

Crucial periods for brown hares (*Lepus europaeus*) in a multi predator environment with regard to their seasonal energy demand

Research report

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Summary:

Agricultural intensification is thought to be the main reason for the hare population decline. Agricultural intensification causes loss of landscape diversity- and quality and improves the accessibility- and impact of predators on hare populations. Hare numbers are positively associated with landscape diversity, also their body condition seems to be better in areas with high diversity. Available data suggests that hare numbers have declined in areas where the landscape has been simplified by field enlargement and block farming.

Along with intensification of agriculture, predation is the most mentioned cause for hare declines. There are two pathways through which predation can influence the density of prey species; these are direct predation and predation pressure or risk effects. The main predator of the brown hare in Europe is generally acknowledged to be the red fox (*Vulpes vulpes*), which has increased strongly in Europe during the last 50 years. The diet of the red fox consists between 3-46 % of brown hare, depending on the region and the number of hares and foxes present in this region. The Game Conservancy in the UK estimates that a family of foxes would consume 33 adult hares annually, which is in coherence with other researches. It is found that most young hares are taken by foxes in spring and summer. Adult hares seem to be more vulnerable to predation in mainly spring and winter.

Increased predation pressure most likely occurs in the period where red fox reproduce. The food intake of a vixen during gestation increases approximately by one fourth, and during lactation her food requirement doubles. This increase of food intake by the vixen together with growing young means that red foxes will have to forage more often than under normal circumstances, which would mean that predation pressure is much higher during this period.

European brown hares have high energetic costs of reproduction, mainly due to precocial, rapidly growing young that rely largely on energy-rich milk. When the total litter weight increases, milk production of lactating females does not increase as fast as the body weights of the young. These findings suggest that female hares, like other mammals, may face a physiological limit of energy throughput during peak lactation. In order to fulfill in the needs of the young, hares build up fat stores during winter, and may even partly restore fat depots during the non-reproductive period or during gestation in the breeding season. Milk fat partially originated from maternal fat stores, particularly in spring. Leverets have highest food intake in the 4th and 5th week of lactation. In the 5th week almost half of their food intake is from solid food, which means they have to spend much time foraging for food. This makes the leverets most vulnerable to predation and starvation in these last weeks of lactation.

An increase of predator population numbers in the habitat of the brown hare can reduce their density, especially when this is combined with disease, hunting and/or habitat changes like the harvesting of crops. Hares have to deal with fluctuation of food availability, temperature and predation pressure. These factors go together with fluctuations in energy demand throughout the year. When this energy demand is not met it leads to hares facing crucial periods in a year.

It is found that brown hares have an impeccable need for habitat heterogeneity, and that with a modification of agriculture the crucial periods for brown hares will become increasingly difficult to overcome. Predators create great crucial periods during the breeding period, starting from the second half of spring. Energetic crucial periods were found with regard to reproduction and were found most critical in summer and autumn.

Preface:

We would like to thank Martijn Weterings for giving us the opportunity to participate in his research on the brown hare. We also want to thank our supervisors Theo Meijer and Okka Bangma for their guidance and great commitment during our entire research.

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Table of Contents

1. Introduction.....	5
1.2 Goal	6
1.3 Research questions.....	6
1.3.1 Ecological Niche.....	6
1.3.2 Predation	6
1.3.3 Energetics	6
2. Material & Methods	7
2.1 Data sampling.....	7
2.2 Data analyses.....	7
3. Results	8
3.1 Ecological niche	8
3.1.1 Habitat preference	8
3.1.2 Survival rates	11
3.1.3 Hare density in different landscapes during different seasons.....	12
3.1.4 Litter quality and body condition in relation to habitat.....	13
3.1.5 Food preference	14
3.2 Predation.....	14
3.2.1 Hunting bag records (1961-2009)	15
3.2.2 Distribution of the red fox.....	16
3.2.3 Effects of (direct) predation	17
3.2.4 Effects of predation pressure	21
3.3 Energetics	22
3.3.1 Energetic costs of reproduction	23
3.3.2 Energy expenditure of females, males and young hares	23
3.3.3 The role of ambient temperature on energy expenditure.....	24
3.3.4 Energetic costs of lactation	25
3.3.6 Influence of high- and low fat diet on lactating hares	27
4. Discussion	29
5. Recommendations.....	34
6. References	35
Appendices	

1. Introduction

Brown hares (*Lepus europaeus*) are widely distributed throughout Europe, except for the North of Scandinavia and Island, and throughout the Middle East to Central Asia (also see fig. 1). They have also been introduced in other parts of the world, such as Canada, the United States, New Zealand, and South America. (Lincoln, 1974; Broekhuizen and Maaskamp, 1980).

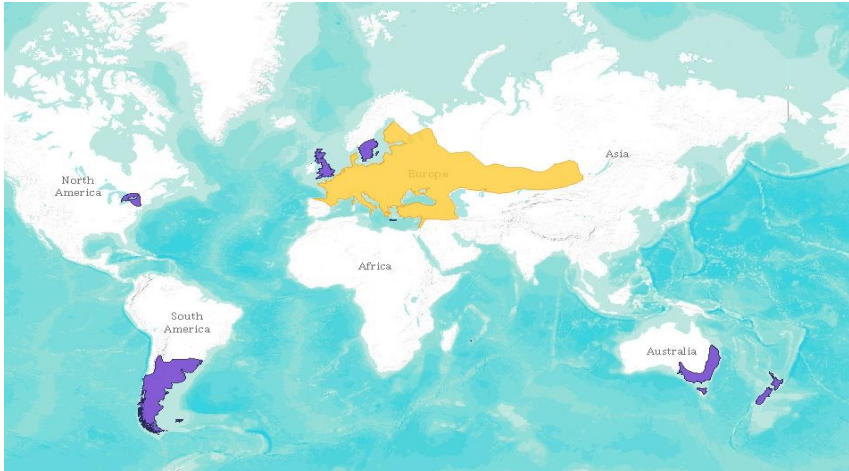


Fig. 1: Distribution of the brown hare. Yellow shows the natural habitat of the brown hare, purple shows where this species is introduced (IUCN, 2013).

Since the 1960's there has been a consistent decline in brown hare population numbers in Europe, according to hunting numbers (Edwards, 2000; Smith et al., 2005). Hunting records indicate a dramatic decline in population numbers during the period 1960-1990 in the UK, Sweden, Denmark, the Netherlands, Germany, Luxembourg, Bulgaria, Austria Poland, Slovakia and Switzerland. (Broekhuizen, 1982; Edwards et al., 2000; Schmidt et al., 2004; Smith et al., 2005; Jensen, 2009; Tapper and Yalden, 2010). In the Netherlands, more recent data shows that the population is stable or even slightly increasing since the late 1990's (NEM, 2013).

