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Assessing potential causes for the population decline of European brown hare in the agricultural landscape of Europe

– a review of the current knowledge



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Assessing potential causes for the population decline of Euro- pean brown hare in the agri- cultural landscape of Europe

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Data sheet

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Abstract: Despite considerable research efforts populations of the European brown hare (*Lepus europaeus*) have been declining throughout Europe since the early 1960s. The hypothesised causal factors for the decline are numerous and act via resource availability, reproduction and survival. Based on a systematic review of the literature the potential causes are discussed and a hypothesis for the underlying cause of the decline is suggested as are future research priorities. Recognising that multiple factors are interacting, modelling integrating resource availability, ecology, behaviour and the environment is required in future research.

Keywords: European brown hare, decreasing density, survival, reproduction, anthropogenic factors

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Summary

Recognising that multiple factors are interacting in the case of the declining European hare populations, modelling integrating resource availability, ecology, behaviour and the environment is required in future research.

Despite considerable research efforts populations of the European brown hare (*Lepus europaeus*) have been declining throughout Europe since the early 1960s. The hypothesised causal factors for the decline are numerous and act via resource availability, reproduction and survival. Based on a systematic review of the literature the potential causes are discussed, a hypothesis for the underlying cause of the decline is suggested, as are future research priorities.

Studies indicate that food shortage in the modern cereal dominated agricultural landscape, possibly caused by the introduction of herbicides reducing weed biomass ten-fold, may result in a summer food bottleneck. If true, this change has postponed minimum resource availability from the winter period to the central reproductive period of the hare with distinct effects on population dynamics. Previously, seasonal variation in resource availability with summer-high and winter-low was well adjusted with the main reproductive output through spring and summer allowing high density in autumn before onset of the hunting season. In this situation the majority of mortality factors, hunting

inclusive, were compensatory, only taking the surplus and thus reducing density according to the pre-winter drop in resource availability. In the modern landscape the situation may be reversed with low resource availability in summer and high during winter. Hence, the food resources available cannot support the new generation of hares resulting in low survival and eventually autumn densities far lower than the resource availability allows in this period. As a consequence most mortality during autumn and winter including hunting act as additive factors, with an elevated risk of reducing the breeding population of the following year.

Predation can not unequivocally be ruled out in having an effect on hare population dynamics, but since fertility of female hares even at reduced population densities seems far beneath the physiological maximum, predation does not appear to be the primary cause of decline.

An average number of litters per female as low as 2.3 in hare populations in intensive agricultural landscapes strongly support the hypothesis of resource limitations during the breeding season. Apparently female hares experiencing limited resources postpone ovulation until a minimum level of internal energy stores are rebuilt, thus limiting the possible number of litters during a reproductive season.

Dansk resumé

Til trods for en betragtelig forsknings- og udredningsindsats har de europæiske harebestande (*Lepus europaeus*) været faldende siden først i 1960'erne. Der er fremsat mange hypoteser om, at årsagerne til tilbagegangen virker gennem resourcetilgængelighed, reproduktion og overlevelse. Med udgangspunkt i en systematisk gennemgang af litteraturen fremlægges i denne rapport en diskussion af de mulige årsager til tilbagegangen; der præsenteres en hypotese om den bagvedliggende årsag, og der fremsættes forslag til fremtidig forskning.

Undersøgelser indikerer, at der i det moderne landbrugslandskab, som er domineret af korndyrkning, kan forekomme en fødemæssig flaskehals om sommeren som følge af brugen af herbicider, der har reduceret mængden af ukrudt i afgrøderne med en faktor 10. Hvis denne hypotese holder, så har disse ændringer flyttet den traditionelle periode med fødeknaphed fra vinteren til væsentlige dele af harens ynglesæson med deraf følgende markante effekter på harens populationsdynamik. Tidligere var der – med forholdsvis meget føde om sommeren og mindre om vinteren – bedre overensstemmelse mellem den sæsonmæssige variation i fødemængden og harens killingeproduktion gennem forår og sommer, hvilket gav mulighed for opbygning af høje bestandstætheder forud for jagtsæsonen om efteråret.

I denne situation var de fleste dødsårsager, herunder jagt, kompensatoriske, idet disse kun fjernede bestandsoverskuddet og reducerede tætheden til et niveau, der passede til nedgangen i føderessourcer-

ne forud for vinteren. I det moderne landbrugslandskab kan situationen være vendt, så der nu er forholdsvis mere føde om vinteren og mindre om sommeren. Derfor er de tilgængelige føderessourcer ikke længere tilstrækkelige til at ernære årets killinger i sommerperioden, og det resulterer i lav killingeoverlevelse og i sidste ende bestandstætheder langt under det niveau, som de nuværende efterårsressourcer ellers ville kunne bære. Derfor er det meste af dødeligheden om efteråret og vinteren nu additiv, og dermed er der en forøget risiko for, at der sker en reduktion af næste års ynglebestand.

Prædation kan ikke entydigt udelukkes at have en effekt på harens bestandsdynamik, men eftersom hunharenes fertilitet – selv i bestande med stærkt reduceret tæthed – synes at være langt under det fysiologiske maksimum, så er prædation næppe den primære årsag til tilbagegangen.

Et gennemsnitligt antal kuld per hunhare så lavt som 2,3 i harebestande i intensivt dyrkede landbrugslandskaber understøtter hypotesen om fødebegrænsning i ynglesæsonen. Hunharer, der oplever en sådan begrænsning, ovulerer tilsyneladende ikke, før de har opbygget et minimum af energidepoter, og det begrænser antallet af kuld i en ynglesæson.

Årsagen til tilbagegangen i harebestandene skal findes i et komplekst samspil mellem mange faktorer. I den fremtidige forskning er det derfor nødvendigt at inddrage modeller, som integrerer resourcetilgængelighed, økologi, adfærd og landskab.

1 Introduction

Populations of the European brown hare (*Lepus europaeus*) have been reported declining throughout Europe since the early 1960s (Strandgaard & Asferg, 1980; Tapper & Parsons, 1984; Hutchings & Harris, 1996; Marboutin et al., 2003). Although still widespread in Europe, the brown hare is protected under Appendix III of the Convention of the Conservation of European Wildlife and Natural Habitats (Bern Convention). In UK it is classified as a “priority species of conservation concern” (Vaughan et al., 2003) and in Switzerland it is included in the national red list (Pfister et al., 2002).

There are numerous hypothesised causal factors for the decline including changes in landscape structure, agricultural management, climate, predation, and disease affecting food supply, reproduction and survival. Considerable effort has been put into research to understand the underlying causes and to develop mitigating management strategies, but populations are not recovering. Whether the observed population trends mirrors a dynamic change of the environment, by which the hare populations are responding to a new level of landscape carrying capacity, or whether the decline will continue and lead to the disappearance of the hare as a key species of the open landscape in Europe, is unknown. In the search for a common explanation for the decline of the brown hare in Europe one has to look for common factors acting in those countries with synchronous declines. Hence, it seems unlikely that factors such as non-sustainable hunting or diseases would affect all regions of Europe simultaneously, although they could be important locally. However, this analysis is hampered by the fact that one of the

basic keystones for investigating these trends, the accumulation of representative national data on the densities of hare populations, is not widely available across Europe.

The aim of this work is to review and evaluate the literature on the causes of decline in European hare populations, and to target areas of future research priority. The time frame considered is from the 1940s up till the present time, in gross terms representing a period in the 40s and the 50s with a stable population trend followed by a successive decline from the 60s and onwards. The review focuses on hare populations in the agricultural landscape of Europe but to improve the understanding of the changing living conditions, comparisons to introduced hare populations outside Europe and to undisturbed natural habitats are occasionally drawn. Literature has been retrieved by searching relevant databases in 2005 (Web of Science, BIOSIS and Current Contents), personal literature collections and specific reference lists in key papers. Papers were selected according to their relevance and scientific quality to the overall theme or key ecological and population dynamic factors.

