surveys were started at least one hour after sunset and finished before 23:30 hours, while day-time transects were only walked between 10.00 and 14.00 hours when most hares would be inactive in their forms (Hutchings & Harris 1995; Smith et al. 2004). Days with poor visibility due to fog or heavy rain and particularly cold nights or those with bright moonlight were avoided as these negatively influence the proportion of active hares at night (Barnes & Tapper 1985; Reid, et al. 2007). Surveys were carried out by two people walking slowly and silently along the transect scanning an arc of 180^{o} with a 1 mega-candlepower spotlight (Clubman CB2, Cluson Engineering Ltd, Hampshire, UK) and 8 x 42 binoculars. Observations of animals were made by the same observer to avoid between observer differences. A trained and experienced observer collected all day-time data. All sites were surveyed on foot to avoid contravening the recommendation that transects do not follow existing linear structures such as roads or paths (Buckland et al. 2001) and equally to be able to include fields irrespective of road access.

In order to assess whether hares were reacting to the observer prior to detection, the behaviour of each individual sighted was recorded. Five classifications were used:

- *Crouching* Hare lying on the soil surface with the entire body parallel to the ground; not feeding.
- *Running* Hare running at the moment of detection.
- *Standing* Hare immobile in a vigilant position; not feeding.
- *Feeding* Hare actively feeding whether sitting or lying.
- *Feeding + chasing* Hares in a group, alternating feeding with short, 5-20m, chases in the direction of another individual.

During night time surveys all hares that were displaced by the surveyors were followed with the lamp as they moved away to establish with precision the direction of movement to ensure that no animals were counted twice while moving through successive fields. Hares were subsequently ignored if they relocated to other fields that were on the transect route and as such were seen for a second time. Hare detections were facilitated by the very short grass swards during the months of surveys and a combination of eye shine, the sight of the entire animal and its movement were employed for detecting individuals throughout the study. Transect sections were recorded using GPS and superimposed on 1:10,000 Ordnance Survey maps in ArcGIS version 9.1 (ESRI California, USA) in order to calculate total distance walked. Distances to sighted animals were measured using a laser range finder (Leica LRF900, Germany) with 1m precision and 7 x magnification. Angles between the transect line and the location of the observed animal were measured using a compass to the nearest degree. Typically hares were easily distinguished in the field from rabbits, which were largely sympatric, but in cases when identification was problematic angle and distance were recorded and subsequently the animal was approached by the observer until the species could be identified with certainty. Distance sampling could not be employed to establish rabbit densities in our sites due to the fact that very large numbers of rabbits were present on many of the transects surveyed. In addition, rabbits were more mobile and easier to displace by the surveyor than hares making angle and distance recording highly problematic. As the majority of fields had average sward height of less than 5cm and only 3 fields had average sward heights > 12cm at the time of the surveys it was assumed that detectability was largely unaffected by sward height.

2.2.3.2 **Night time versus daytime surveys**

Two sites (C & G) were selected for an evaluation of the differences between day and night time surveys. Transects were walked twice during night time and three times during daytime using the same network of transects. These surveys were carried out during autumn and winter seasons (October to March 2008-2009) but for simplicity here will be referred to as ‘winter’ surveys.

2.2.4 Data analysis

A detailed explanation of the theory of distance sampling and practical aspects of the analysis is provided by Buckland et al. (2001). Program DISTANCE version 6.0, release 2 (Thomas et al. 2009) was used to calculate the density and abundance of brown hares in the surveyed sites. Detection functions were calculated across sites for each season and pooled seasons while specific density estimates were generated by post-stratification at the levels of site, season or year. Where counts were sufficient (i.e. > 40 observations) a separate detection function was calculated for each site to investigate the differences in the detection of animals in different areas and at different densities. Since all surveys took place in the same habitat type (grassland) and with the same species, for comparisons between daytime and night time surveys separate detection functions were generated for each of these pooled across sites and seasons. Global density was calculated as the mean of stratum estimates weighted by stratum area (Buckland et al. 2001, Thomas et al. 2010). No left truncation or the forcing of data into arbitrary bins was applied but instead a combination of analysis using ungrouped data or data grouped at different intervals and different right-hand truncations were used in order to select for the model with the best fit. Distance data were modelled by fitting three key functions and three series expansions to the data (Buckland *et al*. 2001). Model performance was evaluated using a combination of Quantile quantile (q-q) plots, Goodness of fit tests, Kolmogorov-Smirnov and Cramer-von Mises family tests for ungrouped data and Akaike's Information Criterion (AIC) for both grouped and ungrouped data, with the best model, in terms of parsimony, selected on the basis of the lowest AIC value. Variance was calculated using a combination of the default empirical calculation and in some instances an advanced analytic encounter rate option with post-stratification with over-lapping strata made of adjacent samples as this method was shown to give more robust estimations of variance when there were strong spatial trends in the studied area (Fewster *et al*. 2009). In this case consecutive field transects rather than parallel systematic lines were used in order to account for the variance in encounter rate. Comparisons of density estimates between seasons, years or between night time and daytime surveys were performed using the *z test* (Buckland *et al.* 2001).

We assessed the relative efficiency of daytime versus night time surveys by comparing coefficients of variation using the formula:

$$L = \frac{L_0 \{cv(\hat{D}_0)^2\}}{\{cv_t(\hat{D})^2\}}$$ Buckland *et al.* (2001)

where L is the total transect length, L_0 is the transect length covered in the study, $cv(\hat{D})$ is the coefficient of variation in the pilot study and $cv_t(\hat{D})$ is the target value for the coefficient of variation. The relationship between survey efforts required for two sets of surveys to achieve equivalent coefficients of variation (i.e. $cv_{tN}(\hat{D}) = cv_{tD}(\hat{D})$) can be described by:

$$L_N / L_D = \left[L_{0N} \cdot \frac{\left\{ cv\left(\hat{D}_0\right)_N^{\,2} \right\}}{L_{0D} \left\{ cv\left(\hat{D}_0\right)_D^{\,2} \right\}} \right]$$

Which we define as the ‘survey efficiency ratio’.

2.3 Results

2.3.1 Population density estimates

Hares were recorded at all seven sites but despite the fact that all sites were situated within the same region and were superficially similar in composition and management, densities varied widely between them (Table 2.1). The overall mean density was 20.6 hares km^{-2} (95% CI 18-23 km^{-2}) with a post-breeding (autumn) density of 22.6 hares km^{-2} (95% CI 18-28 km^{-2}) and a pre-breeding (spring) density of 18.9 hares km^{-2} (95% CI 15-23 km^{-2}). Encounter rates varied between 0.4 and 11.1 hares km^{-1} (mean = 3.8; SD = 3.6; n = 7) for autumn and 0.5 and 6.7 hares km^{-1} (mean = 3.0; SD = 2.3; n = 7) for spring (Table 2.1). The minimum spring density estimate at any site was 2.9 hares km^{-2} (95% CI 1-7 km^{-2}) while the highest was 39.9 hares km^{-2} (95% CI 25-64 km^{-2}).

Site	**Transects (number)**	**Effort (km)**	**Observations (hares seen)**	**Encounter rate (hares km^{-1})**	**Density (hares km^{-2})**	**95% CI**	**CV(%)**
A	73	17.5	63	3.4	21.2	15-29	16.4
B	109	22.2	10	0.4	2.9	2-5	35.4
C	149	28.1	141	4.8	30.0	24-37	11.6
D	43	16.6	30	1.7	10.8	7-18	25.6
E	30	13.0	12	0.9	5.8	3-11	35.4
F	72	17.6	56	3.0	19.0	13-27	19.3
G	40	15.6	139	8.9	52.8	39-71	14.9
Pooled	516	130.6	451	3.3	20.6	18-23	7.81

Table. 2.1. Hare density estimates, total effort, observations and encounter rates in the autumn 2007-spring 2008 surveys in seven pastural sites in NE England (Fitted model was a Hazard-rate key function with a cosine adjustment term, with 16m intervals, 130m truncation

Of all hares with recorded behaviour at the moment of detection (n = 577) only 10% were observed running while the majority (58%) were observed feeding (Figure 2.2). “Feeding +chasing” behaviour was almost entirely recorded in fields with high numbers of hares situated in site G. The proportion of individual hares exhibiting different types of behaviour at the moment of sighting was compared between seasons and hare behaviour was significantly different ($\chi^2 = 36.03$, $p = 0.01$, df = 8). However, the small percentage of hares observed running suggests that most animals were detected at their original position, prior to evasive movement away from the observer, a fact also confirmed by the histogram of pooled night time observations (Figure 2.3) and the visual inspection of data fit to the model (Figure 2.4).

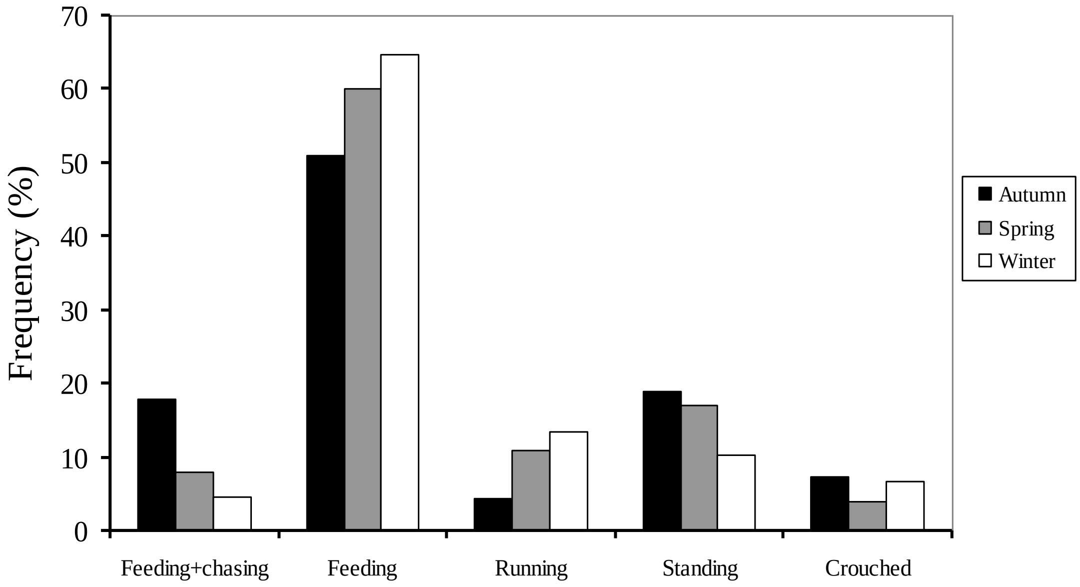

Figure 2.2. Observed hare behaviour at the moment of detection during 2007-2009 night time surveys.

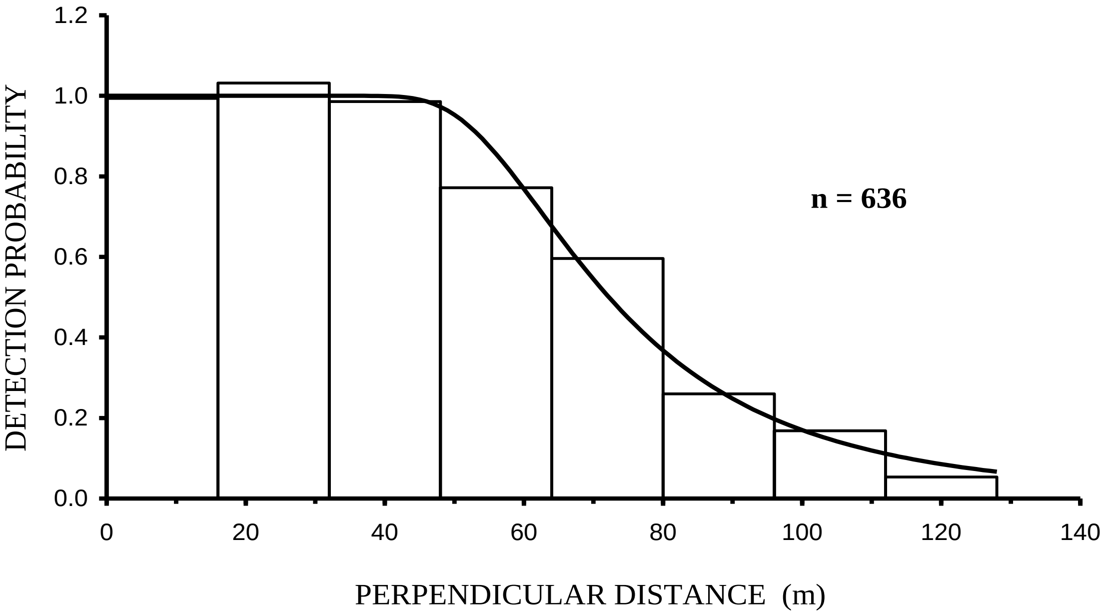

Figure 2.3. Histogram of total night time hare observations in all seven sites surveyed during 2007-2009. Fitted model is a Hazard-rate key function with a cosine adjustment term, with 16m intervals, 130m truncation

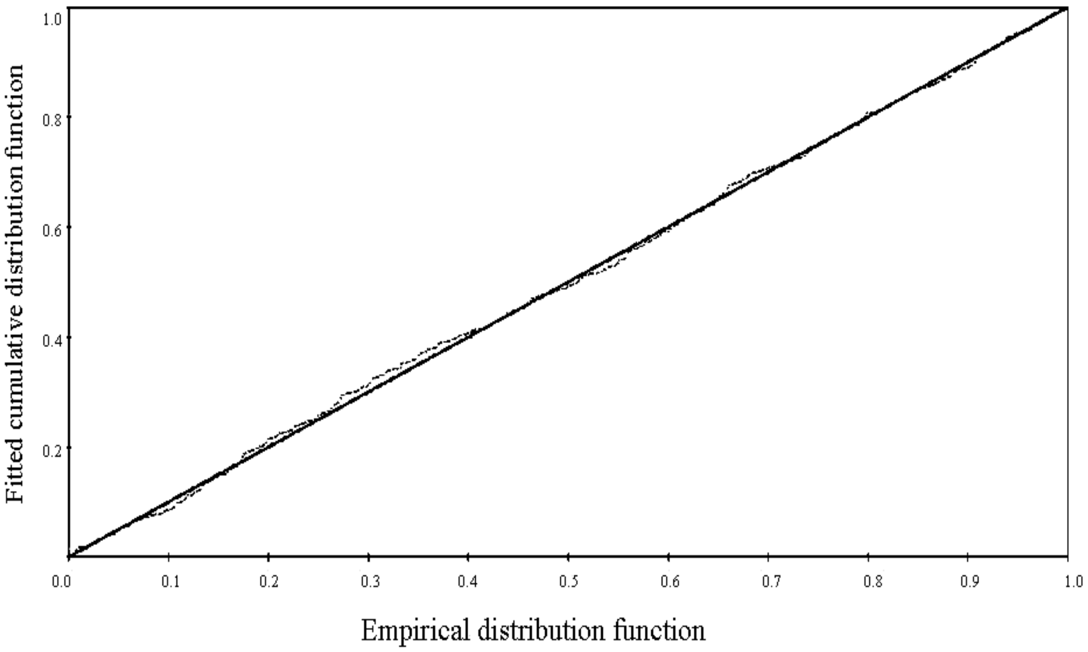

Figure 2.4. Quantile- quantile (q-q) plot of fits of hare observations (n = 651) obtained during 2007-2009 line transect sampling in all seven sites. Fitted model is a Hazard-rate key function with a cosine adjustment term, no interval, no truncation. The model fit to the data is near perfect.

*(q-q plots only show a maximum of 500 randomly selected observations)

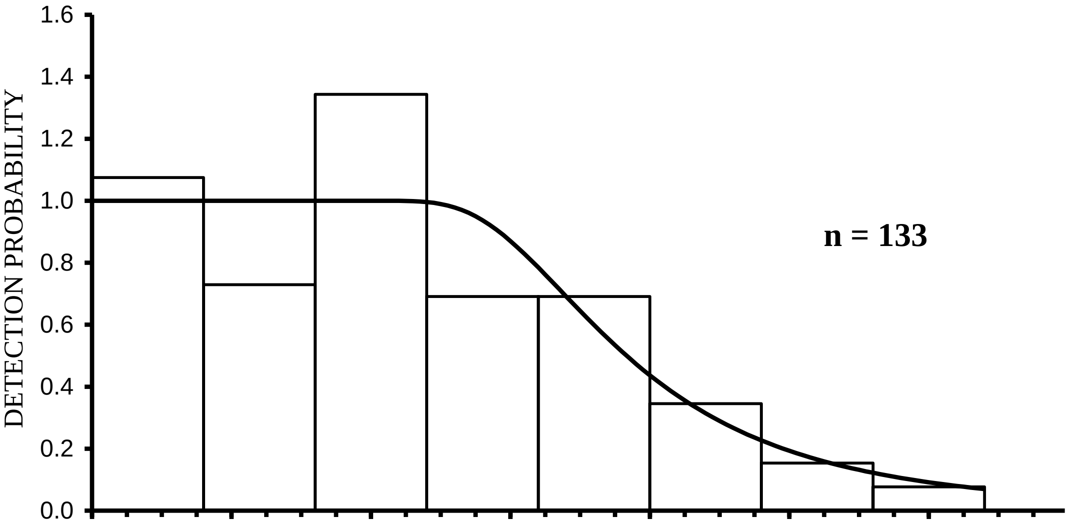

Figure 2.5. Histogram of total night-time hare observations in the highest density site (site G) during pooled autumn-spring 2007-2008. Fitted model is a Hazard-rate key function with a simple polynomial adjustment term, 16m intervals, 5% right truncation.

At the highest density site, G, the detection probability remained similar during both seasons, with a spike in detections around 40m, probably indicating over-dispersion of frequency in observations (Figure 2.5).

2.3.2. Detecting changes in population density

The decrease in number of hare observations between autumn 2007 and spring 2008 for all seven sites was reflected in a 16.4% decrease in the mean calculated density. This apparent decline in observations was most noticeable at the highest density site, G (Table 2.2). For most other sites density estimates were very similar between seasons and the overall autumn and spring densities were not significantly different (Z-test, $Z = 1.158$; $P = 0.246$). The overall detection function and the distribution of radial distances for all seven sites was different for autumn and spring, with fewer observations near the transect line during spring, possibly as a reflection of increased activity during that time. At the highest density site, G, the detection function remained similar during both seasons. Extrapolating from the overall regional estimate of hare density of 20.6 hares km^{-2} (95% CI 18-23 km^{-2}) derived from the pooled autumn and spring surveys and based on consecutive iterations of 5% hypothetical changes in population, a separate further survey replication might have been sufficient to detect significant population changes of around 25% (based on the Z test) if the precision of the new estimate was the same as the previous estimate.

For sites C and G, where between-year comparisons were possible, density estimates for winter 2009 were almost identical to the ones obtained for spring 2008; for site C these were 26.8 hares km^{-2} and 25.6 hares km^{-2} respectively, and for site G 40 hares km^{-2} and 41.8 hares km^{-2} respectively. This was also reflected by the very similar encounter rates between spring 2008 and winter 2008 (Table 2.2).

Site	Year	Season	Transects (number)	Total effort (km)	Observations (hares seen)	Encounter rate (hares km^{-1})	Density (hares km^{-2})	95% CI	CV(%)
C	2007	Autumn	78	13.9	77	5.5	32.9	24-45	15.9
C	2008	Spring	71	14.1	64	4.2	26.8	20-36	15.0
C	2008-2009	Winter	119	23.3	96	4.1	25.6	19-35	15.9
G	2007	Autumn	20	7.7	86	10.5	66.4	45-99	19.5
G	2008	Spring	20	7.9	53	6.5	39.9	25-64	23.0
G	2008-2009	Winter	47	15.3	106	6.8	41.8	31-57	15.2

Table 2.2. Estimates of hare density, effort and encounter rates for night time surveys at two sites during 2007 - 2009 (calculated with Uniform key function with cosine adjustment term, 16m interval, 115m truncation)

2.3.2 Night time versus daytime surveys

Daytime encounter rates (0.7 hares km^{-1}) were 7.4 times lower than night time encounter rates (5.2 hares km^{-1}) on the same transects (Table 2.3). Effective strip width (ESW) was much lower in daytime than night time surveys (8.9m and 64.4m respectively; Figures 2.6 and 2.7). Mean pooled density estimates for daytime surveys for the two sites (41.2 hares km^{-2}; 95% CI 29-59 km^{-2}) were considerably higher than night time estimates (32.3 hares km^{-2}; 95% CI 26-40 km^{-2}) but due to the very large confidence intervals for daytime estimates the results of a Z-test of differences between the two was not significant (Z=1.01, P=0.31).

Site	**Total effort (km)**	**Observations (hares seen)**	**Encounter rate (hares km^{-1})**	**Density (hares km^{-2})**	**95% CI**	**CV(%)**
C (N)	23.3	96	4.1	25.6	19-35	15.9
C (D)	41.1	27	0.6	38.0	25-57	20.7
G (N)	15.3	106	6.8	41.8	31-57	15.2
G (D)	21.6	17	0.8	45.0	27-76	26.7

Table 2.3. Estimates of hare density, effort and encounter rates in the two sites surveyed during winter 2008 - 2009 (calculated with Hazard-rate key function, cosine adjustment term, 16m interval, 115m truncation for night time surveys and Uniform key function with cosine adjustment term, no interval, no truncation for daytime surveys)
(N) – night time surveys
(D) – daytime surveys

For site C survey efficiency of daytime surveys was 0.33 that of night time surveys; for site G efficiency of daytime surveys was 0.29 that of night time surveys.

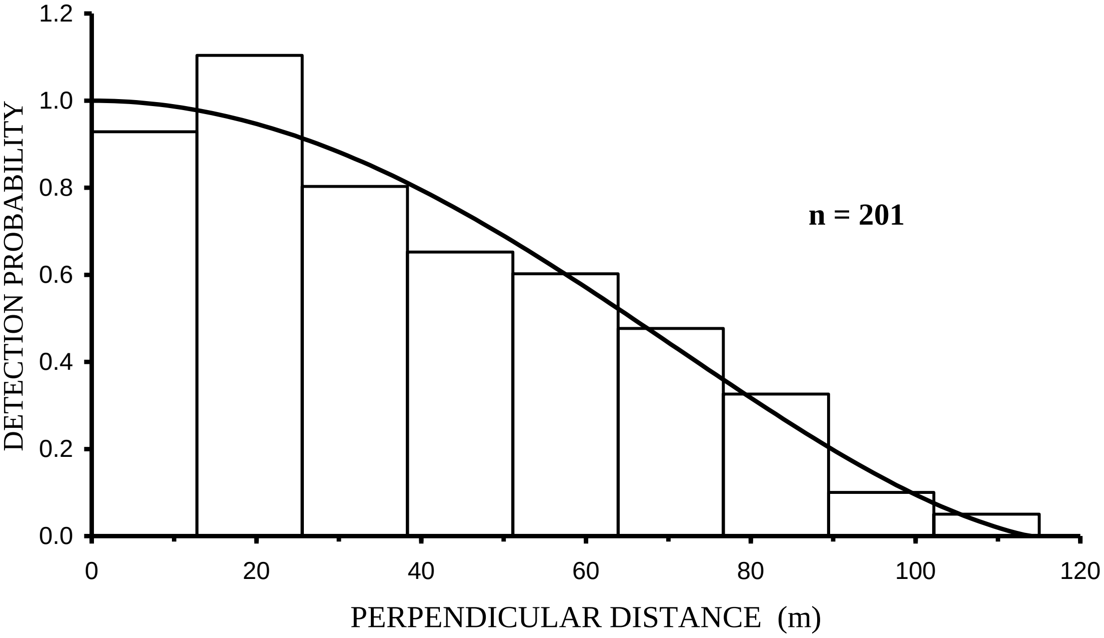

Figure 2.6 Histogram of total night time hare observations in the two sites surveyed twice during winter 2008-2009. Fitted model is a Uniform key function with a simple polynomial adjustment term, no intervals, 115m right truncation.

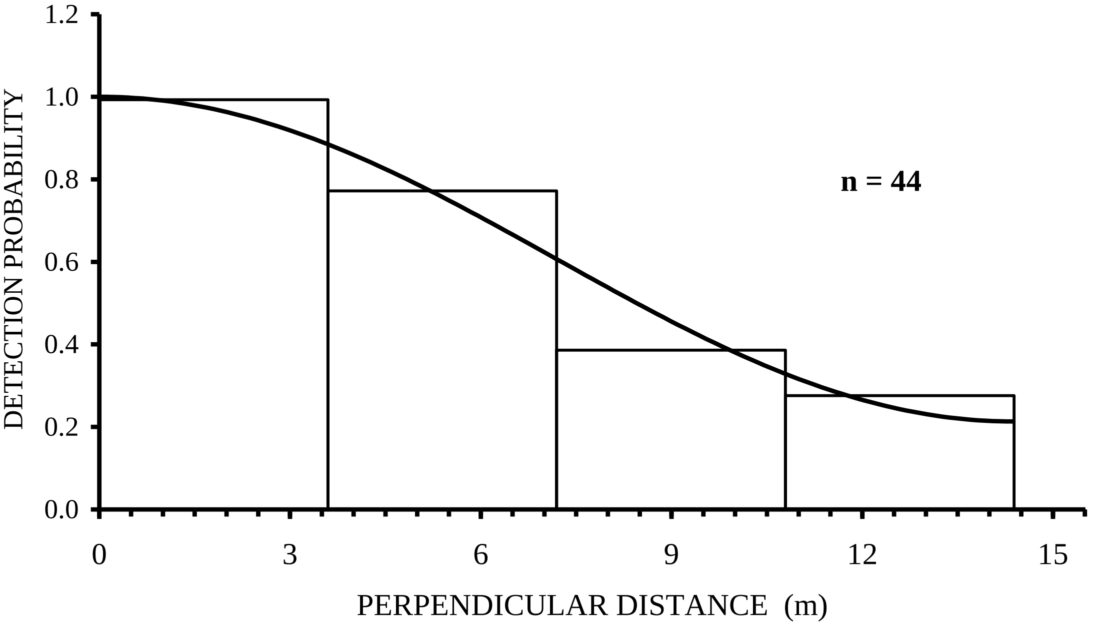

Figure 2.7 Histogram of total day time hare observations in the two sites surveyed three times during winter 2008-2009. Fitted model is a Uniform key function with a cosine adjustment term, no intervals, no truncation.

In order to understand the effect of different daytime and night time encounter rates on hare detections at all sites we converted our observed (night time) encounter rates to hypothetical daytime encounter rates by dividing by the ratio between daytime and night time encounter rates from our comparison study in sites C and G (i.e. 7.65). We used these to compare the probability of detecting one or more animals on a 1 km transect were surveys to be carried out during the day or during the night. We used a simple Poisson model for hare encounters with the mean as the observed or hypothetical encounter rate for night time and daytime rates respectively (Table 2.4). While the Poisson model may not be suitable for hares at high densities, where encounters are likely to be clumped, we consider it to be a reasonable approximation for hares at these moderate densities and a useful didactic model in this case.

Site	**Night time**		**Daytime**	
	Encounter rate (hares km^{-1})	**Probability of detecting ≥ 1 animal**	**Encounter rate (hares km^{-1})**	**Probability of detecting ≥ 1 animal**
A	3.4	0.97	0.44	0.36
B	0.4	0.33	0.05	0.05
C	4.8	0.99	0.63	0.47
D	1.7	0.82	0.22	0.20
E	0.9	0.59	0.12	0.11
F	3.0	0.95	0.39	0.32
G	8.9	1.00	1.16	0.69
Overall	3.3	0.96	0.43	0.35

Table. 2.4. Encounter rate and probability of encountering at least one hare on a 1-km transect at each site. Daytime encounter rates were calculated by dividing night time encounter rates by the ratio between daytime and night time encounter rates at sites C and G (see Table 2.3).

Over all sites there was a high probability (96%) of detecting at least one hare within 1 km on night time transects, but a relatively low probability (35%) on daytime transects. Only the highest density site (site G, hare density 53.9 hares km^{-2}) had a probability of detection > 50% in daytime surveys, while all but the lowest density site (site B, hare density 2.9 hares km^{-2}) had detection probabilities > 50% in night time surveys.

2.4 Discussion

Conservation targets for the brown hare in the Britain have been set based on population assessments and repeated surveys are necessary to evaluate whether these targets can be or have been met. Our results demonstrate how low hare detectability during day time surveys can affect the results of such surveys with potential wide-reaching implications for setting and monitoring of conservation targets for this species.

2.4.1 Hare density estimates

Our average density estimate of 20.6 hares km^{-2} for the study region is several times greater than the average for brown hares from the national hare survey but is by no means extreme. Given the right conditions continental European populations of brown hares can reach densities in excess of 100 hares km^{-2} (Smith et al. 2005a). In Britain hare densities of 87.3 hares km^{-2} in ‘optimum conditions’ (the presence of predator control and habitat improvements in arable areas) and 28.5 hares km^{-2} in ‘suboptimal conditions’ (mixed rough pasture/arable areas with no habitat improvements and only 3 years of predator control) have been recorded (Reynolds et al. 2010). In our study hare density was not clearly related to sites with effective predator control (sites B, C, D, G; Petrovan et al. 2011). This suggests that predator control alone is not sufficient to explain the relatively high densities of hares in some of our sites. While it is possible that hare numbers in our study region have increased since the time of the national survey, we propose two possible alternative explanations for the discrepancy. The first, and one that is relevant to widespread studies of any species with low daytime detectability, is that daytime surveys result in under-sampling and consequently, across wide spatial scales, underestimated density. The results from our seven sites show variability in population density greater than a factor of ten between superficially similar nearby sites (e.g. sites B, C and G, Table 2.1). The low encounter rate during daytime surveys means that the probability of detecting hares in these surveys, even at relatively high densities, is remarkably low over 1 km transect walked. At site B, where estimated densities were approximately equal to the British average for pasture land, detection probability in a 1-km transect was 5% in the daytime, and at site C, with density over 10 times higher, detection probability was 46%. Extrapolating these figures to the national hare survey, where participants surveyed 3 km in each site on 3 occasions in each of the two years, the estimated probability of detecting one or more hares at our site B (2.9 hares km^{-2}, just below the national average for pastures) in any one daytime survey would be 19% and over the course of all surveys and both years would be 59% (assuming a binomial distribution of detection probabilities and independence between temporal replicates at a site). This implies that in many sites where hares are present at modest densities, even extensive daytime surveys risk not detecting their presence. Regional or national hare density estimates based on such data would rely on a weighted average of those sites where hares were encountered and those with null counts, artificially reducing the overall estimate. Furthermore, distribution maps would likely indicate low levels of presence at regional scales where in fact hares might be widely, if sparsely, distributed. This problem would be exacerbated by a low-efficiency sampling method requiring individual sites to be surveyed multiple times in order to generate sufficient encounters.

A second possible explanation for the discrepancy between our density estimates and those of the national hare survey is that pastures in the North East of England are, for some reason, more suitable for hares than those in the west, a region that is dominated by pastural landscapes and where most data for hares in pastures in the national survey were obtained. There is some evidence that juvenile hares can suffer high mortality in wet conditions (Edwards et al. 2000; Hackländer et al. 2002) and it is possible that the higher rainfall in western Britain reduces recruitment of juveniles to the adult population. One would, in that case, expect pastures in eastern Britain to support higher density populations. Equally, it is very likely that at least in some of our sites hare populations had benefited from measures put in place for game rearing, such as the presence of small blocks of woodland and herbaceous strips in field margins, as well as predator control, all of which have been shown to positively influence hare densities (Vaughan et al. 2003; Reynolds et al. 2010).

2.4.2 Assessing hare populations with day time surveys

Our case study demonstrates that detectability is an important determinant of data quantity and quality when using distance sampling to generate density estimates. Nocturnal species, like hares, typically use different habitats throughout the 24-hour cycle. Brown hares use discrete patches for nocturnal feeding and daytime resting (Smith et al. 2004) and the latter can be located in areas unsuitable for distance sampling due to poor visibility or limited access, such as mature crops left standing over winter or dense woodland (Heydon et al. 2000). Additionally during day time surveys the surveyor typically relies on flushing resting animals (Langbein et al. 1999). As is clear from our day time survey data, this only happens when in close proximity, which results in a very narrow strip width being surveyed and not only a small number of observations (Tables 2.3 and 2.4), but also data from a very small proportion of the survey area with greater potential biases from errors in measuring distances and non-random placement of survey transects. The robust nature of our estimates from night time surveys is supported by the very similar density estimates generated from a variety of models and narrow confidence limits from the best fitting model (Tables 2.1 & 2.2). A combination of low encounter rates and the narrow effective strip width in daytime surveys led to estimates with high variability and a relatively poor model fit. However, brown hares often feed in social groups during the night to increase vigilance (Monaghan & Metcalfe 1985) and at the high end of hare densities in our sites (site G) night time line-transect surveys became less efficient due to the increased possibility of encountering aggregations of up to 20 individuals. Treating these as individual sightings violates the object independence assumption in Distance and although the programme is considered very robust to such violations (Thomas et al. 2010) it can result in increased variance due to large differences in encounter rates between transects and consequently poor precision (Buckland et al. 2001). In such circumstances either day time distance sampling or cluster analysis for night time surveys might provide adequate solutions for minimising variance.