Multiple in- and external factors have effect on brown hare population dynamics. Figure 2 shows a conceptual model of all factors influencing the population dynamics of brown hare. The loss of landscape diversity- and quality is a result of agricultural intensification and improves the accessibility- and impact of predators on hare populations (Edwards, 2000; Smith et al, 2005). Much research has been conducted on the influence of agricultural intensification and loss of associated habitat diversity- and quality. And although some studies have been conducted on the impact of predators on brown hare population numbers, it remains unknown what the precise effects are. An increase of predator population numbers could reduce hare densities, especially when this is combined with disease, hunting and/or habitat changes like the harvesting of crops. These habitat changes could lead to fragmentation of the landscape and reduce the effectiveness of the hiding of leverets in between vegetation from predators (Cowan, 2004; Smith et al., 2005). These factors go together with fluctuations in energy demand throughout the year. When this energy demand is not met it could lead to hares having crucial periods in a year. Crucial periods, in this research, are defined as periods where hares are heavily affected by limiting factors on their survival and/or reproduction

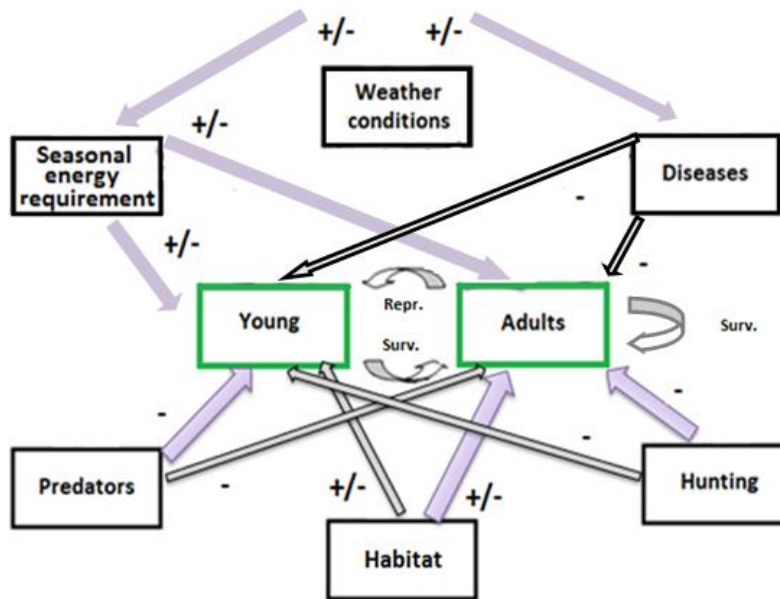


Fig 2: Conceptual model of brown hare population dynamics. The different factors that influence the brown hare survival may be either positive or negative. The thick arrows represent an estimation of factors with high influence on survival and the thin arrows show a minor influence on survival. Reproduction, young survival and adult survival are given. Hares are counted as young until they reach sexual maturity (>8 months). More arrows could be drawn in between the different factors.

1.2 Goal

This research focuses on the impact of predation (and predation pressure) on brown hares (adult and young) in a multi predator environment, in relation to the seasonal energy requirement of hares. It will thus give an insight in the crucial periods for the brown hare within a year and it will broaden the knowledge about the role of the main predators on hares.

1.3 Research questions

What are the crucial periods for the brown hare (*Lepus europaeus*) in a multi predator environment with regard to their seasonal energy demand?

1.3.1 Ecological Niche

- What is the ecological niche (habitat) and food preference of the brown hare during the four different seasons?

1.3.2 Predation

- In which seasons of the year are predators most abundant in the habitat of the brown hare and therefore is the impact of direct predation at its largest?
- What are the effects of predation pressure on brown hare population dynamics?

1.3.3 Energetics

- What is the seasonal energy demand of the brown hare (male/female/leveret)?

2. Material & Methods

2.1 Data sampling

This research focused on the crucial periods for a brown hare in a year. To get a good insight in the different factors causing these crucial periods, information was gathered about the ecological niche of the brown hares, the main predators of the brown hare, the effects of predation, and the energy demand of the brown hare. This research focussed on the hare populations in Europe, therefore all data were gathered from studies carried out in Europe. All data were classified in four seasons (spring, summer, autumn and winter).

- In this research the ecological niche of the brown hare was divided in: Habitat preference, survival rates, hare density in different landscapes during the four seasons, Litter quality and body condition in relation to habitat, food preference, and in home range.
- Information was collected about most important predators of the brown hare. Data about the social structure, home range, food requirement and preference, and distribution of the concerning predators were gathered from 1946 until now. Data was gathered about the influence of direct- and indirect (predation pressure) predation on brown hare population.
- In order to get a good insight in the energetic demand of brown hares (male, female and leverets) during different seasons, firstly data was gathered about the reproductive system of the brown hare. Data was taken from studies that focused on the energetic costs of reproduction and lactation for female hares. Also the milk intake of leverets was taken into account in order to see how high energetic needs are during the first weeks after birth. The role of ambient temperature was also investigated because this has a significant effect on the energetic costs of brown hares.
- Beside these main points information was collected about the effects of hunting, disease and weather conditions.

2.2 Data analyses

This study is a quantitative research. All information is gathered from existing literature. The results are divided in three different subjects: ecological niche of the brown hare, predation and energetic demand. A distinction will be made between adult males, adult females, and leverets, with a focus on the different life stages (in energy requirements).

In this research we used the four different seasons as periods to present our findings. We used the meteorological method to index the four different seasons: Spring starts on 1 March, summer at 1 June, autumn at 1 September and winter at 1 December (KNMI, 2013).

3. Results

3.1 Ecological niche

One of the most mentioned reasons for the decline in hare numbers in several European countries is the intensification of agriculture, which leads to a loss in habitat diversity (Smith et al., 2005). A study of Bertóti (1975) showed that following the modification to a monoculture, hare density was reduced by almost 90% in Hungary. In Bulgaria the decline of hares started at the same time and in the same areas as where habitat diversity decreased (Petrov, 1976). In such areas food availability decreased during the summer as crops reach maturity simultaneously and alternative food resources are not available because of the loss of hedgerows and fallow land (Frylestam, 1980a; Frylestam, 1986; McLaren, 1996).

In the text below the ecological niche of the brown hare in Europe will be shown. The niche of a species is defined as the functional role and position of the species in its community (Sinclair et al., 2006). This paragraph will focus mainly on the habitat preference of the brown hare in Europe and density in different habitats. Multiple studies and books were combined to give an insight in the home range, density in different habitats, survival rates and habitat preference of the brown hare in Europe during different seasons.

3.1.1 Habitat preference

Tapper and Barnes (1986) performed a two year study on the influence of farming practice on the ecology of the brown hare. In this research the movements of individual hares were studied by radio-tracking on a mixed arable farm, and these numbers were compared with farming patterns at 9 farmland sites in different parts of England. The study farm was a mixed arable and livestock enterprise of approximately 650 ha. Wheat and barley covered 50% of the ground, most of the remainder being grass. Some of the grass leys were strains of ryegrass grown for seed or for silage, to be used later as pastures. Other leys, mostly established by under sowing, were mixtures of grass and wild white clover for cattle and sheep grazing. Permanent pastures represented only 6% of the farm area. Turnips and kale were regularly sown into 40 ha of cereal stubbles as winter fodder for sheep and cattle.