The starting point for this work is the literature on human induced changes affecting general living conditions of European hare populations. These changes clearly act on classical biological factors such as resource availability, reproduction and survival. The basic knowledge on these key factors is evaluated separately, although source literature not necessarily directly connected to the overall theme of declining populations.

2 Fluctuations and trends in hare populations

Long time series of direct measurements of hare densities are rare. Most studies of long temporal trends are therefore based on indirect data material such as hunting records. Hunting records from a range of European countries show that hare populations in Europe have been decreasing simultaneously over the last forty years (Table 1).

Although older data on local hunting bag indicate large-scale fluctuations in England from the early 1900 up till the 1960s (Tapper & Parsons, 1984), the prevalence of the present decline makes it unlikely that the situation is part of a naturally occurring fluctuation. The most consistent and reliable data on national hunting bag is from Denmark where all hunters have been obliged to report their personal bag record annually since 1940. Concurrent with the Swiss and English data, Danish hare bags fluctuate

around an annual bag of 400,000 during 1940-1960. Subsequently the bag has decreased to the present level of 71,000 in 2002 (Asferg, 2004). In Eastern Europe the rate of decline appears to be more moderate and taking effect somewhat later than in Western Europe (Table 1). The trend in Europe is not however, a global one, since the European hare has been successfully introduced into New Zealand and Argentina, colonising the majority of the available land areas with stable or increasing population sizes (Flux, 1997; Bonino & Montenegro, 1997). Cyclic population fluctuations has been reported for other Lagomorph species (Finerty, 1981), but no such true cycles have been found for populations of the European hare (Tapper & Parsons, 1984). Given that the population decline is not part of a natural cyclic fluctuation, common denominators responsible should be identifiable.

Table 1. Trends in European brown hare populations in different countries. Where decrease/increase factor is missing, no national hunting records are available. * Introduced populations.

Country	National trend	Decrease factor (bag numbers)	Year span studied	Source
Sweden	Decrease	2-3 (120000-45000)	1940-1975	Frylestam, 1976a
Denmark	Decrease	4-5 (475000-71000)	1940-2001	Bregnballe, 2003; Asferg 2004
England	Decrease	5-6	1961-1989	Tapper, 1992
Germany	Decrease	2-3	1960-1993	Schäfers, 1996
Poland	Decrease since 1970	2 (400000-200000)	1981-1995	Wasilewski, 1991; Panek & Kamieniarz, 1999
Switzerland	Decrease	5 (35000-7000)	1960-1989	Pfister et al., 2002
Austria	Decrease	2	1961-1990	Edwards et al., 2000
France	Decrease	?		Marboutin & Peroux, 1996
Slovakia	Decrease	?		Slamecka, Hell & Jurcik, 1997
New Zealand*	Stable	?		Flux, 1997
Argentina*	Stable, Increasing	?		Bonino & Montenegro, 1997

3 Anthropogenic impacts

Although the general decline in hare populations throughout Europe may be affected by abiotic factors, predation or diseases it seems likely that a central part of the complex of causes should be sought for in the spectrum of anthropogenic impacts changing the environment of the hare. In particular agricultural exploitation has dramatically altered the landscape structure concurrent with hare declines.

3.1 The agricultural landscape

The relationship between the pattern of agricultural intensification, and associated changes in landscape structure in Europe, and the decrease in hare populations has been intensively studied (Table 2 and 3). In a recent review of 77 research papers from 12 European countries Smith et al. (2005a) concluded that habitat changes caused by agricultural intensification are the ultimate cause of hare population declines but effects of changes in climate or predator numbers are magnified by the loss of high-quality year-round forage and cover.

The most pronounced changes which have shaped the modern European landscape are: 1) urban growth, roads and railways, habitat fragmentation, and diminishing agricultural areas, 2) mechanisation and intensification of agriculture through the use of pesticides and fertilisers. The result is large farm and field units with high yielding monocultures and reduced diversity of crops and landscape types (Stoate et al., 2001; Lundström-Gilliéron & Schlaepfer, 2003; Smith et al., 2004, 2005a, 2005b). An example of the remarkable increase in efficiency of the agricultural sector is the raise in cereal yield from an average of 2 tonnes per hectare in the 1940s up to the present average level of 7 tonnes per hectare. This raise in yield follows an equivalent raise in applied fertilizer and spraying with herbicides, insecticides and fungicides (Robinson & Sutherland, 2002). Modern weed control has reduced the previous need for crop rotation, now allowing continuous cereal cropping. This possibility has led to a higher degree of agricultural specialisation and change in land use where intensive cereal farming is concentrated in areas where soil quality is good and climate is mild (oceanic), whilst cattle farming and pasture land is concentrated on the poorer soil types.

The general pattern of change in crop types is a pronounced increase in the use of winter cereals, especially winter wheat and winter barley during the 1980s and 1990s. Concurrently areas with root crops have been reduced. In Denmark winter cereals now cover approximately 70% of the whole agricultural area (Olesen et al., 2002; Schmidt et al. 2004). In 1993 arable subsidies were linked to farmers entering land as set-aside as a tool of production control in the European Union. In general, set-aside has not improved the nature content of the agricultural landscape as much as one could hope for, as an increasing part is assigned to permanent set-aside on poor soil types. Plant species diversity is high in the first year of set-aside, but is successively reduced through competition from perennial plant species, mainly grass species. In connection with the agricultural intensification small biotopes in the open land as for example hedgerows has been reduced markedly (Robinson & Sutherland, 2002).

Originating from open steppe grassland, the hare has successfully exploited open agricultural areas (Frylestam, 1980a). In the modern agricultural landscape hares are closely associated with arable land (Hutchings) & Harris, 1996; Kiliás & Ackermann, 2001; Pfister et al., 2002; Vaughan et al., 2003) and even ploughed fields with no available food are often used as resting sites (Pepin, 1987a). Habitat preference studies show that in general the hare exploits the common crop types in agricultural areas by a strict seasonal selection of winter cereals and rape from their early emergence in September throughout the winter until stem extension in mid-May (northern temperate zone). From mid-May to harvest winter cereals are generally avoided. Peas and spring cereals are only preferred in the early spring growth phase, whereas permanent grass and clover fields are selected throughout the year, although most intensively during summer (Frylestam, 1980b; Frylestam, 1986; Hansen, 1997b) Data on diet composition, dealt with in detail later, shows that food item species diversity increases markedly during summer, reflecting a change from cereals to a variety of naturally occurring species of grasses and herbs. This pattern reveals a strategic use of the natural seasonal variation in plant growth phenology (Chapuis, 1990; Hansen, 1990). Evidence from the landscape scale (Tapper & Barnes, 1986), underlines the importance of non-crop forage, showing

Table 2. Factors affecting population density or habitat preference of European hares in the literature. Methods used are different variations of regression and principal component analyses usually based on hunting statistics.