2.4.3 Implications for future monitoring programmes

Adaptive wildlife management is gathering support amongst academics and professional wildlife biologists as an effective and efficient approach to informed decision making. Wildlife monitoring plays a central role in such schemes (Nichols & Williams 2006; Field et al. 2007; Lyons et al. 2008; Lindenmayer & Liekens 2009; 2010) and there is growing acknowledgement that monitoring programmes as well as management actions must be adaptive (Mattfeldt, et al. 2009). The UK BAP and national hare survey pre-date the formal move towards adaptive management, and the brown hare Species Action Plan is not an explicitly adaptive management programme. The survey identified broad scale patterns in the distribution and abundance of hares, but was unable to resolve hare densities at scales that were useful to local or regional land and conservation managers. It has therefore been impossible to evaluate whether the management interventions that were intended to increase hare numbers, such as conservation headlands and set-aside (UK BAP, 1995; Smith et al. 2004), that can benefit hares at farm level (Browne & Aebischer 2003) have had any impact at regional or national levels (http://www.ukbap-reporting.org.uk/). Our analysis indicates that a straightforward modification of the methods of the national hare survey is far more likely to provide appropriately detailed data to overcome this problem. Such methods might therefore feed into a new adaptive management programme for the species at regional and national levels.

There has been no recent repeat of the two national hare surveys, perhaps because of the significant effort and cost involved in co-ordinating its 550 volunteers (Hutchings & Harris 1996). Consequently, it is unclear to what extent the target of doubling hare numbers has been achieved. There is currently no clear prospect of a repeat national survey in the near future but brown hare numbers are being recorded as part of a number of wildlife monitoring schemes (Battersby 2005). While such schemes might provide information on general trends, particularly for culled populations, the fact that hares were only recorded in 2.6% to 30.5% of all squares surveyed in these schemes (Battersby 2005) suggests that the same issues of low detection probability will restrict the value of these schemes at regional scales.

The involvement of volunteers in data collection for wide-scale ecological surveys (an example of ‘citizen science’) has increased substantially in recent decades (e.g. Newman et al. 2003; Lepczyk 2005; Silvertown 2009), was the basis for the national hare survey and is employed especially in widespread monitoring of birds (e.g. Risely et al. 2009). Using volunteers as survey assistants appears desirable but restricts the nature of work that can be carried out. Given the very much greater efficiency that we have demonstrated for night time surveys of hares, we suggest that future surveys for brown hares and other species could incorporate this method by using a smaller number of trained fieldworkers over an intensive period rather than a larger number of volunteers over a longer period; the benefits would be ease of organisation and a regional-scale, habitat-specific and management-relevant level of detail. Such a survey would provide local managers with the information required to implement management directly relevant to national conservation targets. Surveys of other species with low detectability may benefit from a similar approach, and a full assessment of costs and benefits of using volunteers in their monitoring ought to include the role of detection probability in determining data quality and quantity.

Chapter 3 Factors affecting hare distribution and abundance in grasslands

Summary

Grazing represents the primary factor influencing sward height and composition in grasslands and small herbivores can be facilitated or suffer as a result of competition with large herbivores. Brown hares have declined dramatically throughout the UK in the past decades and the decline seems to have been more pronounced in grassland areas. Increased stocking density in pastures has been blamed for transforming previously favourable habitat into suboptimal habitat for hares in Western Europe through the reduction in areas of suitable cover from both weather and predators. However, few studies have focused specifically on hares in pastures and the factors influencing hare presence and abundance in grasslands remain poorly understood.

In this study we investigated hare populations in seven large areas of pastural farmland in north east England through night time surveys between autumn and early spring and collected information on sward height, field type and management. We compared hare distribution and abundance with that of the European rabbit, a largely sympatric species causing important economic damages in agricultural areas.

Hare distribution was far patchier than that of rabbits and their density was greatly reduced. Hare presence and density were significantly and positively associated with larger fields used for cattle grazing at both local and landscape scale while sheep grazing had a negative effect on hare density but positive on rabbit density at transect level. Sheep grazed fields had consistently shorter swards than other fields including mixed sheep-cattle grazed fields. There was no association between hares and fox Kilometric Abundance Index. We suggest that changes in the grazing regimes and increased densities of stock, particularly sheep, in the UK may have had significant but opposing impacts on both lagomorph species and recommend that future studies focus on mechanisms for hare selection of taller swards for foraging in order to provide better founded solutions for their conservation management.

3.1 Introduction

In grassland-dominated environments herbivores may compete for food or facilitate one another depending on body size, morphology and grazing behaviour (Illius & Gordon, 1992; Arsenault & Owen-Smith, 2002; Bakker et al. 2009). The occurrence and density of medium and small sized herbivores have been shown to be affected by large herbivores in grasslands (Wheeler, 2008; Petrovan et al. in press) and this relationship is likely to be influenced by both food availability and perceived predation risk (Iason et al. 2002; Evans et al. 2006). Large herbivores have a longer digestive tract, lower mass-related food requirements and are able to tolerate lower quality forage than smaller herbivores (Iason & Van Wieren, 1999) and small herbivores select higher quality forage to compensate for the lower intake of biomass, have different metabolic requirements to body size relationships and can survive on shorter swards than larger animals (Hulbert & Andersen, 2001).

Grazing represents a core determinant of sward structure and composition in grasslands since grazing by livestock creates a shorter, denser and more nutritious canopy of plant material than ungrazed areas (Bakker et al. 2009). However, grazing reduces available cover and may increase competition and/or reduce food availability for small herbivores particularly at high stocking densities or in areas of low productivity (Evans et al. 2006; Wheeler, 2008). This is particularly relevant for sheep grazing in the UK, where sheep density has increased considerably in post war years (Fuller & Gough, 1999) and includes both productive areas, such as improved or semi-improved pastures and areas of low productivity, such as uplands and moorlands. In addition, sheep grazing is largely different from cattle grazing in that it produces shorter, more homogenous grass swards (Smith et al. 2004; Petrovan et al. 2011).

The agricultural landscape of North Yorkshire offers suitable conditions to investigate the relationships between four herbivore species, two domestic, cattle and sheep, and two wild and introduced species, the brown hare and the European rabbit. Brown hares have been shown to be facilitated by cattle grazing in a saltmarsh environment (Kuijper et al. 2008) and hares were selecting cattle-grazed areas in a radio-tracking study but avoided sheep-grazed areas for most of the year (Smith et al. 2004, Chapter 5). On the other hand, rabbits have also been shown to be facilitated by both cattle (Bakker et al. 2009) and sheep (Petrovan et al. 2011) probably as a result of the rabbit preference for shorter swards during foraging, irrespective of biomass intake (Iason et al. 2002). Competition between hares and rabbits has been investigated in the past but results remain unclear (Flux, 2008) with confirmation of extensive overlap in the diet of the two species in some studies (Kuijper et al. 2004) but not in others (Katona et al. 2004).

Brown hares have declined dramatically in the UK and this decline has been more pronounced in grasslands (Hutchings & Harris, 1996; McLaren et al. 1997). Proposed reasons for this include increased livestock densities and a consequent reduction in suitable cover which could make the hares expend more energy and become more susceptible to adverse weather, diseases and predation (Smith et al. 2004; 2005). However, our research in North Yorkshire pastures indicated that hares can reach far higher densities than previously reported for grasslands but with very large variation in density between individual sites (Chapter 3).

This study had two objectives: a) to investigate the role of habitat and management variables, in particular those related to grazing, in order to explain differences in hare occurrence and densities in several large grassland-dominated sites and to establish measures to reverse their declines and b) to relate the patterns in hare distribution with that of the rabbits, which are largely sympatric and which could potentially act as competitors.

3.2 Methods

3.2.1 Study site and sampling design

The study took place in seven sites located in a lowland/marginal upland pastural landscape in North Yorkshire, England during autumn-early spring between October 2007 and March 2009. A series of 2-6 transect routes that encompassed between 6 and 22 fields each were established in all of the seven grassland-dominated sites aiming to cover as much of the site area as possible. A detailed description of the study area and data collection protocol is provided in Chapters 2 & 4 and Petrovan et al. (2011).

3.2.3 Data collection

Hare and rabbit surveys were carried out during the night in autumn-winter (October to December) and early spring (January to March), when the short vegetation allowed good detectability of both species. During autumn 2007 and spring 2008, all transects at all seven sites were surveyed twice and two of the seven sites (C and G) were surveyed again twice in autumn 2008 and spring 2009.

Hare and rabbit densities were assessed by spotlight counts with numbers of hares recorded as an exact number while the very high rabbit densities were recorded as an estimate in intervals of 5 or 10 (Chapter 4, Petrovan et al. 2011). Due to the necessity of data at field or transect level both hare and rabbit densities were computed as the total number of individuals detected in each field divided by field size.

Fields were classified into four types according to their grazing management (sheep only, mixed sheep-cattle, cattle only and rough pastures). Starting in spring 2008 sward height data were collected concurrently with spotlight counts by the direct measurement method (Chapter 4, Petrovan et al. 2011). In each field the presence of livestock was recorded, either as a direct count or as an estimate for large groups of sheep or cattle. Field size and proximity to woodland or bracken patches, representing shelter for hares or harbourage for rabbit warrens, were also measured and was taken as a four-level categorical variable (Chapter 4, Petrovan et al. 2011).

3.2.4 Data analysis

Due to the complex structure of the data and the low presence at field level the factors influencing hare presence were investigated using linear mixed models (Zuur et al. 2009) with ‘hare presence’ taken as a binary dependent variable. Field identity nested within transect route and within site were included as random factors. Sward height and heterogeneity, field area and type, proximity of the field to woodland or bracken patches, the presence of field margins, and predator and rabbit control and percentage of land used by sheep were included as the fixed components in the model. To avoid collinearity problems, one of each pair of highly correlated explanatory variables ($r>0.6$) were excluded from the model. The analysis was performed using a backward selection procedure based on AIC to compare nested models. Rabbit density, sward height and field area were log transformed to achieve normality. Similarly, at the transect route level hare presence expressed as the percentage of fields on each transect route where hares were present and the percentages of fields occupied by different field types on each transect route were arc transformed to achieve normality. Statistical analysis was performed using SPSS statistical software for Windows version 13.0 (SPSS Inc., Chicago, IL). The following models were fitted as the starting points for the model selection at the field and transect route scales respectively:

Model formula field scale (Equation 1):

ArcHare Presence = β_1(Lgrass height)+ β_2(Lfield size) + β_3(Field type) + β_4(Proximity to woodland) + β_5(Presence cattle) + β_6(Presence sheep) + β_7(season) + (1 | Site/Transect/ FieldId)

Model formula transect scale (Equation 2):

LHare density = β_1(Lgrass height) + β_2 (LMeanField size) + β_3(ArcTypeSheep) + β_4(ArcTypeMixed) + β_5(ArcTypeCattle) + β_6(ArcTypeRough) + β_4(Fox KAI) + β_5(LMeanRabbit density) + (1 | Site)

3.3 Results

Overall, 94 fields from two sites were surveyed four times while all the rest were surveyed twice (Chapters 2 & 4; Petrovan et al. 2011). A total of 649 hare observations were recorded in the 260 individual fields surveyed by spotlighting between October 2007 and March 2009.

Hares were present in only 35% of fields, compared to rabbits in 63%. As expected, hare presence varied significantly between study sites (ANOVA, F = 54.871, $p < 0.001$). At the field level hare presence was significantly associated with field type and field area (Table 3.1). Hare presence was positively influenced by field area while field type impacted hare presence differently, with positive effect of both cattle grazed fields and rough pasture but no significant effects of sheep grazed fields and mixed sheep-cattle fields (Table 3.1). Mean sward height was significantly different between field types, with sheep grazed fields having the shortest swards (Figure 3.1). However, neither the proximity to woodland or bracken patches, rabbit density and field margins, nor the presence of livestock in the fields during the survey, were significantly associated with hare presence, and were therefore excluded from the final model.

	Estimate (±SE)	z value	P
(Intercept)	-16.1878(±2.7675)	-5.849	0.0001
Lfieldsize	1.4420 (±0.2637)	5.468	0.0001
fTYPE2 (mixed)	-0.2697 (±0.3843)	-0.702	0.4827
fTYPE3(cattle)	1.5287 (±0.4269)	3.581	0.0003
fTYPE4(rough)	2.0800 (±0.5807)	3.582	0.0003

Table 3.1 Binomial generalized mixed model fixed effects at field level. Lfieldsize = Log transformed field area; fTYPE2 = field type mixed; fTYPE3 = field type cattle grazed; fTYPE4 = field type rough grazing. Number of observations 684. Dependant variable was hare presence.

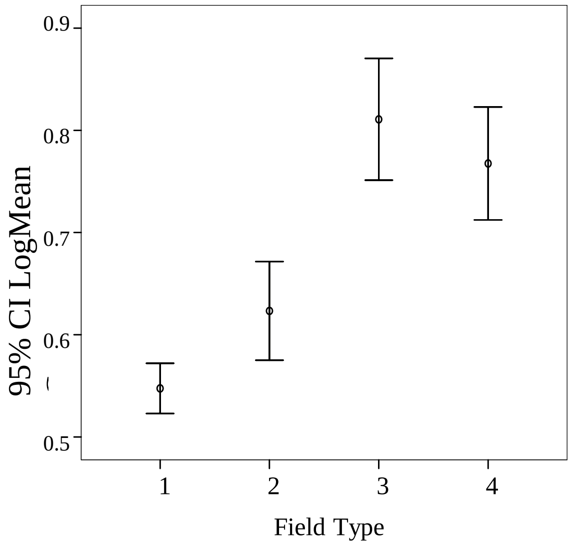

Figure 3.1. Log transformed mean sward height and 95% CI in all four field types (ANOVA; F = 84.836; P < 0.001; df = 381). Field type 1 = sheep; Field type 2 = mixed sheep-cattle; Field type 3 = cattle grazing; Field type 4 = rough grazing.

At the transect route level hare density varied between the seven sites (Figure 3.2) and was significantly associated with the percentage of either cattle grazed or sheep grazed fields but not mixed sheep-cattle pasture or rough pasture (Table 3.2; Figures 3.3 & 3.4). The percentage of cattle grazed fields positively influenced hare density at the transect level while the percentage of sheep grazed fields negatively influenced hare density at this scale. However, there were no significant associations between hare density and fox KAI, mean field size or mean rabbit density and these variables were removed from the final models.

At this same transect scale rabbit density was negatively associated with both fox KAI (ANOVA; F= 9.516; P < 0.003; t = -3.085; P = 0.03) and field area (ANOVA; F= 27.434; P < 0.001; *t* = -5.238; P < 0.001) and positively associated with the percentage of sheep grazed fields (ANOVA; F= 5.729; P = 0.029; *t* = 2.393; P = 0.021). Therefore the analysis of rabbit density at transect scale confirmed the results of both local and landscape scale analysis (Chapter 4) suggesting that this analysis at transect level is relevant.

Source	Estimate (±SE)	df	F	P
Intercept	0.291(±0.599)	1	184.042	0.0001
Site		4	19.090	0.0001
ArcType1 (sheep)	-0.244 (±0.565)	17	10.248	0.001
Fox KAI	-0.042(±0.399)	5	1.849	0.199

Table 3.2. Linear mixed model at transect scale. ArcType 1 = arcsine transformed percentage of fields occupied by sheep grazing at transect level. Dependant variable was log transformed mean hare density in each transect.

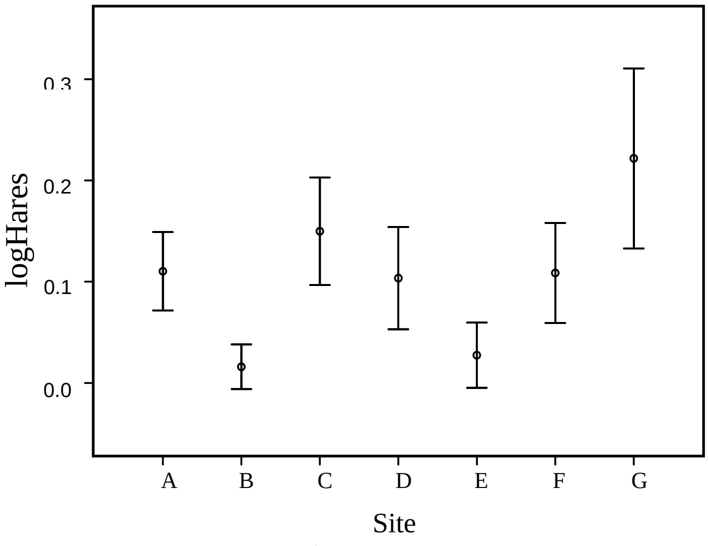

Figure 3.2. Log transformed mean hare density (number of hares/ha) at the transect route level and 95% CI in all seven sites surveyed (ANOVA; F = 4.560; P = 0.038; df = 50).

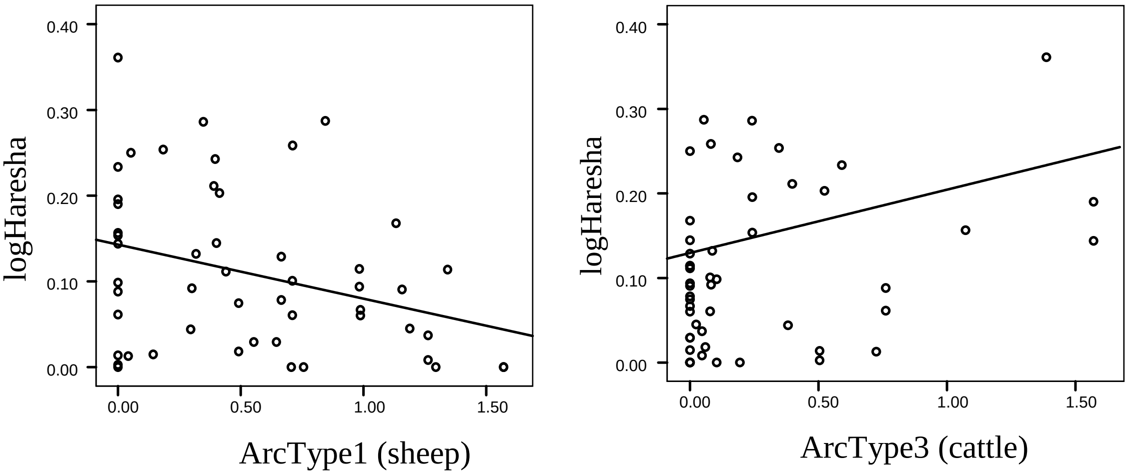

Figure 3.3. Relationship between log transformed mean hare transect density and arcsine transformed percentage of sheep grazed fields on each transect (ANOVA; F = 5.771; P = 0.020; df = 50; R^2 = 0.105) and arcsine transformed percentage of cattle grazed fields on each transect (ANOVA; F = 5.824; P = 0.020; df = 50; R^2 = 0.106).

3.4 Discussion

Due to the low hare presence at the field level as well as the spatial and temporal data structure with repeated measures the data at field level could only be analyzed using a binomial response of hare presence/absence and not with a measure of density (i.e. hares/ha). Nevertheless, this study suggests that hare presence in grassland areas is affected by both grazing type and field area. Large fields were found to be beneficial for hares (Vaughan et al. 2003) up to a limit after which further increases could be neutral or even detrimental (Chapter 5). In the present study hare presence was higher in larger fields but overall, the mean field size (3ha) was much smaller than in comparative studies from the continent (Reitz & Leonard, 1994; Ruhe & Hohmann, 2004) and fields larger than 10ha represented less than 5% of more than 260 surveyed fields. In contrast with rabbits, which largely depend on field boundaries for their burrows and as such select smaller fields (Chapter 2) hares probably require larger open fields to make the best of their predator escape strategy using high speed (Goszczynski & Wasilewski, 1992).

Despite the fact that hares actively select blocks of woodland during the daytime (Tapper & Barnes, 1986; Chapter 5) hare presence at the field level was not influenced by the proximity to woodland or bracken, probably due to the fact that small blocks of woodland were homogenously distributed between all sites. Equally, fox abundance had no effect on hare density but fox control was significantly associated with increased rabbit densities (Chapter 4, Petrovan et al. 2011).

Both hare presence at the field level and hare density at the transect level were associated with variables describing grazing management. Hare density in particular was negatively associated with sheep grazed fields and positively with cattle grazed fields, in contrast with rabbit populations which were highest in sheep grazed fields. However, the underlying mechanisms for hares selecting fields grazed by cattle and not sheep and therefore with taller and more heterogeneous swards remains unexplained.

Differences in herbivore body mass result in differences in optimal food intake and can provide an important mechanism for niche differentiation in communities of grazing species (Ritchie and Olff, 1999). However, body mass differences between hares and rabbits are relatively small and major differences between the two species mostly involve different social, breeding and foraging strategies.

A herbivore’s selection for particular sward heights is likely to be a function of its anti-predator strategy and the optimization of food abundance and availability (Whittingham and Devereux 2008). If rabbit populations are facilitated by intensive sheep grazing their increased densities could potentially help maintain the sward height at low levels, therefore creating unsuitable conditions for hares which prefer taller grass swards for foraging.

3.5 Conclusions

In this study we have identified that grazing regimes and sheep grazing in particular may impact differently on lagomorph abundance through the creation of grass swards of different heights and structure. The large increases in sheep numbers in Britain in the post-war years (Fuller and Gough 1999) may have had a significant impact on hare densities both directly, by creating unsuitable conditions for hare populations through the reduction in food and cover and indirectly, by increasing habitat suitability for rabbits in pasture land and therefore promoting competition between hares and rabbits. Future studies designed to investigate the competition between hares and rabbits should focus on the mechanisms for hare selection of taller swards and use field trials to test the impact of swards of different heights on both hare and rabbit populations in order to provide sound conservation and management advice.

Chapter 4 Farming for pests? Local and landscape-scale effects of grassland management on rabbit densities

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Summary

In recent decades in the UK there has been an increasing trend in numbers of the European wild rabbit, a significant agricultural pest typically associated with grassland habitats. However, the relationship between rabbit abundance and grassland management, in particular grazing, has not been sufficiently explained. We studied rabbit densities in 7 pasture dominated sites in north-east England between autumn and spring in two consecutive years, and used generalised linear mixed models and generalised additive models to explore relationships between habitat and management variables and rabbit abundance at local (field) and landscape scales. At the local scale high rabbit densities were significantly associated with small fields and the very short, homogeneous swards created by intensive sheep grazing during autumn and winter. At the landscape scale, high rabbit numbers were associated with sites with most field boundaries and a predator removal policy. Our results indicate that landscape management may play a central role in explaining rabbit abundance and distribution in grasslands. We suggest that current pasture management may create favourable conditions for high rabbit densities, and consequently boost numbers of this important pest species.

4.1 Introduction

In Great Britain, populations of the European wild rabbit (*Oryctolagus cuniculus*) have recovered from the myxomatosis epidemic of the 1950s, which eliminated over 99% of the population (Lloyd 1970) and there has been a subsequent increase in rabbit numbers (Lees and Bell 2008; Trout et al. 1986). Contrary to the situation within the rabbit's native distribution range in the Iberian Peninsula, in which the slow recovery of rabbit populations has only recently led to emerging pest situations (Barrio et al., in press) and despite recent reports of declines following the spread of Rabbit Haemorrhagic Disease in both England and Scotland (Battersby 2005) in many areas in the UK rabbits have reached pest status causing approximately £115 million of damage to the British agricultural industry (Smith et al. 2007). The impact of rabbits is especially important in grass-dominated areas, which are the typical habitat for the species (Hulbert et al. 1996; Iason et al. 2002) and which dominate much of the British agricultural landscape, covering around 68% of the total agricultural area (approximately 12.7 million ha) (Anonymous 2009). Damage and crop losses associated with rabbits may be more easily overlooked by farmers in pastures and silage grass areas than in other types of crops and can result in little or no control even when rabbit numbers are high (Dendy et al. 2003). For these reasons understanding the factors that shape rabbit distribution and densities in grassland could allow more effective targeting of resources for rabbit management.

Previous studies in the United Kingdom investigating the factors associated with rabbit abundance at a national scale have identified several variables which positively influenced rabbit densities such as aspects of woodland, soil wetness, predator removal policy and inclusion in agri-environment schemes (Reid et al. 2007; Trout et al. 2000). Pest species, such as the European rabbit, are capable of utilizing much of the landscape in which they live (Hamilton et al. 2006) and this is particularly the case in a highly anthropogenic and productive landscape, such as UK farmland, where rabbits can be found in almost every type of habitat (Trout et al. 2000). In such heterogeneous landscapes resources are spread relatively continuously across a wide area but with variation in resource quality (Hamilton et al. 2006). In grassland habitats grazing is a primary determinant of sward structure and composition since grazing livestock create a short, dense canopy of highly nutritious plant material and there is some evidence that this can affect rabbit distribution. Bakker et al. (Bakker et al. 2009; Bakker et al. 2004) demonstrated that rabbit grazing is facilitated by the presence of cattle grazing in a productive agroecosystem. Experimental evidence suggests that at the local scale rabbits select for foraging areas with short sward irrespective of low crop biomass (Iason et al. 2002). Preference for shorter swards by rabbits is attributed to anti-predator strategies, as the perceived predation risk may be lowest in short vegetation (Bakker et al. 2009; Iason et al. 2002).

Here we investigate the role of habitat and management variables at two spatial scales in explaining rabbit densities in several large grassland-dominated sites in north east England. At a wide, multi-farm scale, variables reflecting land use, patchiness of the landscape and management practices, i.e. culling of predators or rabbit populations, were considered. At a local scale, additional variables describing habitat features, field management and survey season were also included. We aimed to identify which habitat, pest/predator and grazing management factors most parsimoniously explained variation in rabbit densities both at local and landscape scales.

4.2 Methods

4.2.1 Study site

Rabbit distribution and densities were recorded in seven study sites located in a lowland/marginal upland pastural landscape in North Yorkshire, England at altitudes between 30 and 250m. Sites were selected by investigating remotely sensed images using Google Earth (http://*earth.google.com*) and searching for large areas dominated by pastures, subsequently verified in the field. Sites were spaced between 3.5-14 km apart (mean 10.4 km).

Mean annual temperature and mean annual precipitation for the past 30-40 years were 8 ^{o}C (SD = 0.5) and 704 mm (SD = 63) for three of the study sites, situated closer to the coast and 7 ^{o}C (SD =0.5) and 924mm (SD = 85) for the other four sites (Environment-Agency 2009; MetOffice 2007)

Sites were dominated by improved and semi-improved grassland (<50% *Juncus spp.* dominated and no artificial fertilisers) but also included a few arable fields, patches of woodland and rural development. In most areas the landscape was undulating, with gentle sloping hills and wide, flat valleys. Grass fields were used in a rotational system and were extensively grazed by sheep *Ovis aries* and cattle *Bos taurus* at variable stocking densities. A small percentage of fields were used for silage production with 2-3 cuts per year and sheep grazing during autumn and winter. Fields were bounded by dry stone walls, hedgerows and barbed wire fences and size varied considerably (mean = 2.98 ha, SD = 2.91, range = 0.33-22.72 ha). Shooting for game birds took place at most sites but only 4 sites included a permanent gamekeeper whose role included predator and pest control.

4.2.2 Sampling design

In each of the seven selected sites we established a series of 2-6 transects, each approximately 2-3 km in length (Table 1), by identifying farmers who would give permission to survey their land at night while aiming to cover as much of the area as possible throughout the site. Only 3 of more than 60 farms identified did not grant access for surveys. To minimize the possibility of double counting of animals in each site transects were spaced at a minimum of 300-400m distance or separated by natural or artificial barriers such as streams, large blocks of woodland or robust fences. Transects did not follow any landscape or manmade features, such as streams, valleys, roads or foot paths and each transect encompassed between 6 and 22 fields (mean= 9; SD=2.3).

4.2.3 Data collection

4.2.3.1 Rabbit surveys

Rabbit density surveys were carried out between October 2007 and March 2009. Sampling effort was concentrated during autumn-winter (October to December) and early spring (January to March), when vegetation was generally short and when rabbit population surveys are most effective (Poole et al. 2003). However, due to the poor weather conditions in spring 2008, with high rainfall and frequent fog, surveys were extended until early May for a small number of transects. During the first survey periods, i.e. autumn 2007 and spring 2008, all transects at all seven sites were surveyed twice, once in autumn and once in spring (Table 4.1). These surveys were used in landscape scale analyses. In addition, two of the seven sites (C and G) were surveyed again twice in autumn 2008 and spring 2009 using the same transects. Local scale analyses used these data from sites C and G in conjunction with data from all sites (A-G) collected in spring 2008 when detailed measures at the field level were taken.

Rabbit densities were assessed by spotlight counts which have been shown to produce accurate and consistent estimations of rabbit densities in a comparative study (Poole et al. 2003). Rabbit numbers were recorded as an exact number or as an estimate in intervals of 5 or 10 when densities were very high. All night-time surveys were started at least one hour after sunset and finished before 23:30. In accordance with previous rabbit studies, surveys were not performed on days where visibility was poor due to fog or heavy rain; similarly particularly cold, windy or bright nights were also avoided due to their negative impact on rabbit activity (Reid et al. 2007). Surveys were carried out by two people, with the same observer (SP), collecting all data in order to avoid between-observer differences in detecting animals while the second person recorded the data. Transects were paced slowly and silently in a straight line through the middle of the field while continuously scanning the area in front in a semicircle with 8 x42 binoculars and a 1 million candlepower spotlight (Clubman CB2, Cluson Engineering Ltd, Hampshire, UK). For all transects that were surveyed more than once in the same season there was an interval of at least a week between visits to minimize any effect of animal disturbance due to spotlighting. To ensure that no animals were counted twice while moving through successive fields, all rabbits which were displaced by the surveyors were followed with the lamp as they moved away to establish with precision the direction of movement and were consequently discounted if they relocated to other fields that were on the transect. The distance walked was recorded at all times as tracks with a GPS (Garmin GPSMAP76C, Garmin International Inc., Kansas, USA) and later superimposed on 1:10 000 scale Ordnance Survey digital map data tiles of the area provided by the Digimap service (http://edina.ac.uk/digimap). Tracks were manipulated in ArcGIS 9.1 (ESRI, California, USA) to remove sections where rabbits were not surveyed (e.g. distance walked to and from the access point in the field, avoidance of farm buildings or woodland). The remaining sections were used to calculate transect length to the nearest metre in each field. Rabbit densities were computed as the total number of rabbits detected in each field divided by field size.

4.3.2.2 Habitat variables

We considered several variables reflecting field management and surrounding habitat structure both at a local and a landscape scale.

At the local scale, fields were classified into four types according to their grazing management (sheep only, mixed sheep-cattle, cattle only and rough pastures).. Sward height data were collected concurrently with spotlight counts by the direct measurement method which has been shown to be the only method capable of producing accurate measurements in short swards (Stewart et al. 2001). Measurements to the nearest 1mm, were collected in each field along the transect, from the moment of the entrance into the field until the exit, every 50 paces in large fields and every 25 paces in smaller fields, with a minimum of 6 measurements per field. The minimum number of sward height measurements needed to give a stable mean for sheep grazed fields was verified at an early stage of the project. Additional measurements were taken in fields where sward height was very heterogeneous to account for the greater variability.

Field margins can provide diversity and additional habitat for a range of animal species (Marshall and Moonen 2002), and they form an important part of Agri-Environment Schemes which can have a positive effect on rabbits, but also on fox abundance (Reid et al. 2007). For each field we quantified the extent of field margins inside the field by giving them a class between I and IV; I corresponding to field margins between 0-10 cm wide (in which the vegetation was taller or more diverse than the rest of the field), II for 10-20 cm, III for 20-30 cm and IV for 30cm and above.

In each field we recorded the presence of livestock, either as a direct count or as an estimate for large groups of sheep or cattle. Field size and proximity to woodland or bracken patches, representing shelter for rabbits or harbourage for their warrens, were also measured. The proximity to these refuges was taken as a four-level categorical variable, separating those fields adjacent to woodland or bracken, those up to 100 m away, those lying between 100 and 200 m away, and those further away.

At the landscape scale, the area occupied by sheep pastures was assessed. The patchiness of the landscape was indirectly measured through ‘edge density’, which was computed in ArcGIS for each site as the length of field borders per unit area (m ha^{-1}). For analysis purposes site area was calculated as the sum of field areas that were surveyed in each season (mean = 94.51ha; range 18.59-143.00 ha; SD= 41.92). Management practices such as the presence of rabbit or fox *Vulpes vulpes* control were determined by detailed interviews with farmers, gamekeepers and landowners and were included as a binary (presence-absence) variable. The season in which all field surveys for each site were conducted (i.e. autumn or spring) were also considered. Additionally, the number of foxes encountered in each site during the surveys was taken as a surrogate of predation pressure. Fox records were expressed as foxes seen per km walked. In the case of the field scale analyses we took into account the date of field sampling by pooling survey journeys into bimonthly periods.