Figure 3 shows that in this research (Tapper and Barnes, 1986) hares had a preference for pasture landscape during spring and summer, with respectively 58 and 66% against 37 and 17% of arable landscape. In winter, hares had a preference for arable landscape, with 63% against 22% of pasture landscape. In autumn the hares were equally distributed over the two landscape types, with 43% of hares in pasture and 37% in arable landscape. The hares preferred to feed on short crops and their preference for cereal declined as crops grew, meaning hares shifted their activities between fields according to crop size. Pastures were important feeding areas throughout the year. Woodlands and hedges were used most frequently by day since this was primarily a sheltering habitat (see figure 3). Smith et al. (2004) suggests that hares select a variety of habitats for both feeding and resting throughout the year, as found by Tapper and Barnes (1986). When habitats were suitable for both, hares often used the same one for feeding and resting, as found by Reitz and Léonard (1994) and Marboutin and Aebischer (1996). This study showed that for most of the year hares did not select arable habitats over other habitat types, but instead they selected pasture grazed by cattle and fallow land, for both foraging and resting. Hares selected arable habitats (cereal and grass ley crops) above others only when crops were short and suitable to eat, a preference also found by Tapper and Barnes (1986).

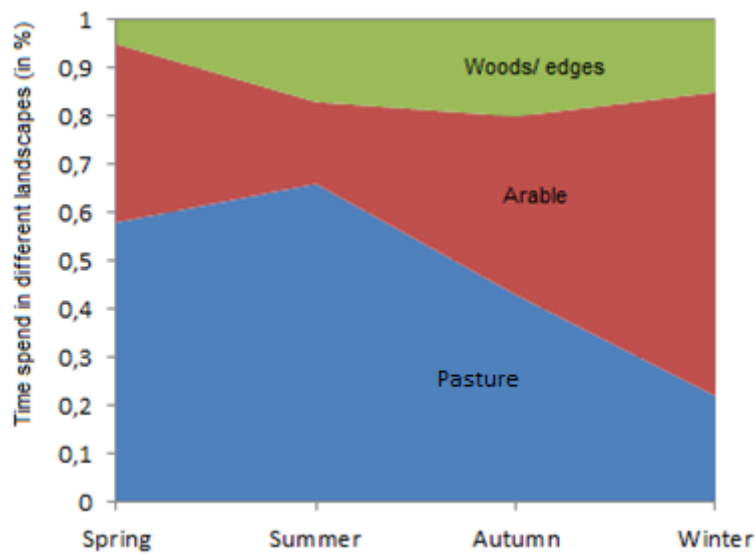


Fig. 3: Time spend in different landscape types by radio fixed hares (N=15) in four seasons during 1981 and 1982 in the UK; average of 2 years. The area shows pasture landscape (long grass, grass with livestock and grass without livestock), the red area represents arable landscape (winter cereal, spring cereal and stubble turnip), the green area represents woods and edges (data obtained from Tapper and Barnes, 1986).

Preferences for the different crop types in the arable landscape, given in figure 3, are shown in figure 4. The most important area for hares from October to May on arable farms in France and the UK are winter cereals and this also expected for the rest of Europe, see figure 4 (Chapuis, 1990; Marboutin and Hansen 1998; Tapper and Barnes, 1986). In the study of Tapper and Barnes (1986) hares were recorded on winter cereal fields for almost the entire year (except for August and September), with a peak in winter (63%) and on it's highest in January (80%). Stubble turnip was used at night for feeding when it was short in the early stages of its growth, but as it became longer it was used primarily during the day as cover.

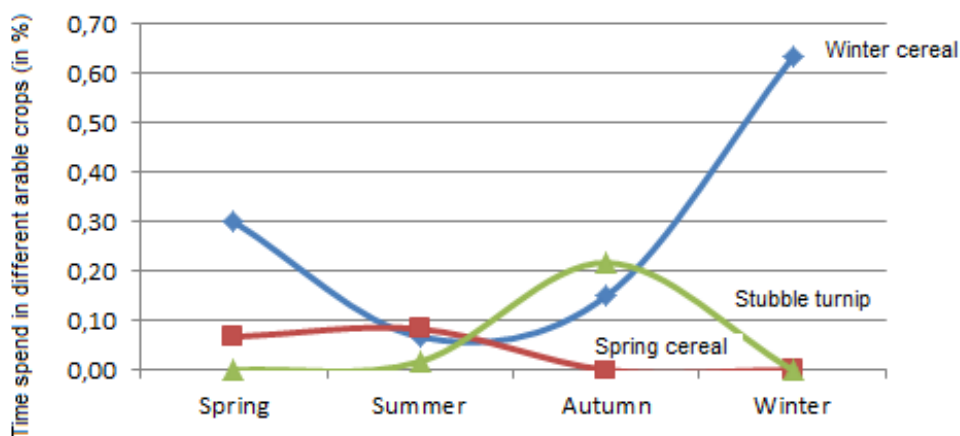


Fig.4: Time radio fixed hares spend (%) in different arable crops (N=15) in four seasons during 1981 and 1982 in the UK; average of 2 years. The blue line shows winter cereal, the red line shows spring cereal and the green lines represents stubble turnip. The total percentages of the three arable crops represent the red area in figure 3 (data obtained from Tapper and Barnes, 1986).

Preference for the different grass types in the pasture landscape, given in figure 3, is shown in figure 5. Second most important forage areas for hares in the UK are grass fields without livestock (also shown in figure 5), especially when winter cereals are not available during summer and early autumn. Hares were found in grass field with- and without livestock during the entire year. Respectively 35% in spring, 27% in summer, 35% in autumn and 12% in winter (see figure 5). Long grass fields and fields with livestock were also used primarily at night as feeding areas and little during the day. How often these grass fields were used during the year can also be found in figure 5 (Frylestam, 1976; Tapper and Barnes, 1986).

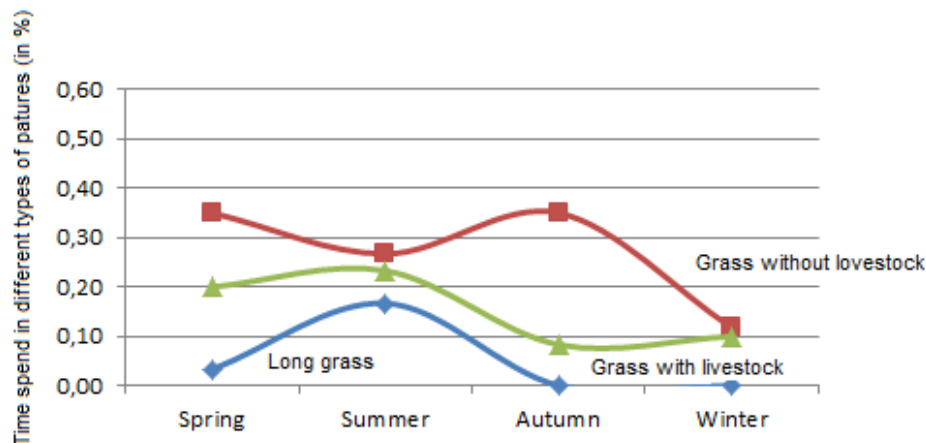


Fig 5: Time ratio fixed hares spend (%) in different types of pastures (N=15) in four seasons during 1981 and 1982 in the UK; average of 2 years. The blue line shows long grass, the red line shows grass without livestock and the green line represents grass with livestock. The total percentages of the three grass types represent the blue area in figure 3 (data obtained from Tapper and Barnes, 1986).