Value of the factor studied in relation to density or preference of the hare (+, -)	Landscape type of study area	Country	Material	Year span	Method	Source
+ mild climate - traffic	Mixed agricultural landscape	Switzerland	Hunting statistics	1980-1985	Correlation matrix Multiple regression	Lundström-Gillieron & Schlaepfer, 2003
+ % arable land + dry soil types + diversity of crop types - high stem fruit farm areas	Mixed agricultural landscape	Switzerland	Night spotlight counts	1991-1999	Multiple regression	Pfister et al., 2002
- forest + winter cereals + potato fields + root crop fields + grassland	Mixed agricultural landscape	Germany (North-central)	Hunting statistics	1962-1973	Multiple regression	Schröpfer & Nyenhuis, 1982
- forest - roads - pastures - set aside + cereals and maize + root crops	Agrarian lowland	Germany (North)	Hunting statistics	1990-1997	Principal component analyses	Nyenhuis, 1999
+ % arable land + diversity of crop types - mean farm size	Nation wide agriculture land	Germany (West)	Hunting statistics	1959-1993	Regression	Schäfers, 1996
+ mild climate, lowland + % arable land + diversity of crop types	Mixed landscape	Germany (Bayern)	Night spotlight counts	1999	Principal component analyses	Kiliass & Ackermann, 2001
- forest - large field size	Mixed agricultural landscape	Poland	Hunting statistics & census	1981-1995	Simple and multiple correlation	Panek & Kamieniarz, 1999
- ploughed fields (spring) - Maize and rice fields (autumn) + meadow grassland + field edges + poplar groves	Mixed Landscape and poplar plantations	Italy (North)	Night spotlight counts	1978-1979	Simple and multiple correlation	Meriggi & Alieri, 1989
+ arable fields or woodland in typical pasture land + hunting - fox seen	Mixed landscape	England	Questionnaire	2000	Ordinal logistic regression	Vaughan et al., 2003

Table 3. Factors affecting population density or habitat preference of European hares in the literature. Methods used are either direct observations or calculation of habitat preference.

Value of the factor studied in relation to density or preference of the hare (+, -)	Landscape type of study area	Country	Material	Year span	Method	Source
+ winter-wheat (April) + ploughed fields (March-April) - harrowed fields (March-April) - pastures (April)	Large scale farming area	France	Daylight flushing counts	1975-1978	Observed density	Pepin, 1987a
+ habitat diversity + field margins - rape fields	Mixed landscape	Poland (North-east)	Daylight flushing counts	1988-1990	Habitat preference index	Lewandowski & Nowakowski, 1993
- fields near urban areas - fields near forest + small tree biotopes (no effect of agrarian structure)	Mixed agricultural landscape	Poland	Capture	1974-1976	Observed density	Bresinski, 1983
+ w. cereals (Oct-May) + Clover fields (May-Oct) - ploughed fields - pastures (June-Oct) - discontinuity in food supply	Agricultural areas (South lowland)	Sweden	Night spotlight counts	1974-1976	Habitat preference index	Frylestam, 1980b; Frylestam, 1992
+ grass without livestock - arable crops (May-Aug) + forest edge + hedgerows + landscape diversity (summer-autumn) - field size	Agricultural Landscape	England	Conventional radio-tracking & day & night counts	1980-1982	Habitat preference index	Tapper & Barnes, 1986

that small semi-natural habitats and field margins are highly preferred by hares, particularly in intensive agricultural areas where they are rare. The common agricultural use of winter cereals in Europe offers sufficient food in autumn to spring, with hares only using 2.6% of available biomass (Nesvadbova & Zejda, 1989); but seasonal continuity in availability of food seems to be a problem (Frylestam 1980b). Where the classical view has been resource limitation during winter, focus is now on a possible nutritional discontinuance or bottleneck during summer. This assumption is enhanced by the fact that weed biomass and diversity has decreased strongly over the past 40 years in agricultural land (Hald & Reddersen, 1990; McCollin et al., 2000; Robinson & Sutherland, 2002). More specifically, the level of weed abundance in cereal fields have declined with about 2/3 in mid-field plots in Denmark from the 1960s to 1990 (Hald, 1998). Since then, the levels have declined even more so that often less than 1 g DM/m² of weeds are present in

cereal fields in June, and species diversity is low (Topping et al., 2004a). A further constraint is that the modern tightly sown cereal crops are difficult for the hare to penetrate from May to harvest due to mechanical resistance, leaving only approximately 35% of a typical agricultural area as potential habitat (Rühe, 1999). In some areas of intensive agriculture this percentage can even be as low as 4% (Frylestam, 1980b). Although winter cereals are eaten from autumn to spring, even in this period the low nutritional diversity of oversimplified agricultural areas with almost no alternative food items may be suboptimal for the hare (Schröpfer & Nyenhuis, 1982; Marboutin & Aebischer, 1996; Vaughan et al., 2003).

In herbivores, the carrying capacity of a landscape is primarily determined by the period with lowest amount of available food resources, especially if the duration of the period of negative energetic balance and costs exceeds the energetic storing capacity of

the animal (Caughley & Sinclair, 1994). In the case of the hare, the negative influence of the potential lack of summer food is exacerbated because the main breeding season, which exerts heavy energetic demands for lactation, coincides with the period of low availability of food in modern intensively managed agricultural landscapes.

As the landscape becomes more and more homogeneous the importance of small semi-natural habitats in the landscape might increase, but this facet of landscape change has received little attention. Smith et al. (2004) found that hares selected habitats that were heterogeneous in structure with taller vegetation during spring and summer, and that hares in pastoral landscapes were more likely to be limited by habitat in terms of cover than food. Another neglected area is the importance of the landscape mosaic, despite the fact that high crop diversity has been found to be associated with relative high hare density (Tapper & Barnes, 1986; Pepin, 1987a; Schäfers, 1996; Kiliyas & Ackermann, 2001).

The methods used for evaluating the importance of the landscape, as reflected in Table 2 and 3, range from density counts and radio tracking to the use of hunting statistics and even questionnaires on landowners' subjective evaluation of hare densities. Each method has advantages and disadvantages, but it is out of the scope of this paper to evaluate the single methods. However as modern technology may soon be available one should encourage future research using GPS-radio collars, enabling high precision and objective time scheduled fixes (day and night) which would improve our knowledge on hare preferences even including smaller landscape elements. This kind of preference study combined with a thorough quantification of available biomass of preferred food items in selected landscape structures is essential for understanding the constraints of the modern landscape as a habitat for hares.

3.2 Pastures and domestic stock

Low relative hare densities are reported for pastoral landscapes in England, Sweden and Germany (Table 2 and 3) (Frylestam, 1976b; Frylestam, 1980b; Barnes et al., 1983; Tapper & Barnes, 1986; McLaren et al., 1997; Nyenhuis, 1999; Vaughan et al., 2003). The same pattern has also been seen for mountain hare (*L. timidus*) (Hewson, 1989; Dingerkus & Montgomery, 2002). The reasons are not unequivocal but Barnes et al. (1983) show that hare density drops sharply when livestock is moved into a field and raises again within a week after livestock is re-

moved. In this study, the hares always maintained at least a 10m distance from the cattle (Barnes et al., 1983), indicating that disturbance from the presence of livestock is important. If this behaviour is significant, the aggregation of specialised pastoral areas through the second half of the 20th century could have had a bearing on the decline of hare populations. However, these relationships have never been thoroughly investigated. The disturbance from livestock is not the only negative factor associated with intensive livestock production. Leveret mortality from intensive silage cutting may also be critical (McLaren et al., 1997). Another hypothesis suggests that the high qualities of culture grasses used for cattle are a sub-optimal food item for the hare (Frylestam, 1986). Frylestam's data indicate that hares on pastures prefer wild grasses to sown culture grasses.

3.3 Pesticides

Direct detrimental effects on hare populations due to herbicide application to arable crops has not been reported, even though incidents of poisoning have occurred (Chlewski, 1976; Rimkus & Wolf, 1987; Edwards et al., 2000). Negative effects of hormone based herbicides on reproductive fitness of hares has been suggested as an explanation of high frequencies of non-reproductive female hares, but this has never been verified. Indirect effects of applying herbicides, reducing an important alternative food resource, could certainly have a deleterious effect on the resource availability of modern landscapes. In fact the introduction of herbicides in agriculture from the late 1950s and the rise in use (Robinson & Sutherland, 2002) has reduced the abundance of weed in cereal fields with at least a factor 10 (Hald, 1998; Topping et al., 2004a). As the summer diet of the hare to a large extent consists of different weed species (Hansen, 1991) it is likely that the use of herbicides in agriculture has played an important role in the concurrent decline of the European hare.