4.2.4 Data analysis

To investigate the factors that explain variation in rabbit densities at both the field and landscape levels we used linear mixed models (Zuur et al. 2009). Site and field identity nested within site were included as random factors in both analyses. In both cases, the response variable was rabbit density, which was log transformed to achieve normality. Sward height and heterogeneity, field size and type, proximity of the field to woodland or bracken patches, the presence of field margins and domestic stock, and bimonthly sampling period were included as fixed components in the local scale approach. Edge density, sampling season, predator and rabbit control and percentage of land used by sheep were included as the fixed component in the landscape model. To avoid collinearity problems, one of each pair of highly correlated explanatory variables ($r>0.6$) were excluded from the model (i.e. foxes seen per km and sward height heterogeneity); remaining variables had variance inflation factors (VIF) < 2 (Graham 2003). Model selection was based on Akaike’s Information Criterion (AIC) and likelihood ratio tests. In the local scale model, we added a variance structure to account for the heterogeneity in residual spread across sampling months (Pinheiro and Bates 2000). The following models were fitted for the local and landscape scales respectively, as the starting points for the model selection:

Local scale

$\text{Log(rabbit density+1)}_{ij}=\alpha+\beta_1(\text{grass height})_{ij}+\beta_2(\text{field size})_{ij} + \beta_3(\text{bimonth})_{ij}+ \beta_4(\text{field type})_{ij} + \beta_5(\text{field margins})_{ij} + \beta_6(\text{proximity to woodlands})_{ij} + \beta_7(\text{livestock})_{ij} +a_i+ \varepsilon_{ij}$
$\varepsilon_{ij}\sim N(0,\sigma_j^2)$; $a_i\sim N(0,d^2)$

Landscape scale

$\text{Log(rabbit density+1)}_i=\alpha+\beta_1(\text{\% sheep})_i+\beta_2(\text{edge density})_i + \beta_3(\text{season})_i+ \beta_4(\text{rabbit control})_i + \beta_5(\text{predator control})_i +a_i+ \varepsilon_i$
$\varepsilon_i\sim N(0,\sigma^2)$; $a_i\sim N(0,d^2)$

Where the subscripts *i* and *j* refer to each field and sampling month respectively. a_i is the random intercept that differs for each field *i*, and is assumed to be normally distributed with mean 0 and variance d^2. The residual terms ε_i and ε_{ij} are also assumed to be normally distributed with mean 0 and for ε_{ij} variances are allowed to differ by sampling month *j*.

Additionally, to investigate the shape of the relationship between sward height and rabbit occurrence in fields we used univariate binomial Generalized Additive Models (GAM) with a logit link (Hastie and Tibshirani 1990). Visual inspection of GAM plots can be used as an exploratory tool to infer the relationship, linear or otherwise, between variables (Pueyo and Alados 2007). The response variable was the presence or absence of rabbits in each field, and the predictor variable, i.e. grass height, was modelled using cubic regression splines, and the optimal amount of smoothing was estimated via cross-validation (Zuur et al. 2009). To improve the fit of the model, grass heights were log-transformed.

Modelling assumptions of normality, homogeneity and independence were checked (Zuur et al. 2009). All statistical analyses were performed using R 2.8.1 (R Development Core Team 2008) and particularly the packages *nlme* (Pinheiro and Bates 2000) and *mcgv* (Wood 2006).

4.3 Results

During the two years of this study we surveyed 260 individual fields on 170 km of transects by spotlighting, collected over 2700 grass height measurements and recorded a total of 4543 rabbit observations. We surveyed 94 fields in two sites four times while all the rest were surveyed twice (Table 4.1). Rabbits were present in 63% of all surveyed fields but densities varied widely, with only a small proportion of fields (16%) exhibiting very high rabbit abundances. Overall, we recorded an average rabbit density of 4.7 rabbits ha^{-1} (SD = 8.77; range = 0.00-69.68). Rabbit densities varied between study sites (Figure 1; ANOVA, F = 43.275, $p < 0.001$). We recorded a total of 33 foxes (mean = 0.25 foxes km^{-1}; SD = 0.24; range = 0.00-0.67), and fox sightings were significantly lower in sites where predator control was carried out (t-test; t=4.130, n=7, p=0.035; Figure 4.1).

Site	Season surveyed	Fields (number)	Transect (number)	Effort (km)
A	Autumn 07	39	5	9.4
	Spring 08	38	5	9.2
B	Autumn 07	58	5	11.8
	Spring 08	53	5	10.5
C	Autumn 07	78	6	13.9
	Spring 08	75	6	13.2
	Winter 08-09	119	12	23.3
D	Autumn 07	23	3	8.4
	Spring 08	21	3	8.2
E	Autumn 07	17	2	6.5
	Spring 08	17	2	6.5
F	Autumn 07	38	4	9.3
	Spring 08	34	4	8.3
G	Autumn 07	24	3	8.0
	Spring 08	22	3	7.8
	Winter 08-09	47	6	15.3
Total per season	Autumn 07	277	29	67.3
	Spring 08	260	29	63.4
	Winter 08-09	166	18	38.6
Total				169.6

Table 4.1. Sampling design. Autumn 07 = Oct-Dec; Spring 08 = Feb-May; Winter 08-09 = Oct-Mar. Field identity, transect position and survey effort were the same in all repeat surveys of individual sites with minor exceptions caused by fields changing management (i.e. grassland in autumn but sown in spring). In sites C and G during winter 2008-2009 transects were surveyed twice.

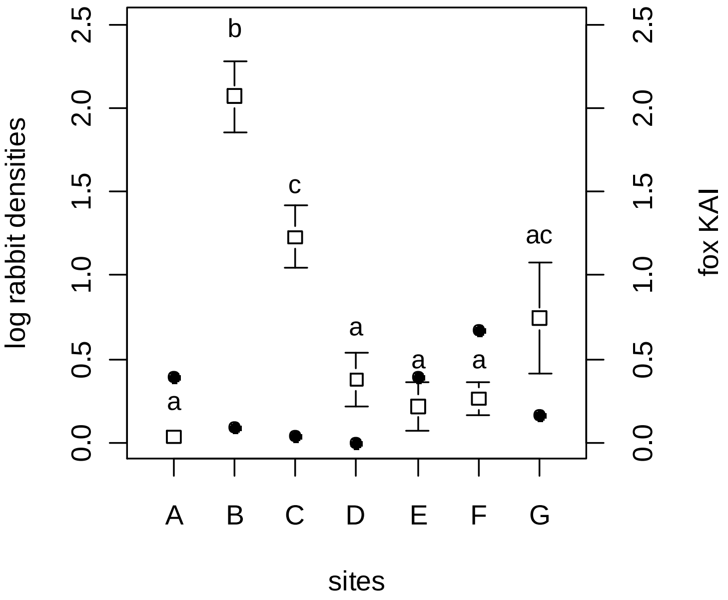

Figure 4.1 Rabbit densities and foxes per km, i.e. numbers of foxes seen per km walked at seven sites in NE England. Open squares are log mean rabbit densities and corresponding 95% confidence intervals; letters indicate significant differences between groups (p<0.01). Filled dots indicate foxes seen per km values in each site. Predator control was carried out at sites B, C, D and G.

At the landscape scale log-transformed rabbit densities across sites were significantly associated with the field boundary length per unit area (‘edge density’) and the presence of predator control policy at a site (Table 4.2).

At the local scale rabbit densities were correlated with grass height, field size and field type with sheep grazed fields and rough grazing fields having the highest densities. However, due to the fact that rough grazing fields were in small numbers and included large variation in sward height and some field types were correlated with other factors (e.g. mixed grazing and fox KAI) a simpler field type classification was used, specifically weather fields were grazed by sheep or not. Rabbit densities were correlated with grass height, field size and field type (Table 4.3). Grass height ranged from 0.5 to 17.9 cm (mean = 3.7, SD = 2.7), and was negatively correlated with rabbit densities; it was also significantly different between field types (ANOVA, F=75.768, p=0.0001; Figure 4.2). Field size was negatively related to rabbit densities, with smaller fields having higher rabbit densities. Field type, specifically those fields devoted to sheep grazing, was positively associated with rabbit densities. However, neither the proximity to woodlands or bracken patches, field margins, nor the presence of livestock in the fields during the survey, were significantly associated with rabbit densities, and were therefore excluded from the final model.

Grass height showed a non-linear relationship with rabbit presence (Figure 4.3). After cross-validation, the effective degrees of freedom were set to 5.51. Effective degrees of freedom reflect the ruggedness of the smoothing parameter: values close to 1 represent straight lines, higher values indicate non-linearities (Zuur et al. 2009). The smoothing term was highly significant (χ^2 = 22.93, p = 0.001). The density of rabbits was greatest at grass heights of 1.12 cm, and again but to a lower extent at 4.31 cm and declined at higher grass heights.

Linear mixed model for rabbit densities – Landscape scale				
	Estimate (±SE)	**Df**	**t-value**	**Sig.**
Intercept	-1.640 (±0.718)	7	-2.284	0.056
Edge density	0.009 (±0.003)	4	2.808	0.048
Predator control	1.036(±0.357)	4	2.898	0.044

Table 4.2. Linear mixed model results for rabbit densities at the landscape scale. Response variable: rabbit densities log-transformed. Random factor: sampling site. Log Likelihood: -11.11

Linear mixed model for rabbit densities – Local scale				
	Estimate (±SE)	**Df**	**t-value**	**Sig.**
Intercept	0.763 (±0.284)	229	2.690	0.008
Grass height	-0.042 (±0.015)	137	-2.838	0.005
Field size	-0.051 (±0.017)	137	-2.920	0.004
Field type - sheep	0.310 (±0.103)	137	2.994	0.003

Table 4.3. Linear mixed model results for rabbit densities at local scale. Response variable: rabbit densities log-transformed. Random factor: field within sampling site. Variance structure: different standard deviations per sampling period. Log Likelihood: -442.10

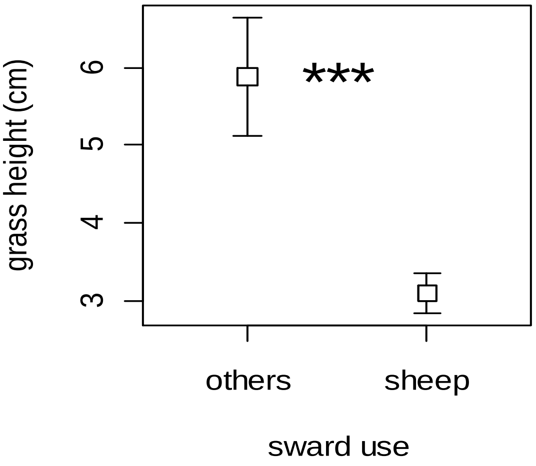

Figure 4.2 Mean grass height (cm) +/- 95% confidence intervals for swards used by sheep and those used for other grazing. A significant difference between means at p=0.001 is indicated by the stars.

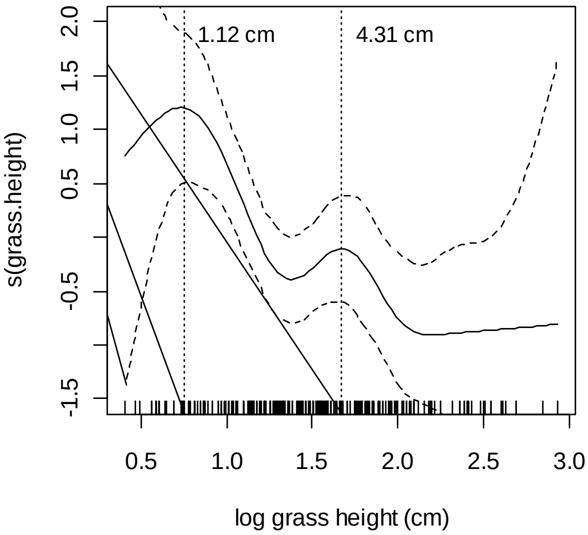

Figure 4.3 Estimated smoothing curve (cubic regression splines) and point-wise 95% confidence intervals for the Generalized Additive Model containing log-transformed grass height as the predictor variable, and the presence/absence of rabbits in each field as the response variable. The horizontal axis shows the observed values of grass height (short vertical lines), and the vertical axis the contribution of the smoother to the fitted values. Critical values of untransformed grass height are indicated (vertical dashed lines).

4.4 Discussion

This study aimed to create a better understanding of the mechanisms through which habitat and farming management, in particular livestock grazing, influences rabbit abundance in grasslands at both the field and the landscape scale and as a consequence, to identify ways that management practices could be used to manipulate rabbit densities and, by extrapolation, the economic impacts associated with their presence in pastures. While we have identified different factors associated with rabbit density at different spatial scales, variables associated with livestock grazing were highly significant at the local scale, implying that grazing management may play a central role in explaining rabbit density in individual grasslands.

4.4.1 Relationship between habitat management and rabbits at the field scale

At the field level, which represents a spatially and temporally distinct management unit (Atkinson et al. 2005), higher rabbit densities occurred in small fields containing improved sheep pastures. Sheep grazing generates short and homogeneous swards which Iason et al. (2002) demonstrated, through manipulative experiments, were preferred foraging areas for rabbits but to our knowledge there are no published field-scale evaluations of a link between grazing management and rabbit abundance.

Sward height selection in herbivores has been attributed to different anti-predator strategies and optimization of food abundance and/or availability (Whittingham and Devereux 2008). In animals relying on visual cues to detect predators, the level of visual obstruction offered by the vegetation within a foraging patch is likely to have a greater influence on their perception of predation risk than the degree of protection it offers (Whittingham and Devereux 2008). In this sense, rabbits' preference for shorter swards in spite of the apparent reduced food resource they represent, can be explained as an anti-predator strategy (Bakker et al. 2004; Iason et al. 2002). On the other hand, shorter swards are of higher nutritional quality, as forage quality of grasses per unit weight declines with increasing sward height (Riddington et al. 1997). In our study, rabbits were most abundant in sward heights shorter than 1.5 cm; the further, minor apparent selection for sward heights around 4 cm could be explained by a higher availability of swards of that size. Our data suggest that maintaining autumn and winter sward heights above those associated with highest rabbit densities in this study may reduce local abundance of rabbits. This suggestion is supported by small-scale experimental studies: removal of sheep from experimental grazing plots led to abandonment of the area by rabbits (Iason and Hester 1999). However, it is impossible to quantify what proportion of the short sward height in our survey area is due to sheep grazing and what is a consequence of intense rabbit grazing. Rabbits can facilitate habitats for themselves and their conspecifics by creating and maintaining vegetation in a favourable state through repeated grazing (Bakker et al. 2005). It has been shown that grazing by rabbits, particularly at high densities, can represent a significant contribution to overall grass offtake; in Iason and Hester's (Iason and Hester 1999) 0.4 ha experimental plots, rabbit offtake was as great as that by sheep. However rabbits are central-place foragers, foraging closest to their burrows (Bakker et al. 2005); in our study, with mean field sizes of almost 3 ha and grass measurements taken from the middle of fields, i.e. away from most burrows, it is likely that the sward heights we measured were determined for the most part by sheep and not rabbit grazing, although this might not be the case at the very short sward heights of less than 1.5 cm where high rabbit densities might play a significant role in creating and maintaining such short swards.

Woodland was positively and strongly associated with rabbit abundance in a country-wide study (Trout et al. 2000) and surface-living rabbits were found to intensely use the dense cover provided by woodland or scrub rather than burrows during winter (Kolb 1991) but here the proximity to woods or bracken had no significant relationship with rabbit numbers at the field scale. This might be explained by different processes governing distribution at this scale, or the fact that numerous small blocks of woodland were distributed fairly homogenously throughout most of our sites.

4.4.2 Relationship between habitat management and rabbits at the landscape scale

At the wider, landscape scale edge density and predator control were the most significant factors in determining rabbit densities. Similar results were found by Reid et al (2007) in Northern Ireland and by Trout et al. (2000) in England and Wales. Both of these previous studies suggest that the presence and density of field boundaries positively influences rabbit abundance.

The presence of a predator control policy explained differences in fox sightings between sites. It has been suggested that predator control might be a consequence of the high numbers of foxes attracted by the abundance of rabbits therefore making it impossible to distinguish between cause and effect (Trout et al. 2000). However, it is likely that in our sites predator control was implemented irrespective of rabbit densities due to the local economic importance of pheasant and grouse shooting for which fox control represents a key management practice even at low predator density (Trout and Tittensor 1989). The fact that lagomorphs, most likely rabbits, represent the most important prey item in fox diets in the UK (Webbon et al. 2006) and the observed relationship between fox control and rabbit abundance (Banks et al. 1998) supports our finding of higher rabbit densities in areas with fox control, and suggests that this relationship is causal.

4.5 Conclusion

Our counts indicated relatively high rabbit densities in several of our sites, but such spotlight counts may represent only ~60% of the total rabbit population using that area and even that percentage can vary widely (Poole et al. 2003). At the local scale, sheep grazing appears to have a substantial influence on rabbit density, in part through its impact on sward height. The results from such a correlatory study as this must not be viewed as confirmation of the relationships reported, which should instead be the basis of further investigation. While there is strong experimental evidence for the local preference of rabbits for foraging in areas with short grass, our results suggest that other relationships, particularity at the landscape scale, should be explored through manipulative studies in the field.

Sheep numbers in Britain more than doubled in the post-war years (Fuller and Gough 1999) and even in upland areas over this long timescale there has been a change from mixed grazing regimes toward those dominated by sheep (Sydes and Miller 1988). If the relationships described here are causative and hold true across the country, recent trends in grazing management in Britain may have had a significant impact on rabbit densities at local and landscape scales by increasing habitat suitability for rabbits in pasture land with the potential for significant concomitant economic losses.

Chapter 5 Age structure, demography and population dynamics in harvested populations of brown hares in pastures

Summary

In the past decades pastures are considered to have become suboptimal habitat for brown hares in the UK and hares from pastures exist at lower population densities, have poorer body condition, smaller size and lower breeding rates than hares in arable habitats. However, data on hare density and demography from pastures are relatively scarce throughout the UK and the rest of Europe. Understanding the associations between habitat and population demography may present tools for halting the hare declines in grasslands and for a more successful management of this species.

In this study we examined hare carcasses from grassland-dominated areas in the study region where hare populations reach moderate and high densities. We investigated age structure, body size and condition, as well as productivity and impact of hunting and compared our results with data from both England and continental Europe. We used chemically coloured placental scar counting, a modern method for estimation of female productivity that had yet to be employed in the UK and we present the first data on hare productivity, age structure and survival from UK pastures derived with this method.

Female hares from pastures in our sites were able to produce a high number of leverets. However, both percentage of female fertility and leveret survival were relatively low although higher than reported from other pastural sites in the UK. The hare population had the potential to increase at a low rate, but only in the absence of hunting. Previously described differences in skeletal size and fat deposits between hares from arable and pastural areas were not evident in our study and female hares were capable of reaching similar sizes to those from arable sites. Female fertility appeared to be influenced by pathological processes which should be further investigated. We suggest hares in pastures are not necessarily in poor condition in the UK and population increases should focus on identifying and preventing the causes of juvenile mortality.

5.1 Introduction

Adult and juvenile survival, population structure and body condition are fundamental parameters for understanding species population ecology and this is especially relevant for managing rare, declining or harvested species such as the brown hare *Lepus europaeus*. Populations of brown hare have declined dramatically over most of their European range in the past 50 years and in the UK this decline has been most pronounced in pastures (McLaren et al. 1997). In the UK, hares in pastural landscapes have been reported at lower population densities (Hutchings & Harris, 1996; Vaughan et al. 2003), with poorer body condition, smaller size and less participation in breeding than in arable habitats (Jennings et al. 2006). Yet, data on hare density and demography from pastures, particularly from the UK, are scarce (Smith et al. 2005a).

Identifying the age distribution of the population can provide a powerful mechanism for understanding how culling rates and habitat management influence juvenile and adult survival and as such, the dynamics of the population as a whole (Langvatn & Loison, 1999). Several methods have been employed in the past for age determination for hares including the weight of the eye lens (Suchentrunk et al. 1991), the ossification of the ulna and radius cartilage “Stroh’s Sign” and counting of the periostal growth lines in the mandible (Frylestam & von Shantz, 1977, Iason, 1988). The dry weight of the eye lens can only be used successfully to separate young from adults and to indicate the age in months of animals less than 7-8 months. The ossification of the epiphyseal cartilage of the ulna and the radius can be used to separate between juveniles and adults (older than 7-8 months). However, the annual growth lines in the lower mandible are the only method capable of indicating with accuracy the actual age in years of adult lagomorphs. Annual growth lines in the mandible are believed to form during winter time, when the slower metabolic rate results in the formation of thinner and more compacted growth layers than those formed during summer months, thus creating the impression of lines in the bone tissue (Frylestam & von Shantz, 1977).

Body condition has been evaluated in a variety of ways in mammalian species including size adjusted body mass (Garcia-Berthou, 2001), skeletal size, perirenal fat stores, bone marrow fat index and ratio of urea nitrogen to creatinine (Jennings et al. 2006). Perirenal or kidney fat deposits can provide a good indication of the nutritional status of hares for a short period up until death, while bone marrow fat is usually only mobilised as a last resort following prolonged periods of restricted diet (Henke & Demarais, 1990) and is therefore indicative of longer-term nutritional status. In many mammal species, including the brown hare, perirenal fat deposits show regular annual cycles (Parkes, 1989) which have been related to their breeding status, with non breeding females having larger fat deposits than breeding ones (Pepin, 1987; Valencak et al. 2009). In males, mating is associated with increased activity and fat deposits are likely to be used to sustain the breeding process (Flux, 1987). As such, the presence and extent of fat deposits is likely to have a strong influence on the reproductive success of both sexes.

Annual female fertility is a vital parameter for understanding population demographics and to determine sustainable hunting rates. In brown hares reproduction can occur in almost any month of the year but in the Northern hemisphere there is typically a period of quiescence in both males and females from October to early January when most animals do not breed (Lincoln, 1974; Flux, 1987). Obtaining data on annual fertility relies on carcass analysis and this is best exploited at the end of the breeding season when placental scars can provide information on total fertility in the past breeding season (Bray et al. 2003).

This study aimed to: a) obtain information on hare populations from pastures in the studied area including age and sex structure, demographics and body condition and b) to use this dataset in order to draw conclusions on the population status, dynamics and sustainable hunting levels. Ultimately it aimed to build a matrix population model for brown hares in pastures and to provide a powerful tool for conservation and management action in pastural areas, where hare declines have been most pronounced (Hutchings & Harris, 1996).

5.2 Methods

For the purpose of this study 88 hare carcasses were collected from 5 locations in grassland-dominated sites spread across North Yorkshire, UK. Two sites produced most carcasses (site C n = 28; site G n = 50). Most animals (76 hares) had been shot and were collected from hunters and shooting estates while the remaining 12 were either road kills or animals found dead in the field. Hares are culled in almost any month of the year in the UK but unlike most of Europe, the main shooting season is in January-March (Cowan, 2004) coinciding with the end of the pheasant shooting season. However, as at this time most females are already pregnant (Lincoln, 1974) and data on annual reproduction can not be acquired, most culled hares in this dataset were obtained in late autumn, between 10th of October and 10th December, in three consecutive years, from 2007 to 2009.

4.2.1 Age

Age was estimated using a simplified version of Iason's protocol (Iason, 1988) for counting the annual growth lines in the lower mandible, a method developed for large samples of culled mountain hares *Lepus timidus,* but which is based on the same principles that have been used for brown hares in the past (Frylestam & von Shantz, 1977). Fresh eye lenses were not available for analysis since most of the shot hares were stored in cooling boxes or freezers for periods of 5 to 48 hours prior to collection.

Mandibles were collected and frozen at -20^0 C until analysis when they were immersed in warm water for 15 minutes to help remove any remaining flesh from the bone. The entire cleaned jaw was later immobilised in a protective cloth in preparation for sectioning. A bone section of approximately 0.8-1 cm was removed by making a transverse cut through the lower jaw bone with a 22 x 0.6 mm cutting disc (RotaCraft, Shesto Ltd, UK) at 10 000 rotations/second, with the first cut just after the first premolar and the second cut just after the last molar (Iason et al. 1988). The bone sections were later polished with very fine wet emery paper and dried at room temperature for 48 hours before being analysed under the stereo microscope at 30 x magnification. Each bone section was inspected twice with repeat inspections carried out blind; in the case of differences between age estimations the section was analysed for a third time. A sub-sample of 26 of these bone sections were analysed independently by an experienced observer and results were identical between the two observers for 24 of these (92.3%), indicating the high degree of consistency of this method.

5.2.2 Body condition and skeletal size

To asses body condition whole body weight of the hares was recorded using a digital scale with 10 g precision (Sensas 25, Sensas, France). The deposits of fat around the kidney and on the interior abdominal wall were assessed and the length of the hind foot was measured. Perirenal fat scores were classified using a 7 group classification based on the size and extent of these deposits where score 0 represents “no fat deposits” and score 7 represents “very large” fat deposits (Appendix, Image A). Hind foot length is a commonly used measure of skeletal size for lagomorphs (Jennings et al. 2006, Wincentz et al. 2009); the length was recorded using a tape measure with a precision of 1.0 mm after completely defrosting the samples for two hours at room temperature in order to minimize any possible effect of muscular contractions or rigidity which could be present in the fresh carcass.

5.2.3 Reproduction

Annual fertility was estimated from counts of the placental scars on the surface of the uteri (Bray et al. 2003). This technique is based on the fact that in brown hares the placental scars fade over winter and as such, the scars counted in females at the end of the breeding season represent the total reproductive output in the preceding breeding season and none from the season before (Bray et al. 2003; Marboutin et al. 2003).

The entire female reproductive tract was removed from the carcasses and stored at -20^o C until analysis when the uteri were allowed to thaw under cold water and then separated from ovaries, mesometrium and oviducts. These were subsequently cleaned and sectioned along the entire length of the uteri duplex opposite the mesometrium to avoid damaging the placental scars. The subsequent staining technique followed the protocol of Bray et al. (2003) based on Turnbull's reaction using potassium hexacyanoferrate (20%) and a mixture of weak hydrochloric acid (1%) and a solution of ammonium sulphide (10%). The stained uteri were then immediately analysed under a binocular microscope fitted with an air suction pump. Due to the corrosive nature of the staining process each uterus was analysed for a maximum of 45-60 min after which the modifications of the endometrium made the sample unreliable. All chemical procedures were performed in agreement with the University of Hull health and safety policies and regulations.

5.2.4 Population parameters and dynamics

Life tables were constructed based on two methods, a simple static life table based on analysis of the age of brown hares at harvest following Milner-Gulland & Rowcliffe

(2007) and a life table including data on annual production following Brockhuizen (1980) and Owen-Smith (2007). In the second case the expected production of leverets, had hunting been carried out during the reproduction period, was calculated by dividing the number of adult hares by 2, correcting the percentage of fertile females and multiplying the rest by the average number of scars counted in fertile adult females. Due to the small sample sizes and since female fertility was similar between the two sites that contributed most carcasses these values were used to construct the life-tables taking the collected samples as a single population (Table 5.2). Given that no values of negative mortality were obtained the data were not smoothed.

Using the data obtained in the life table (Table 5.2) and the formulas developed by Pianka (1994) Gross reproductive rate (GRR), net reproductive rate or replacement rate of the population (R_0), expectation of life for each age class (E_x), reproductive value (v_x) and generation time (T) were calculated for brown hares in North Yorkshire pastures (Table 3). The intrinsic rate of population growth (r) which is interchangeable with the finite rate of population growth (λ) was calculated using the Euler-Lotka equation considering that population growth is stationary when $r = 0$ and $\lambda = 1$ and it assumes a stable age distribution and a stationary population size.

Equation 1:

$$GRR = \sum_{x=0}^{w} m_x$$

Equation 2:

$$R_0 = \sum_{x=0}^{w} l_x m_x$$

Equation 3:

$$T = \frac{\sum_{x=0}^{w} x l_x m_x}{R_0}$$

Equation 4:

$$r = \frac{\ln R_0}{T}$$

Equation 5:
$$E_x = \frac{\sum_{y=x}^{w} l_y}{l_x}$$

Equation 6:
$$v_x = \sum_{y=x}^{w} \frac{l_y}{l_x} m_x$$
(Pianka, 1994)

Equation 7 (Euler-Lotka equation):
$$1 = \sum_{x=0}^{w} l_x m_x e^{-rx}$$
(Pianka, 1994)

where $\boldsymbol{x}$ is the age interval, $\boldsymbol{w}$ is the maximum age class, $\boldsymbol{n_x}$ the number of individuals alive at start of age $\boldsymbol{x}$, $\boldsymbol{l_x}$ is the percentage of individuals still alive at age x $\boldsymbol{m_x}$ is the number of female offspring per female of age $\boldsymbol{x}$, $\boldsymbol{p_x}$ is the age-specific survival rate from age $\boldsymbol{x}$ to age $\boldsymbol{x+1}$, $\boldsymbol{e}$ is the base of the natural logarithms and $\boldsymbol{r}$ is the instantaneous rate of increase per individual.

Using the data obtained from life tables a conceptual model and a projection matrix model for the hare population in the study sites were created following the methodology of Milner-Gulland & Rowcliffe (2007) (Figure 5.1). Based on the conceptual model a simplified three stage age-structured model was constructed based on the survival of juveniles, sub-adults and adults as well as fecundity and hunting rate to explore population growth rate and to perform a sensitivity analysis by adjusting all parameters by the same proportion (i.e. 10% and 20%) or an elasticity analysis where single parameters were modified by the same ratios and these were compared with similar age structured models including different harvesting rates which were run in the program USHER (TrueBasic, Owen-Smith 2007). Generated models were run for 20 years.

Brown hare conceptual model

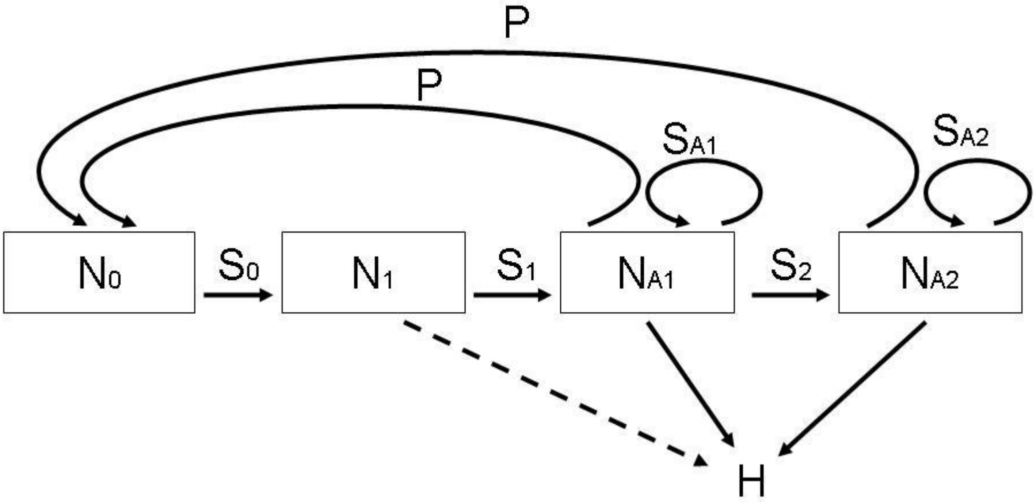

Figure 5.1 Flow diagram summarising an age structured conceptual model of a brown hare population hunted post-breeding. In the UK most hare hunting is concentrated pre-breeding, so there is only limited hunting off-take at the N_1 stage (dotted line). Boxes represent numbers of hares in each age class, arrows represent vital rates.

Figure 5.1 shows the flow of individuals through different age classes. Due to the structure of our data a four stage dynamic conceptual model was constructed following Milner-Gulland & Rowcliffe, (2007) with N_0 (age 0-0.4 years), N_1 (age 0.4-1 years), N_{A1} (adults age class 1-3) and N_{A2} (adults age class over 3 years). The symbol S represents the survival of different age classes from one stage to the next. Adults in N_{A1} and N_{A2} are also subject to a hunting off-take, H. Adults participate in breeding and have a fecundity P, which produces the next year's individuals (N_0). The main difference between the two adult stages N_{A1} and N_{A2} is represented by the smaller survival rate calculated for old adults (S_{A2}). For the purpose of this study it was assumed that annual population emigration is equal to population immigration or that the population is closed (dispersal is null in both scenarios). The model was density independent as there is no unambiguous evidence that brown hare populations exhibit density dependent regulation (Marboutin et al, 2003); furthermore the densities of brown hares in these sites (Chapter 2) are less than half of hare densities reported in other areas in continental Europe (Smith et al. 2005a).

For demographic models an Usher matrix was used to summarize the transitions in the age classes and used matrix algebra to quantify next year's population size as a function of this year's. Usher matrices are generally recommended instead of the more common Leslie matrix when adult survival and fecundity are similar between years (Owen-Smith, 2007). The equation used was:

$$N_{t+1} = AN_t$$

Where N_t is a vector of the number of individuals in each class and A is the transition matrix:

$$A = \begin{pmatrix} 0 & 0 & P & P \\ S_1 & 0 & 0 & 0 \\ 0 & S_2(1-H) & S_{A1}(1-H) & S_{A2}(1-H) \end{pmatrix}$$

5.2.5 Diseases

Lagomorph populations can be very susceptible to disease outbreaks, such as myxomatosis and the Rabbit Haemorrhagic Disease (RHD), which have devastated populations of European rabbits, and hare populations can be host and suffer significant impacts from European Brown Hare Syndrome (EBHS) or pseudotuberculosis (Wibbelt & Frölich, 2005). In addition, pseudotuberculosis is a zoonotic disease which brown hares can transmit to both domestic stock and humans. As such, as a preliminary assessment of disease impact in hare populations in the studied area all collected hare carcasses were investigated macroscopically during the post-mortem examination for signs of disease.