Hares seem to have two basic ecological requirements. Firstly, a feeding area which is usually open ground with a short growing crop, secondly a resting area which may also provide shelter if it is a tall, dense crop, hedgerow, or woodland (Broekhuizen and Maaskamp, 1980; Tapper and Barnes, 1986). Hares mainly feed at night in a different area from the place where they shelter during the day. This results in some hares moving between habitats daily. The kind of crop or habitat used by hares during the day was also influenced by weather. They sought shade in sunny weather in summer and at this time 52% of radio fixes were in long crops or hedges, whereas during rainy weather only 21% of fixes were in such habitats. In winter during sub-zero temperatures in daytime 55% of fixes were from long crops or woods and hedges, whereas in warmer weather only 33% of fixes were from such habitats (Tapper and Barnes, 1986; Tapper and Yalden, 2010).

Brown hares prefer edge habitats (Tapper and Barnes, 1986; Pépin, 1989; Goszczyński and Wasilewski, 1992; Reynolds and Tapper, 1995; Roedenbeck and Voser, 2008; Tapper and Yalden, 2010) and especially edges toward tree stands, which appear to have a positive effect on the growth of the hare. Also the mean condition of female hares in Denmark was positively affected by the coverage of grass-leys and the amount of edge habitat towards tree-stands in the sampling area (Jensen, 2009). This is probably because there is more suitable food available in these areas when crops mature and hares are able to switch onto younger vegetation nearby. In all seasons, except winter, but particularly during the spring and summer, hares avoided both short, even vegetation and pasture grazed by sheep (characterized by a short homogeneous structure) (Smith et al., 2004; Benton et al. 2003). This suggests that during the main part of the breeding season, hares select habitat structures that provide more cover from predators and unfavourable weather conditions (Tapper and Parsons 1984; Smith et al., 2004; Jennings et al., 2006).

3.1.2 Survival rates

Leveret survival is estimated at 0.25-0.50 in an arable landscape, depending on particular year and the farming area (also shown in figure 6) (Pépin 1989). Average survival rate in arable landscapes is estimated on 37%. Survival rates in a mixed agricultural landscapes and mainly pasture landscapes were respectively 0.23 and 0.18 (Frylestam 1980a). The lower survival rate in pasture landscapes is partly caused by the fact that these areas normally support higher numbers of red fox than arable landscapes and because there is little cover for weather conditions (Webbon et al., 2004). In appendix I, II, and III life tables of the (female) brown hare are given for respectively arable-, mixed-, and mainly pasture landscape. For these life tables a starting population of 1000 females was set, and corresponding leveret survival rates (birth to first autumn) were used. For calculating the proportion of original cohort surviving, survival rates for adult females (0,57) given by Jensen (2009) were used. An average of three surviving offspring per female per year was set to calculate the total number of surviving offspring per year (Broekhuizen, 1982). The number of female and male hares being born is estimated to be equal (Broekhuizen, 1981; Jensen 2009). Through dividing the total number of offspring by two, the total number of female offspring after a period of 8 years could be given. The total number of female offspring after 8 years in arable, mixed-, and mainly pasture landscape were respectively 1277, 795, and 621. This suggests that in mixed- and pasture landscapes the number of females would reduce with respectively 20 and 38% in a timeframe of 8 years. And in arable landscape the number of females would increase with almost 28% in a timeframe of 8 years. These results are only calculated numbers based on known survival rates of leverets and adults of different countries, and therefore population changes might be slightly different in different countries. But they clearly show that the large production of young hares and their survival is crucial for the existence of the brown hare. The life tables in the appendix show that when leveret survival rates are high, the age at which adult females die has almost no effect on the total population change.

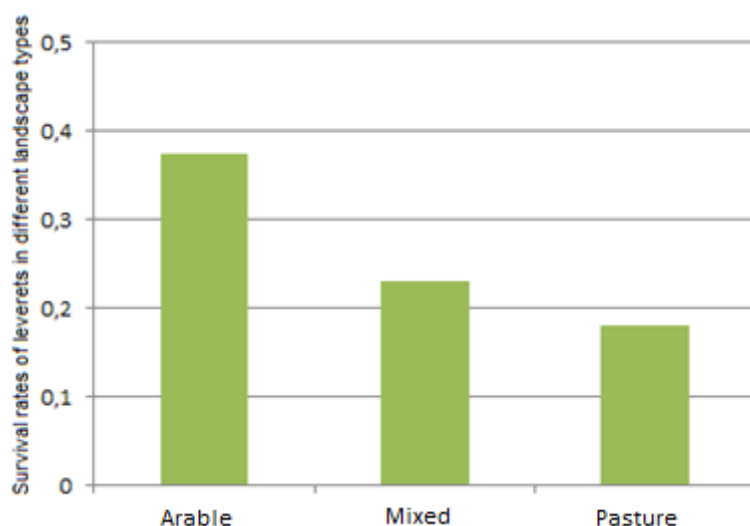


Fig. 6: Estimated leveret survival rates in different landscape types. The survival rates are given as percentages of total annual leveret production per year (data obtained from Pépin, 1989 and Frylestam, 1980b).

Jensen (2009) estimated the survival rates of leverets to be approximately 14%. Leveret survival rates in Poland, Bulgaria and Sweden were expected to be respectively 20-30% (Pielowski and Raczynski, 1976), 25% (Petrov and Dragoev, 1962) and 22% (Frylestam, 1980b). Adult hare survival rates in Denmark are estimated to be approximately 40% for males and 57% for females

(also shown in figure 7) (Jensen, 2009). Broekhuizen (1979) estimated leveret survival rate to be 23%. Adult survival rates in the Netherlands were estimated to be approximately 45% for females and 38% for males (also shown in figure 7) (Broekhuizen, 1979). Marboutin and Hansen (1998) found that the survival rates of males and females in an area without predators were respectively 0.50-0.61 and 0.44-0.56. Female survival rates were not significantly influenced, but this would mean that males, on average, have 10 to 21% higher survival rate in an area without predators than in an area with predators. It is expected that males have lower survival rates than females because they disperse further and move more between different habitats, which could possibly increase the chance of being eaten by predators such as the red fox (Broekhuizen, 1979; Jensen, 2009).

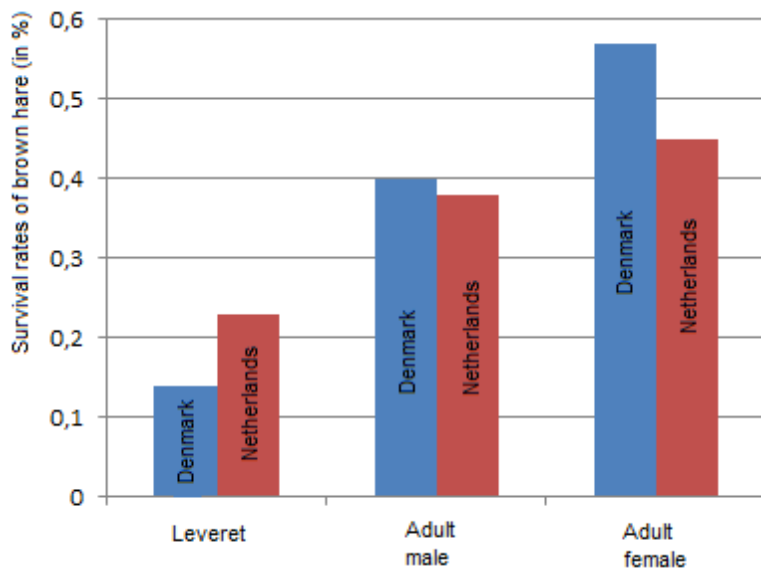


Fig. 7: Estimated survival rates of leverets (birth to first Autumn), adult males (older than 1 year), and adult females (older than 1 year) in Denmark and the Netherlands (Broekhuizen, 1979; Jensen, 2009).