3.4 Machinery and traffic

Modern crop harvesting operations with large and fast machinery is an important source of mortality, particularly for leverets taking cover in grass and alfalfa used for silage production (Milanov & Dimov, 1990; Milanov, 1996). Even older studies report losses of 15.4% of the natural increase in hare populations by agricultural machinery. The highest losses being in grass and lucerne for green fodder (45%), moderate losses in grass meadows and clover

(18%) and low losses in cereals (4-6%) (Kaluzinski & Pielowski, 1976). A more recent study in Denmark confirmed the level of mortality due to agricultural machinery at approximately 15% of the leveret production (Hansen, 1997a; Marboutin & Hansen, 1998). On the other hand harvesting operations do not cause mortality among adult hares (Marboutin & Aebischer, 1996).

Traffic definitely affects mortality in hare populations. Reichholf (1981) recorded mean values of 0.64-0.28 killed hares per km main road per year from 1976 to 1980, the decrease linearly related to the decrease in hunting bag. Extrapolating these

results to the whole of Germany, 60,000 hares are killed amounting to well over 10% of the annual hunting bag. Traffic is perhaps not a cause of decline in hare populations, but could be used as an indicator of this. However traffic kills averaging over 10% of the annual hunting bag might affect local population levels (Reichholf, 1981). Earlier results from East-Germany give far higher values for traffic kills, but hare population densities were also considerably higher at that time (Ueckermann, 1964). A possible effect of the general rise in traffic intensity and area of roads in Europe has not been investigated.

4 Home range

Although there are marked variations in home range sizes (26-190 ha), the general pattern seems to be large home ranges in areas of intensive agriculture and limited landscape diversity, and small home ranges in areas with a higher degree of natural habitats and thereby higher landscape diversity. An overview of results is given by Marboutin (1997) and Kunst et al. (2001).

Kunst et al. (2001) clearly demonstrate that home range size does not vary seasonally in natural habitats of salt marsh areas in contrast to large seasonal variations in areas of intensive farming. The reason for this is suggested to be the high level of patchiness in the salt marsh, insuring food availability and shelter throughout the year within a limited area (Kunst et al., 2001). In a large scale cereal farming area (50% wheat) in France average home range size was as large as 190 ha. Neither light cycles nor harvest operations changed the pattern of habitat use

within home ranges, but compared to the structure of the whole study area habitat availability did influence home range establishment. Pastures, set aside and woodland habitats were significantly underrepresented (Marboutin & Aebischer, 1996).

Interpretation of the biological meaning of home range size is difficult since it is influenced by more than one factor e.g. food resources, shelter, social organisation and reproductive behaviour. Different methods used in estimating home ranges, different time scales and the fact that home range size is usually influenced by the number of fixes used, adds to these difficulties (Marboutin, 1997).

Despite these difficulties future studies on seasonal shifts in home range size and location in relation to landscape structure could contribute significantly to our understanding of the present status of the brown hare in Europe.

5 Reproduction

Maximum life span for the European hare is reported to be 7-12 years although average length of life in free living hare populations ranges between 2.0-2.9 years (Pielowski, 1971a; Abildgård et al., 1972; Marboutin & Peroux, 1995). Female hares are generally considered to live longer than males, although this was not the case in the study of Abildgård et al. (1972), where the sex ratio was male biased. Considerable research has been done on reproductive fitness of the female hare, as post mortem dissections of the uterus allow reconstruction of individual annual reproductive history (Bray et al., 2003). Applying this method it was revealed that not all adult females reproduce. Reproducing females have up to 5 litters annually and top annual fertility is 20-25 leverets (Bensinger et al., 2000; Hackländer et al., 2001). In the study of Bensinger et al. (2000), 16% of the adult females did not reproduce and 21 out of 30 of these were found to have pathological changes in the uterus, most pronounced for the age group 5 years or older. Hackländer et al. (2001) confirm these results, although age determination was based on eye lens weight. The cause of the pathological changes is not known. However, these findings result in an age dependent reproduction where all females aged 1-2 years reproduce, 90% of the cohort aged 2-3 year reproduce, 85% of 3-5 year olds reproduce and only 54% are reproductive when over 5 years old (Bensinger et al., 2000). Although the percentage of non-reproductive does where higher in low density populations than in high density populations, the proportion of non-reproductive females could not be ascribed to density dependence, but related to eye lens weight (Hackländer et al., 2001). Given that fertility decreases with age the highly variable proportion of non-reproductive females and variations in fertility (Table 4) may be explained by differences in age structure of hare populations (Hackländer et al., 2001).

It still remains an open question if the proportion of adult female hare not taking part in the reproduction is a natural response to unfavourable living conditions. However, the existence of non-reproductive females is not a new phenomenon, as it was referred to already in 1962. In the study of Hewson & Taylor (1975) the percentage of adult female hares not pregnant in the main breeding season (March-August) was as high as 32% (annual variations between 0 and 32% in a 12 year study). These findings suggest that the percentage of non-reproductive females is probably not the primary cause of the decrease in hare populations, although imposing a negative effect on population growth when mortality of juveniles are high and the age structure of the population becomes distorted.

As described, placental scars are usually counted to reveal number of offspring produced. This number is then often compared to the proportion of juveniles in the hunting bag to calculate survival. However, Bonino & Montenegro (1997) found that pre-natal mortality in European hares in Argentina was as high as 57% of all ova ovulated, where 22% were lost after implantation, indicating an even larger reproductive potential. In Holland pre-natal mortality in pregnant female hare was found to be 6% (Broekhuizen & Maaskamp, 1981). The reasons for this kind of losses have not yet been studied. Reproductive output is enhanced by the potential for females born early in the year to breed in the year they are born, as they usually reach maturity at the age of approximately 6 months (Broekhuizen & Maaskamp, 1981), and in some occasions even before (Caillol et al., 1992). In France, all female hares born in January and February reproduced in the same year, as did 26% of those born in March-April and 6% of those born in May-June (Marboutin et al., 2003). The chances of survival of early leverets are low, but given good conditions, this potential enhances the re-

Table 4. Overview of published levels of reproducing does and fertility in European hare populations.

Reproductive does (%)	Annual fertility	Method of calculating fertility	Country	Source
85-100	12-15	Reproductive females	France	Marboutin et al., 2003
83-84	11.2	Reproductive females	Germany	Bensinger et al., 2000
73-93	8.0	Reproductive females	Austria	Hackländer et al., 2001
?	6.8-8.9	Reproductive females	Sweden	Frylestam, 1980a
79-86	4.1-5.9	All females	Denmark	Hansen, 1992
?	9.4	All females estimations	France	Pepin, 1989

productive capability of the species. The major cause of variability in reproductive potential seem to be the number of litters more than litter size (Bensinger et al., 2000); the further north the shorter reproductive season and consequently a reduced number of litters. Despite the effect of latitude hares, in Europe do not seem to maximise their number of litters during the reproductive season. Given that the reproductive season starts 2-4 weeks after winter solstice (Flux 1965), the first litter is often seen in late February. With the last litter often seen in late September, the potential period of giving birth is up to seven months in Europe. As the European hare is capable of superfoetation, i.e. mating up to 4 days before giving birth, the minimum duration between successive litters is 38 days, which in theory makes at least 6 litters per reproductive season possible. In reality, this is far from the case, e.g. as reported by Hansen (1992) where the average number of litters per female reproducing amounted to only 2.86 (2.33 including 18.6% not reproducing), indicating a possible duration between litters of up to 100 days. In captivity where hares were fed *ad libitum* 46% of 37 litters were borne 37-39 days after last litter and the average duration between litters were 45.5 days (Petersen 1990). In this case the aver-

age number of litters was 3.9. These results suggest that it is indeed physiologically possible for female hare to increase the number of litters and overall reproduction much further than currently seen in the wild, given optimal conditions.