5.2.6 Comparisons with the national data

The raw dataset on 1018 hare carcasses collected at a national scale during 1998-2001 (Jennings et al. 2006) was used for comparisons with the carcass data in this study. This national hare carcass dataset (NHCD) included the name of the estate where the hare was collected, the date of collection, sex, body weight, hind foot length, reproductive status (number of foetuses present and lactating status), the cause of death (shot or killed with dogs, road kill, euthanasia, disease), an age classification (subadult, young adult, age 1, 2 or 3 and old adult) as well as the Centre for Ecology and Hydrology (CEH) land use class (using the 30 class system of land use classification) of a 1 km $^{-2}$ around the point where the hare was collected. Before analysis data were pooled based on the CEH classes so that only three categories were used: arable (n = 801), pastural (n = 98) and marginal upland (n = 31). Other categories (i.e. upland or other rarer land use classes) were either absent or very rare in this study area and were removed from further analysis. The majority of hares in this dataset had been collected in February-early March, during the main shooting season for hares in the UK.

Adult body weight and hind foot length were investigated between hares from the study sites and hares from NHCD arable and NHCD pastural-marginal upland using General Linear Models (GLM) in order to test for differences in indices of body size and skeletal size between different sexes and habitats. Not all data categories were normally distributed but since general linear models are robust to moderate violations of the assumption of normality of variables and the variables considered (body weight and hind foot length) were continuous data no data transformation was undertaken prior to analysis to facilitate interpretation of results (Garcia-Berthou, 2001). However, as a supplementary precaution the analysis was performed and results were compared both with and without transformation. Body weight is largely a function of skeletal size and this was accounted for in the model by taking “Body weight” as the dependant variable, “Sex” and “Habitat” as fixed factors and “foot length” (hind foot length) as a covariate in order to test for the effect of habitat and sex on body weight between different carcass datasets (hares from North-Yorkshire and hares from NHCD arable and pastural-marginal upland areas). Statistical analysis was performed using SPSS for Windows version 13.0 (SPSS Inc., Chicago, USA).

5.3 Results

5.3.1 Age structure

Of the 88 hare carcasses collected from North Yorkshire sex could not be established in 5 individuals which had been found dead on roads or partially scavenged; the remaining 83 animals comprised 42 females and 41 males. Age could not be established in 7 carcasses, due to damaged or missing jaw bones.

Lines were found in all jaw bone sections used for analysis; however in each single section line identification and counting could only be performed in certain areas of the jaw bone, especially in the upper lateral side. All three types of lines described in the literature were observed: resorption lines, adhesion lines and annual growth lines (Frylestam & von Shantz, 1977) but only lines judged to be annual growth lines based on their size and aspect were used in aging animals.

The overall calculated percentage of young of the year was 38.7% and the percentages of young of the year were similar between the two sites that produced the highest number of carcasses, with 35% in site C and 37% in site G, while the female proportion in site C was 46% and 62.5% in site G. The oldest animal in the sample was a 6 year old female, and 8% of all hares for which age was determined were older than 3 years (Figure 5.2). However we found no males older than 3 years (Figure 5.3). The sex ratio of young of the year hares was slightly imbalanced with more males than females present (Figure 5.3).

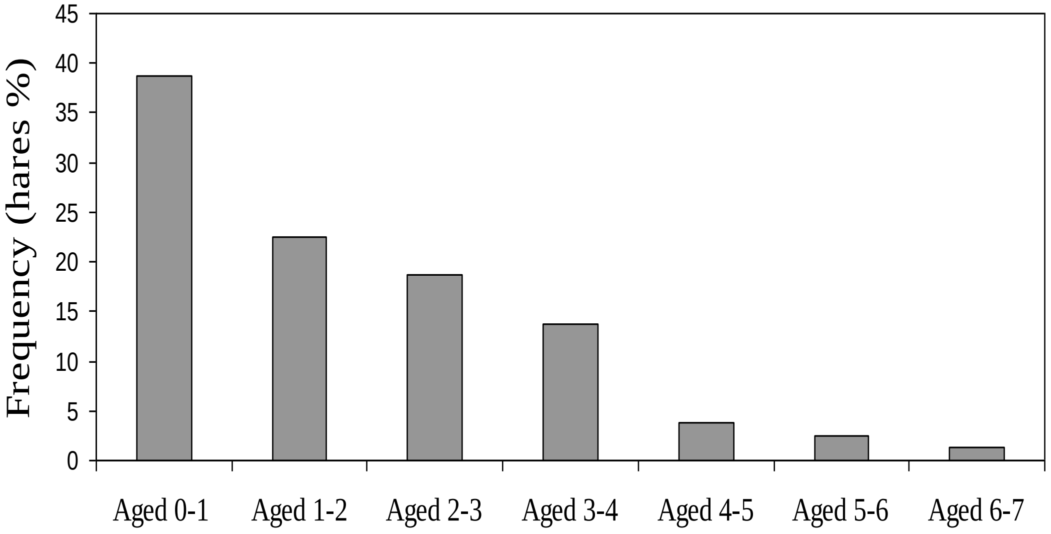

Figure 5.2 Age structure pooled across sexes in 81 brown hares from pastural sites in NE England

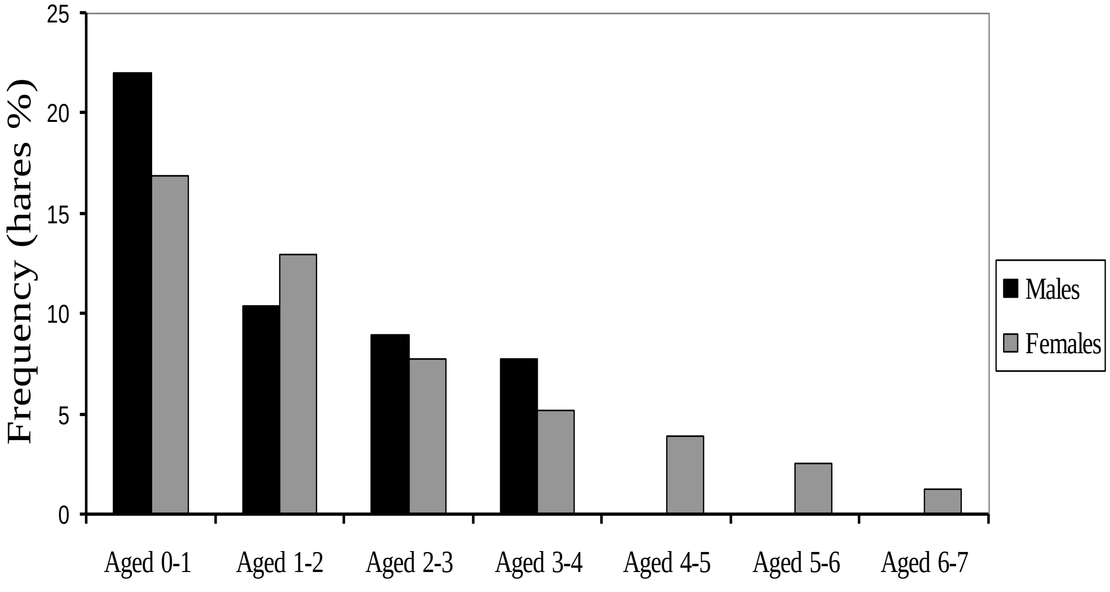

Figure 5.3 Age and sex structure in 77 brown hares from pastural sites in NE England

There was no significant association between site and age in sites C and G ($\chi^2 = 2.93$, $P > 0.05$, df = 4).

5.3.2 Body condition and skeletal size

Total mean body weight was 3.28 kg and ranged between 1.52 and 4.45 kg (SD = 0.43 kg, n = 82). Overall, females were significantly heavier than males (female 3.40 kg, n =41; male = 3.15 kg, n =41) (Table 4.4). Mean weight of young of the year of 3.06 kg was smaller than mean adult weight of 3.41 kg (z test, z = 3.69, P = 0.01). Average weight in the two sites which produced most carcasses was very similar, 3.33 kg in site G (SD = 0.39 kg, n = 45) and 3.31 kg in site C (SD = 0.32 kg, n = 28).

Mean hind foot length (MHFL) was 14.3 cm and ranged between 11.7 cm and 15.3 cm (SD = 0.56, n = 77). Perhaps because of the large variation caused by pooling of young born in 3 or 4 litters into one category, MHFL of young of the year of 14.2 cm (SD = 0.76, n = 30) was similar to the MHFL of adults of 14.4 cm (SD = 0.39, n = 47) (z test, z = 1.69, P = 0.05). Hind foot length was positively correlated with body weight (r = 0.698, P = 0.01, df = 72) (Figure 5.4).

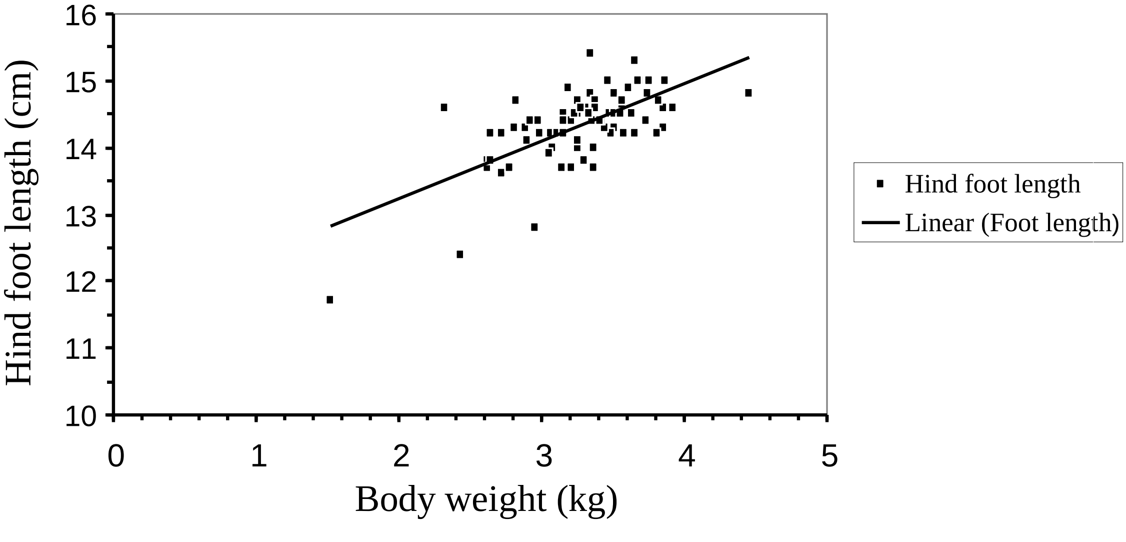

Figure 5.4 Relationship between hind foot length and body weight in 74 brown hares from pastures in North Yorkshire (R^2 = 0.4325; y = 0.86x + 11.5)

Perirenal and abdominal fat deposits were present in 84% of the 82 hare carcasses analysed but the size and extent of deposits and consequently body condition scores varied widely (Figure 5.5).

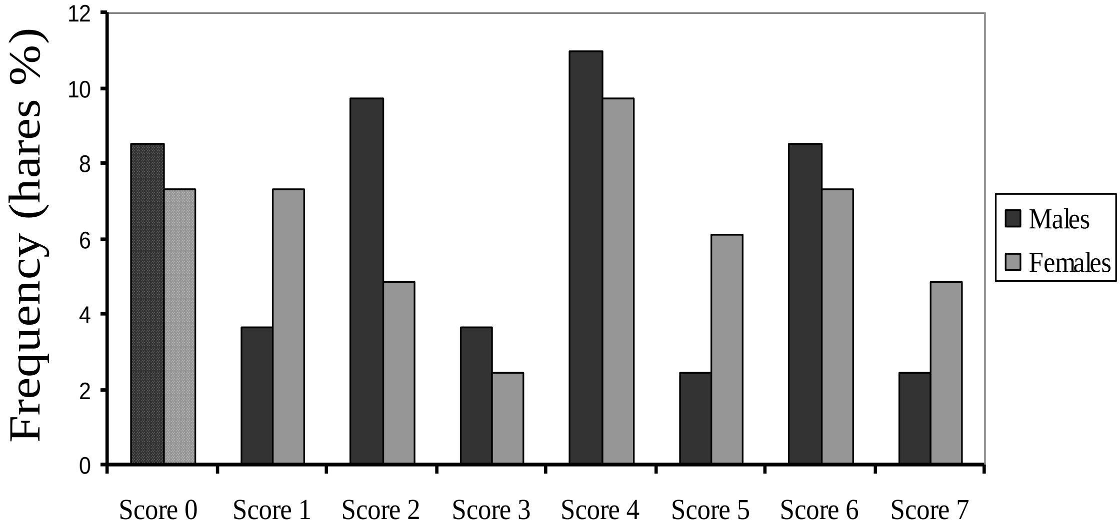

Figure 5.5 Body condition (fat deposits) score distribution in brown hares from pastural sites in NE England (n = 82). Dotted bars indicate males and females with no fat deposits.

After grouping the fat deposit scores into 3 categories only (score 0-2, 3-4 and 5-7), as dictated by the small sample sizes for some categories, the size and extent of perirenal fat deposits where significantly associated with the reproductive status in adult females, with non-reproducing females hares having higher than expected fat deposit scores ($\chi^2 = 6.34$; $P < 0.05$; df = 2).

Reproductive status could not be quantified for adult males in late autumn. Fat deposit scores for males varied widely despite the fact that almost all were collected between the months October and December. After grouping of the fat deposit scores into three categories (score 0-2, 3-4 and 5-7) there was a significant association between culling period and fat deposit scores with hares culled in the second half of the period (after 11th November) having significantly higher fat deposit scores than those culled prior to that date ($\chi^2 = 9.25$; $P < 0.01$; df = 2).

For young of the year the time of culling was not significantly associated with the fat deposit scores, most likely due to the fact that animals of different birth rates and as such at different stages in their growth, were pooled into this one category ($\chi^2 = 7.17$; $P > 0.05$; df = 7).

5.3.3 Reproduction

Of the 41 female carcasses collected 5 individuals had missing or damaged uteri and were not included in the analysis. Of the rest, all 12 females aged as young of the year were nulliparous, which was confirmed by the status and condition of their uteri, with short reproductive tract, small diameter of the duplex uteri and smooth uterine wall (Bray et al. 2003). An additional 5 adult females (20%) were non-reproducing, with no leverets produced in the previous breeding season. In 4 of the cases of non-reproducing adult does the uteri presented signs of pathological transformations including the presence of numerous large cysts on the endometrial surface. The aspect of these transformations was typical for cystic endometrial hyperplasia (CEH), a disease previously described in female brown hares in Germany (Besinger et al 2000) and Australia (Stott et al 2008) (Appendix, Image B).

Reproduction was recorded in 19 females, with an average of 11.4 placental scars and ranging from 3 to 18 scars per female giving a total of 210 embryos produced (Figure 5.6; Image C). An additional 14 placental scars (6.4%) were typical for the resorption type, indicating post-implantation loss of embryos (Appendix, Image D). However, of the 19 reproducing females 3 individuals were collected before the end of the breeding season, between June and August of which one female was pregnant and had 4 well developed embryos at the time of her death in July. Removing these three females from the analysis the average number of embryos produced per adult fertile female was 12.4. Female fertility was not significantly different between the two sites that contributed most carcasses with a mean of 10 placental scars per female in site C (range = 0-13, SD = 4.61, n = 8) and 9 placental scars in site G (range = 0-18, SD = 6.87, n = 13) (t test, t = 0.518, P = 0.31). Excluding all infertile adult females the mean number of placental scars in site C was 11.7 (SD = 1.38, n = 7) and 13 in site G (SD = 3, n = 9). The number of scars was significantly higher in heavier females (R^2 = 0.328; df = 16; F = 6.83; P = 0.020). No pregnant females were found in the sample of hares culled between October and December but two females culled in early October showed weak signs of lactation with small quantities of milk production.

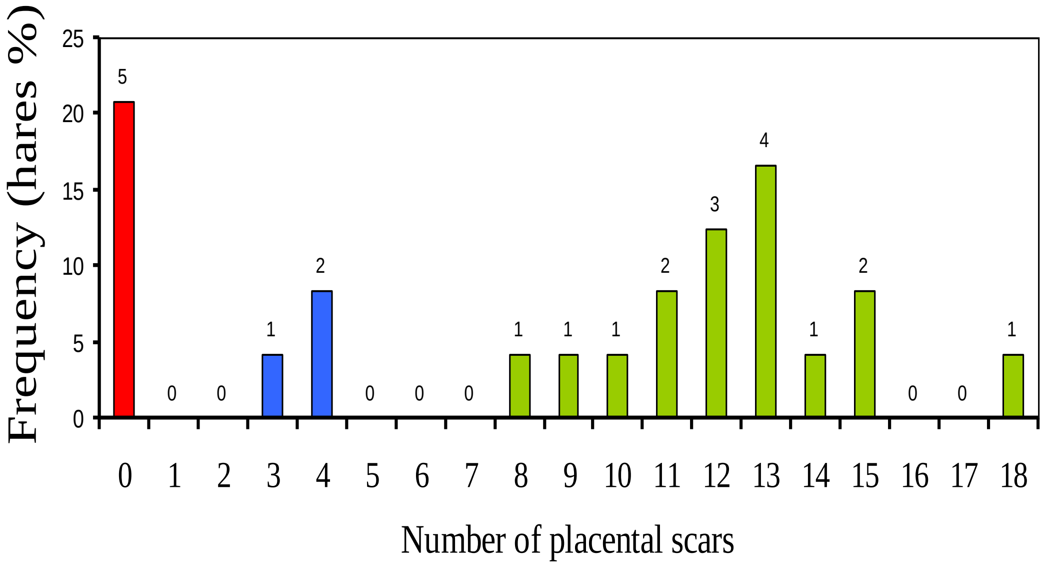

Figure 5.6. Annual fertility in adult female hares in North Yorkshire (n = 24). Corresponding numbers of females in each category are shown for each bar. Red bar indicates adult females infertile in the previous breeding season. Blue bars indicate females collected before the end of the breeding season.

5.3.4 Population demographics and dynamics

Age structure and annual reproduction values were used to create life tables for brown hares in the study sites. The number of leverets produced over the entire breeding season was calculated by averaging the total number of embryos produced by fertile females over the course of the year (Table 5.2).

Age (years) a	Number sampled N_a	Survival rate $S_a = n_{a+1}/n_a$
0.4-1	31	0.58
1-2	18	0.83
2-3	15	0.73
3-4	11	0.27
4-5	3	0.66
5-6	2	0.5
6-7	1	0

Table 5.1. Static life table for the hare populations pooled across sites in North Yorkshire, based on age composition of a non-selective cull

As only one individual in the entire sample weighed less than 2.43 kg (i.e. one male of 1.52 kg) it is reasonable to assume that juveniles of less than 4 months, when they approach adult weight of around 2.8-3.4 kg, were not represented in the collected sample. Therefore, category 0-0.4 year old (leverets) was not included in this table.

Age (years) x	N	Frequency a_x	Survival l_x	Mortality d_x	Mortality rate $q_x = d_x/l_x$	Survival rate $p_x = (1-q_x)$
0	248*	329	1.00	0.75	0.75	0.25
0.4	31	81	0.25	0.09	0.38	0.62
1	18	50	0.15	0.06	0.36	0.64
2	15	32	0.1	0.05	0.47	0.53
3	11	17	0.05	0.03	0.65	0.35
4	3	6	0.02	0.01	0.50	0.50
5	2	3	0.001	0.01	0.67	0.33
6	1	1	0.00	0.00	1.00	0.00
Total	329					

Table 5.2. Life table for the hare population pooled across sites in North Yorkshire, based on age composition of a non-selective cull, and calculated productivity in all adult females.
*** -** annual leveret production value calculated from the mean female productivity and estimated percentage of fertile females

Using this method the estimated mean survival rate for all age classes is 0.40 and 0.42 for all age classes except leverets. However, the numbers of hares in the collected sample surviving 4 or more years is less than 10 % and as such all hares aged more than 3 can be pooled in a single category. In this case the mean estimated survival rate for all age classes was 0.41 or 0.45 for all hare classes except leverets. In both scenarios the survival rate of leverets (age class 0-0.4 year) is around 0.25.

Using the formulas developed by Pianka (1994) a Gross reproductive rate and a net reproductive rate (GRR = 23.75; R_0 = 1.52) were calculated and which indicate that the brown hare population used in this study is increasing ($R_0 > 1$). GRR represents the number of offspring that would be produced by an individual in the absence of mortality while the net reproductive rate (R_0) represents the average number of offspring produced by an average individual during its entire lifetime (Pianka, 1994). Generation time (T =

1.82) represents the number of time units needed for the average female to produce a female offspring and since the population was increasing it was corrected by dividing it with the net reproductive rate R_0 (Pianka, 1994). The Euler-Lotka equation is considered an improved method for estimation of r from life table data and in this study using this equation r = 0.24 ($\boldsymbol{r_{est}}$ = 0.23 using $\boldsymbol{r_{est}} = \ln R_0/T$) at 1.02 confirming that the population was stable or increasing at a very small annual rate.

Age (years) (x)	Survival l_x	Fecundity m_x	Realised fecundity $l_x m_x$	Age weighted by realised fecundity $x l_x m_x$	Expectation of life E_x	Reproductive value v_x
0	1.00	0.00	0	0	1.571	1.52475
0.4	0.25	0.00	0	0	2.284	6.099
1	0.15	4.75	0.7125	0.7125	2.14	10.165
2	0.1	4.75	0.475	0.95	1.71	8.1225
3	0.05	4.75	0.2375	0.7125	1.42	6.745
4	0.02	4.75	0.095	0.38	1.05	4.9875
5	0.001	4.75	0.00475	0.02375	1	4.75
6	0.00	0.00	0	0	0	0
Total		23.75 (GRR)	1.52 (R_0)	2.77 (T for stable pop.)		

Table 5.3. Estimated fecundity, net reproductive rate, life expectancy and reproductive value for an increasing hare population pooled across pastural-marginal upland sites in North Yorkshire based on a post-breeding non-selective cull.

These suggest that 1 year old hares have the greatest reproductive value based on their survival and fecundity.

Brown hare elasticity analysis and projection matrix

In the absence of hunting the adult population of brown hares described by the three stage age-structured model appeared to be increasing at an annual rate of around 10% suggesting that a level of annual hunting of 10% post-breeding affecting in the same proportion both subadults and adults would be compensatory to population growth. Equally in the absence of hunting an increase of 20% of juvenile survival to 0.3 meant that the adult population could double in less than 6 years. Alternatively, the population would undergo a slow decline of only 1% in adult numbers with a 20% reduction in fecundity.

The four stage population projection matrix model suggested a modest growth rate and a steady population increase in the absence of hunting (A), a stable population at 10% hunting (B), a slow decrease at 15% hunting rate (C) and probable extinction in 20 years time at 30% (C) (Figure 5.7). However, considering the small number of carcasses available for this study and the fact that population parameters are temporally and spatially restricted these results should be interpreted with caution. One potential problem with these projections is the fact that they do not incorporate variation in parameters due to stochastic events, such as major episodes of adverse weather or diseases which could significantly alter both survival and fecundity of different age groups. Equally, it is likely that hunting levels would be adjusted once the population is showing strong signs of decline.

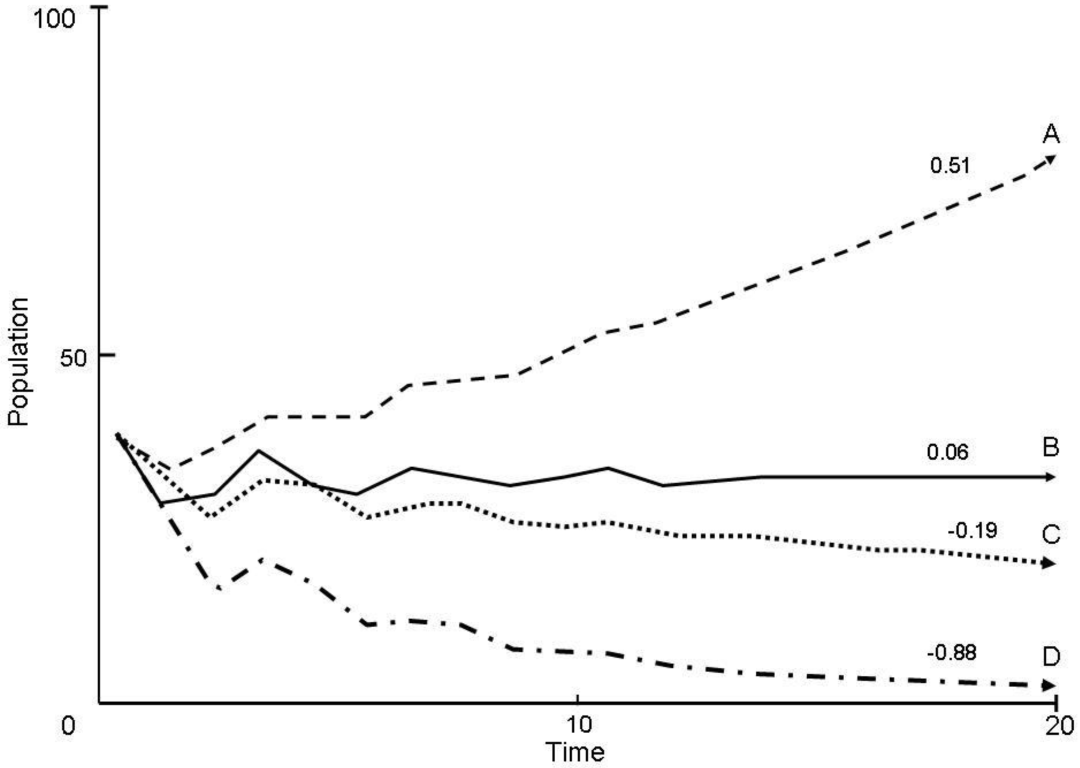

Figure 5.7. Projection matrix modelling results for brown hare population in North Yorkshire over 20 years showing growth rates A in the absence of hunting (λ = 1.051), B with 10% hunting (λ = 1.006), C 15% hunting (λ = 1.051) and D with 30% hunting (λ = 0.912)

5.3.5 Comparisons with the NHCD

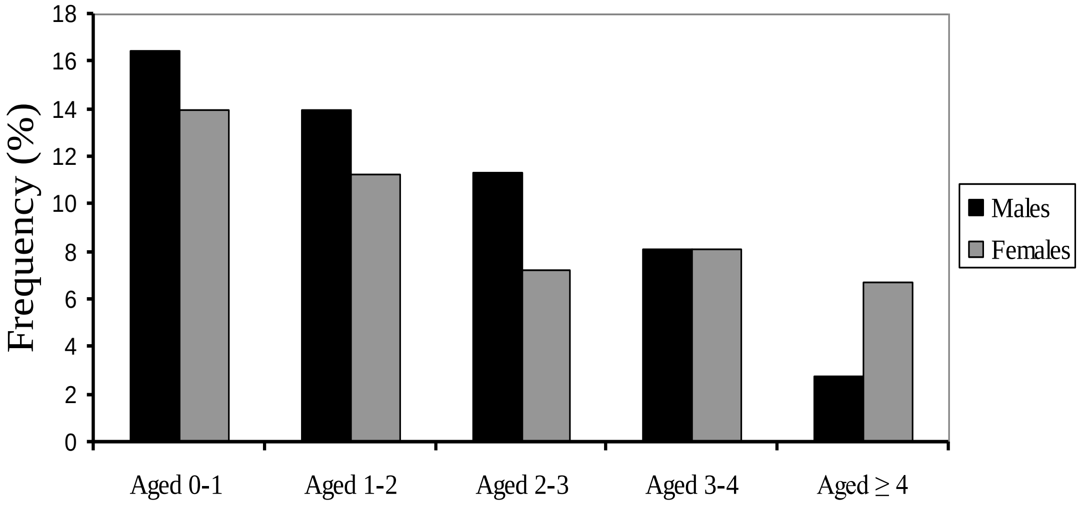

Figure 5.8. Age and sex structure of brown hares in NHCD Arable (n = 801)

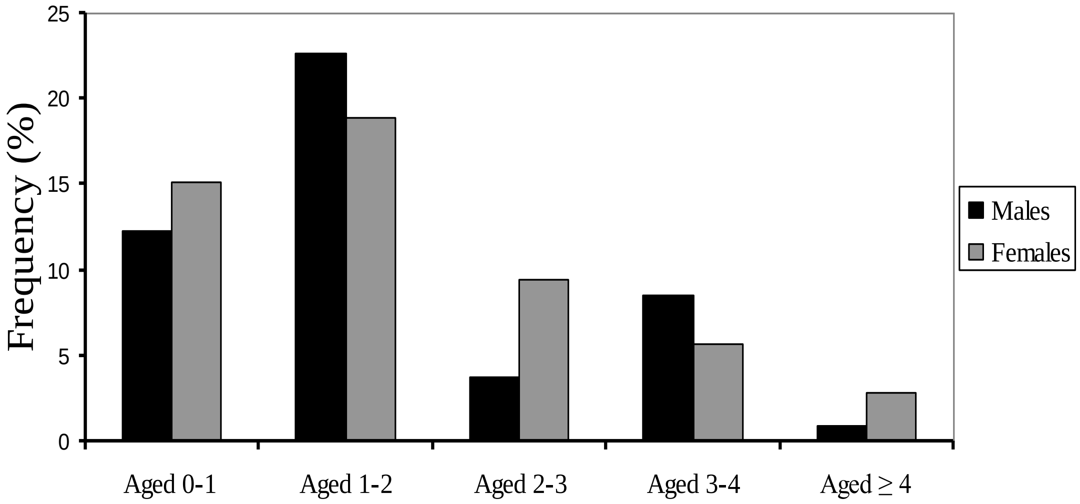

Figure 5.9. Age and sex structure of brown hares in NHCD Pastural-marginal upland (n = 106)

Sex and age structure were similar between NHCD arable and NHCD pastural-marginal although the proportion of young of the year was slightly smaller in pastures-marginal upland at 27% than in arable at 30%. Since most animals were collected at different times of the year (post-breeding in North Yorkshire and pre-breeding in the NHCD) and in different regions, comparisons between the two datasets are difficult but there were significant differences between the age structure of the three datasets ($\chi^2 = 12.59$; $P < 0.05$; df = 4) with a higher proportion of animals < 1 year in the North Yorkshire sample and a higher proportion of individuals age 1-2 in NHCD arable.

Despite the differences in timing of carcass collection the total mean weight of hare carcasses in this study of 3.28 kg was almost identical to the total mean weight of the 1018 hares collected during the NHCD of 3.26 kg (SD = 0.54 kg).

Of all adult hares from pastural-marginal upland areas in the NHCD 17.4% (15 individuals) had not been killed (by shooting or with dogs) or road-kills but instead were found dead for unknown reasons or from disease. It would be logical to assume that such animals might therefore be in poorer body condition and that body measurements might be affected compared with the normal, healthy population. One adult male hare from the sample in North Yorkshire which was found dead due to a severe infection that had affected most organs but particularly the lungs, had a body weight almost 30% lower than other adult males from the same area. In fact, mean adult body weight for this category in the NHCD of 2.6 kg (SD = 0.49) was significantly lower compared to 3.2 kg (SD = 0.50) (*t test* t = 1.998; P < 0.05; df = 64) and equally adult MHFL for individuals of unknown cause of death or diseased was 13.7 cm (SD = 0.36) compared to 14.28 cm (SD = 0.38) (*t test* t = 1.993; P < 0.05; df = 73) for all the other adults from the same type of habitat. As a consequence these individuals were considered unrepresentative of the population and were removed from further analysis. An additional male with no recorded body weight but an MHFL of 12.3 cm was excluded from further analysis as a possible error in the aging classification process. The remaining NHCD sample contained 63 adult individuals from both pasture and marginal upland habitats with 34 males and 29 females.

Mean adult body weight was significantly different between sites and sexes (Table 5.4) but not between all groups and categories (Figure 5.10).

Source	df	MS	F	P
Corrected Model	3	7.13	50.00	0.001
Intercept	1	2437.57	17079.75	0.001
Habitat	2	0.65	4.60	0.010
Sex	1	19.88	139.31	0.001
Error	649	0.14		
Total	653			
Corrected Total	652			

MS = mean square; df = degrees of freedom

Table 5.4. Results of ANCOVA with ‘Body weight’ as the dependant variable and ‘Habitat’ and ‘Sex’ taken as fixed factors

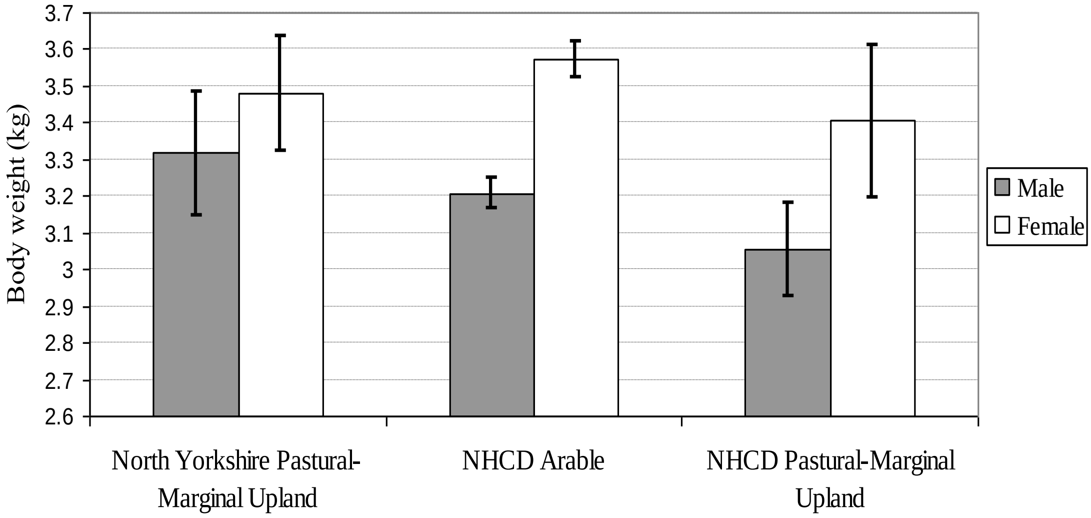

Figure 5.10. Mean adult body weight comparison between brown hares from this study, (males n = 21, females n = 25), NHCD arable (males n = 285, females n = 266) and NHCD pastural-marginal upland (males n = 31, females n = 26). Error bars indicate 95% CI.