3.1.3 Hare density in different landscapes during different seasons

Hare numbers are positively associated with landscape diversity. Available data suggests that hare numbers have declined in areas where the landscape has been simplified by field enlargement and block farming (Tapper and Barnes, 1986). As can be seen in figure 8 and 9, hare populations in pasture landscapes in the UK are very low compared to arable landscapes in spring and autumn (McLaren et al., 1997). Reasons for this may include grassland improvement, leading to higher stock density, leveret mortality from silage cutting and digestive problems from cultivated grasses (McLaren et al., 1997; Frylestam, 1986).

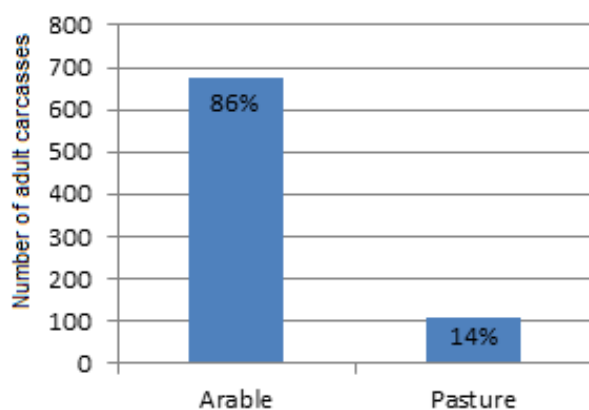


Fig. 8: Sample sizes (expressed as numbers of adult carcasses; total N = 808) among two farmland types in England and Wales between 1997- 2000. Percentages are of total number shown; levels of variables from which < 5% of hares originated are not shown (data obtained from Jennings et al., 2006).

Population densities of brown hare in Europe are estimated to range from 0.1/ha to 3.4/ha (IUCN, 2013). Figure 9 shows a hare density ranges from 16 hares per 100 ha in a pasture landscape to 48 hares per 100 ha in an arable landscape. European hares in the UK are positively associated with arable habitats. This is shown by the lower hare densities in pasture landscapes than in mixed and arable habitats, also mixed habitats have lower hare densities than arable habitats (also see figure 8 and 9)(Pépin, 1985, 1987; Marboutin and Aebischer, 1996). It seems that when pasture habitat makes up a small proportion of the landscape, its effect is positive, but wide-ranging pasture has a negative effect (Petrak, 1990; Hutchings and Harris, 1996). The variation in density with habitat type throughout Europe shown in figure 8 agrees with findings of individual studies comparing densities in different habitat types (Frylestam, 1976; Hutchings and Harris, 1996). However, Smith et al. (2005) found that density was similar in arable and mixed habitats in autumn (also see figure 9), but that in spring mixed habitats had lower densities than arable habitats. This suggests that winter survival rate is lower in mixed habitats than in arable habitats. It also suggests that mixed habitats have higher reproduction rates and/or survival of young than arable areas, since they reach a similar density by the end of the breeding season. Hares from pasture areas are generally smaller, lighter and have less fat than those from arable areas, this is because they probably spend more energy on foraging and are unable to maintain body condition as well as those from arable areas (Goszczyński and Wasilewski, 1992; Jennings et al, 2009).

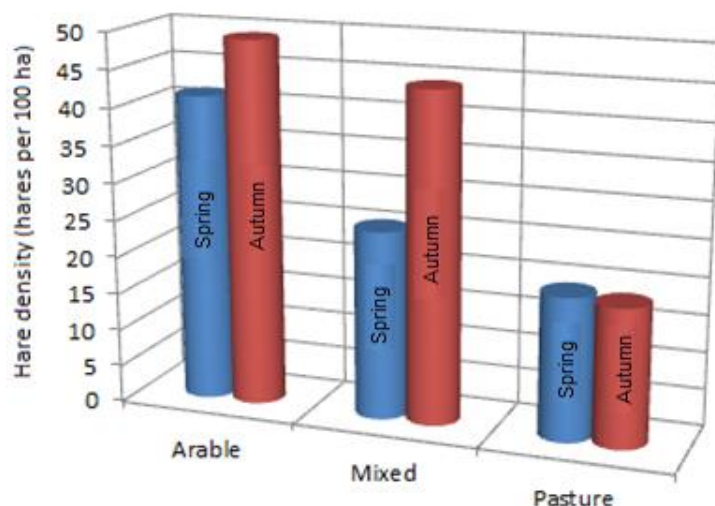


Fig. 9: Hare density (hares per 100 ha) in spring and autumn among different landscapes. The blue bars represent spring, the red bars represent autumn. This figure shows the average hare density (hares per 100 ha) within each landscape type. Results of 77 research papers from 12 European countries are summarized (data obtained from Smith et al., 2005).

3.1.4 Litter quality and body condition in relation to habitat

Jensen (2009) found that brown hares rely heavily on habitat quality during the breeding period. Females in heterogeneous habitats are likely to produce more litters, larger litters and/or larger off-spring at birth. This was also found by Vaughan and Keith (1981). Frylestam (1980b) found that lighter hares produced fewer litters, and similarly, Jennings et al. (2006) found poor body condition and lower reproductive output in hares in pasture areas compared to arable areas. This is also in accordance with the results of Goszczyński and Wasilewski (1992), who found that hares from pasture areas are generally smaller, lighter and have less fat than those from arable areas. Frylestam (1980b) noted that hares living in low landscape-diversity areas had higher mortality rates and lower body weights than hares living in more diversified landscapes, and that lighter hares produced fewer litters.

3.1.5 Food preference

The brown hare prefers parts of weeds and grasses with high energy content (Frylestam, 1980a). This high energy content is not only of great advance for the energy assimilation but also foraging may decrease and therefore the predation risk. If the energy content of this food is high, the animals have to eat less which means the weight of the ingested load is lower than when these animals are feeding on food containing low amounts of energy. Without this extra load hares are logically faster and also should be able to outrun predators more easily (Hackländer et al., 2002a).

In Sweden, Frylestam's (1980b) study on seasonal differences in hare preference for different crops suggests that hares preferred grass fields in summer and avoided other arable crops at this time. He also suggested that hares may experience a food shortage in summer as crops mature in farming areas where large blocks of arable land contain the same crop. However, these observations were restricted to short crops only. Tapper and Barnes (1986) found that in the UK hares had a preference for pasture landscape during spring and summer. In this study grass was practically the only crop used by hares in late summer, which supports the data found by Frylestam (1980b).