In a decreasing population with a very low percentage of juveniles (38%) as reported by Hansen (1992) and 18.6% adult females not reproducing, average real production per female (including non-reproductive females) was as low as 5.0 leverets – even excluding adult mortality during the reproductive season. Using these figures and an adult survival of 0.5 in a simple population model reveals that at least 22% of the leverets have to survive just to sustain the population (Olesen, unpublished).

Although recognising the large reproductive potential of hares recent modelling of population dynamics in hare stresses that the survival of leverets is one of the most important factor affecting density (Marboutin et al., 2003). This approach is supported by the findings of Pehrson (1984) showing that suboptimal feeding in captive mountain hares does not result in lower fitness but reduced birth weight, eventually resulting in reduced leveret survival.

6 Survival

As previously noted, many researchers indicate that the most important factor in understanding the nature of the declining populations of hare is leveret survival; hence leveret survival rates have been the focus of several studies (Table 5). Being regarded as a reproductive specialist (Krebs, 1986), the strategy of the hare should be relatively low maternal investment and high reproductive output, enduring a rather low offspring survival. However when juvenile survival are down to 0.14 (Marboutin et al., 2003) or even as low as 0.067 (Marboutin & Peroux, 1995), it is crucial to investigate the nature of these excessive losses. Regrettably, most studies fail to attribute a cause to the low survival rates reported.

Table 5. Overview of published levels of survival rates of leverets in European hare populations (hunting mortality is not included).

Survival rate	Country	Source
0.14 – 0.29	France	Marboutin et al., 2003
0.23 (average)	Poland	Pielowski, 1981
0.20 – 0.31	Denmark	Hansen, 1992
0.35 – 0.45	France	Pepin, 1989

Modelling hare population dynamics adds interesting perspectives to the meaning of factors affecting population growth, survival of leverets not unconditionally being the most important factor. Hence, population growth rate is more sensitive to changes in maintenance (survival of yearlings and adults) than to changes in internal recruitment (i.e. proportion of breeding females + fecundity + juvenile survival) if the proportion of juveniles in the population is low (42%), typical for decreasing populations (Marboutin & Peroux, 1995). However, the variability in young production is about twice as large as in adult survival, and perhaps in reality counterbalances the differential in population growth rate caused by adult survivorship. Marboutin & Peroux, (1995) conclude that once a hare population has poor recruitment, its growth rate becomes very sensitive to any kind of mortality imposed on the breeding adults, such as that related to hunting. Excluding hunting in the model, population growth rate increased by 5.9%, twice as much as if the same percentage increase was assigned to one of the other recruitment parameters, but still not enough to prevent a population decrease (Marboutin & Peroux, 1995). In this case density dependent regulation of recruitment, if present, could not counterbalance hunting exploitation.

Density dependence also works directly on survival of leverets. In the classic 13 year study of Abildgård et al. (1972) in a non-hunted island population without mammalian predators, survival of leverets was inversely proportional to density giving a low autumn young/adult proportion (annual variation 32-71%) in years of high density and vice versa. Wasilewski (1991) found the opposite pattern in Poland, but his material was based on 5 different populations in a study period of only two years, making it more difficult to exclude the influence of differences in range quality.

Leveret survival seems favoured by high body weight, although results were obtained in a study with released hand reared and wild leverets (Marboutin et al., 1990). In yearlings results on the relationship between body weight and survival are more substantial. Grouping yearlings according to body mass of less than 3 kg and equal to or over 3 kg, survival was 0.40-0.68 for heavy males and 0.20-0.44 in lighter males, and 0.31-0.52 and 0.22-0.40 for heavy and lighter females respectively. Yearling survival was found to depend also on year of study and winter severity in this island population without mammalian predation (Marboutin & Hansen, 1998).

Survival of adult hares is rather variable due to the influence of hunting. Excluding hunting, adult survival range was 0.51 to 0.59 and exposed to hunting survival ranges between 0.35 and 0.52 (Abildgård et al., 1972; Broekhuizen, 1979; Kovacs, 1983; Pepin, 1987a; Marboutin & Peroux, 1995; Marboutin & Hansen, 1998). Also in adults, survival was found to be sex dependent, males surviving better than females ($\text{survival}_{\text{male}}=0.50-0.61$, $\text{survival}_{\text{female}}=0.44-0.56$) (Marboutin & Hansen, 1998). None of the studies on adult survival account for the fact that mean life span of adult hares is only between two to three years. Some indirect evidence is given by Wasilewski (1991), who found that survival of adult hares during breeding was twice as high in field-forest habitats than in field habitats. He presumes that living in mixed field-forest habitat reduces adult mortality mainly caused by agricultural practices, but on the other hand raises mortality of leverets due to higher predation pressure.

One of the main drawbacks of the studies and models published so far are that they cannot include

landscape dynamics and its influence on survival. Hence, current models are incapable of visualising direct effects of possible resource limitations due to, for instance, changes in agricultural practice.

6.1 Predation

The question usually discussed is whether predation drives the prey population or vice versa. As species like the red fox and the European hare have co-existed for thousands of years, predation seems to be a compensatory mortality, only taking the 'doomed surplus', which is also the basic principle of sustainable hunting by humans. However it is extremely difficult to quantify precisely predation on hares under field conditions, and most published results are therefore more or less indirect measures. Recent studies indicate that the red fox may have a significant impact on the density of hare populations (e.g. Schmidt et al., 2004; Smith et al., 2005a). Following the introduction of sarcoptic mange in Sweden, fox density was reduced and hare density increased simultaneously. When the infection died out, fox densities increased and density of hares decreased to previous levels (Lindström et al., 1994). Results from Germany where a fox population was treated against rabies by oral immunisation supports the findings in Sweden. In Germany the fox population rose by 170% followed by a reduction of the hare density to 1/8 of its previous level (Ahrens et al., 1995).

Using computer simulations Reynolds & Tapper (1995) demonstrated that the number of hares eaten by foxes easily exceeded their breeding density and amounted to 76-100% of annual production. As the degree of compensation between mortality factors was unknown it was impossible to prove that fox predation per se limited the hare population, but it played a major role in hare population dynamics (Reynolds & Tapper, 1995). In England predator control is used as a traditional management tool for small game populations, potentially raising hare densities from 15/km² to 60/km² or from 5/km² to 65/km² if habitat improvement and predator control is combined (Reynolds & Tapper, 1995). In fact it is argued that hare density only increases as a result of habitat improvement if fox density is also suppressed (Stoate et al., 1995). Erlinge et al. (1984) evaluated from analyses of pellets of raptors and owls and scats and prey remnants of carnivores that at least 40% of the annual production in hares were consumed by predators. The red fox and the domestic cat were responsible for 84% of this predation. The red fox does not only prey on leverets, but was

shown to take approximately 10% of the population of adult hares during summer (45% of adult mortality) (Goszczynski & Wasilewski, 1992). This result is supported by a recent study where 10 of 13 radio marked adult hares were predated by the red fox (Olesen & Berthelsen unpublished).