Adult foot length, taken as an index of skeletal size, was not significantly different between sites but was significantly different between sexes (Table 5.5) (Figure 5.11).

Source	df	MS	F	P
Corrected Model	3	0.74	2.51	0.058
Intercept	1	45237.64	152602.58	0.001
Habitat	2	0.18	0.63	0.528
Sex	1	1.80	6.09	0.014
Error	648	0.29		
Total	652			
Corrected Total	651			

MS = mean square; df = degrees of freedom

Table 5.5. Results of ANCOVA with ‘Foot length’ (HFL) as the dependant variable and ‘Habitat’ and ‘Sex’ taken as fixed factors

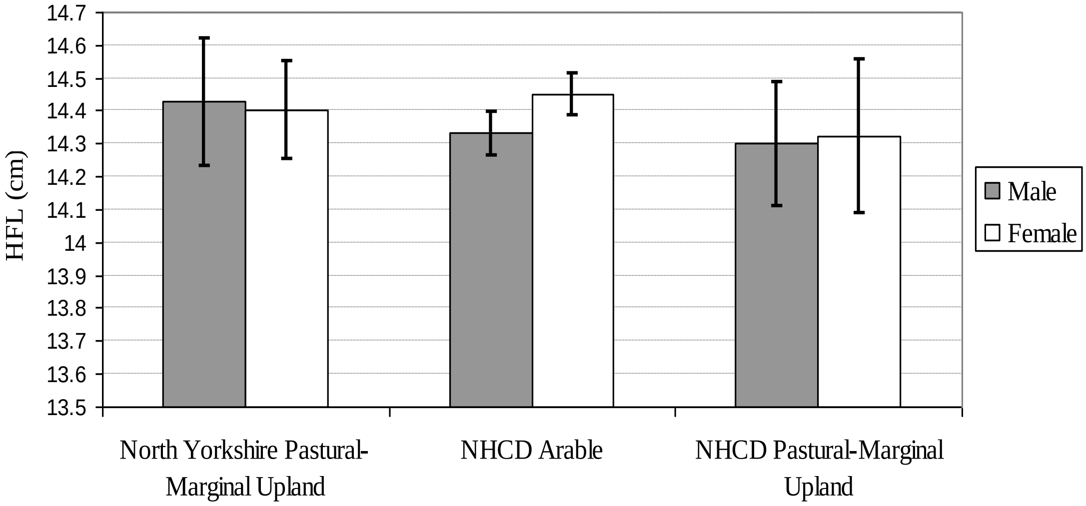

Figure 5.11. Mean adult HFL comparison between brown hares from this study, (males n = 21, females n = 25), NHCD arable (males n = 289, females n = 266) and NHCD pastural-marginal upland (males n = 34, females n = 28). Error bars indicate 95% CI..

Adult body weight was significantly correlated with hind foot length in all three datasets (North Yorkshire data, NHCD pastural-marginal upland and NHCD arable) and for both sexes (Adjusted $R^2 = 0.161$; $F = 22.02$; $df = 640$; $P < 0.001$). Using univariate GLM with ‘Body weight’ as the dependant variable, ‘Foot length’ (HFL) as covariate and ‘Habitat’ and ‘Sex’ taken as fixed factors there were significant effects of both Sex and Habitat on hare body weights from NHCD arable, NHCD pastural-marginal upland and from North Yorkshire pastural-marginal upland (Table 5.6). Hares from NHCD arable were generally heavier than those from NHCD pastures and marginal upland but not those from North Yorkshire and skeletal size was not significantly influenced by habitat between the three datasets.

Source	df	MS	F	P
Corrected Model	4	9.015	75.097	0.001
Intercept	1	1.094	9.113	0.003
Habitat	2	0.481	4.009	0.019
Sex	1	16.390	136.525	0.001
Foot	1	14.825	123.496	0.001
Error	647	0.120		
Total	652			
Corrected Total	651			

Table 5.6. Results of univariate GLM with ‘Body weight’ as the dependant variable, ‘Foot length’ as covariate and ‘Habitat’ and ‘Sex’ taken as fixed factors

5.3.6 Diseases

The only male (H120WYK060210) found dead as a certain consequence of disease (most likely pseudotuberculosis), at the start of February, had no fat deposits and a total weight almost 30% smaller than individuals of the same age group consistent with prolonged infection prior to death. One adult female (H008DAL030807), which was found dead in August, presented symptoms usually associated with the European Brown Hare Syndrome, a viral disease which can cause mass mortality in hares and which produces acute hepatitis and diffuse haemorrhages in different internal organs including the lungs (Frolich et al. 2003). This female had no fat deposits and the second lowest fertility of all adult fertile females with only two litters produced and a total of only 4 placental scars. Two other individuals, one male and one female also showed symptoms usually associated with infection with *Yersinia* (*Y. pseudotuberculosis* and possibly *Y. enterocolitica*), with white-yellowish granulomatous nodules in the lungs, liver and mesenteries as well as collection of opaque fluid in the pericardium.

In 4 cases female hares displayed signs of pathological transformations of the uteri surface, particularly at the endometrial level, with typical aspect for cystic endometrial hyperplasia (CEH), a disease known to affect both herbivores and carnivores.

5.4 Discussion

5.4.1 Age and sex structure

The overall observed proportion of young of the year of 38.7% seems low when compared to the 48-66% found in France (Marboutin et al. 2003), 62% in Netherlands (Broekhuizen, 1979), 54% in mainland South Sweden (Frylestam, 1979) and 66.7% in Australia (Stott & Harris, 2006) but very similar to the 39.5% found in a recent study in Denmark (Wincentz, 2009). At the European level a review found 32-52% young of the year in the population (Smith et al. 2005) with variation due both to intensity of farming and farming type but there was no inclusion of data specifically from pastural areas. In the UK, the proportion of individuals <1 year old in the population, mostly obtained from animals shot in February at a national scale, was 32% for males and 29% for females (Jennings et al. 2006) but with a pooled proportion of only 27% in pastural-marginal upland areas (Figure 5.7). The difference between the present study, where most individuals had been collected in late autumn, from October until mid December and the proportion of animals <1 year old observed mostly in February in the NHCD could be an indication of winter mortality during this period. However, juvenile survival and mortality are both spatially and temporally variable and despite the fact that any weather effects were probably condensed since both datasets combined three years it is likely that for the juvenile survival estimated in this study in North Yorkshire it would be inappropriate to extrapolate beyond the spatial and temporal limits of the study.

The sex ratio of adults was roughly equal in the present study but females reached older age than males, with no males older than 3 years. This is in contradiction with other studies from France where males were found to survive better than females (Marboutin & Hansen, 1998). However, it is similar to studies on hare populations from Denmark (Wincentz, 2009), Poland (Pielowski, 1971), Australia (Stott & Harris, 2005) and the UK (Jennings et al. 2006), all of which found more old females than males in the population. In agreement with the findings of Jennings et al. (2006) in arable areas and Wincentz (2009) at a national scale in Denmark, the sex ratio of the young of the year in North Yorkshire pastures was slightly imbalanced, with more males present in the sample than females. Although numbers were small, if this apparent difference is true it could be linked to the fact that in brown hares dispersal is largely male biased, with young males typically dispersing before 5 months of age (Avril et al. 2010) and as a consequence, their survival could be affected.

5.4.2 Reproduction

At the European level, the mean number of leverets of 9.5 per adult female or 12.4 per fertile adult female derived from this study is comparable with data from other studies on brown hares in France with means of 12-15 leverets (Marboutin et al. 2003), 6.8-8.9 in southern Sweden (Frylestam, 1980a) and 9.8-11.1 in Denmark (Wincentz, 2009). However, brown hares from the continent typically have higher body mass and larger skeletal size, a fact that was confirmed by the present dataset, with adult hares in the samples from our sites being on average 16% lighter than in Denmark. Considering that hare litter size and/or number of litters have been shown to correlate positively with female body mass (Frylestam, 1980b; Marboutin et al. 2003; the present study) and that female productivity fluctuates across the geographical distribution of the species and appears to decrease with latitude (Flux, 1967), hares in Britain are consequently expected to have lower annual fertility. Flux (1967) estimated mean annual production of leverets at 9.8 in New Zealand, where brown hares were introduced from England

(and therefore smaller in size) and experience similar weather conditions, and this value compares very well with the 9.5 reported in this study.

UK pastures are considered to be suboptimal habitat for brown hares (Vaughan et al, 2003, Jennings et al, 2006) as body condition, size and participation in breeding were reduced when compared with hares from arable areas. However, recent research from Denmark (Wincentz et al. 2009) found a positive association between the proportion of grass ley areas and the mean number of placental scars per female, but a negative association between the percentage of breeding adult females and such areas. In Sweden, Frylestam (1980a) found significantly higher annual fertility in female hares from pastural areas compared with other populations while in France, Marboutin et al. (2003) estimated mean fertility of 13.8 per fertile doe in an area with 80% grassland and 10% cereal. The data presented from the sample of carcasses of brown hares from North Yorkshire suggests that at least in these study sites hares were capable of reaching high annual fertility.

The method used in the present study for placental scar counting, as described by Bray et al. (2003), seems to indicate higher female fertility than previously described by other methods, such as estimates based on mean litter size and mean number of litters (Pepin, 1989, Brokhuizen & Maaskamp, 1981) or by placental scar counting without chemical coloration or after bleaching of the uterus (Frylestam, 1980, Hansen, 1992). Nonetheless, the methodology used by Bray et al. (2003) is the only one to have been calibrated against the productivity of hand reared brown hares, with an observed overestimation of only 2.5% of total fertility.

The proportion of placental scars of the resorption type indicating post-implantation mortality of the embryo, were, at 6 % in the present study, fewer than other datasets, with Bray et al. (2003) reporting 12%. However, the time of collection of carcasses in Bray et al. was September rather than October-December as in the present work and given that the highest proportion of post-implantation loss of embryos typically occurs during the first litter it is likely that some of the very early scars had been missed during the analysis of uteri from North Yorkshire.

The high levels of female productivity in this study from NE England pastures are somewhat decreased by the fact that no female < 1 year old (n = 12) had any evidence of breeding in the past breeding season. Brown hare leverets can reach adult body size around the age of 4 months and sexual maturity between 5 and 6 months (Lincoln, 1976; Caillol et al. 1992) or 6 to 7 months (Broekhuizen & Maaskamp, 1981) and hence, juveniles born after April, when litter size is at a peak, will only breed in the following year. Mild weather during autumn was found to extend the breeding season (Hewson & Taylor, 1975) and the breeding season is usually shorter in colder climates. As a consequence, the percentage of females breeding in the first year of life is generally low in temperate Europe, between 0% in southern Sweden (Frylestam, 1980a), 13% in France (Marboutin et al. 2003) and 4 % in East Anglia, UK (Lincoln, 1974) but not in Australia where females of 3 months old were already breeding and where young of the year females contributed 54% of the total reproductive output (Stott et al. 2008).

The adult female fertility of 80% estimated in this study, even if based on a relatively small sample size, is at the lower limits when compared with other European populations of 85-100% in France (Marboutin et al. 2003), 82% in Austria (Hacklander et al. 2001) but very similar to the 79% in Denmark (Nielsen, 2006). The low percentage of adult females breeding in semi-natural pastures in Denmark combined with the high fertility of the remaining females in the population were suggested to act as a compensatory mechanism where females that lost early litters produced additional ones later in the year (Wincentz et al. 2009). In the NHCD, Jennings et al. (2006) found similar pregnancy rates and litter sizes in arable and pastural habitats but lower lactation rates in pastures, suggesting reduced juvenile survival or shorter suckling periods due to poor body condition as the cause.

This is the first dataset on annual fertility of the brown hare in the UK based on placental scar counting and as such interpretation of these regional results is difficult at a wider, national scale. In addition, the relatively small sample size of carcasses of adult females analysed here means that these results should be interpreted with caution. However, the results of this study suggest that female hares in pastures in NE England were capable of high annual fertility but the percentage of adult females breeding was at the lower limits for hare populations in Europe, perhaps as a consequence of pathological processes affecting female hares in such habitats.

5.4.3 Population demographics and dynamics

The relatively low proportion of young of the year in the hunting bag in autumn from this study combined with the high female fertility suggest that leveret survival during the first months of life was very low in these sites and this was confirmed by the life tables. However, while post-breeding hunting using beaters is assumed to be non-selective (Pepin, 1987), shooting at night from a car with the help of a spotlight, as done in the present study, could potentially select against small individuals from late litters which would therefore be underrepresented in the hunting bag. On the other hand, litter size is smaller at the start and the end of the breeding season and most juveniles should be old enough in mid October-December to be difficult to distinguish based on body size from adults. During hare surveys at night in October-December 2007 and 2008 (Chapter 2) identification of juveniles was possible in less than 5% of all hare observations (352) and only in October.

Leveret survival is influenced by predation (Erlinge et al. 1984), climate (Hackländer et al. 2002b, Smith et al. 2005) and disease (Edwards et al. 2000), all of which are likely to be linked with habitat management and potentially with agricultural operations (Pepin 1989). McLaren et al.(1997) and Reid et al. (2010) suggested that the timing and increase in silage grass cutting operations in recent decades could be responsible for high leveret mortality in grasslands, but this could not be confirmed by direct observations, due to the difficulties of catching and monitoring a sufficiently large number of leverets. An estimated 0.05-0.15 survival rate for juveniles between birth and autumn was observed in a study in Poland (Wasilevski, 1991) and 0.16-0.19 over three years in a pastural sandy area in mainland south Sweden (Frylestam, 1980b). In contrast, Pepin (1989) found leveret and juvenile survival of 0.25-0.50 for arable areas in France. A figure for juvenile survival of 0.20 was used when modelling hare populations from pastural areas in a recent study (University of Bristol, 2003) but the authors suggest that this figure might be an overestimate. The 0.25 survival of leverets to subadults derived from the present study in pastural areas with moderate hunting levels compares well with such figures and suggests that at least in the pastures of north east of England, which are comparatively colder and dryer than the western parts of Britain, leveret survival might be higher than previously reported for UK pastures.

Despite potential differences in hunting pressure and significant differences in hare densities (site C 30 hares km^{-2}; site G 52.8 hares km^{-2}; Chapter 2) adult age did not vary significantly between populations, suggesting that adult mortality is similar between the two sites that contributed most carcasses. A relatively constant adult survival rate around 0.50 is generally assumed in hares (Marboutin & Peroux 1995) with 0.50-0.61 for adult males and 0.44-0.56 for adult females in a non-harvested population (Marboutin & Hansen 1998). The 0.45-0.51 survival rate for adults obtained in this study indicates that such values are consistent with previous studies on hare populations of moderate or high densities. By comparison, a combined annual adult-subadult survival rate during a radiotracking study of a non-harvested hare population in pastural areas in the south west of England was 0.35 (0.17 - 0.52; 95%CI) (University of Bristol, 2003).

The survival and fecundity data from this study suggests that taking the separate sites as a single population there is evidence for an annual increase; however, this increase is limited by culling rates even at very modest levels of less than 10% of the population. Brown hares are culled at varying rates but intensive shooting can reduce the pre-breeding population by as much as 40% in areas of high density in the UK (Hutchings & Harris, 1996) or even an average of 49% (Stoate & Tapper, 1993). More recent population modelling suggests sustainable hunting rates in populations in France between 20 and 35% depending on population post-breeding size (Marboutin et al. 2003) but these are based on populations with higher demographic parameters than those in the UK. There were indications that the levels of hare hunting in site G between 2004 and 2008 (100-150 individuals culled annually in 1010 ha, or 23-35% of the current winter population) had been too high and that the population was declining which led to a halving of the culling rate the following years (Estate Manager, personal communication). However, poaching activities in the form of coursing with dogs were frequent events and meant that the success of any reductions in culling quotas was difficult to quantify.

In order to increase the ‘shootable surplus’ and to manage the population at sustainable levels efforts should be directed at increasing the demographic parameters which could have most impact. The elasticity models created in this study indicate that while both juvenile and adult survival would benefit the population growth rate at similar levels the very low juvenile survival calculated in these sites suggests that this is the area where most gains could be obtained. Based on current knowledge achieving such increases might be difficult since the main causes of leveret mortality remain largely unclear and are likely to differ between regions, habitats and years. It is likely however that improving the provision of adequate resting areas for both adults and leverets and focusing future research on identifying the exact causes of juvenile mortality could provide strong suggestions for increasing leveret survival rates in agricultural areas.

5.4.4 Body condition and skeletal size

The results of this study confirm the fact that in brown hares both the accumulation and the utilisation of fat deposits follow the timing of the reproductive cycle in both sexes. In females, previous research has indicated that gestation induces fat deposition, at least in the first litters, which can then be mobilised during lactation (Parkes, 1989). However, as income breeders female hares also utilize the fat obtained directly from ingested food for milk production (Valencak et al. 2009). Reproduction is a very energy-demanding process in brown hares due primarily to the particularity of producing precocial and rapidly growing young that largely depend on the high fat milk produced by the mother for at least the first two weeks of life (Valencak et al. 2009). As expected, there was a significant association between the size of fat deposits and reproductive status, with non-breeding females having higher fat deposits than breeding ones although in the present study the non-breeding condition was largely associated with a pathological process (i.e. CEH). However, the small sample sizes presented here mean that these results should only be interpreted as preliminary findings.

In adult males, the size and extent of perirenal fat deposits was greater for those individuals which were culled in the second part of autumn, confirming the hypothesis that fat deposition increases towards late autumn, in preparation for the breeding season when fat stores are being mobilised (Flux, 1987; Parkes, 1989). Male hares increase their home ranges during the breeding season (Smith et al. 2004), fight off competitors and are involved in long chases of the females and mating activities (Flux, 1987), all requiring high levels of energy consumption. Fat stores should therefore increase up to a peak in adult males with the onset of the breeding season in mid to late January. As such, comparing the data from carcasses collected in late autumn with the ones from winter (February-March) collected in the NHCD is difficult and probably inadequate but the distribution of fat deposit scores, particularly of adult male hares in late autumn from North Yorkshire pastures seem to indicate good body condition.

5.4.6 Diseases

Pseudotuberculosis is one of the main mortality factors in adult brown hares of both sexes and has been positively linked with increased hare densities in a study in northern Germany where 55% of hares tested positive for Yersinia antibodies (Frolich et al. 2003). This is particularly relevant since this disease can remain subclinical and can be transmitted through infected faeces to domestic species such as sheep and cattle or to humans. Two individual hares in our sample with strong signs of pseudotuberculosis infection at the time of their culling in October-November seemed in relatively good body condition, with moderate fat deposits and average body weight. However, this disease typically kills adult hares in winter (Marboutin et al. 2003), probably as a consequence of the added environmental stress of cold and wet weather on an already weakened individual and it is possible that these individuals would have suffered the same fate. All three individuals presenting symptoms of pseudotuberculosis were from site G but from different years which suggests that more investigation is required to establish the prevalence and of this disease and its importance as a contributor to the mortality of hares in this site.

All 4 cases of pathological transformations of the uteri, very likely caused by cystic endometrial hyperplasia (CEH), were also found in site G. This disease has a poorly understood aetiology and pathogenesis but it has been linked with prolonged or excessive exposure to hormones, usually estrogens in herbivores (Radi 2005, Stott & Wight, 2004; Stott et al. 2008) and can lead to permanent infertility in domestic animals by preventing implantation or fertilisation (Radi, 2005). Interestingly, if high levels of estrogens were the cause of this disease they might also promote a shorter puberty in females and higher levels of young females breeding in the population but this was not confirmed in this study. While numbers are small, the apparently high prevalence of this disease in adult females in the sample collected from this site indicates that further research would be warranted in order to identify both the proximal and the underlying cause for this pathology. If, as previously suggested the proximal cause is the exposure to high levels of estrogens it is likely that the same symptoms could develop in domestic animals grazing in the same areas. Potential sources of estrogens and progesterone could be external such as irrigation water contaminated with hormones not separated at sewage treating plants or phytoestrogens or mycoestrogens produced by plants and funguses growing in the sward (Stott et al. 2008). If the percentages obtained in this sample would hold true across the population this disease may play a significant role in the population dynamics through limiting the fertility of adult females.

5.4.5 Comparisons with the NHCD

Given that carcasses were collected at different times of the year in the present study compared to the dataset obtained in the NHCD comparing the body weight and MHFL of animals aged <1 year old is difficult. As such, all analysis was focused on differences between adults of different sexes based on their respective habitat. Considering that overall, hares in North Yorkshire pastural-marginal upland areas were at far higher densities compared to the average for pastures at a national scale (Chapter 3) it would be reasonable to assume that this might be indicative of suitable environment and could be also reflected in the condition of individuals. However, after removing all animals with disease or an unknown cause of death from the NHCD pastural-marginal upland sample there were no significant effects of habitat on skeletal size (HFL) between hares from any of the three groups used in the analysis. Similarly, the total weight of adults was only significantly different between males from NHCD arable and pastural-marginal upland but not for females. Although these results might be a consequence of small sample sizes for adult individuals from pastures and the large variation, the fact that we could not confirm the differences presented by Jennings et al (2006) suggests that the relationship between body weight, size and condition in hare populations from pastural or arable areas might not be as straightforward as previously thought and almost certainly requires more information from areas of different densities in order to be adequately explained.

5.5 Conclusions

The annual fertility figures derived from carcass analysis from North Yorkshire suggest that females from pastures, at least from the eastern part of the country are able to produce a high number of leverets and although leveret survival is low, it might not be as low as previously reported for other pastural areas in the UK (University of Bristol, 2003). There is strong evidence that the population would be increasing in the absence of hunting in these sites but given the low juvenile survival and low female fertility this trend is likely to change at even relatively modest hunting rates of 15-20%.

Adult survival in this study was also higher than previously reported for other pastural areas (University of Bristol, 2003, Jennings et al. 2006) but compared well with studies from continental Europe. However, the full scale and impact of the adult female infertility needs further investigation as, for the moment, the underlying cause for the relatively low proportion of fertile adult female hares within the sample remains unknown since body size and condition indicated that females in these habitats were not in poor condition.

This study could not confirm the differences in skeletal size and fat deposits between hares from arable and pastural areas and whilst this might be a consequence of the small sample sizes there are strong indications that adult hares from pastural-marginal upland areas from North Yorkshire were capable of reaching similar sizes to those from other areas of moderate to high densities, such as arable sites. While climatic differences between the eastern and western parts of Britain could have an important role to play in explaining both the higher densities and the apparently good body condition and survival of brown hares from north east England it is also likely that hares in the sites investigated here were benefiting from measures put in place for game rearing and through agri-environment schemes, such as the provision of field margins, blocks of woods, as well as predator control, all of which have been shown to positively influence hare densities (Vaughan et al. 2003; Reynolds et al. 2010).

Population growth rate is more sensitive to adult survival in areas with low juvenile recruitment (Marboutin & Peroux 1995) and at 0.25 juvenile survival in the present study this might be the case in our study sites. As such, to achieve sustainable hunting harvesting, of maximum 15% of the pre-breeding population in our study area, quotas should be kept under this value and both adult and juvenile mortality should be minimised in order to ensure maintenance in areas of low recruitment. Reduced juvenile recruitment was blamed for the decline of brown hares in Denmark (Wincentz, 2009) but the underlying causes, probably involving changes in agricultural management, increased predation and/or precipitation, remain yet to be fully explained. Further research should focus on identifying the major causes of juvenile mortality and ways to reduce it if increases in hare populations are to be achieved in the UK.

Chapter 6 Brown hare range selection for farmed and non-farmed habitat features in an agricultural mosaic

A manuscript based on this chapter has been submitted as:

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Summary

Agricultural intensification in the post-war years has led to dramatic changes of the European farmland landscape with losses of heterogeneity, increased simplification and reductions in associated biodiversity. Previous studies have linked the declines of the brown hare with agricultural intensification and changes in timing of agricultural practices and recommend that agri-environment schemes could be used to increase populations of hares. However, the results of such schemes have been equivocal in their success in increasing hare populations and there is no apparent consensus on how these can be improved in order to benefit hare populations without causing negative impacts on other farmland species, such as some birds. Understanding of space use and range selection of hares in agricultural areas, in particular in relation to the habitat structures created or maintained through agri-environment schemes could contribute to their successful conservation using such schemes.

We radio-collared and studied hares for one calendar year in a mixed agricultural area dominated by grassland and investigated the hares' selection for different habitats and habitat structures during both active and inactive periods. Home ranges were generally small but tended to be larger in arable fields. Using 'homing in' as a radio-tracking technique we show that hares strongly selected field margins during both active and inactive periods of time and used the areas in the middle of the fields less frequently than those closer to the field boundaries. Hares selected habitats in terms of both between field and within field heterogeneity. Pasture fields, mostly sheep grazed were generally avoided throughout the year. We suggest that agri-environment schemes targeted at increasing non-farmed habitat features and reducing sward depletion through less intensive or mixed grazing regimes could prove beneficial for hare populations. Future studies should focus on identifying the underlying reasons for hare's selection of field margins and on the most suitable management of such areas.

6.1 Introduction

The intensification of agriculture is regarded as the main cause for the decline of several species typically associated with farmland over the past 50-60 years in Europe (Benton et al. 2003) and this includes the brown hare (Smith et al 2005a). Intensification has resulted in the simplification of the landscape, with homogenous fields and increased field size, an increase in agricultural practices such as spraying with pesticides and harvesting operations (i.e. cutting grass for silage rather than hay) as well as the reduction in non-farmed habitat features such as field margins, hedgerows, fallow land and trees (Tscharntke et al. 2005) and a general reduction in biodiversity (Robinson & Sutherland, 2002).

As a result of the declines of brown hares in the UK they are considered a “priority species” and have a Species Action Plan (BAP, 1995). The causes for the hare decline given in the BAP include the conversion of grassland to arable, loss of farmland biodiversity and the shift in harvesting from hay to silage. However, brown hares can benefit from large fields (Vaughan et al. 2003; Chapter 6) and in Britain hare densities are the highest in areas dominated by arable land with relatively low habitat diversity (Hutchings & Harris, 1996; Vaughan et al. 2003). Previous research has suggested that in pastural areas hares could benefit more from within-field heterogeneity rather than between-field heterogeneity (Smith et al, 2004) and recommended that agri-environment schemes focus at this level in order to increase available cover. Despite this it is still unclear to what extent such schemes can increase numbers of hares as results have been few and contradictory (Browne & Aebisher, 2003; Reynolds et al. 2010). Irish hares (*Lepus timidus hibernicus*), which show a closer ecological resemblance to brown hares than mountain hares (Reid et al. 2010), did not show an increase in farms where agri-environment schemes had been put into place (Reid et al. 2007).

At the national scale brown hares from grassland areas were positively associated with both improved grassland and woodland but not with set-aside (Hutchings & Harris, 1996; Vaughan et al. 2003) and there are several studies indicating that landscape diversity is important for hares, especially in intensively managed areas (Frylestam, 1980; Tapper & Barnes, 1986; Pepin & Angibault, 2008). However, whether hares select specific habitat features associated with landscape diversity such as small blocks of woodland or with agri-environment schemes, such as uncultivated field margins, hedgerows or stands of trees remains largely unknown and poorly understood. This might be a consequence of the fact that most non-farmed habitat features, such as field margins, are relatively small, narrow habitat features, usually less than 10m wide and radio-telemetry studies that rely on triangulation (the most common approach taken to study habitat use by hares) have error polygons that are too large to reliably assess use of such features. However, if hare declines are to be reversed using agri-environment schemes targeted at increasing population densities through habitat modifications understanding the associations between hares and farmed and non-farmed habitat structures could significantly contribute to their success.

This study had two aims: a) to investigate the habitat use of hares in relation to farmed and non-farmed features in a grassland-dominated agricultural area and b) to relate the selection or avoidance of particular agricultural fields to their condition and management.

6.2 Methods

6.2.1 Study site

The study site (311 ha) was a flat grassland dominated area located in a lowland mixed arable-pastoral landscape in North Yorkshire, north east England, UK (54°20’N, -

0°50’E). Habitats were ground truthed and digitised at a scale of 1:10000 using ArcGIS 9.2 software (ESRI, California, USA). Fields were used in a rotational system and the proportion each land cover type was different between seasons and years. During summer and early autumn 2009 the site consisted predominantly of improved grassland (41%), semi-improved grassland (25%), arable fields with maize and barley (12%), blocks of woodland (9%), fields used for biofuel production (*Miscanthus giganteus*) (6%), with small patches of unimproved grassland (1.2%), as well as some farm buildings and secondary roads. During late autumn, winter, spring and summer 2010 the site was still dominated by improved grassland (27%) and semi-improved grassland (25%) but with an increase in arable fields, mostly barley and some maize, to 27%. The proportion of other, smaller categories remained unchanged.

Field size varied widely (range = 0.3-24.7 ha, mean 4.2 ha; SD = 4.3 ha; n = 70) but fields were generally larger when compared with other pasture-dominated sites from North Yorkshire (Chapters 2 & 3) and were often separated by drainage ditches. As part of a long term Countryside Stewardship Scheme several large fields, mostly with arable crops, silage grass or *Miscanthus*, contained grassy field margins typically 2 and 6 m wide or in a few cases 6 m margins planted with game cover crops. All grassy field margins had been seeded with a field margin grass mixture, were not sprayed and were cut once every 2-3 years to prevent weed expansion. In addition, alongside drainage ditches and streams there were similar 2 m wide seeded grassy field margins. Overall, field margins accounted for around 3.5 % of the entire area.

Pasture fields were grazed by sheep and cattle at varying stocking densities with improved grassland fields used primarily for silage production for most of the year and sheep or cattle grazing during the winter. The site lies within an area where shooting activities play an important economic role, primarily for pheasants (*Phasianus colchicus*) and red-legged partridges (*Alectoris rufa*). As a consequence, predator control was enforced throughout the year, mostly focused on the removal of foxes (*Vulpes vulpes*) and stoats (*Mustela erminea*) in order to prevent damage to stocks of game birds.

The density of hares during winters of 2007-2008 and 2008-2009 in a part of the study area which was almost entirely pastural, calculated with night time line transect distance sampling, wast 41.8 hares km $^{-2}$ (Chapter 2), which is very high compared with that in other pastural areas in England of 3.3 hares km $^{-2}$ (Hutchings & Harris, 1996). The study population was subject to hunting in the form of shooting mainly in February-March (Chapter 5) and despite the ban on hunting with dogs in the form of coursing there were constant reports of poaching in this site during 2007-2010.

6.2.2 Capture technique

Hares were captured from June 2009 to April 2010 using simultaneously up to three 5 m and one 75 m long 6z gauge static nylon long nets (Euroguns, Yorkshire, UK). Hares were usually captured between 9 and 11:30 am, during their daytime inactive period, after being flushed by a line of 3-10 beaters and sometimes with the additional help of 1-2 well-trained hunting dogs. Flushed animals were driven into nets placed across openings in hedgerows and access points to and from the fields. Captured hares were quickly immobilised and had their head covered with a cloth bag to minimise handling stress. They were later sexed and ear tagged using lamb plastic tags (Rototag, Dalton, UK). Hares were radio-collared with TW-3 cable-tie small mammal radio collars with a lifespan of 18 months (Biotrack Ltd., Dorset. UK). The combined weight of the ear tag and collar was less than 1% of the animal’s body weight. Brown hares are known to be susceptible to shock and to minimise capture stress the processing of hares was kept to a minimum and animals were released back into the same area within 6-10 minutes from capture.

In total 27 hares including one recapture were caught using this method with a capture rate averaging <1 hare per day. Juveniles of less than 2 kg and leverets were not collared to avoid potential injuries since the collars were not expandable. Considering the winter hare density assessed during night-time in a part of the site and the amount of suitable habitat area (i.e. grassland and arable fields but not roads, buildings, blocks of woods, etc) the collared hares represented between 10-15% of the population in the study area. All work procedures were carried out in accordance with University of Hull Ethical Committee protocols and standards for non licensed animal species.

6.2.3 Data collection

13 hares were tracked independently over one calendar year between July 2009 and August 2010. Hares were located using a Telonics TR4 radio receiver (Telonics Inc, Arizona, USA) with a handheld Lintec flexible 3-element Yagi antenna (Biotrack Ltd., Dorset. UK).

Locational fixes collected during the first five days after capture as well as fixes collected initially at the site of capture were used to determine the status of the animal and the effect of capture on its movements but were removed from any further analysis. To avoid autocorrelation of locational fixes (Harris et al. 1990), each animal was discontinuously tracked with 1-4 fixes collected each week during both their inactive and active periods with at least a 3-hour interval between consecutive fixes. For all collared individuals that died during the study period the apparent cause of death was recorded.

The active period included the crepuscular and nocturnal period from one hour prior to sunset until one hour after sunrise while the inactive period was the diurnal period from one hour past sunrise until one hour prior to sunset. The seasons were defined as spring (01 March-31 May), summer (01 June-31 August), autumn (01 September-30 November) and winter (01 December-27 February). Different numbers of hares were tracked in each season and several individuals were tracked in multiple seasons; 7 females and 5 males in summer, 5 females and 2 males in autumn, 4 females and 4 males in winter and 6 females and 2 males in spring.