3.1.6 Home range

At the beginning of the breeding season (late winter), during peak breeding (spring), females are searching for suitable sites in which to give birth and males are searching for females. Low levels of mating activity occur in summer and autumn (Lincoln, 1974). In these months Smith et al. (2004) found range sizes to be at their minimum. Brown hares have home ranges that normally range from 10 to 100 ha (Broekhuizen and Maaskamp, 1982). Within their home range, the need of have food availability all year round is necessary to cover the energetic costs. Crop and landscape diversity is important for availability of suitable nutrients (Tapper and Barnes, 1986). Tapper and Barnes (1986) gave an average range size of 38 ha (max. = 78 ha; min. = 16 ha), which is comparable to Broekhuizen and Maaskamp's (1982) results for hares living in arable and pasture landscapes in the Netherlands, with an average range size of 29 ha (max.= 72 ha; min.= 7,5 ha). The range sizes are calculated for individual animals that were radio tracked. The given ranges of 38 ha in the UK (Tapper and Barnes, 1986) and 29 ha in the Netherlands (Broekhuizen and Maaskamp, 1982) are shared by more than one hare (for density per 100 ha also see figure 9).

3.2 Predation

Along with intensification of agriculture, predation is the most mentioned cause for hare declines (e.g. Schmidt *et al.* 2004, Panek *et al.* 2006). Mammalian predators that feed on hares are the red fox (*Vulpes vulpes*), stoat (*Mustela erminea*), the wolf (*Canis lupus*) and the lynx (*Lynx lynx*). Avian predators are birds of prey, such as the buzzard (*Buteo buteo*), tawny owl (*Strix aluco*) and the goshawk (*Accipiter gentilis*). Avian predators normally feed on brown hare leverets (Tapper and Yalden, 2010). Scientific studies on the influence of predators on brown hare in general only focus on the red fox. This might be because the effects of other predators on hare populations are of low impact and so are rarely taken into account. Even though research is mainly conducted on the red fox, population numbers and distribution of avian predators show changes in the past 4 decades (See appendix IV, V and VI). The goshawk and the buzzard increased <5% each year since 1980. These avian predator species massively inhabited the Netherlands for the last 4 decades (also see appendix IV, V and VI) (Broekhuizen, 1992). Because there is too little known about the effects of other predators on brown hare populations, this research will focus on the influence of red fox.

The main predator of the brown hare in Europe is generally acknowledged to be the red fox (Pielowski, 1976; Von Schantz, 1980; Erlinge et al., 1984; Goszczyński and Wasilewski, 1992; Reynolds and Tapper, 1995; Jensen, 2009). In red fox the basic social unit is a pair, but a territory can have groups up to six members (usually one adult male and 2-5 possibly related females), depending on the habitat. Depending on the climate and habitat home ranges of red fox can vary from 10 to over 5000 ha (Macdonald, 1987; Voigt et al., 1987). Broekhuizen (1992) estimated home range of red fox in the Netherlands to be 100 ha for a pair. Mating occurs between December and February. After a gestation period of 49-55 days, the pups are born from March to May. Most females only have one litter per year. Lactation lasts for four weeks, and the pups are fully weaned at 6-8 weeks. They reach sexual maturity at 9-10 months. The proportion of breeding females in the group, and litter size (3-12 young per litter) which varies with food availability (Wilson and Mittermeier, 2009). Fox populations that are dense related to food resources are generally less productive than those that are less dense. Red fox populations do not rely on the density of the brown hare, given the range of alternative prey (functional predation response) (Cowan, 2004). The red fox is a generalist and also feeds on rabbits, birds and rodents (Dell'Arte et al., 2007). Research showed that red fox populations are increasing in Europe (also see figure 10) (Chautan et al., 1998). In the Netherlands, recent data shows that the red fox population is stable (also see appendix VII) (NEM, 2013).

3.2.1 Hunting bag records (1961-2009)

The Game and Wildlife Conservation Trust created an index of brown hare and red fox in the UK over a period 1961-2009 by using hunting game bags. Figure 10 shows that there has been a significant decline in hare hunting bags between 1961 and 2009, brown hare bags declined with 46% over this time period. This decline in hare numbers has been linked to the reduction of agricultural diversity through intensification, and the increased predation pressure as fox numbers increased. Since the introduction of set-aside and agricultural-environment schemes, that have restored some habitat diversity on farmland, there is a slight increase of hare bags in the last years (2000-2009).

Between 1961 and the early 1990s there has been a continuous increase in red fox hunting bags (see figure 10). Over the period 1961-2009 the fox hunting bag index has tripled. Changes in fox control methods, including the use of spotlights for night shooting and the banning of Cymag poison, have undoubtedly affected the size of the fox hunting bags. The rearing and releasing of game birds, like pheasants, has probably also improved food supply for red fox in autumn and winter.

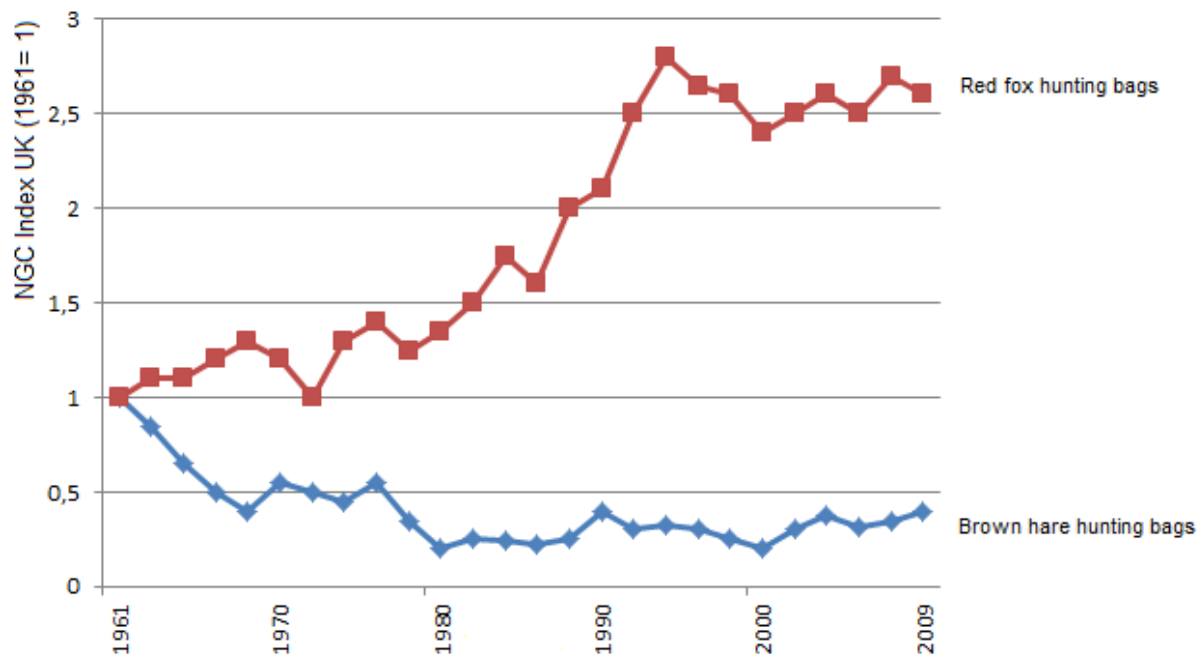


Fig. 10: National Game bag Census index of brown hare and red fox in the UK, change over time period 1961- 2009. The blue line represents the brown hare, and the red line represents the red fox. The small squares in the lines represent the different years