Differences in density of predators in relation to density of prey seem to be the reason for results on red fox predation varying between 10-100% of the annual hare leveret production (Pielowski, 1976; Erlinge et al., 1984; Goszczynski & Wasilewski, 1992; Reynolds & Tapper, 1995). A compilation of the limited amount of results published reveals a pattern of asymptotic decreasing importance of the fox predation as the ratio of hare/fox density increases. As previously mentioned, 75-100% of annual production could be eaten by the red fox in a case where the hare/fox ratio was approximately 15 (Reynolds & Tapper, 1995). Assuming that the hunting statistics reflect population levels the average hare/fox ratio in Denmark is now less than 2, primarily due to the decline of the hare bag as the bag of red foxes has been stable or decreasing since the 1960s. However, evaluating the impact of the red fox on hare populations it is important to realise the nature of this predator being an alternative prey selector. In years where voles are abundant the fox is known to shift to this prey species (Angelstam et al., 1984).

Other predators than the red fox, domestic dog and cat also prey on hares. In a study where mammalian predators were effectively excluded by fencing, birds took at least 15% of the leverets produced annually. Of this 50% was taken by hooded crows, 20% by ravens, 20% by common buzzards, 8% by goshawks and 2% by long-eared owl (Hansen, 1997a).

Until now there has been only limited focus on the combined impact of predation and change of agricultural management. Vaughan et al. (2003) suggested possible interactions between habitat and predation after finding that changes in land management that provide year-round cover may make farms more attractive to hares. Swift removal of the major part of all cover by cereal harvesting, thereby exposing new-born leverets to predation from crows, ravens, birds of prey, domestic cats and dogs, mustelids and the red fox presents another problem. The only possible way to investigate this is monitoring prey populations in comparable study areas with and without predator control. This type of study was carried out for mountain hare populations in Finland. The surprising result was an in-

crease in hare populations in areas where predators were protected and proliferating (Kauhala et al., 1999).

6.2 Hunting

In France hare populations have been shown to be resilient to heavy hunting pressure of between 40-46% of the autumn population where juvenile/adult ratios prior to hunting ranged between 1.2-2.4 and densities between 52-71 animals/km² (Pepin, 1989). In some areas of high hare density in England, a hunting bag of up to 69% of the autumn population was maintained over several years (Stoate & Tapper, 1993). Given that the hare is declining in Europe a central question is whether hunting can be sustainable or is a contributing factor to the decline. The definition of sustainability is that the population growth rate is larger than or equal to one, i.e. where populations are either stable or growing.

Marboutin et al. (2003) have constructed a dynamic population model for evaluating sustainable harvest rates in hare. Although they have presumed that hunting is entirely an additive mortality factor they reach interesting results defining sustainable harvest rates at different levels of leveret survival, density and initial population size. The model illustrates that a population of less than 250 hares at a density of less than or equal to 5/km² could only sustain harvest rates up to 20%. If density is higher than or equal to 10/km² in an initial population of 500 or more harvest was sustainable at a rate of approximately 30%. Harvest rates higher than 35% were not sustainable even in very large populations. These results suggest that excessive hunting may be regarded as an aggravating factor, but not as the primary cause of population decline (Marboutin et al., 2003). The difference between older findings of apparent sustainability at harvest rates up to 46% (Pepin, 1989) and results of modelling (max 35%) is probably due to dissimilarity in age structure, fertility and mortality of the populations studied.

Hunting not being the primary factor responsible for the decline in hare populations is supported by the fact that density is still only a fraction of previous levels in large areas of central Germany where hunting was markedly reduced or fully abandoned (Eskens et al., 1999).

6.3 Climate

Generally mild climate with limited precipitation and warm temperatures have a positive impact on hare populations (Andersen, 1957; Spittler, 1987; Nyenhuis, 1995). The global climate trend (Global Warming) is raising average temperatures, but is also believed to elevate annual precipitation in Europe (Hurrell, 1995), the latter not necessarily an advantage for the hare.

In the early study of Andersen (1957) 40-50% of the variance in time series of local bags could be attributed to climate factors. The authors listed in Table 6 agree that excess precipitation in the breeding season affects hare populations probably through an elevated mortality of new-born leverets. If impact of climate on hare populations primarily works through the mortality pattern of leverets, it seems likely that the months of prime reproduction (June-August) should be the most important. On the other hand if climate influences availability of food and energetics of adults, hence the reproductive fitness, one should also expect impacts of snow cover and temperature during winter. In the literature both high monthly mean temperatures, length of dry and sunny periods in the central reproductive season is shown to be advantageous for the hare (Spittler, 1987; Nyenhuis, 1995), whereas mean precipitation and days with frost during winter acts as negative factors (Andersen, 1957; Nyenhuis 1995).

The precocial leverets of the brown hare are able to maintain normothermic body temperatures from the first day of life during cold exposure down to minus 8°C (Hackländer et al., 2002a). Despite this ability leverets during their first week of life spent more energy than they received via milk when the ambient temperature was lower than 8°C. Low litter size in the cold part of the reproductive season seems to counteract this as individual energy supply via milk is higher than in large litters (Hackländer et al., 2002b). This compensation mechanism is confirmed by Petersen (1990) who show that each extra leveret in the litter reduces body weight at weaning by 52 g (approximately 7%).

Table 6. Overview of published climate indices with an impact on hare populations.

Value of climate indices studied in relation to density, reproduction or survival of the hare (+, -)	Country	Material	Year span	Method	Source
- monthly mean precipitation June-July + monthly mean temperatures March-June - Number of frost days December-March	Denmark	Hunting statistics	1902-1950	Multiple regression models	Andersen, 1957
+ length of dry periods March-September	Germany	Hunting statistics	1957-1986	Subjective comparison of records	Spittler, 1987
+ Number of days with > 10 hours of sunshine July-August + monthly mean temperature April-August - monthly mean precipitation Feb., Mar., July, Aug.	Germany (Nordrhein-Westfalen)	Hunting statistics	1957-1988	Multiple regression	Nyenhuis, 1995

6.4 Disease

The European hare is reported to suffer from a variety of bacterial and viral diseases (Borg, 1987; Poli et al., 1991; Fuchs & Weissenboeck, 1992; Duff et al., 1994; Frölich et al., 1996; Lamarque et al., 1996; Rattenborg, 1997; Deutz & Hinterdorfer, 2000; Haerer et al., 2001). The occurrence of a range of parasitic infections is also well documented (Irvin, 1970; Forstner & Bayreuth, 1982; Soveri & Valtonen, 1983; Sedlak et al., 2000). However, as none of the studies of disease in the European hare has shown a connection between disease and the decline of hare populations it is outside the scope of this review to give details on types of diseases generally identified.

Diseases cause mortality and interesting evidence is given that young animals and animals with low body weight are overrepresented in dead hares found and autopsied. It also seems clear that most hares are found dead in autumn and winter (Lamarque et al., 1996; Haerer et al., 2001). Seasonal changes in mortality caused by disease could be connected to climate as for instance for coccidiosis, which is proliferating under humid conditions. However, since it is believed that most diseases are density dependent it is hard to imagine that disease has been a prime factor behind the decrease of hare populations. In addition, veterinary surveys on what usually is only a fraction of natural mortality give no more than a qualitative picture of diseases occurring. From these surveys it is hard to evaluate the impact of diseases on the population level.