Given the small size and narrow aspect of most non-farmed habitat features (i.e. field margins or small blocks of trees) animals were located by 'homing in' (White & Garrott, 1990) rather than triangulation, which produces error polygons that are relatively large compared to the features of interest. This technique involved approaching each animal silently following the strength of the signal until its position could be determined with certainty, usually by direct observation through binoculars and with the additional use of a spotlight at night. This had obvious advantages over triangulation due to its comparatively high precision, however it required far more effort and was more time consuming. Disturbance was kept to a minimum when locating individuals but where a collared animal was disturbed and it relocated to another area as a consequence of being approached with the antenna, no other fixes were recorded during that day to avoid interference effects on the tracking data. However, in most situations, especially during inactive periods, the precise location of the animal could be determined without causing it to flee.

Locational fixes, and the locations of several easily identifiable structures of known position, such as crossroads, buildings or electric posts were plotted on digitised 1:10000 OS maps and were determined to be accurate to within 5m .

For each collected locational fix, information on habitat use and management as well as number and type of stock in the fields were recorded. Additionally, habitat measurements were taken during each week when radio-tracking took place with vegetation type (grasses or arable crops) and height being recorded in each field that was occupied by collared hares as well as all immediately surrounding fields.

6.2.4 Statistical analysis

Range size was determined using a combination of 100% MCP and the more robust fixed kernel method (Worton, 1987) using individual smoothing parameters determined by least squares cross-validation (LSCV). 100% MCPs were produced to allow comparisons with other studies as these are the most commonly reported range estimators in previous studies (Smith et al. 2004). However, MCPs are generally considered to be poor estimators due to the fact that they rely on outer fixes, can increase almost indefinitely in relation to number of fixes and may include areas that are rarely or never frequented by animals (Kenward, 2003). Smoothed kernel estimators are considered more robust due to the fact that they incorporate a measure of density and not just location of the radio fixes and have been shown to produce stable area estimates with as few as 15 or 17 locational fixes (Kenward, 2003; Pellerin et al. 2008). Currently 95% smoothed fix kernel ranges are regarded as a robust way of calculating home ranges and although the 5% decrease from 100% is an arbitrary value (White & Garrott, 1990) it helps by removing outliers from the dataset. Using the terminology of Smith et al. (2004) these will be referred to as ‘ranges’ whereas 50% kernel ranges will be referred as ‘core ranges’. ‘Core ranges’ represent half of the range and for a species like brown hares with defined home ranges they include the areas of maximum density of radio fixes and as such provide an indication of areas which were frequented the most. All the radio-tracking analysis was performed using Ranges 6, version 1.2207 (Anatrack Ltd. Dorset, UK).

‘Ranges’ were analysed using a repeated measures ANOVA procedure in a generalised linear model where ‘activity’ (active or inactive ranges) was taken as a within-subject factor while ‘sex’ and ‘habitat’ (arable or grassland) were used as between-subject factors. Due to the structure of the data with some fields changing use during the period of study and small number of fixes seasonal differences in ranges were not tested. The number of fixes within active and inactive periods varied between animals and as a consequence the number of fixes used in range calculation was accounted for in the analyses by inclusion as a covariate.

Hares’ use of space within fields was investigated by relating locational fixes to proximity to field boundaries. Boundaries of all fields in the study area were digitised and a ‘distance surface’ raster of distances to the nearest field boundary was generated in ArcGIS. Separate mean distances to field boundaries for active and inactive hares were calculated using Zonal statistics in ArcGIS Spatial Analyst and were then compared with the mean calculated distance of all pixels from the field boundaries in the entire study area. Distances from field boundaries were analysed using a repeated measures ANOVA where activity (active or inactive ranges) was taken as a within-subject factor while sex and number of fixes were used as between-subject factors. The values produced for all fields in ArcGIS were compared with the mean value of distances of locational fixes from field boundaries calculated for each individual hare with a Welch’s t test for unequal sample size with unequal variances, where degrees of freedom were calculated using the Welch-Satterthwaite equation.

Following the protocol used by Smith et al. (2004) habitat selection during both active and inactive periods was analysed at three levels using compositional analysis (Aebischer et al. 1993). The three levels of analysis were: a) 95% fixed kernel active and inactive ranges within the total study area, b) 50% fixed kernel active and inactive within the total study area and c) 50% fixed kernel active and inactive within 95% fixed kernel active and inactive ranges. Compositional analysis allows the comparison between the proportions of used habitat and available habitat by means of MANOVA analysis of transformed log-ratios. All analysis was performed using Smith Ecology Microsoft ® Excel tool for Compositional Analysis version 6.3 (Smith Ecology Ltd., Monmouthshire, UK).

The size and proportion of habitat available and used by hares was calculated in ArcGIS where both fields and field margins were digitised and categorised. Areas deemed unsuitable for hares such as those occupied by streams, roads and farm buildings were removed from the analysis by adjusting the total areas of available and utilised habitats for each individual. To avoid excluding habitat variables or individuals for each individual hare the proportions of utilised habitat that equalled zero were replaced by a value of 0.001 (Aebischer et al. 1993). Habitat categories that were not available to more than 50% of all hares were removed from the analysis.

Identification of habitat selection in each analysis (active and inactive ranges at different levels) was based on the significance of Wilk's lambda and of t-values with randomisation achieved using 1000 iterations (Manly, 1997) and habitats were ranked by relative use. As recommended by Aebischer et al. (1993) in order to compensate for variation in number of radio locations between individuals the weighting of the log-ratio differences was introduced by using the square root of the individual number of locational fixes.

6.3 Results

The 13 radio-collared individuals in this study comprised 8 females and 5 males. Of these one female died less than 30 days after being collared (found dead, exact date of death unknown), possibly due to capture related stress, and was removed from any further analysis. For all other individuals home range size and habitat selection were analysed. The number of locational fixes collected for each individual varied, depending on the length of time it had been collared, but ranged between 17 and 52, with a mean of 29. Incremental analysis with 5% steps of annual active and inactive ranges suggested that an asymptote was reached for several (7) of the individuals tracked for a longer period of time, at around 30-35 fixes.

Survival was relatively poor; over the 13 months of the study 6 hares died due to various causes (Table 6.1). The cause of death included human intervention in two cases: one male was culled during the typical hunting season for hares in early February; a second male was accidentally killed in a snare set for fox control during spring. This indicates an average survival rate of 0.46 for the period when the adult hares were radio-tracked in this study which compares well with the estimates from age-structured modelling (previous chapter).

Hare ID	Sex	Capture date	Survival (days)	Cause of death
H730	F	March 2010	220	*
H740	F	July 2009	58	Possibly fox
H750	F	July 2009	421	*
H760	M	February 2010	136	Fox
H770	F	November 2009	342	*
H780	F	December 2009	318	*
H790	F	April 2010	191	*
H800	M	April 2010	185	*
H810	F	November 2009	310	*
H830	M	August 2009	162	Snare
H840	F	July 2009	< 30	Unknown
H850	M	July 2009	47	Stoat
H870	M	July 2009	182	Culled

F = female; M = male; * = still alive at the end of the study

Table 6.1 Capture date, survival period and cause of death in hares in this study (n=13)

Range size (95% fixed smoothed kernel) varied significantly with activity and there was a significant interaction between the effects of activity and habitat type on range size (Table 6.2). Active ranges were larger than inactive ranges (active ranges mean 17.04 ha, SD =10.02, n = 12; inactive ranges mean 9.69 ha, SD = 6.94, n = 12) (Figures 6.2 & 6.3) and active ranges were larger for hares in arable fields than in grassland fields (Table 6.2). Mean ranges were larger for males (16.48 ha, SD = 9.07 ha; n = 5) than for females (11.12 ha, SD = 9.20 ha; n = 7) but the effect was not significant and ‘Sex’ was removed from the model. The number of locational fixes collected for each individual did not affect the range size.

Source of variation	Df	MS	F	P
Intercept	1	114.921	2.521	0.146
Fixes	1	38.6477	0.847	0.381
Habitat	1	60.981	1.338	0.277
Error	9	45.576		
Active	1	331.263	5.280	0.047
active * Fixes	1	141.797	2.260	0.167
active * Habitat	1	522.199	8.323	0.018
Error(active)	9	62.741		

Table 6.2 Repeated measures ANOVA on range size (n = 24) for within-subject effect: activity (active and inactive) and between-subject factors (fixes and habitat).
df = degrees of freedom; MS = mean square; * = interaction term

The distances from each locational fix to the field boundaries were not significantly different between active or inactive periods of time or sexes (Mean active = 27.59; SD = 25.46; n = 135; Mean inactive = 22.66; SD = 20.75; n = 148) (Table 6.3). However, pooled active and inactive distances from field boundaries were significantly smaller than the mean values between field boundaries and all pixels as calculated in ArcGIS (mean distance = 36.57; n = 32911) (*Welch t test*; t = 5.47; df = 23; P<0.01) indicating that hares did not use all areas in the fields equally, but mainly used areas situated closer to the field edges than in the middle of fields.

Source	df	MS	F	P.
Intercept	1	1323.968	59.641	0.000
Fixes	1	3.251	0.146	0.711
Sex	1	0.326	0.015	0.906
Error	9	22.199		
Active	1	57.838	0.371	0.557
active * Fixes	1	174.654	1.121	0.317
active * Sex	1	177.666	1.141	0.313
Error(active)	9	155.768		

df = degrees of freedom; MS = mean square; * = interaction term

Table 6.3 Repeated measures ANOVA on distance from margins (n = 24) for within-subject factors: activity (active and inactive) and between-subject factors (sex and number of fixes).

For space use in woodland, the distances from each locational fix to the woodland boundary (mean distance = 15.82 m; SD = 9.4; n = 46) were significantly smaller than the mean values between woodland boundaries and all pixels in each block of woodland as calculated in ArcGIS (mean distance = 25.06; n = 32911) (*Welch t test*; t = 2.48; df = 7; P<0.05). Inactive hares did not use all areas in the blocks of woodland equally and mainly used for resting areas situated closer to the woodland edges.

During the visual inspection of the total ranges it became apparent that some fields in the study area were not selected at any time by hares throughout the year (Figure 6.1), probably as an artefact of the selection of areas where most hare captures took place. As a consequence, during compositional analysis the fields that had never been visited by hares were removed from available habitat proportions within the study area in order to test for potential differences in habitat selection. However, there were no differences in the results of the habitat selection analysis once these fields were removed.

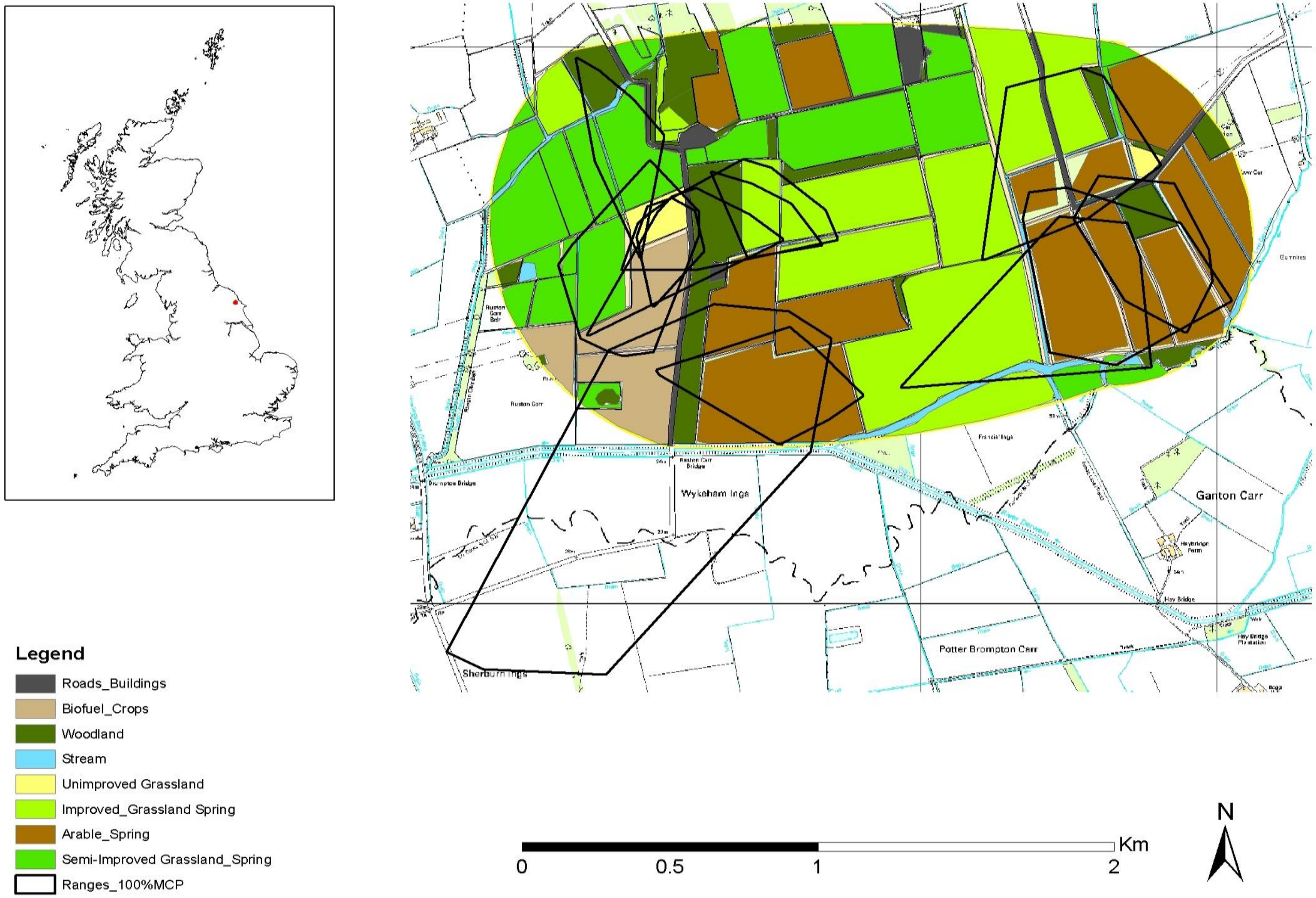

Figure 6.1 Study area, land use during spring 2010 and total 100% MCP ranges for brown hares (n=12)

Figure 6.2 Total 'Active' fixed kernel 95% 'ranges' and 50% 'core ranges'(n=12)

Figure 6.3 Total 'Inactive' fixed kernel 95% 'ranges' and 50% 'core ranges'(n=12)

a) 95% kernel ranges within total study area	Wilks’λ	χ^2	df	P
Active	0.0786	30.5259	6	< 0.0001
Inactive	0.1064	26.8862	6	0.0002
b) 50% kernel ranges within total study area				
Active	0.0069	59.7783	6	< 0.0001
Inactive	0.0227	45.4499	6	< 0.0001
c) 50% kernel ranges within 95% kernel ranges				
Active	0.2375	17.2518	5	0.0040
Inactive	0.7059	4.1800	4	0.3822

Table 6.4 Results of compositional analysis (MANOVA). Active and inactive habitat utilization, was significantly different from random in terms of land use both within the study area and within the 95% fix kernel ranges in all but one case

Habitat selection was non- random during both inactive and active periods (Table 6.4) and habitats were ranked in order of relative use (Table 6.5).

a) Active – Fixed 95% kernels (used) vs. Area (available).	**a) Inactive - Fixed 95% kernels (used) vs. Area (available).**
Margin***	Margin
Woodland	Woodland
Arable	Arable
Unimproved Grassland	*Miscanthus*
Improved Grassland	Unimproved Grassland
Miscanthus	Improved Grassland
Semi-improved Grassland	Semi-improved Grassland
b) Active - Fixed 50% kernels (used) vs. Area (available).	**b) Inactive- Fixed 50% kernels (used) vs. Area (available).**
Margin***	Margin
Arable	Woodland
Unimproved Grassland	Unimproved Grassland
Woodland	*Miscanthus*
Improved Grassland	Arable
Miscanthus	Improved Grassland
Semi-improved Grassland	Semi-improved Grassland
b) Active - Fixed 50% kernels (used) vs. fixed 95% kernels (available).	**b) Inactive - Fixed 50% kernels (used) vs. fixed 95% kernels (available).**
Margin	
Arable	
Unimproved Grassland	NS
Improved Grassland	
Semi-improved Grassland	
Woodland	

Table 6.5 Ranked habitat types relative to utilization versus availability. Utilisation decreases from top to bottom. Significance between consecutive habitat types are indicated with *.

Field margins were ranked higher than any other habitats in relation to their availability at all analysis levels for both active and inactive ranges while semi-improved grassland (mostly sheep pasture) was ranked lower than any other habitat type except woodland for core (50% fix kernels) active ranges within ranges (95% fix kernels). Arable fields were ranked higher than grassland fields at all levels except unimproved grassland for core inactive ranges.

Habitat composition of core (50%) kernel ranges was different from that of ranges (95% kernel), especially in relation to the selection for woodland which was ranked higher than both arable and grassland for range selection but least selected for active core ranges within ranges and lower than both arable and unimproved grassland for active core ranges within the entire study area (Tables 6.5, 6.6 & 6.7). Habitat composition for inactive core ranges within ranges was not significantly different from random but woodland was ranked highest for this analysis, with core inactive ranges comprising on average 30.4% woodland compared to 8.6% for active core ranges (Figure 4). Biofuel crops (*Miscanthus*) ranked lower than most other habitats for active ranges and core ranges Tables 6.6 & 6.7.

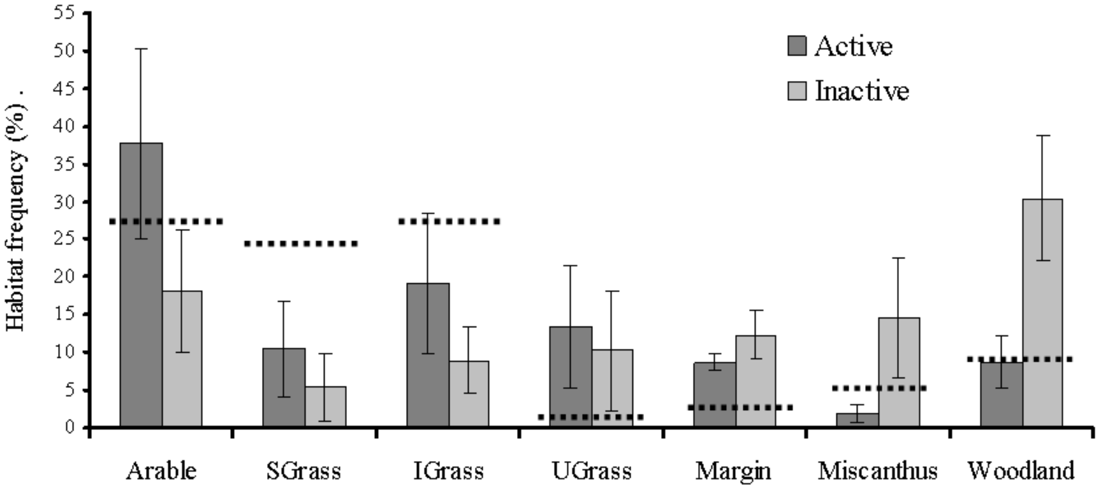

Figure 6.4 Core range percentage mean composition of habitats (error bars indicate SE, n = 24) versus availability for brown hares. Dotted lines represent percentage availability of different habitats in the study area. SGrass = semi-improved grass (pasture); IGrass = improved grass; UGrass = unimproved grassland.

	Arable	SGrass	IGrass	UGrass	Margin	*Miscanthus*	Woodland	Rank
Arable		+	+	+	---	+	+	**5**
SGrass	-		-	--- (-)	---	-	-	**0**
IGrass	-	+		-	---	+	-	**2**
UGrass	-	+++ (+)	+		---	+++	+	**4**
Margin	+++	+++	+++	+++		+++	+++	**6**
Miscanthus	-	+	-	---	---		-	**1**
Woodland	-	+	+	-	---	+		**3**

Table 6.6 Active core areas (50% kernels) versus total available area simple matrix ranking of habitats. Significance levels and ranks are shown according to randomization results, but where significance levels from standard *t-tests* of observed data differ these are shown in parentheses.

	Arable	SGrass	IGrass	UGrass	Margin	*Miscanthus*	Woodland	Rank
Arable		+	+	-	---	-	-	**2**
SGrass	-		-	-	---	-	---	**0**
IGrass	-	+		-	---	-	---	**1**
UGrass	+	+	+		---	+	-	**4**
Margin	+++	+++	+++	+++		+++	+	**6**
Miscanthus	+	+	+	-	---		-	**3**
Woodland	+	+++	+++	+	-	+		**5**

Table 6.7 Inactive core areas (50% kernels) versus total available area simple matrix ranking of habitats. Significance levels and ranks are shown according to randomization results.

Vegetation was higher in field margins than in semi-improved grassland during the entire year (mean margins = 15.11, range 5 -80 cm, n = 47; semi-improved grass mean = 4.57, range 2.5-9 cm; n = 76) (*t test*; t = 4.83; P < 0.0001) and during all seasons except late spring and summer in arable crops. Sheep grazed fields were the least selected of all available habitats and had consistently shorter vegetation than other grassland fields (Chapters 3 & 4).

6.4 Discussion

As previously observed by Smith et al. (2004) the method of capture using static long nets was more successful in capturing females than males, although the exact mechanisms for this are unknown. Females survived for longer periods of time than males (Table 6.1), possibly as a consequence of males moving further than females during the breeding season and becoming more exposed to hunting or predation (Chapter 5).

Radio-tracked hares in this study showed strong site fidelity, with only one adult male progressively shifting its range during January- February by more than 1.5 km to a site situated outside the study area and where it remained until it was culled during the shooting season. In brown hares dispersal is male biased but typically occurs in juveniles less than 5 months old and only 0-5% of hares disperse after this age (Avril et al. 2010). Due to the fact that the movements of this male corresponded with the onset of the breeding season it is impossible to tell whether they represented true dispersal or simply an increase in home range associated with mating behaviour. Individual ranges overlapped and sometimes to a large extent (Figures 6.2 & 6.3).

To our knowledge this is the first study that examines range and habitat selection for adult brown hares using ‘homing in’ as a technique for radio-tracking in order to identify with precision their location and the selection for both farmed and non-farmed habitats. The 100% MCP ranges from this study 24±23 ha (range 6.6 – 94 ha; n = 12) were at the lower limit when compared with values from other UK studies of 25-38 ha in mixed pasture-arable areas (Bradshaw, 1995; Smith et al. 2004; Tapper & Barnes, 1986) but similar to the 26 ha in a pastural area in the Netherlands (Broekhuizen & Maaskamp, 1982). However, the results of this study from North Yorkshire included two females only radio-tracked during spring and summer when ranges are generally smaller than in winter (Smith et al. 2004). Removing these two individuals the mean 100% MCP was 28±24 ha. Equally, field size was on average considerably smaller in this study area than in comparable studies from the continent of 6.7 ha to 10 ha (Ruhe & Hohmann, 2004; Reitz & Leonard, 1994) and hares could therefore access different fields and habitats without the need to cover extensive areas. Home range size is a function of habitat productivity and resource distribution as well as individual energy needs (Mitchell & Powell, 2004) and as such, habitats rich in resources allow individuals to meet their requirements within relatively small areas.

The fact that hares used areas of the field differently in relation to the distance from the field boundary supports the idea of optimal field sizes existing for hares (Cowan, 2004; Vaughan et al. 2003). Previous studies found that small fields can be beneficial for hares (Slamecka 1991; Lewandowski & Nowakowski, 1993; Panek & Kamieniarz, 1999) but hares might benefit from increasing field size (Vaughan et al. 2003, Chapter 3) up to a threshold after which further increases might be detrimental. This is especially the case in intensive farmland or in monocultures where hares have to expand their ranges and move increasing distances in order to access a variety of resources.

However, optimal field size is likely to depend on field use and to vary with both field diversity and between- field diversity.

As expected, range sizes (95% fixed smoothed kernels) were larger during the night which reflects the lifestyle of this species. In common with other lagomorph species brown hares are generally active during the night, and at dawn and dusk, and spend much of the day inactive and motionless, often in a shallow excavation in the soil surface known as a ‘form’ (Holley, 2001).

Throughout the year hares moved varying distances in order to select a variety of habitats for active and inactive periods and inactive ranges were outside active ranges for several hares (Figures 6.2 & 6.3), similar to the findings of Tapper & Barnes (1996). However, other individuals used the same habitats for both feeding and resting as previously found by Smith et al. (2004), Marboutin & Aebischer (1996) and Reitz & Leonard (1994). Areas selected for both active and inactive periods typically encompassed field margins, unimproved grassland, arable crops (barley but not maize) and improved grassland.

Active ranges were larger for hares in arable fields than those in grassland as previously found in studies concentrating on extensive arable areas where ranges could increase up to several hundred hectares (Marboutin & Aebischer, 1996). This might be explained by the fact that arable fields are generally larger in size than pastural ones (in this study area mean arable field area was 6.9 ha compared to 3.5 ha for semi-improved grassland fields). Also, hares typically avoid crossing mature crops (Ruhe et al. 2004) and always seem to avoid harrowed fields for resting (Pepin & Angibault, 2008). This could increase the area covered by the animal in order to access other fields or habitats. Equally, hares might face food shortages during the summer in arable areas when most cereal crops reach maturity and become unpalatable (Reichlin et al. 2004) or once the crops are harvested, forcing them to use other fields for foraging.

Selection of daytime resting areas indicated a strong preference for non-farmed areas with tall vegetation such as woodland and stands of trees in field boundaries, field margins, unimproved grassland and *Miscanthus*. Several hares used the same resting areas for most of the study period, although not continuously, probably as an anti-predator strategy. Hares selected woodland during inactive periods at a higher rate than its availability but the majority of locational fixes in this habitat came from edges (< 20m from boundary) indicating that hares preferentially selected these over areas situated further inside blocks of woods. Most resting places allowed a good open view across the surrounding fields, suggesting that hares favoured these probably to avoid possible ambushes by approaching predators, such as foxes (Angelici et al. 1999; Tapper& Barnes, 1986). However, hares in arable fields often selected cereal crops over woodland as resting areas during late spring and summer, once the crop height was at its highest.

Evidence from other studies in relation to the selection for and associations between hares and woodland are contradictory, with broad-scale studies suggesting that woodland is positively associated with hares in pastures (Hutchings & Harris, 1996; Vaughan et al. 2003) and hares selected woodland and hedgerows for resting sites at the local scale in some studies (Tapper & Barnes, 1986) but not in others (Marboutin & Aebischer, 1996). The fact that few hares were found in areas with more than 20% woodland (Panek & Kamieniarz, 1994) supports the findings from our study that hares select edges of small blocks of woodland for resting periods but avoid woodland altogether during active periods.

The strong selection for field margins as both active and inactive habitats for hares in this study could be linked with the fact that such areas typically have taller vegetation for the entire year when compared to semi-improved grassland and for most of the year, except late spring and early summer, in arable fields. Additionally, there are suggestions that hares preferentially select wild plants and weeds and field margins, which might therefore provide a source of diverse and rich in fat food (Tapper & Barnes, 1986; Frylestam, 1986; Reichlin et al. 2004).

Sheep pasture was the least selected habitat type in this study for both active and inactive ranges and even when hares were present in such fields they selected field margins rather than the field itself. Smith et al. (2004) found similar results in south west England, where hares avoided sheep pasture in all seasons except winter and suggested that the underlying reason might be lack of cover. Intensive sheep pastures typically have shorter and more homogenous vegetation height than most other grassland fields but the fact that hares avoided this habitat type for foraging, during active periods in the present study, suggests that this avoidance might be related to a lack of food rather than cover or a combination of the two. There are no published studies investigating hare preference for swards of a certain height but these might explain the fact that hares select for the taller grass swards created by cattle grazing (Smith et a. 2004; Chapter 3) but generally avoid sheep pastures as feeding areas.

6.5 Conclusions

Habitat heterogeneity appears important for brown hares in an intensive farmland environment at both between field and within field levels. Using radio-tracking with a ‘homing in’ technique for brown hares we recorded a strong selection for non-farmed habitat structures such as field margins, stands of trees and blocks of woodland and an avoidance of the very short grass swards within sheep grazed fields. It is likely that with adequate design field margins could be used to provide both cover and food for hare populations while benefiting general farmland biodiversity at the wider level.

Hares used areas of the fields situated closer to the field edges more than those closer to the middle of the fields suggesting that hares might suffer as a consequence of increasing field size over a certain limit. Equally, large blocks of woodland might support few hares except for the areas closer to the edges, but the establishment of small blocks of woodland or even stands of trees in field margins could provide hares with suitable cover opportunities and would very likely be beneficial for hares in both pastural and arable areas.

Future studies should be focused on optimal strategies for creating and maintaining field margins in a variety of pastural and arable habitats in order to increase numbers of hares and on identifying the causes of hare’s selection for field margins by separating the effects of dietary preferences and vegetation height.

Given the suggestions that agri-environment schemes might increase numbers of pests or predators, such as rabbits and foxes (Reid et al. 2007), these aspects should be further investigated and taken into account in future schemes. An increase in fox abundance could potentially offset benefits for hare populations (Reynolds et al. 2010) although recent studies suggest that suitable agricultural management that increases diversity results in fox predation focusing on voles rather than hares (Panek, 2009).

The ultimate causes for the hare avoidance of sheep grazed areas should be investigated, ideally through experimental manipulations of sward height by means of exclosures and by manipulating the livestock density.

Chapter 7 General discussion, conclusions & future work

With around 75% of the UK and 40% of EU land area being farmed in one way or another and more environments in unfavourable or poor condition in such areas than in habitats not associated with agriculture (IEEP, 2009 report) the state of biodiversity in Europe is inextricably linked with agricultural management. Intensification and changes in agricultural practices in the past decades have led to well documented declines in a range of species (Robinson & Sutherland, 2002; Benton et al. 2003) and impoverished associated biotic communities (McLaughin & Mineau, 1995). However, the conversion of complex natural or semi-natural environments to simplified and intensively managed systems can impact differently on different species with decreases in rare and specialist species but an increasing effect on invasive and generalist species (Tscharntke et al. 2005).

Both European rabbits and brown hares are introduced game species in the UK, typically associated with the farmed environment and which, at high densities, can cause damage to the agricultural and forestry economy. However, while rabbit populations have increased substantially since their catastrophic decline in the 1950s and have reached pest status once again in some areas, hare populations are showing no clear sign of a recovery since their mid-20th century declines and there is evidence that populations in pastural areas are in poor body condition (Jennings et al. 2006) and might be still declining (McLaren et al. 1997; Battersby, 2005). Rabbit populations are largely regarded as pests, causing important economic damage, although they are important for biodiversity conservation in some UK areas and are probably an important prey species for several threatened bird and mammalian predators (Lees & Bell, 2008). Recent estimates suggest that rabbit numbers, while still being a long way from pre-myxomatosis levels, might be 40 times as high as hare numbers in the UK (Battersby, 2005). Brown hares however, are an iconic farmland species, an important quarry animal and have as such received a lot of attention in recent years due to their declines resulting in their classification as a “priority species of conservation concern” (UK BAP, 1995).

As a consequence, part of the focus of this work was to investigate the status of both hare and rabbit populations in grassland areas in NE England and to identify the major factors affecting their densities and distribution in such areas. This information should create a better understanding of the local and landscape-scale processes linking habitat and agricultural management with the ecology of these two species and could allow for better targeted wildlife management measures.

7.1 Brown hare and European rabbit populations in grasslands in NE England

The results of this study show that both hares and rabbits were widely distributed and could reach high densities in grassland-dominated areas in this region but with large variation between different sites. Brown hare population densities in the studied region of 20.6 hares km^{-2} were surprisingly high and several times higher than the average for pastures at the national scale. However, hare densities varied tenfold even within nearby superficially similar sites which, combined with the large area of most of these sites suggests that regional climatic factors such as rainfall or average temperature might play only a secondary role in regulating populations of this species in the studied area.

In this study I developed and tested a new method aimed at accurately surveying hare populations at large spatial scales using night-time distance sampling along walked transects. The fact that surveys were performed on foot means that fields could be surveyed without the potentially substantial biases associated with road-based surveys. The comparisons of the methodology used in this study with daytime distance sampling clearly demonstrate the benefits of using our approach and suggest that large scale monitoring programmes, such as regional or national schemes could greatly benefit from employing this method in the future. In addition, our results suggest that the same method could concurrently produce large numbers of observations of other wildlife species, especially crepuscular and nocturnal mammals which typically suffer from low detectability, such as rabbits, foxes, badgers, roe-deer and hedgehogs. The downsides are that this method is probably more logistically complex and costly, requiring some specialised equipment (e.g. spotlight), specific agreements with farmers, gamekeepers and landowners and needs adequate measures to minimize risks associated with fieldwork during the night. However, it is very likely that the significant benefits, such as the substantially higher number of observations and higher precision, the relatively low manpower and shorter time frame required would largely outweigh any additional costs. One example of how such a monitoring program can be run and financed is the German Wildlife Information System where hunting associations survey hare populations using spotlights, although the method employed in this case in not distance sampling but strip censuses (Strauß et al. 2008).

The main implication of this study for hare surveys in pastures is the suggestion that national figures may suffer from serious underestimation in areas where hare densities are low and that hares might be far more widely distributed than previously thought.