3.2.2 Distribution of the red fox

The red fox is distributed throughout Europe and other continents of the world and can be found in the most diverse habitats. For a generalist feeder such as the fox, habitat heterogeneity may be the main factor underlying a broad ecological niche. The preferred habitat of the red fox is mixed field-forest habitats, but Pielowski (1976) found that around the 1970's the fox was also settling in open farmland in western Poland. In central Poland Goszczyński (1985) found that all of the fox's breeding dens were located in forests, and the searching intensity on farmland was at least several times smaller at distances 2 km away from forest than in nearby forest. Around the 1970's, 43% of breeding sites in western Poland were found in farmland, although no breeding dens located in crops had been recorded at that time (Pielowski 1976). In the same period it was estimated that in a nearby area and during the winter-spring season, the fox penetrated crop fields located > 0.6 km away from forest between 2 and 15 times less often than fields <0.4 km to the forest edge (Goszczyński 1985). By the end of the 1990's, the searching intensity of farmland by red fox was independent on the distance from forest, and the proportion of breeding sites located outside of forests almost doubled (Goszczyński and Wasilewski, 1992). Panek and Bresiński (2002) found 83% of fox dens in farmland. Red fox prefers cover rich habitats for resting and for movements in daylight. The increased use of shelters and breeding sites located in agricultural landscape may have resulted in smaller distances between the places of day-time rest and feeding grounds (Goszczyński and Wasilewski, 1992). In Southern Finland, Kurki et al. (1998) found that fox density increased with the ratio of agricultural areas among forest, reaching its maximum at 20–30% of farmland and afterwards decreased as the proportion of this habitat increased. Settling in agricultural landscape also means that the red fox has settled in the habitat of the brown hare, which could result in the fox having a bigger impact on hare dynamics. Webbon et al. (2004) showed that red fox population density is positively related to coniferous woods, lowland mire/marsh and grassland leys and negatively related with areas with roads and upland. Different landscapes were measured of which 3 different arable lands (73.179 km² of rural area) and 2 pasture lands (62.821 km² of rural area). The

mean fox density of arable land was 1,33 fox per km² (0,46-3,43) where the mean density in the pasture lands was 1,64 per km² (0,7-2,74). Thus it appears that overall density of the fox is higher in pasture lands. In the Netherlands the red fox population inhabited a larger range of the area throughout the years (see figure 11). The distribution shows to be going West where different types of landscape are found (like sand grounds and dunes) (Broekhuizen, 1992).

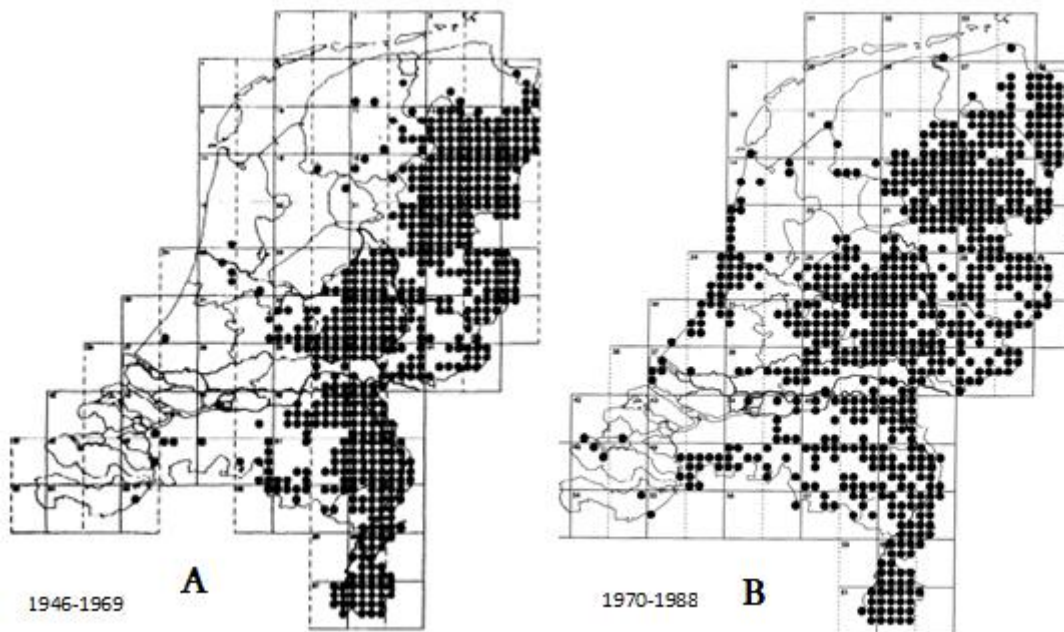


Fig 11: Distribution of the red fox in the Netherlands. Map A shows the distribution of the red fox (1946-1969) based on observations, map B shows the distribution (1970-1988) based on observations, captures and found individuals (data obtained from Broekhuizen, 1992).

3.2.3 Effects of (direct) predation

The diet of the red fox consists between 3-46 % of brown hare, depending on the region and the number of hares and foxes present in this region (Pielowski, 1976; Von Schantz, 1980; Erlinge et al., 1984; Goszczyński and Wasilewski, 1992; Reynolds and Tapper, 1995). The Game Conservancy in the UK estimates that a family of foxes (a breeding pair and eventual offspring) would consume 33 adult hares annually (Pépin, 1989; Reynolds and Tapper, 1995). It is assumed that, on average, an adult red fox has a food requirement around 500g per day. The food intake of a vixen during gestation (beginning of February – end of March) increases approximately by one fourth, and during lactation (April) she doubles her food intake. The food intake of growing young (May- November) is assumed to be around 450g per day per animal (Goszczyński and Wasilewski, 1992). An overview of the food requirement of red fox during different life stages can be seen in figure 12. If the diet of red fox would consist of 25% brown hares, it can be calculated that a breeding pair would consume approximately 28 adult hares per year (when average bodyweight of adult hare is assumed to be 3,5 kg). This would be in coherence with the estimation of the Game Conservancy in the UK, but as mentioned before in the text, the amount of brown hare in the diet of red fox can vary between different regions.

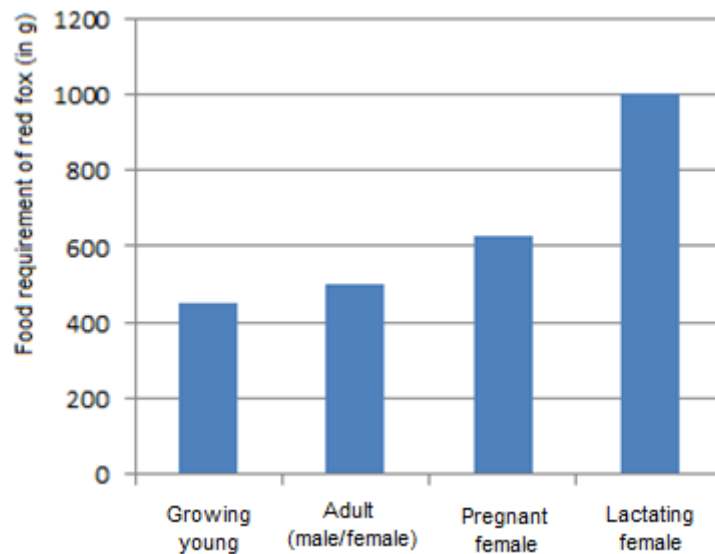


Fig. 12: An overview of the food requirement of the red fox during different life stages. The y-axis shows the amount of food a fox requires per animal per day in grams. The x-axis is divided in growing young (May- November), adult (9-10 months after birth), pregnant female (beginning of February – end of March) and lactating females (April) (data obtained from Goszczyński and Wasilewski, 1992).