7 Food and body condition

Research on the diet composition of hare is done either using stomach content or faecal samples. Homolka (1986a) has compared the two methods and found a high degree of accordance in results. It is important to understand that the diet of hares is dynamic in terms of availability of selected species, diet composition changing with season and type of landscape (Table 7). It appears that the diet of hares closely reflects the pattern of vegetation in the specific home range and the phenology of individual plant species. Hares living in agricultural areas with intensive cereal production preferentially select green parts of cereals (up to 95%) during the earliest growth phases of these crops but in summer when cereals ripen the use of wild dicotyledonous plant species raises in proportion to their appearance and abundance. On average half of the stomach content

is made up by wild dicotyledonous plant species in this period. In pastoral landscapes hares have a far more species diverse diet of forbs (weeds) year around and if present they feed on root fruits, wild grasses, clover and lucerne. In arable landscapes, during late summer, up to 20% of the stomach content may consist of cereal grains. In the winter period hares in the arable land again turn to cereals, whereas hares living in the vicinity of forests consume greater amounts of needles, woody parts of herbs and shoots of trees and shrubs. In the arable landscape hare and roe deer remove 63% of the available biomass of shoots of trees and shrubs in hedgerows during winter (Homolka et al., 1988). In areas of high plant diversity dandelions (*Taraxacum sp*) and blackberries (*Rubus sp*) are selected. Dandelions are an important high fat resource for

Table 7. Overview of results on seasonal variation in dietary composition of the European hare. Data are recalculated to enable comparability and reflect range of results in the chosen period. Numbers are vol % or % relative abundance. Figures do not necessarily add up to 100% due to aggregation of periodical data and a percentage of unidentifiable material. “+” : <1%.

Plant fraction, group or species	Winter (Dec-Mar) (%)	Spring (Apr-May) (%)	Summer (Jun-Sep) (%)	Autumn (Oct-Nov) (%)	Landscape Country	Material & method	Source
Poaceae (incl. cereals)	45-50	50	45-55	30	Mixed landscape	Digestive tract samples (vol %)	Homolka, 1983
Green herbs	30-35	45	30-35	40	Central Bohemia		
Shoots trees & shrubs	3-5	3	0	1			
Seeds & grains	2-5	3	3-17	14			
Woody herbs	6-10	1	0-3	8			
Poaceae (incl. cereals)	46-47	97	94	99	Meadow and woodland complex	Faecal samples (vol %)	Homolka, 1982
Green herbs	5-6	3	4-6	1	Czechoslovakia		
Seeds & grains	0	+	2	+			
Woody herbs	7-23	+	0	0			
Needles (Picea)	15-32	+	+	+			
Bark	8-10	+	+	+			
Zea mays	0	+	5-40	0	Intensive arable farming	Faecal samples (% relat. abund.)	Chapuis, 1990
Triticum sativum	85-98	78-92	5-75	80-90	France		
Seeds of grasses	0	0	0-18	0			
Inflorescence of grasses	0	0-5	5-42	0			
Other grasses	5-18	2-18	2-40	5-15			
Green herbs	+	1-5	1-12	0-5			
Monocotyledon, cereals	25-65	35-50	8-25	25-50	Agricultural area and golf course	Stomach samples (vol %)	Hansen, 1990
Monocotyledon, wild and domestic grasses	25-60	22-25	25-30	35-55	Denmark		
Dicotyledon, wild herbs	2-4	8-20	12-26	3-5			
Dicotyledon, crops	0	0-15	18-45	2-3			
Bark, twigs and buds of trees and shrubs	2-14	0-4	0-2	1-2			
Seeds and fruit	0-3	0	0-3	0-1			

nutritionally stressed pregnant and lactating hares (Hackländer et al., 2002b). Only Homolka et al. (1988) and Nesvadbova & Zejda (1989) quantify biomass production and consumption of hares, applying useful data for energetic modelling. For mountain hare diet choice was well correlated with crude protein and phosphorus content (Lindlöf et al., 2004). No such analyses of feeding strategy have yet been conducted for the European hare. However, Smith et al. (2005b) found that in pastoral landscapes seasonal differences in active range size could not be explained by variation in nutritional quality.

To a large extent research on diet composition confirms the findings of researchers studying the impact of landscape change. Especially in some periods of the year previously selected food items have become rare due to the use of herbicides. This factor may account for part of the population decline in hares. Extension of home range to maximise food diversity and quantity is of course an energetic trade-off. Nocturnal travel distances of more than the reported average of 3.9 km (Pepin & Cargnelutti, 1994) could be a problem, because feeding activity occupies as much as two-thirds of the night-time during winter (Homolka, 1986b; Hansen, 1996).

Weight and growth pattern of the European hare is given by Pielowski (1969, 1971b) stating that body weight increases until the fourth year. Leverets are borne precocial with full fur and open eyes able to maintain normothermic body temperatures from the first day of life, even at temperatures as low as minus 8°C (Hackländer et al., 2002). Juveniles may reach maturity already at the age of 4-6 months, enabling early female offspring to breed in the year of birth (Caillol et al., 1992). Kidney fat deposits are high in full grown embryos but quickly decreases in new born leverets, reaching an absolute low in juveniles under 2 kg. This pattern emphasises the potential risk of mortality in juvenile hares due to limited energy resources (Parkes, 1989). Accumulating fat depots is an ultimate necessity for the ability of the hare doe to lactate. The seasonal changes of perirenal fat depots in hare does are induced by lactation. Depots build up from the weaning of the last litter of the year through winter reaching approximately 4 g in February, whereas non-productive (infertile) adult females reach depots of up to 18 g. Depletion down to zero occurs from early spring (1st litter) to midsummer (Pepin, 1987b; Parkes, 1989). The modern landscape, presumably with excess of food during winter, should improve the possibility of filling fat depots and secure lactation to a certain extent. However, the results on

perirenal fat depots of does show that depots are empty in the prime period of lactation, i.e. mid-summer (Pepin, 1987b; Parkes, 1989).

7.1 Nutritional ecology and physiological requirements

Little is published on the nutritional ecology and physiological requirements of the hare. The only option is adapting the present knowledge on rabbits, although this could be misleading. Nutritional recommendations for rabbits are shown in Table 8.

Table 8. Energy requirements and recommended nutrient levels for rabbits Adapted from Maertens & de Groote (1991).

Energy requirements and dietary composition. DM = 89-90 %	Reproduc- ing does	Young rabbits	Fattening rabbits
Maintenance energy requirements (kJ DE/kg MW/day)	420 - 460		
Digestible energy (MJ/kg)	> 10.5	> 9.5	9.8-10
Crude fibre (%)	> 11.5	> 15.5	> 14.5
ADF (%)	> 15	> 20	> 18.5
Indig. crude fibre (%)	> 10.0	> 14.0	> 12.5
Crude fat (%)	4 - 5	3 - 5	3 - 5
Crude Protein (%)	17.5 - 18.0	15.5 - 16.0	16.0 - 16.5
Lysine (%)	> 0.9	> 0.75	> 0.7
Starch (%)	free	< 13.5	free

The order Lagomorpha represent a group of mammals with a specialised digestive system filling in a niche between ruminants and the single stomach digesters, with or without hind gut fermenting, sometimes refereed to as pseudo-ruminants. The reason for this naming is the ability to ferment plant fibre in the large caecum (40% of the digestive system), followed by oral reingestion of faeces (coprophagy) from caecum material. Caecum selectively admits only fine fibre, coarse fibre being excluded and excreted in day faeces. Coprophagy allows these animals to capture microbial protein and vitamins like the ruminant system where fermenting takes place in the rumen before the enzymatic degradation of protein in the abomasum. Volatile fatty acid (VFA) absorption covering approximately 30% of resting metabolism in rabbits, and bacterial nitrogen contribution to total nitrogen intake is up to 24%. The adaptive advantage of this digestive system is probably to overcome the limiting effect of rapid rate of food passage, due to high energy demand relative to the small size of their gastrointestinal tract. This strategy permits these small sized animals to consume fibre, improve nitrogen supply and still be able to maintain a high level of energy

intake (van Soest, 1996; Gidenne, 2003). Recent research focuses on the need for cellulose and lignin in rabbit diets to prevent incidence of diarrhoea. Most young growing plants contain less than 5% lignin, the recommendations in rabbit diets being at least 5% of dry matter (DM) (Gidenne, 1997). These findings might be associated with possible nutritional problems of hares due to the high quality of culture grasses used in modern pastures. Results on

rabbits show a sharp decrease in caecal VFA production after only few hours of starvation (Gidenne, 1997), which may be relevant to the possible situation of starvation of hares during summer.