Rabbit distribution in the studied region was very high with rabbits occupying a remarkable 65% of all fields surveyed but with similarly large differences in densities between sites as for hares. The very high values of observed densities of up to 6978 rabbits km^{-2}, with an average of 470 rabbits km^{-2}, are consistent with substantial rabbit induced economic losses in such areas (Dendy et al. 2003). These would include not only direct and indirect losses in plant yield and biomass consumed by rabbits but also damage of pasture fields through intense digging of burrows, undermined walls and fences as well as pasture contamination with faeces and potential transmission of parasites and diseases, such as paratuberculosis, to domestic stock (Daniels et al. 2003). For silage grass fields rabbit damage has been shown to produce losses of around 200 kg per rabbit over a three year period (Dendy et al. 2003). Economic losses for other, more expensive crops are more difficult to quantify but can be substantial even at relatively low rabbit densities (Bell et al. 1999; Barrio et al. 2010).

7.2 Brown hare body condition, population dynamics and harvesting rates

In this study I report the first results from the UK on brown hare annual productivity using placental scars counting on chemically treated uteri and demonstrate that females from pastures in the eastern part of the country were capable of high productivity. However, both leveret survival and female fertility were low and there was some evidence that female participation in breeding was restricted by pathological transformations of the uteri. Both adult and juvenile survival were higher than values reported for other pastural areas in the UK (University of Bristol, 2003, Jennings et al. 2006) but were comparable with populations from continental Europe.

Hare carcass data from grassland-dominated areas in North Yorkshire did not confirm the differences in skeletal size, total body weight and condition between hares from arable and pastural areas and suggests that hares from pastures in other regions of the UK might not necessarily be in poor condition relative to their arable-inhabiting conspecifics. Such differences might be more a reflection of regional conditions than a broad habitat type influence and it is likely that more carcass data from pastures would be required before a clear conclusion is drawn. However, it is particularly difficult to collect a sufficient and unbiased sample of hare carcasses from areas of low density where they might be in poor condition, especially given the large variability that we present here.

In the UK hares are probably hunted in most farmland areas where their densities are moderate or high, either as a game species or to prevent damage to crops or forestry and culling can remove as much as 40% or even 69% of the hare population (Hutchings & Harris, 1996; Stoate & Tapper, 1993). This study presents evidence that the studied hare population could increase in the absence of hunting but due to poor juvenile survival the population could decline even at relatively modest hunting rates of 15-20%. Although such estimates should be interpreted only in relation to the studied population and as such can not be extrapolated more widely, they represent an interesting model and case study for the management of this species in the UK.

To prevent further declines in hare numbers and to achieve sustainable hunting levels harvesting quotas should be designed in parallel with adequate monitoring of the population. Ideally such monitoring would incorporate a measure of annual productivity and age structure as is the case in some continental European countries (Marboutin et al. 2003), where hunting associations are responsible for collecting data from culled carcasses including body parts, such as eye lenses and uteri. Such programmes can offer wide ranging benefits including early detection of potential threats to the population, such as decreased female fertility or emerging diseases and can ensure an adequate and informed design of harvesting quotas and management.

However, at present the implementation of such a scheme would be very challenging in the UK given that hares in this country are typically hunted in February and March, when most females are already pregnant or nursing young and placental scar counting cannot be performed.

7.3 Brown hare habitat selection in farmland

In agreement with previous studies the results of this study suggest that hares require a certain degree of habitat heterogeneity in order to satisfy their needs for both quality forage and adequate shelter. However, such habitat heterogeneity appears important at both between field and within field levels and in addition we demonstrate that different areas of the fields are not used with the same frequency. The apparent strong selection for non-farmed habitat structures such as field margins, stands of trees or blocks of woods suggests that these might be successfully used to increase the suitability of grass-dominated or mixed areas for hare populations. Their establishment and maintenance could be encouraged as part of existing or future agri-environment schemes and are likely to benefit a variety of other taxa in agricultural areas (Marshall et al. 2006). However, radio-tracking and habitat selection *per se* do not give information on whether a particular selected habitat is ‘crucial’ or not for a species (White & Garrott, 1990) and these should ideally be tested using controlled manipulations in order to assess their importance and impact. This could be performed by tracking animals in areas where access to field margins and other non-farmed habitat structures could be temporarily restricted for hares and equally where field margins of different size and age since establishment could be either introduced or simulated.

It remains unclear whether the hare selection for field margins during both active and inactive periods is related to a selection of particular food plants or the increased height of the sward compared to the rest of the field but this might prove instrumental in providing sufficiently targeted and informed measures through agri-environment schemes to benefit hare populations across the country.

7.4 Implications of agricultural management for hare and rabbit populations in pastures

The current work demonstrates that the management of agricultural land and grazing regimes in particular are important components influencing the distribution and densities of both lagomorph species in North Yorkshire pastures. Grazing by sheep and cattle creates different structures of the swards in terms of both mean height and height heterogeneity. The data indicates that rabbit populations were positively associated with intensive sheep grazing and small size fields while hare populations typically showed a strong negative association with such areas but despite their importance the mechanisms and underlying reasons remain unclear.

Densities of two lagomorph species, a hare (*Lepus californicus)* and a rabbit (*Sylvilagus nuttalli)* were correlated with the abundance of plant biomass and were negatively associated with grazing by both sheep and cattle in a semi-natural habitat (MacCraken & Hansen, 1982). Moreover, mountain hares (*Lepus timidus*) can be outcompeted by a larger herbivore, roe deer (*Capreolus capreolus*), when resources are scarce (Hulbert & Nadersen, 2001). Equally, when resources are limited, small hindgut fermentors such as hares and rabbits, which are more tolerant of poor-quality diets, can compete directly with the more efficient, larger ruminants (Illius and Gordon 1992). Hares and rabbits have different digestive strategies to cope with decreases in food quality (Kuijper et al. 2004) and previous studies have identified evidence for niche or spatial separation of the two species (Barnes & Tapper, 1986; Chapuis, 1989), and between rabbits and mountain hares (Hulbert et al. 1996).

Rabbits are social animals, living in communal burrows (Cowan, 1986) whereas hares are mainly solitary animals that only form aggregations during the night-time when at high density or when food resources are clumped, in order to benefit from increased group vigilance (Monaghan & Metcalfe, 1985). The fact that rabbits are central place foragers capable of living in high density groups suggests that they might have become more adapted to intra-specific competition. In fact, rabbits can modify the environment to suit their needs and have been shown to be able to facilitate conditions for themselves by creating and maintaining a preferred vegetation state through repeated grazing (Bakker et al. 2005) and rabbit grazing is often density-independent (Lees &

Bell, 2008). No direct evidence of competition was found between rabbits and hares at a national scale using questionnaires in the UK (Vaughan et al. 2003) or in a semi-natural area of juniper scrub in Hungary following a population crash in rabbits (Katona et al. 2004) and proposed reasons relate to niche separation in feeding strategies of the two species. This is supported by the present study, with higher rabbit densities occurring in small fields containing improved sheep pastures (Chapter 4) and hare presence positively influenced by cattle grazing and rough pastures containing taller swards than sheep- grazed fields.

In addition, the control of predators such as foxes was significantly and positively associated with rabbit populations but not with hare populations.

This suggests that the future management of both rabbits and hares could be significantly improved, either for their conservation or for limiting their populations through manipulations of grazing regimes and potentially, through predator control. However, the full role and implications of predator control need to be studied in relation to other factors, such as alternative prey in agricultural areas of different management (Panek, 2009).

7.5 Recommendations and future work

1. The development of hare surveys using line distance sampling at night in a variety of new sites and regions in the UK would create a much stronger basis for adequately monitoring of their status and would provide the detail required for local conservation or management actions. Ideally all monitoring should be preceded by a night time pilot study. This would be particularly important in order to detect potential density trends of the hare population in the survey area. Such trends need to be considered and taken into account during the placement of transects in order to minimize variance and obtain maximum precision.

Equally, the results of this study suggest that sites with high hare density (more than 30 hares km^{-2}) could continue to be surveyed during the day time if sufficient observations can be obtained without the need for supplementary replicates (> 40-60 observations with 1-2 replicates per season).

2. Unravelling the mechanisms why hares largely avoid sheep-grazed fields while rabbits benefit from them could provide important tools for both conservation and pest damage prevention. This should be tested using field manipulations and experiments and future research should incorporate such studies. One possible solution for achieving this would be through selecting specific areas where the grazing pressure by both cattle and sheep can be controlled and modified while continuously monitoring the impact on rabbit and hare activity, during both diurnal and nocturnal periods.

3. Future studies on hare conservation should aim to create better targeted agri-environment schemes for this species. Such schemes could be designed and implemented in both arable and pastural landscapes once the optimal parameters of field margins are identified in relation to their establishment, species composition and management (i.e. cutting regimes).

4. A potential review of the current hunting regime for brown hares should evaluate the benefits and costs of a change in timing of the culling period to bring it in line with continental Europe. In addition to the advantages of using placental scars for a better defining of the harvest rates and management of hare populations it could also benefit animal welfare as culling animals in October-November would minimize the killing of pregnant or lactating animals and therefore sacrificing their dependent young (Cowan, 2004).

5. More work is required to understand the spread and full impact of diseases such as pseudotuberculosis or cystic endometrial hyperplasia in hare populations in

the region and generally in the UK. This could create a better understanding of potential threats facing the hare populations. Equally, it could contribute to the early detection and prevention of the spread of diseases to domestic livestock and humans in areas where diseases such as pseudotuberculosis or brucellosis have a high prevalence in the hare population. This could be achieved through a more detailed laboratory analysis of carcasses and a simple monitoring scheme could be put in place with the help of hunting associations during the culling season for hares.

References

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, 74; pp 1313-1325.

Alves P.C., Ferrand N., Suchentrunk F. and Harris D. J. (2003) Ancient introgression of Lepus timidus mtDNA into L. granatensis and L. europaeus in the Iberian Peninsula – *Molecular Phylogenetics and Evolution* Vol. 20, Issue 1 , pp 70-80

Andrzejewski R. & Jeziershi W. (1966) Studies on the European hare. XI. Estimation of population density and attempt to plan the yearly take of hares *Acta Theriologica* 11 (21-29): 433-448

Angelici, F.M., Riga, F., Boitani, L. & Luiselli, L. (1999) Use of dens by radio-tracked brown hares *Lepus europeaus*. *Behavioral Processes* 47, pp 205–209

Anonymous (1995) *Biodiversity; The UK Action Plan*. HMSO, London. UK.

Anonymous (1979) *Convention on the conservation of European wildlife and natural habitats*. Bern Convention. Council of Europe, Strasbourg. available at http://conventions.coe.int/Treaty/FR/Treaties/Html/1043.htm#Mammals/Mammifères

Anonymous (2009) June Survey of Agriculture and Horticulture (Land use and livestock on agricultural holdings at 1 June 2009) UK provisional results DEFRA Report

Atkinson PW, Fuller RJ, Vickery JA, Conway GJ, Tallowin JRB, Smith REN, Haysom KA, Ings TC, Asteraki EJ, Brown VK (2005) Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *Journal of Applied Ecology* 42: 932-942.

Arsenault, R. & Owen-Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97, pp 313-318.

Avril, A., Léonard, Y., Letty, J., Péroux R., Guitton, J.B. & Pontier, D. (2010) Natal dispersal of European hare in a high-density population. *Mammalian Biology* doi:10.1016/j.mambio.2010.07.001

Baillie, S. R., Sutherland, W. J., Freeman, S. N., Gregory, R. D. & Paradis, E. (2000), Consequences of large-scale processes for the conservation of bird populations. *Journal of Applied Ecology*, 37, pp 88–102.

Bakker, E.S., Olff, H., Boekhoff, M., Gleichman, J.M., & Berendse, F. (2004) Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138, pp 91-101.

Bakker, E.S, Olff, H. & Gleichman JM (2009) Contrasting effects of large hervivore grazing on smaller herbivores. *Basic and Applied Ecology* 10: 141-150.

Bakker, E.S, Reiffers, R.C, Olff, H & Gleichman, J.M. (2005) Experimental manipulation of predation risk and food quality: effect on grazing behaviour in a central-place foraging herbivore. *Oecologia* 146: 157-167.

Baldi, A. & Farago, S. (2006) Long-term changes of farmland game populations in a post-socialist country (Hungary), *Agriculture, Ecosystems and Environment* 118, pp 307-311

Banks, P.B, Dickman, C.R & Newsome, A.E (1998) Ecological costs of vertebrate predator control: foxes and rabbits. *Journal of Wildlife Management* 62:,pp 766-772.

Barnes, R. F. W., Tapper S.C. & Williams J. (1983) Use of pastures by brown hare - *Journal of Applied Ecology* 20 , pp 179-185.

Barnes, R.F.W. & Tapper, S.C. (1985) A method for counting hares by spotlight. *Journal of Zoology*, London, 206, pp 273-276

Barnes R.F.W. & Tapper, S.C. (1986) Consequences of the myxomatosis epidemic in Britain's Rabbit (*Oryctolagus cuniculus* L.) population on the numbers of Brown Hares (*Lepus europaeus* Pallas) *Mammal Review*, 16, pp 111-116

Barrio, I.C., Acevedo P. & Tortosa, F.S. (2010). Assessment of methods for estimating wild rabbit population abundance in agricultural landscapes. *European Journal of Wildlife Research* 53, pp 335-340

Barrio, I.C., Bueno, C.G. & Tortosa, F.S. (2009), Improving predictions of the location and use of warrens in sensitive rabbit populations. Animal Conservation, 12, pp 426–433

Battersby J. (eds) & Tracking Mammals Partnership. (2005). UK Mammals: Species Status and Population Trends. First Report by the Tracking Mammals Partnership. JNCC/Tracking Mammals Partnership, Peterborough.

Bell, A.C., Byrne, P.M. & Watson, S.. (1998), The effect of rabbit (Oryctolagus cuniculus) grazing damage on the growth and yield of winter cereals. *Annals of Applied Biology*, 133, pp 431–442

Bell, A.C., Byrne, P.M. & Watson, S. (1999). The effect of rabbit (*Oryctolagus cuniculus*) grazing damage on the growth, botanical composition and yield of a rye grass re-seed. *Annals of Applied Biology* 135, pp 417–424

Ben Slimen, H.; Suchentrunk, F.; Shahin, A. A. B.; Ben Ammar Elgaaied, A. (2006) Phylogenetic analysis of mtCR-1 sequences of Tunisian and Egyptian hares (Lepus sp. or spp., Lagomorpha) with different coat colours. *Mammalian Biology* 73 ,4, pp224-235

Bensinger, S.V. Kugelschafter, K., Eskens, U. & Sobiraj, G. & A. (2000). Untersuchungen zur jährlichen Reproduktionsleistung von weiblichen Feldhasen (*Lepus europaeus* Pallas, 1778) in Deutchland. *Zeitschrift für Säugetierkunde.* 46, pp 73-83.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18, pp 182–188.

Branco, M., Monnerot, M., Ferrand, N. & Templeton, A.R. (2002) Postglacial dispersal of the European rabbit (*Oryctolagus cuniculus*) on the Iberian peninsula reconstructed from nested glade and mismatch analyses of mitochondrial DNA genetic variation. *Evolution*, 56, pp 792–803.

Bray Y., Marboutin E., Peroux R. & Ferron J. (2003), Reliability of Stained Placental-Scar Counts in European Hares *Wildlife Society Bulletin*, Vol. 31, No. 1 pp.237-246

Bray Y., Marboutin E., Devillion S., Mauvy B. & Peroux R. (2007) Natal dispersal of European hare in France *Journal of Zoology*, Vol. 273, Issue 4, pp. 326-334

Brockless M. (1995) Game and shooting at Loddington. *Game Conservancy Review* 26, 67-68.

Broekhuizen S. (1976) The situation of the hare populations in the Netherlands. In: *Ecology and management of European hare populations* (eds. Pielowski Z. & Pucek Z.), pp. 105-114. Polish Hunting Association, Warsaw.

Broekhuizen S. (1979) Survival in adult European hares. *Acta Theriologica* 24, pp 465-473.

Broekhuizen S. & Maaskamp F. (1980) Behaviour of does and leverets of the European hare (Lepus europaeus) whilst nursing. *Journal of Zoology* 191, pp 487-50 1.

Broekhuizen, S. & Maaskamp, F. (1981) Annual production of young in European hares (Lepus europaeus) in the Netherlands. *Journal of Zoology* 193, pp 499-516.

Broekhuizen S., Bouman E. & Went W. (1986) Variation in timing of nursing in the brown hare (Lepus europaeus) and the European rabbit (Oryctolagus cuniculus). *Mammal Review* 16 , pp 139-144.

Browne, S.J. &. Aebischer, N.J (2003) *Arable Stewardship: impact of the pilot scheme on the brown hare and grey partridge after five years.* Final report to Defra on Contract ref. RMP1870vs3.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., (2001). *Introduction to Distance Sampling*. Oxford University Press, Oxford.

Burnham K.P. and David R. Anderson (1984) The need for Distance data in transect counts *The Journal of Wildlife Management*, Vol. 48, No. 4, pp. 1248-1254

Caillol, M., Mondain-Monval,M., Meunier,M.& Rossano,B. (1992) Influence of season of birth on onset of gonadotropic and ovarian functions in young doe hares (Lepus europaeus). *Journal of Reproduction and Fert*ility 96, pp 747–753.

Chapman J. A. & Flux J. E. C. (1990) *Introduction and overview of the Lagomorpha. Pages 1–6 in Rabbits, hares and pikas: Status conservation action plan. In:* Chapman J. A., Flux J. E. C., (Eds) Gland, Switzerland*:* International Union for Conservation of Nature and Natural Resources*;*.

Chapman J.A. & Flux J. E. C. (2008) Introduction to Lagomorpha in *Lagomorph Biology- Evolution, Ecology and Conservation* (editors Alves P.C., Ferrand N., Hacklander K.) Springer, Berlin Heidelberg

Chapuis JL (1990) Comparison of the diets of two sympatric lagomorphs, *Lepus europaeus* (Pallas) and *Oryctolagus cuniculus* (L.) in an agroecosystem of the Iˆle-de-France. *Zeitschrift für Säugetierkunde* 55, pp 176–185

Cooper, T., Hart, K. and Baldock, D. (2009) *The Provision of Public Goods Through Agriculture in the European Union*, Report for DG Agriculture and Rural Development, Contract No 30-CE-0233091/00-28, Institute for European Environmental Policy: London.

Corbet G. B. (1986) Relationships and origins of the European lagomorphs *Mammal Review* 16 (3-4), pp 105–110

Cooke, B. (2008) Managing the European rabbit: converging interests between Australian research for rabbit control and European research for their conservation. In: *Lagomorph Biology: Evolution, Ecology and Conservation* (Ed. by P.C.Alves, N.Ferrand & K.Hackländer), pp. 317–326. Springer-Verlag, Berlin, Heidelberg

Cowan D.P. (2004) An overview of the current status and protection of the Brown Hare (Lepus Europaeus) in the UK; A report prepared for European Wildlife Division

Cowan D.P. (2008) Order Lagomorpha Rabbits and hares in *Mammals of the British Isles: Handbook, 4th Edition*, (Eds. Harris S. & Yalden D.) The Mammal Society, Southampton

Cowan, D. P. & Bell, D. J. (1986), Leporid social behaviour and social organization. Mammal Review, 16, pp 169–179.

Cowan, D. P. & Garson P. J. (1984). Variations in the social structure of rabbit populations: causes and demographic consequences. Pp. 537-555 in *Behavioural ecology: ecological consequences of adaptive behaviour* (Ed. By R. M. Sibly & R. H. Smith) Blackwell Scientific Publications, Oxford, United Kingdom

Critchley, C.N.R., Allen, D.S., Fowbert, J.A., Mole, A.C. and Gundrey, A.L. (2004). Habitat establishment on arable land: assessment of an agri-environment scheme in England, UK. *Biological Conservation* 119, pp. 429–442.

Daniels, M.J., Lees, J.D., Hutchings, M.R. & Greig, A. 2003. The ranging behaviour and habitat use of rabbits on farmland and their potential role in the epidemiology of paratuberculosis. *Veterinary Journal* 165, pp 248-257

Delibes-Mateos, M., Redpath, S.M., Angulo, E., Ferreras, P. & Villafuerte, R. (2007) Rabbits as a keystone species in southern Europe. *Biological Conservation* 137, pp 149–156

Dendy J, McKillop G, Fox S, Western G, Langton S (2003) The development of a model to assess the effects of rabbit grazing on grass. *Annals of Applied Biology* 142: pp 317-322.

Dendy J, McKillop G, Fox S, Western G, Langton S (2004), A field trial to assess the effects of rabbit grazing on spring barley. *Annals of Applied Biology*, 145, pp 77–80

Donald P.F, Green R.E, Heath M.F (2001) Agricultural intensification and the collapse of Europe’s farmland bird populations. *Proceedings Royal Society London* B 268, pp 25–29

Dunning, J. B., Danielson, B. J. & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos* 65, pp 169-175.

Duff, J.P., Chasey, D., Munro, R. & Wooldridge M. (1994) European brown hare syndrome in England. *Veterinary Record* 134 , pp 669-673.

Duff, J.P., Whitwell, K. & Chasey, D. (1997) The emergence and epidemiology of European brown hare syndrome in the UK. In: *Proceedings of the First International Symposium On Caliciviruses* (editors D. Chasey, R.M. Gaskell, I.N. Clarke), pp 176-181, ESVV.

Edwards P.J., Fletcher M.R. & Berny P. (2000) Review of the factors affecting the decline of the European brown hare, Lepus europaeus (Pallas, 1778) the use of wildlife incident data to evaluate the significance of paraquat. *Agriculture Ecosystems & Environment* 79, pp 95-103.

Eldridge, D.J. & Myers, C.A. (2001) The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland, *Journal of Arid Environments* 47, pp 325–337.

Environment-Agency 2009. Monthy rainfall figures 1961-2009. Yorkshire and North East database right 2009.

Erlinge S., Frylestam B., Goransson G., Hogsted G., Liberg O., Loman J., Nilsson I.N., Scantz von T. & Sylven M. (1984) Predation on brown hare and ring-necked pheasant populations in southern Sweden. *Holarctic Ecology* 7 , pp 300-304.

Evans, D.M., Redpath, S.M., Elston, D.A., Evams, S.A., Mitchell, R.J. & Dennis, P. (2006), To graze or not to graze? Sheep, voles, forestry and nature conservation in the British uplands. *Journal of Applied Ecology*, 43, pp 499–505.

Ferrand, N. (2008*)* Inferring the evolutionary history of the European rabbit (*Oryctolagus cuniculus*) from molecular markers. *In: Lagomorph Biology: Evolution, Ecology and Conservation (eds* AlvesPC, FerrandN, HacklanderK*).* Springer, Amsterdam, The Netherlands.

Ferreira, C. & Alves, P.C. (2009) Influence of habitat management on the abundance and diet of wild rabbit (*Oryctolagus cuniculus algirus*) populations in Mediterranean ecosystems, *European Journal of Wildlife Research* 55, pp. 487–496.

Fewster, R.M., Buckland, S.T., Burnham, K.P., Borchers, D.L., Jupp, P.E., Laake, J.L. & Thomas, L. (2009) Estimating the encounter rate variance in distance sampling. *Biometrics* 65, pp 225-236.

Field, S.A., O’Connor, P.J., Tyre, A.J. & Possingham, H.P. (2007) Making monitoring meaningful. *Austral Ecology* 32, pp 485-491.

Fletcher, D. J., Moller, H. & Clapperton, B. K. (1999). Spotlight counts for assessing abundance of rabbits (*Oryctolagus cuniculus* L.). *Wildlife Research* 26, pp 609–620.

Flux, J.E.C. (1987) Myths and mad March Hares. *Nature* 325 pp 737

Flux, J.E.C. (1994). World distribution. In: Thompson, H. V. and King, C. M. (eds) *The European Rabbit*, pp. 8–21. Oxford Science Publications, Oxford.

Flux J.E.C. (2008) A review of competition between Rabbits (*Oryctolagus cuniculus*) and Hares (*Lepus europaeus*) in *Lagomorph Biology- Evolution, Ecology and Conservation* (editors Alves P.C., Ferrand N., Hacklander K.) Springer, Berlin Heidelberg

Frylestam, B. & von Schantz, T. (1977), Age determination of European hares based on periosteal growth lines. *Mammal Review*, 7, pp 151–154.

Frölich, K., Meyer H. H. D., Pielowski Z., Ronsholt L., von SeckLanzendorf S. & Stolte M. (1996) European brown hare syndrome in free-ranging hares in Poland. *Journal of Wildlife Diseases* 32, pp 280-285

Frölich, K., Wisser, J., Schmuser, H., Fehlberg, U., Neubauer, H., Grunow, R., Nikolaou, K., Priemer, J., Thiede, S., Streich, W.J. & Speck, S. (2003) Epizootiologic and ecologic investigations of European brown hares (Lepus europaeus) in selected populations from Schleswig-Holstein, Germany. *Journal of Wildlife Diseases*, 39 (4), pp 751-761

Frylestam, B. (1979) Structure, size and dynamics of three European hare populations in southern Sweden. *Acta Theriologica* 24, pp 449-464.

Frylestam, B. (1980a). Growth and body weight of European hares in Southern Sweden. *Holarctic Ecology* 3, pp 81-86.

Frylestam, B. (1980b) Reproduction in the European hare in southern Sweden. *Holarctic Ecology* 3, pp 74-80

Frylestam, B. (1986) Agricultural land use effects on the winter diet of brown hares *(Lepus europaeus* Pallas) in southern Sweden. *Mammal Review* 16, pp 157-16 1.

Frylestam, B. & Schantz, T.V. (1977). Age-determination of European hares based on periosteal growth lines. *Mammal Review* **7**(3-4), pp 151-154.

Fuller R.J. & Gough S.J. (1999) Changes in sheep numbers in Britain: implications for bird Populations *Biological Conservation* 91, pp 73-89

Garcia-Berthou, E. (2001) On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance *Journal of Animal Ecology* 70, pp 708-711

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84, pp 2809-2815.

Genghini M. & Capizzi D. (2005) Habitat improvement and effects on brown hare (*Lepus europaeus)* and roe deer (*Capreolus capreolus)*: a case study in northern Italy, *Wildlife Biology* 11, pp 319-329

Gregory R. D, Noble G. & Custance J. (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom *Ibis* 146, pp 1-13

Goszczynski, J. & Wasilewski, M. (1992) Predation of foxes on a hare population in central Poland. *Acta Theriologica* 37 , pp 329-338.

Hackländer K., Arnold W. & Ruf, T. (2002a) The Effect of Dietary Fat Content on Lactation Energetics in the European Hare (*Lepus europaeus*)*Physiological and Biochemical Zoology* 75(1), pp 19–28.

Hackländer, K., Arnold, W. & Ruf, T. (2002b) Postnatal development and thermoregulation in the precocial European hare (*Lepus europaeus*). *Journal of Comparative Physiology B* 172, pp 183–190.

Hackländer K., Miedler S., Beiglbock C., Zenker W. The assessment of female reproduction and gestational age in European hare (*Lepus europaeus*) using ultrasonography, *Mammalian Biology* 68, pp 187-191

Hamilton, G.S., Mather, P.B. & Wilson, J.C. (2006) Habitat heterogeneity influences connectivity in a spatially structured pest population. *Journal of Applied Ecology* 43, pp 219–226.

Hansen, K. (1992) Reproduction in European hare in a Danish farmland. *Acta Theriologica* 37, pp 27-40.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) *A Review of British Mammals: Population Estimates and Conservation Status of British Mammals other than Cetaceans*. Joint Nature Conservation Committee, Peterborough.

Hastie, T.J. & Tibshirani, R.J. (1990). Generalized Additive Models. Chapman & Hall, London.

Henke, S. E. & Desmarais, S. (1990). Effect of diet on condition indices in black-tailed jackrabbits. *Journal of Wildlife Diseases* 26, pp 128–33.

Heydon, M.J., Reynolds, J.C. & Short, M.J. (2000) Variation in abundance of foxes (*Vulpes vulpes*) between three regions of rural Britain, in relation to landscape and other variables *Journal of Zoology* 251, pp 253-264.

Hewson R. (1977) Food selection by brown hares (*Lepus capensis*) on cereal and turnip crops in north-east Scotland. *Journal of Applied Ecology* 14, pp 779-785.

Hewson R. & Taylor M. (1975) Embryo counts and length of the breeding season in European hares in Scotland from 1960-1972. *Acta Theriologica* 20, pp 247-254.

Holley, A.J.F. (2001) The daily activity period of the brown hare (*Lepus europaeus*). *Mammal Biology,* 66, pp 1-8.

Hulbert, I.A.R., Iason, G.R. & Racey, P.A. (1996) Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies. Journal of Applied Ecology 33, pp 315-324.

Hulbert, I. A. R. & Andersen, R. (2001) Food competition between a large ruminant and a small hindgut fermentor: the case of the roe deer and mountain hare. *Oecologia*, 128, pp 499-508.

Hutchings, M.R.,& Harris, S. (1995) Does hunting pressure affect the flushing behaviour of brown hares (*Lepus europaeus*)? *Journal of Zoology* 237, pp 663-667.

Hutchings, M.R. & Harris, S. (1996) *The Current Status of the Brown Hare (*Lepus europaeus*) in Britain*. Joint Nature Conservation Committee, Peterborough.

Iason, G.R. (1988) Age Determination of Mountain Hares (Lepus timidus): A Rapid Method and When to Use It. *Journal of Applied Ecology* 25, pp 389-395

Iason, G. & Hester, A. (1999) What are the consequences of reducing sheep density on rabbit-grazed grasslands? In Herbivore Feeding Strategies, Population Processes and Impact on Biodiversity, pp. 79-80, Chize, France.

Iason, G.R., Manso, T., Sim, D.A. & Hartley, F.G. (2002) The functional response does not predict the local distribution of European Rabbits (Oryctolagus cuniculus) on grass swards: experimental evidence. *Functional Ecology* 16, pp 394-402.

Iason, G. & Van Wieren, S.E. (1999). Digestive and ingestive adaptations of mammalian herbivores to low-quality forage. In: H. Olff, V.K. Brown & R.H. Drent (eds) Herbivores: Between Plants and Predators. BES Symp. Vol. 38, pp. 337-370.

Illius, A. & Gordon, I.J. (1992). Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* 89, pp 428–434.

Jackson A.L., Broderick, A.C., Fuller, W.J., Glen, F., Ruxton, G.D. & Godley, B.J. (2008) Sampling design and its effect on population monitoring: How much monitoring do turtles really need? *Biological Conservation* 141, pp 2932-2941.

Jennings N., Smith RK., Hacklander K., Harris S. & White P. (2006) Variation in demography, condition and dietary quality of hares *Lepus europaeus* from high-density and low-density populations *Wildlife Biology* 12-179-189

Kaluzinski J. & Pielowski Z. (1976) The effect of technical agricultural operations on the hare population. In: *Ecology and management of European hare populations* (editors Z. Pielowski & Z. Pucek), pp. 205-211. Polish Hunting Association, Warsaw.

Katona K., Altbacker V. (2002) Diet estimation by faeces analysis: sampling optimisation for the European hare, *Folia Zoologica*-51(1), pp 11-15.

Katona, K., Biro, Z., Hahn, I., Kertesz, M. & Altbacker, V. (2004) Competition between European hare and European rabbit in a lowland area, Hungary: a long-term ecology study in the period of rabbit extinction. *Folia Zoologica* 53, pp 255–268

Katona, K., Biro, Z., Szemethy L., Demes, T. & Nyeste, M. (2010) Spatial, temporal and individual variability in the autumn diet of European hare (Lepus europaeus) in Hungary *Acta Zoologica Academiae Scientiarum Hungaricae* 56 (1), pp. 89–101.

Kasapidis P., Suchentrunk F., Magoulasa A., Kotoulasa G. (2005) The shaping of mitochondrial DNA phylogeographic patterns of the brown hare (*Lepus europaeus*) under the combined influence of Late Pleistocene climatic fluctuations and anthropogenic translocations *Molecular Phylogenetics and Evolution* 34, pp 55–66

Kolb, H.H. (1991) Use of burrows and movements of wild rabbits (Oryctolagus cuniculus) in an area of hill grazing and forestry. *Journal of Applied Ecology* 28, pp 892-905.

Kolb, H.H. (1994). The use of cover and burrows by a population of rabbit (Mammalia: *Oryctolagus cuniculus*) in eastern Scotland. *Journal of Zoology* 233(1), pp. 9–17.

Kuijper, D.P.J., Beek, P., VanWieren, S.E. & Bakker, J.P. (2008). Time-scale effects in the interaction between a large and a small herbivore. *Basic and Applied Ecology* 9, pp 126–134.

Kuijper, D.P.J., Van Wieren, S.E. and Bakker, J.P.(2004) Digestive strategies in two sympatrically occurring lagomorphs. *Journal of Zoology* 264, pp 171-178.

Langbein J., Hutchings M.R., Harris S., Stoate C., Tapper S.C. & Wray S. (1999) Techniques for assessing the abundance of brown hares Lepus europaeus. *Mammal Review* 29, pp 93-116.

Lees AC, Bell DJ (2008) A conservation paradox for the 21st century: the European wild rabbit Oryctolagus cuniculus, an invasive alien and an endangered native species. *Mammal Review* 38, pp 304-320.

Legg C. & Nagy, L. (2006) Why most conservation monitoring is, but need not be, a waste of time. *Journal of Environmental Management* 78, pp 194-199.

Lepczyk, C.A. (2005) Integrating published data and citizen science to describe bird diversity across a landscape. *Journal of Applied Ecology*, 42, pp 672-677.

Lewandowski, K. & Nowakowski, J.J. (1993) Spatial distribution of the brown hare *Lepus europaeus* populations in habitats of various types of agricultural. *Acta Theriologica*, 38, pp 435-442.

Lincoln, G.A. (1974) Reproduction and “March Madness” in the brown hare. *Journal of Zoology*, 174; pp 435-442.

Lindenmayer, D. & Likens, G. (2009) Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology and Evolution* 24, pp 482-486.

Lindenmayer, D. & Likens, G. (2010) The science and application of ecological monitoring. *Biological Conservation* 143**,** pp 1317-1328.

Künkele, J. (1992). Infanticide in wild rabbits (Oryctolagus cuniculus). *Journal of Zoology* 73, pp 317–320.

Lloyd, H.G. (1963). Intra-uterine mortality in the wild rabbit, Oryctolagus cuniculus (L.) in populations of low density. *Journal of Animal Ecology* 32, pp 549–563.

Lloyd HG (1970) Post-myxomatosis rabbit populations in England and Wales. *EPPO,* Public series A 58, pp 197-215.

Lyons, J.E., Runge, M.C., Laskowski, H.P. & Kendall, W.L. (2008) Monitoring in the Context of Structured Decision-Making and Adaptive Management. *Journal of Wildlife Management* 72, pp 1683-1692.

MacCracken J.G. & Hansen, R.M. (1982) Herbaceous Vegetation of Habitat Used by Blacktail Jackrabbits and Nuttall Cottontails in Southeastern Idaho *American Midland Naturalist*, Vol. 107 (1), pp 180-184

Manchester, S.J. & Bullock, J.M. (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology,* 37, pp 845–864

Manly, B.F.J. (1997) *Randomisation, bootstrap and Monte Carlo methods in biology*. 2nd Ed, Chapman and Hall. London. UK.

Marboutin E. & Peroux R. (1995) Survival pattern of European hare in a decreasing population. *Journal of Applied Ecology* 32, pp 809-816.

Marboutin E., Bray Y., Peroux R., Mauvy B. & Lartiges, A (2003) Population dynamics in European hare: breeding parameters and sustainable harvest rates *Journal of Applied Ecology* 40, pp 580-591.

Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment* 89, pp 5-21.

Marshall, E.J.P., West, T.M. & Kleijn, D. (2006) Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. *Agriculture, Ecosystems and Environment* 113, pp 36–44.

Martinet L., Legouis J.J. & Moret B. (1970) Quelques observations sur la reproduction du lievre european (*Lepus europaeus* Pallas) en captivite. *Annals Biol. Anim. Bioch. Biophys.* 10 , pp 195-202.

Masetti M. & De Marinis A. M. (2008) Prehistoric and Historic Artificial Dispersal of Lagomorphs in *Lagomorph Biology- Evolution, Ecology and Conservation* Editors Alves P.C., Ferrand N., Hacklander K., Springer, Berlin Heidelberg

Mattfeldt, S.D., Bailey, L.L. & Campbell Grant, E.H. (2009) Monitoring multiple species: Estimating state variables and exploring the efficacy of a monitoring program. *Biological Conservation* 142, pp 720-737.

McLaren, G.W., Hutchings, M.R. & Harris, S. (1997) Why are brown hares (*Lepus europaeus*) rare in pastural landscapes in Great Britain? *Gibier Faune Sauvage*, 14, pp 335–348.

McLauglin, A. & Mineau, P. (1995) The impact of agricultural practices on biodiversity. *Agriculture Ecosystems & Environment* 55, pp. 201–212.

Meriggi, A. & Alieri, R. (1989) Factors affecting brown hare density in northern Italy. *Ethology, Ecology & Evolution* 1, pp 255-264.

Meriggi, A. & Verri, A. (1990) Population dynamics and habitat selection of the European hare on poplar monocultures in northern Italy. *Acta Theriologica* 35, pp 69-76

MetOffice (2007) National Meteorological Library and Archive Climate of the British Isles - Fact sheet No. 4.

Milner-Gulland, E.J. & Rowcliffe, J.M. (2007) *Conservation and Sustainable Use: a Handbook of Techniques* Oxford University Press, Oxford.

Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V. & Zima, J. (1999) *Atlas of European Mammals*. Academic Press, London.

Mitchell, M.S., Powell, R.A. (2004) A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling* 177, pp 209–232

Monaghan, P & Metcalffe, N.B. (1985) Group foraging in brown hares: effects of resource distribution and social status *Animal Behaviour* 33, pp 993-999.

Murray D, Ellsworth E., Zack A. (2005) Assessment of potential bias with snowshoe hare fecal pellet-plot counts. *Journal of Wildlife Management*: Vol. 69, No. 1 pp. 385–395

Newey, S., Bell, M., Enthoven, S. & Thirgood, S. 2003: Can distance sampling and dung plots be used to assess the density of mountain hares *Lepus timidus*? - *Wildlife Biology* 9, pp 185-192.

Newman, C., Buesching, C.D. & Macdonald, D.W. (2003) Validating mammal monitoring methods and assessing the performance of volunteers in wildlife conservation--"Sed quis custodiet ipsos custodies ?". *Biological Conservation*, 113, pp 189-197.

Nichols, J.D. & Williams, B.K. (2006) Monitoring for conservation. *Trends in Ecology & Evolution*, 21, pp 668-673.

Olff, H., Ritchie, M.E. & Prins, H.H.T. (2002). Global environmental controls of diversity in large herbivores. *Nature*, 415, pp 901–904.

Owen-Smith, N. (2007) *Introduction to Modeling in Wildlife and Resource Conservation.* Blackwell Publishing

Panek, M. (2009) Factors affecting predation of red foxes Vulpes vulpes on brown hares Lepus europaeus during the breeding season in Poland *Wildlife Biology* 15 (3), pp 345 - 349

Panek, M. & Kamieniarz, R. (1999) Relationships between density of brown hare *Lepus europaeus* and landscape structure in Poland in the years 1981–1995. *Acta Theriologica*, 44, pp 67–75.

Parkes, J.P. (1989) Annual patterns in reproduction and perirenal fat of hares (Lepus europaeus) in sub-alpine Canterbury, New Zealand. *Journal of Zoology* 217, pp 9-21

Pellerin, M., Saïd, S. & Gaillard, M. (2008) Roe deer *Capreolus capreolus* home-range sizes estimated from VHF and GPS data. *Wildlife Biology* 14, pp 101–110.

Pepin, D. (1987) Dynamics of a heavily exploited population of brown hare in a large-scale farming area. *Journal of Applied Ecology* 24 , pp 725-734.

Pepin, D. (1989) Variation in survival of brown hare (*Lepus europaeus*) leverets from different farmland areas in the Paris basin. *Journal of Applied Ecology* 26, pp 13-23.

Pépin, D. & Angibault, J.M. (2007) Selection of resting sites by the European hare as related to habitat characteristics during agricultural changes. *European Journal of Wildlife Research* 53, pp 183–189

Pérez-Suarez, G., Palacios, F. & Boursot, P. (1994) Speciation and paraphyly in western Mediterranean hares (*Lepus castroviejoi*, *L. europaeus*, *L. granatensis* and *L. capensis*) revealed by mitochondrial DNA phylogeney. *Biochemical Genetics*, 32, pp 423– 437.

Peroux R., Mauvy B., Lartiges A., Bray Y., Marboutin E., (1997) Point transect sampling: a new approach to estimate densities or abundance of European hares. *Game Wildlife Science* 14, pp 525-529

Petrovan, S.O, Barrio, I.C., Ward, A.I. & Wheeler, P.M. (2011) Farming for pests? Local and landscape-scale effects of grassland management on rabbit densities. *European Journal of Wildlife Research* 57, pp 27-34

Pianka, E.R. (1994) *Evolutionary Ecology*, fifth edition. HarperCollins College Publishers.

Pielke, R.A. (2007) *The honest broker: making sense of science in policy and politics*, Cambridge University Press, Cambridge.

Pielowski Z. (1971) The individual growth curve of the hare. *Acta Theriologica*, 16, pp 79-88.

Pinheiro JC, Bates DM 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag, New York.

Poole, D.W., Cowan, D.P. & Smith, G.C. (2003) Developing a census method based on sight counts to estimate rabbit (Oryctolagus cuniculus) numbers. *Wildlife Research* 30, pp 487-493.

Pueyo, Y. & Alados, C.L. (2007) Abiotic factors determining vegetation patterns in a semi-arid Mediterranean landscape: Different responses on gypsum and non-gypsum substrates. *Journal of Arid Environments* 69, pp 490-505.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Raczynski J. (1964) Studies on the European hare V. Reproduction. *Acta Theriologica* 9 , pp 305-352.

Radi, Z.A. (2005) Endometritis and cystic endometrial hyperplasia in a goat *Journal of Veterinary Diagnostic Investigation* 17, pp 393–395

Reichlin T., Klansek E., Hacklander K. (2006) Diet selection by hares (*Lepus europaeus*) in arable land and its implications for habitat management. *European J Wildlife Research* 52, pp 109-118

Reid N. (2006) Conservation ecology of the Irish hare (*Lepus timidus hibernicus*) Unpublished PhD thesis, Queen’s University Befast

Reid N, McDonald RA, Montgomery WI (2007) Mammals and agri-environment schemes: hare haven or pest paradise? *Journal of Applied Ecology* 44, pp 1200-1208.

Reid, N.**,** McDonald, R.A. & Montgomery, W.I. (2010) Homogeneous habitat can fulfil the discrete and varied resource requirements of hares but may set an ecological trap.*Biological Conservation*, 143, pp 1701-1706

Reitz, F. & Léonard, Y. (1994) Characteristics of European hare *Lepus europaeus* use of space in a French agricultural region of intensive farming. *Acta Theriologica*, 39, pp 143–157.

Reynolds, J.C. & Tapper, S.C. (1995) Predation by foxes *Vulpes vulpes* on brown hares *Lepus europaeus* in central southern England, and its potential impact on annual population growth. *Wildlife Biology*, 1, pp 145–158.

Reynolds, J.C, Stoate, C., Brockless, M.H., Aebischer, N.J. & Tapper, S.C. (2010) The consequences of predator control for brown hares (*Lepus europaeus*) on UK farmland. *European Journal of Wildlife Research* 56, pp 541–549

Reitz, F. & Léonard, Y. (1994) Characteristics of European hare *Lepus europaeus* use of space in a French agricultural region of intensive farming. *Acta Theriologica*, 39, pp 143–157.

Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese Branta b. bernicla: interactions between food quality and quantity. *Biological Conservation 81*, pp 153-160.

Risely, K., Noble, D. G. & Baillie, S. R. (2009) *The Breeding Bird Survey 2008*. BTO Research Report 537. British Trust for Ornithology, Thetford.

Robinson, R. A. & Sutherland, W. J. (2002), Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology, 39, pp 157–176.

Rodel, H.G., Volkl, W. & Kilias, H. (2004) Winter browsing of brown hares: evidence for diet breadth expansion, *Mammalian Biology* 69 6, pp 410-419

Ruette S., Stahl P., Albaret M. (2003) Applying Distance-Sampling Methods to Spotlight Counts of Red Foxes *The Journal of Applied Ecology*, Vol. 40, No. 1 pp. 32-43

Ruhe F. & Hohmann U. (2004) Seasonal locomotion and home-range characteristics of European hares (*Lepus europaeus*) in an arable region in central Germany *European Journal of Wildlife Research* (2004) 50, pp 101–111

Sauer, J.R., Hines, J.E. & Fallon, J. (2008) The North American Breeding Bird Survey, Results and Analysis 1966 - 2007. *Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, MD* Available at: http://www.mbr-pwrc.usgs.gov/bbs/.

Schmidt N., Asferg T., Forschhammer M. (2004) Long-term patterns in European brown hare population dynamics in Denmark: effects of agriculture, predation and climate, *BMC Ecology* 4:15, 2004

Seavy, N. & Reynolds, M.H. (2007) Is statistical power to detect trends a good assessment of population monitoring? *Biological Conservation* 140, pp 187-191.

Silvertown, J. (2009) A new dawn for citizen science. *Trends in Ecology & Evolution*, 24, pp 467-471.

Slamečka J (1991) The influence of ecological arrangements on brown hare population. In: Csányi S, Ernhaft J (eds) *Proceedings of the XXth Congress of International Union of Game Biologists*, Hungary, pp 340–346

Smith G.C., Prickett, A.J. & Cowan, D.P. (2007) Costs and benefits of rabbit control options at the local level. *International Journal of Pest Management* 53, pp 317-321.

Smith, R.K., Jennings, N.V., Robinson, A. & Harris, S. (2004) Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? *Journal of Applied Ecology*, 41, pp 1092–1102.

Smith R.K., Jennings, NV. & Harris, S. (2005a) A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate *Mammal Review* 35, No. 1, pp 1–24

Smith R.K., Jennings, NV., Tataruch F., Hacklander K. & Harris, S. (2005b) Vegetation quality and habitat selection by European hares *Lepus europaeus* in a pastural landscape *Acta Theriologica* 50 (3), pp 391–404,.

Stewart K.E.J, Bourn N.A.D. & Thomas J.A. (2001) An evaluation of three quick methods commonly used to assess sward height in ecology *Journal of Applied Ecology* 38, pp 1148–1154

Stoate C, Boatman N.D, Borralho R.J, Rio Carvalho C, de Snoo G.R, Eden P. (2001) Ecological impacts of arable intensification in Europe *Journal of Environmental Management* 63, pp 337–365

Stoate, C. & Tapper, S.C. (1993) The impact of three hunting methods on brown hare populations in Britain. *Game and Wildlife Science*, 10, pp 229–240.

Stoner C.J., Bininda-Emonds, O.R.P. & Caro, T. (2003) The adaptive significance of coloration in lagomorphs *Biological Journal of the Linnean Society* 79 (2), pp 309-328

Stott, P. (2003). Use of space by sympatric European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) in Australia. *Mammalian Biology* 68, pp 317-327.

Stott, P. (2008a). Comparisons of digestive function between the European hare (*Lepus europaeus*) and the European rabbit (*Oryctolagus cuniculus*): mastication, gut passage, and digestibility. *Mammalian Biology* 73 (4), pp 276-286.

Stott P, Harris S, Wight N (2008b) Fertility and infertility in the European hare *Lepus europaeus* in Australia. In: Alves PC, Ferrand N, Hackländer K (eds) Lagomorph biology: evolution, ecology and conservation. Springer, Berlin, pp 225–240

Stott, P. & Harris, S. (2006). Demographics of the European hare (*Lepus europaeus*) in the Mediterranean climate zone of Australia. *Mammalian Biology* 71, pp 214-226.

Stott, P. & Wight, N. (2004). Female reproductive tract abnormalities in European hares (*Lepus europaeus*) in Australia. *Journal of Wildlife Diseases* 40**,** pp 695-702.

Strauß E., Grauer A., Bartel M., Klein R., Wenzelides L., Greiser G., Muchin A., Nösel H. & Winter A (2008) The German wildlife information system: population densities and development of European Hare (*Lepus europaeus* PALLAS) during 2002-2005 in Germany. *European Journal of Wildlife Research* 54, pp 142–147

Suchentrunk F., Ben Slimen H. & Sert H. (2008) Phylogenetic Aspects of Nuclear and Mithochondrial Gene-Pool Charecteristics of South and North African Cape Hares in *Lagomorph Biology- Evolution, Ecology and Conservation* Editors Alves P.C., Ferrand N., Hackländer K., Springer, Berlin Heidelberg

Suchentrunk, F., Willing R., & Hartl, G.B. (1991). On eye lens weights and other age criteria of the brown hare (Lepus-europaeus Pallas, 1778). *Zeitschrift für Säugetierkunde –International Journal of Mammalian Biology*, 56, pp 365-374.

Sydes C, Miller GR 1988. Range management and nature conservation in the British uplands. In Usher MB, Thompson DBA (eds.), *Ecological Change in the Uplands*., pp. 323-337. Blackwell Scientific Publications, Oxford, UK.

Tablado, Z., Revilla, E. and Palomares, F. (2009), Breeding like rabbits: global patterns of variability and determinants of European wild rabbit reproduction. *Ecography*, 32, pp 310–320

Tapper S.C. & Barnes R.F.W. (1986) Influence of farming practice on the ecology of the brown hare (Lepus europaeus). *Journal of Applied Ecology* 23, pp 39-52.

Tapper, S. & Parsons, N. (1984) The changing status of the brown hare (*Lepus capensis* L.) in Britain. *Mammal Review*, 14, pp 57–70.

Tapper, S. & Stoate, C. (1992) Surveys galore - but how many hares? *Game Conservancy Review* 23, pp 63-64.

Thulin, C.G. (2003) The distribution of Mountain Hares (*Lepus timidus*, L. 1758) in Europe: A challenge from Brown Hares (*L. europaeus*, Pall. 1778)? *Mammal Review*, 33, pp 29-42.

Thulin C.G, Stone J, Tegelström H, Walker CW (2006): Species assignment and hybrid identification among Scandinavian hares Lepus europaeus and L. timidus. *Wildlife Biology*, 12, pp 29-38.

Thomas, L., Laake, J.L., Rexstad, E., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Burt, M.L., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. & Marques, T.A. (2009) *Distance 6.0. Release "2".* Research Unit for Wildlife Population Assessment, University of St. Andrews,UK.

Thomas, L., Buckland, S.T., Rexstad, E., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. & Burnham, K.P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size *Journal of Applied Ecology* 47, pp 5-14

Trout RC, Tittensor AM (1989) Can predators regulate wild Rabbit Oryctolagus cuniculus population density in England and Wales? *Mammal Review* 19, pp 153-173.

Trout RC, Tapper SC, Harradine J (1986) Recent trends in the Rabbit population in Britain. *Mammal Review* 16, pp 117-123.

Trout RC, Langton S, Smith GC, Haines-Young RH (2000) Factors affecting the abundance of rabbits (Oryctolagus cuniculus) in England and Wales. *Journal of Zoology* 252, pp 227-238.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters.*, 8, pp 857–874

University of Bristol (2003) Integrating farm management practices with brown hare conservation in pastural habitats. *Final report on Defra Project* BD 1436

Valencak, T.G, Tataruch, F. and Ruf, T. (2009) Peak energy turnover in lactating European hares: the role of fat reserves *The Journal of Experimental Biology* 212, pp 231-237

van Swaay, C.A.M., Nowicki, P., Settele, J. & van Strien, A.J. (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* 17, pp 3455-3469.

Vaughan, N., Lucas, E.-A., Harris, S. & White, P.C.L. (2003) Habitat associations of European hares *Lepus europaeus*. In England and Wales: implications for farmland management. *Journal of Applied Ecology*, 40, pp 163–175.

Yalden D. (1999) *The history of British mammals*. T & A. D. Poyser, London.

Ward A.I, White P.C.L. & Critchley C.H. (2004) Roe deer Capreolus capreolus behaviour affects density estimates from distance sampling surveys. *Mammal Review* 34**:**4, pp 315–319

Wasilewski M. (1991) Population dynamics of the European hare (*Lepus europaeus* Pallus 1978) in central Poland. *Acta Theriologica* 36 , pp 267-274.

Webbon CC, Baker PJ, N.C. C, Harris S (2006) Macroscopic prey remains in the winter diet of foxes Vulpes vulpes in rural Britain. *Mammal Review* 36, pp 85-97.

Wheeler P. (2002) *Distribution of mammals across the upland landscape* Unpublished PhD thesis, University of Manchester

Wheeler, P. (2008), Effects of sheep grazing on abundance and predators of field vole (*Microtus agrestis*) in upland Britain, *Agriculture, Ecosystems & Environment* 123 pp. 49–55.

White, P., Baker, P., Newton Cross, G., Smart, J., Moberly, R., McLaren, G., Ansell, R. & Harris, S. (2000) Report on Contract 5 Management of the population of foxes, deer, hares and mink and the impact of hunting with dogs and Report on Contract 6 Methods of controlling foxes, deer, hare and mink to hunting with dogs. *Report of the Committee of Inquiry into Hunting with Dogs* (by T. Burns, V. Edwards, J. Marsh, L. Soulsby & M. Winter). The Stationary Office, Norwich.

White, G.C. & Garrott, R.A. (1990) *Analysis of Wildlife Radio-Tracking Data.* Academic Press, San Diego

White P., Newton-Cross, G., Moberly, R.L., Smart, J., Baker, P., Harris S., (2003) The current and future management of wild mammals hunted with dogs in England and Wales. *Journal of Environmental Management* 67, pp 187–197

Whittingham, M.J. & Devereux, C.L. (2008) Changing grass height alters foraging site selection by wintering farmland birds. *Basic and Applied Ecology* 9, pp 779-788.

Wibbelt, G. & Frölich, K (2005) Infectious diseases in the European brown hare (*Lepus europaeus*) *Wildlife Biology in Practice*, 1 (1), pp 86-93.

Wincentz Jensen, T.L. (2009) Identifying causes for population decline of brown hare (Lepus europaeus) in agricultural landscapes in Denmark. Unpublished PhD thesis, NERI, Aarhus University, Denmark.

Williams, D.B., Wells, T.C.E. & Wells, D.A.. (1974) Grazing management of Woodwalton Fen: seasonal changes in the diet of cattle and rabbits. Journal of Applied Ecology 11, pp 499-516

Wood, S.N. (2006). Generalized Additive Models: an introduction with R. Chapman and Hall / CRC.

Worton, B.J. (1987) A review of models of home range for animal movement. *Ecological Modelling*, 38, pp 277 298

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). Mixed effects models and extensions in Ecology with R. Springer, New York.

Appendix

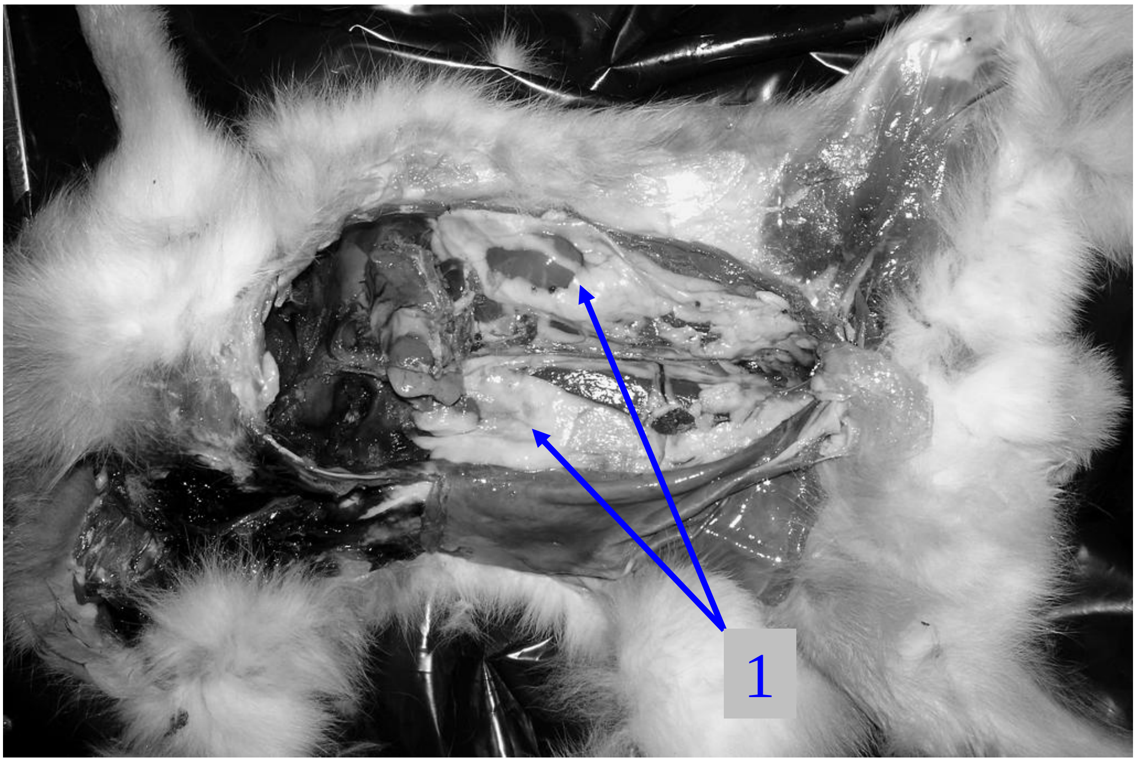

Image A 'Large' perirenal and abdominal wall fat deposits (score 6) in an adult male hare (H040DAN241107) culled at the end of November from North Yorkshire pastures. Photo S. Petrovan

1- Left and right kidney. Note right kidney almost entirely encapsulated by fat.

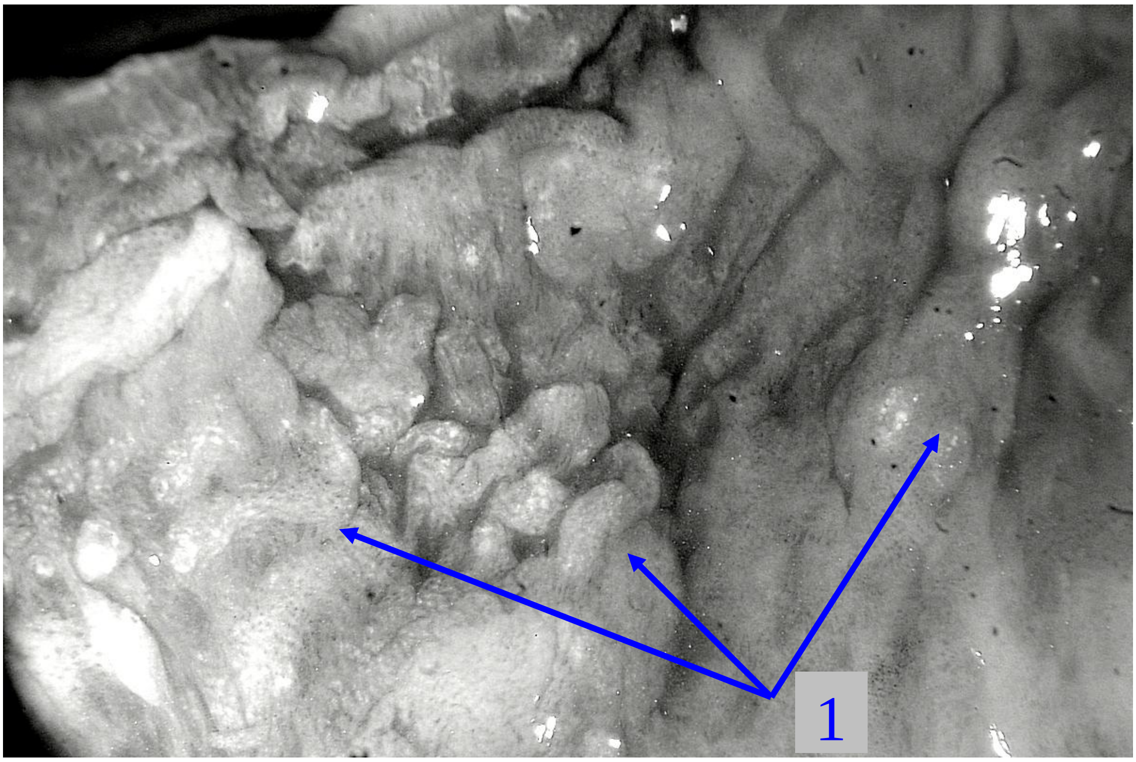

Image B Macroscopic appearance of the endometrium in an infertile female hare (H026WYK101207) with an aspect typical for CEH. Photo S. Petrovan

1- thickened uterus wall with numerous small, translucent cysts containing necrotic debris in the superficial layer of the endometrium. Note the lack of any placental scars

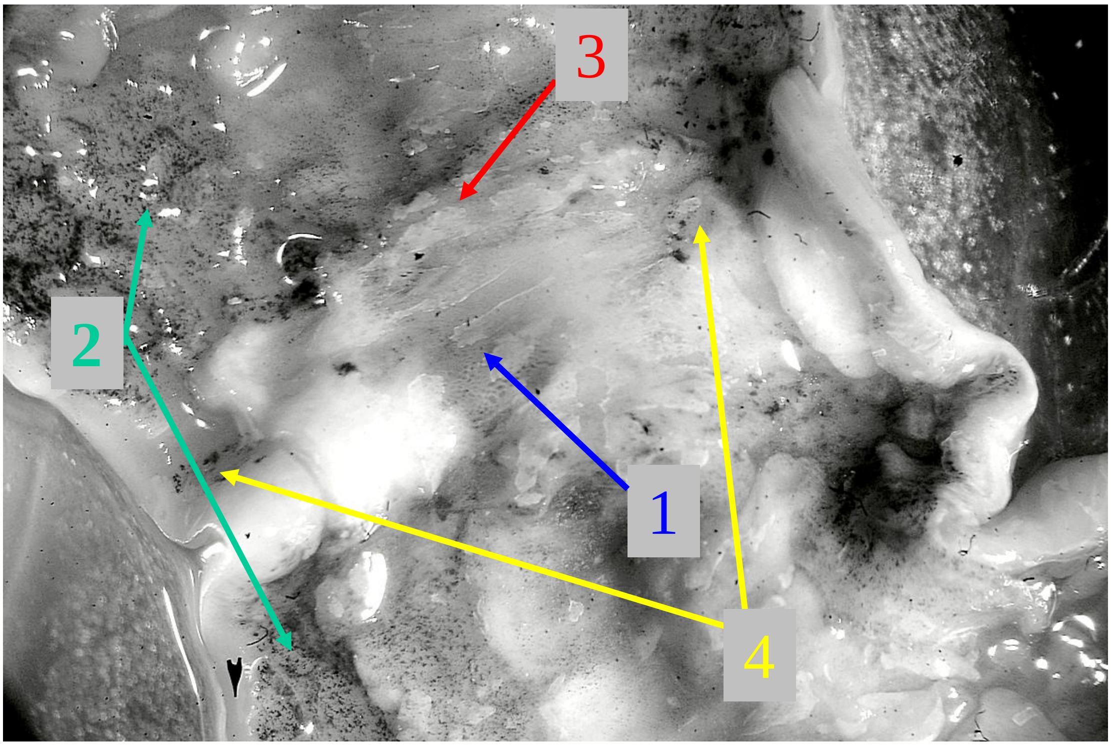

Image C Recent placental scar of a female hare. Photo S. Petrovan
1 Crater at the implantation site
2 Dark bands of macrophages
3 Adjacent to the crater are irregularly distributed knobs
4 Antimesometrial depression caused by pooled blood and macrophages

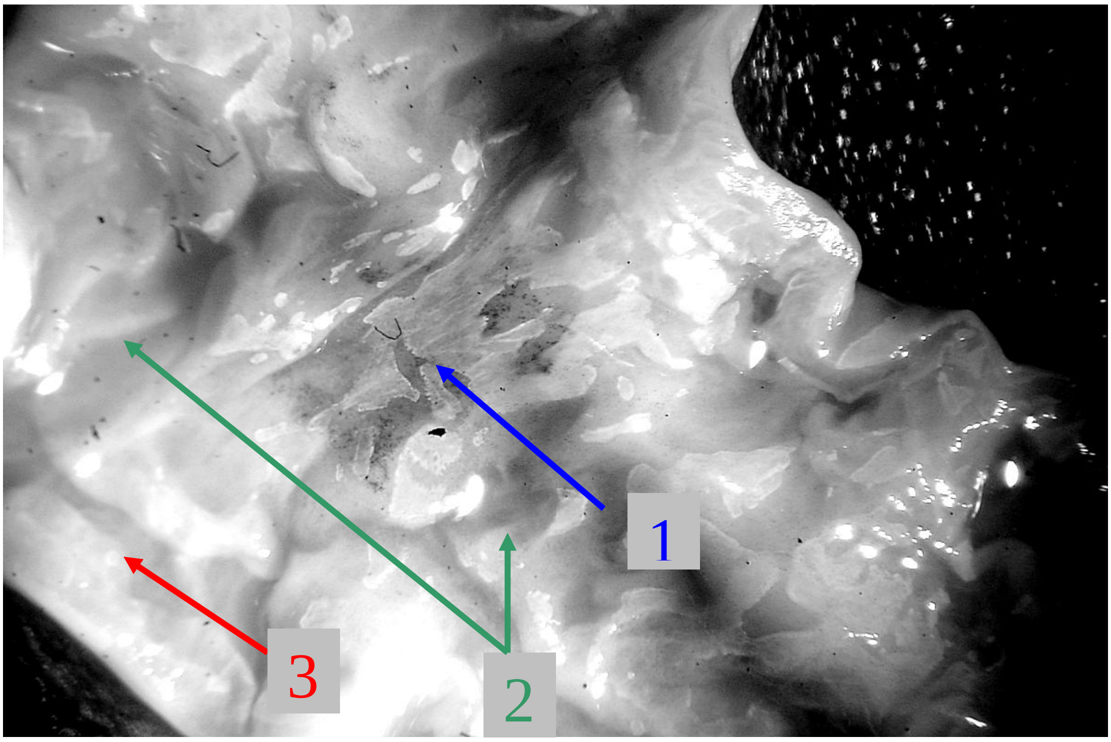

Image D Placental scar typical for resorption type in a female hare. Photo S. Petrovan
1 Shallow and coloured crater at the implantation site without surrounding knobs
2 Lack of bands of macrophages
3 Lack of antimesometrial depression