If the summer food limitation hypothesis is to be investigated an important step would be to create a frame of reference in terms of nutritional need of the hare.

8 Discussion and conclusions

Despite considerable research effort populations of the European brown hare have been declining throughout Europe since the early 1960s. The hypothesised causal factors for the decline are numerous and act via resource availability, reproduction and survival.

One of the hypotheses suggested as a key factor in understanding the present living conditions of the brown hare is the possible shortage of food in the modern cereal dominated agricultural landscape during the summer. The introduction of herbicides in agricultural management has markedly reduced the biomass of weeds, providing the potential for a summer food bottleneck or brake in food continuity. Changes in the agricultural landscape towards pronounced use of wintergreen crop types seem to have postponed minimum resource availability from the winter period to the central reproductive period. If true, this situation has distinct effects on population dynamics. Previously, seasonal variation in resource availability with summer-high and winter-low was well adjusted with the main reproductive output through spring and summer resulting in high density in autumn before onset of the hunting period. In this situation the majority of mortality factors, hunting included, were compensatory, only taking the surplus and thus reducing density according to the pre-winter drop in resource availability. In the modern landscape the situation may be reversed with low resource availability in summer and high during winter. Hence, the food resources available to the new generation of hares cannot support them resulting in low survival and eventually autumn densities far lower than the resource availability allows in this period. As a consequence most mortality during autumn and winter including hunting act as additive factors, with an elevated risk of reducing next years breeding population.

The advantage of this hypothesis is that it allows for all kinds of intermediate situations according to landscape and resource availability, explaining the fact that high density and stable hare populations still exist in certain parts of Europe, e.g. the marshland. The hypothesis also explains why it is often noticed among hunters that the spring density of hares is reasonably good, but at the onset of the hunting season the density is very low. The hypothesis does not rule out the possibility of predation and anthropogenic mortality being important

for hare populations, but focuses on the possible change from acting as compensatory to additive. Mortality factors as hunting and predation become additive when population density is beneath carrying capacity, linking the functionality of mortality to resource availability. In this case the population will not compensate by reducing natural mortality or raising reproduction and the additive mortality will result in a reduction of potential breeding stock. Hence, the relationship between resource availability, reproduction and survival is central for the hypothesis, rather than concentrating on the immediate cause of mortality. Considering reproduction the present knowledge indicates that regulation occurs primarily through the number of litters, more than through litter size or proportion of females not reproducing. However, female hares apparently do not maximise the number of litters. With a minimum period of 38 days between births, superfoetation included, and a reproductive period of 8-9 months, 6 litters in a reproductive season should be possible even in the Northern Temperate Zone, but the observed average number of litters range from only 2.3 to 3.5. A possible explanation to these divergences would be that resources limit the number of litters, lactation draining fat depots of female hares postponing ovulation until a minimum level of internal energy stores are rebuilt. Given that resources are limited for the stationary young leverets in the summer period, a demand for extension of the lactation period could also prolong the duration between births and reduce the number of litters. If prolonging the lactation period is not possible due to the nutritional condition of the adult female, leverets are forced to early roaming exposing them to predation. Resources and predation can also be linked if lactating females are forced to extend their home range to find sufficient food, thereby losing the ability to defend the young leverets. However, these hypotheses still have to be tested.

The impact of resource availability on survival is a key issue of the hypothesis, which predicts resource limitation in the modern agricultural landscape that reduce survival. Adult survival tends to be rather constant if excluding hunting (0.51-0.59); hence leveret and yearling survival which vary with a factor 3 are those of primary concern. In both cohorts evidence is given that survival is affected by bodyweight (Marboutin et al., 1990; Marboutin & Hansen, 1998), indicating that resource availability

does affect survival. Nevertheless direct evidence linking mortality to resource availability is still missing. The most difficult part of this is how to quantify resource availability. The only feasible way to attack this seem to be detailed habitat and food preference studies and botanical quantification of developing standing crop and food quality in preferred habitats of different landscape types.

A more indirect way to verify the hypothesis is to monitor survival of leverets and adults through seasons in contrasting landscapes. If true, summer and winter survival for both juveniles and adults should be contrasting. A capture mark and recapture set-up and analyses of reproductive tracts of females would be ideal, but would suffer from potential compounding effects of predation. A shortcut to verify seasonal variation in quality of food could be analysing the relation between urea nitrogen and urinary creatinine as done by Villafuerte et al. (1997) in cottontails.

Despite the forwarded hypothesis it can not unequivocally be ruled out that the low survival seen in most European hare populations today could be caused by predation. The only evidence contradicting this is that fertility of adult female hares seems rather low in most European populations today. If predation rather than resource availability is the limiting factor one should suspect the remaining individuals to compensate via maximising fertility.

However, quantification of the relative impact of a range of single factors relating to anthropogenic influences and predation have either not been investigated at all or only superficially. Management related factors as supplying slurry, artificial watering or mechanical weeding in organic or conventional arable farming have the potential to increase mortality to new-born leverets, and thus be important in understanding the living conditions of hare populations in the modern landscape. Traffic is another human introduced impact, which has been proven to add to overall mortality in juvenile and adult hares, but in fact we don't know if this relationship is also representative of changes in population size. The consequences of the ever-increasing intensity of traffic are not known either. Clearly all these factors of potential mortality interact. Interaction between agricultural practice and predation could also be suspected as almost all cover is re-

moved over the short cereal harvest period, exposing new-born leverets to avian and mammalian predators.

In short, the most central issue of future research is quantifying the impact of resource availability on the pattern of survival. This may sound concrete and easy to approach, but in reality it involves multiple interacting factors. Hence some sort of integrative modelling is required. Modelling and analysing demographic parameters and plasticity is interesting, equipping us with a useful knowledge on the sensitivity of population growth given certain variations in reproduction and survival. For instance Marboutin & Peroux (1995) could point out the importance of the age structure in the sensitivity of growth rate to changes in maintenance and recruitment. However, not integrating resource availability, the question - why? – can unfortunately always be asked.

A more promising way to improve our understanding of the multifunctional character of the decline of the European hare is the use of mechanistic modelling (Topping & Odderskær, 2004; Topping et al., 2004b). Integrating resource availability, ecology, behaviour and environment in one model permits simultaneous evaluation of a range of factors impacting animals. By developing a model of this type for the hare it will be possible to include the impacts of farm management, landscape structure, hunting, predation, and climate in a single model for specific landscape configurations. In this way the relative impact of different factors may be determined and synergistic or antagonistic effects may be identified. The consequences of the forwarded hypothesis of a changed seasonal pattern of resource availability in the modern landscape and derived shift from compensatory to additive mortality should also be possible to evaluate in such a model. If successful, this approach could be used to test future management strategies for hares.

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9 References

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Despite considerable research efforts populations of the European brown hare (*Lepus europaeus*) have been declining throughout Europe since the early 1960s. The hypothesised causal factors for the decline are numerous and act via resource availability, reproduction and survival. Based on a systematic review of the literature the potential causes are discussed and a hypothesis for the underlying cause of the decline is suggested as are future research priorities. Recognising that multiple factors are interacting, modelling integrating resource availability, ecology, behaviour and the environment is required in future research.