It is seen that red fox populations prevent brown hare populations to reach their carrying capacity. When red fox were excluded from areas with brown hares, the brown hare populations increased in density (Panek et al., 2006) and when the fox population recovered, the hare population decreased again (Lindström et al., 1994). The amount of impact of red fox on these hare populations mainly depends on the habitat type and the initial density (Jensen, 2009). Lindström et al., (1994) performed a research on the density of the red fox and its prey species in Örebro County in Sweden to get an insight in the importance of fox predation on prey density. In this study the researchers conducted an annual questionnaire during 1974-1992, asking 150-355 hunters from all over the area to estimate population changes of red fox, brown hare and other prey animals since the previous hunting season. The hunters could value the population change with increase, stable, or decrease, with assigned values of respectively 1, 0, and -1. The average answers were calculated and can be found in figure 13. During the late 1970s and 1980s an epizootic of sarcoptic mange was prevalent among the Scandinavian red fox, reducing the population density. Figure 13 shows that in years where fox density was low, brown hare density increased, and as fox population increased again, hare density decreased. This study shows that red fox predation, in this specific area, is a crucial factor in limiting the numbers of brown hares (Lindström et al., 1994).

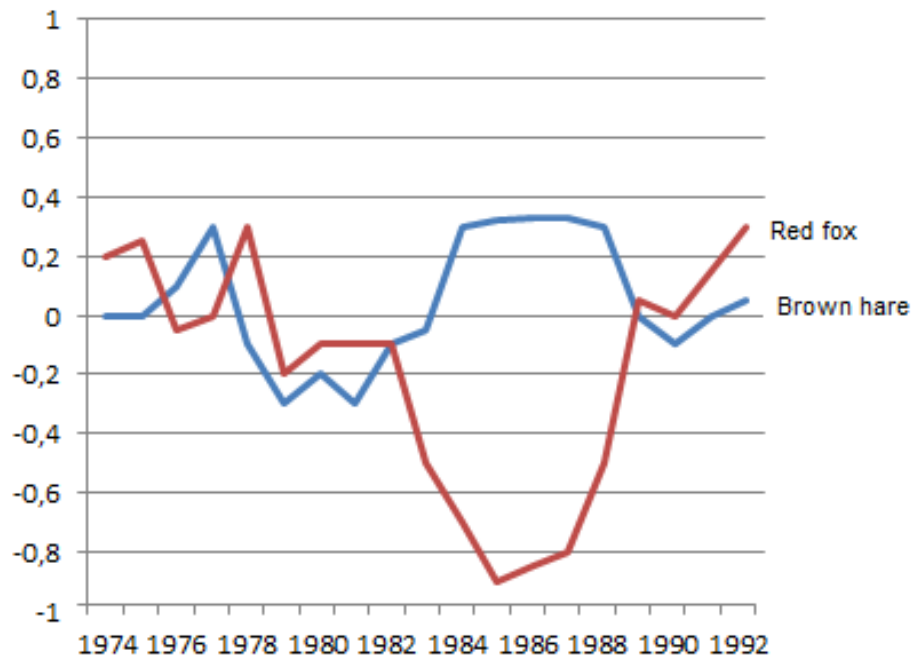


Fig. 13: Questionnaire indices to annual population changes in Örebro County, Sweden. The y-axis shows the average answer of "increase" (1), "stable" (0), or "decrease" (-1). The blue line represents the European hare, and the red line represents the red fox (data obtained from Lindström et al., 1994).

Tapper and Reynolds (1995) conducted a research on the predation of red fox on the brown hare in central southern England. Figure 14 shows both; predation of hares by the fox, as well as the additive non-fox mortality of leverets. The initial population density of adult hares at the beginning of the year was set on 15 hares/km². The productivity was set on 75% of the physiological maximum, which resulted in a total annual production of 53,1 leverets. The predation (killing) of the red fox on the brown hare leverets is the highest in the months April (second half), May, June, July and August. The early (March- April (first half)) and the late (September) born leverets had the lowest mortality rate due to fox predation; 8% and 25%, respectively. The predation mortality rate by fox was about 25% for the early and late born leverets. The leverets that were born in the period of May-August had the lowest survival rate, and as can be seen in figure 14, more than half of all leverets died as a result of predation by red fox (Reynolds and Tapper, 1995).

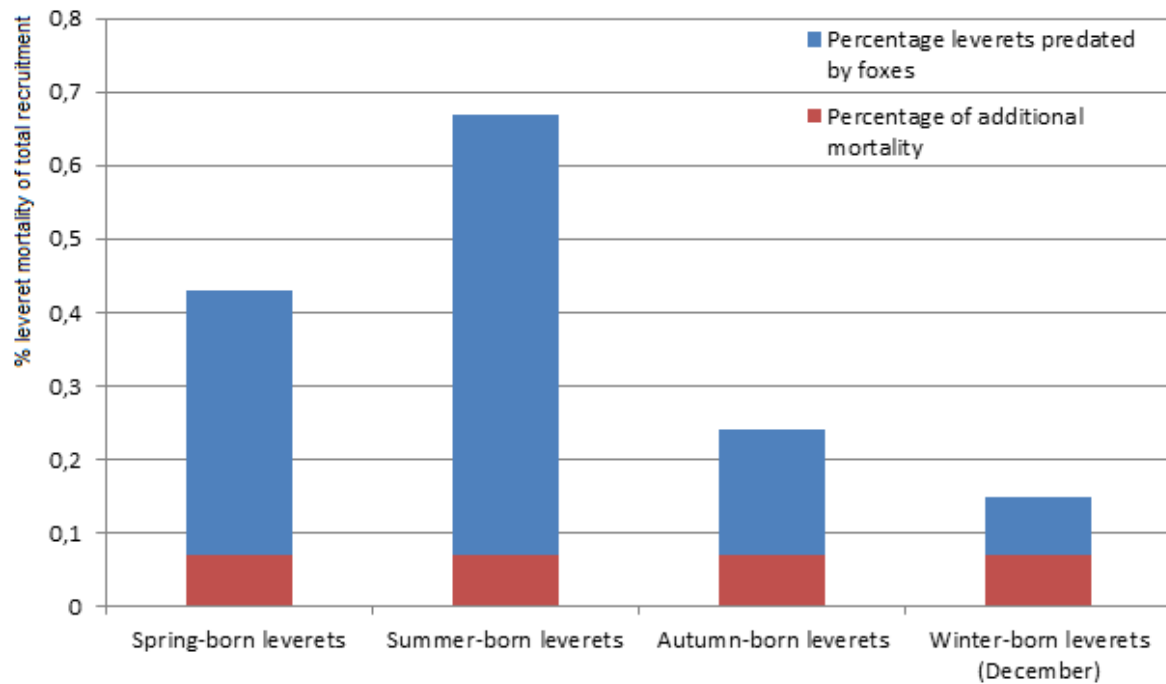


Fig. 14: An overview of leveret mortality with the focus on period of birth (per season or part of season). Combining the blue bars and the red bars gives the total percentage of leverets that died per season (data obtained from Reynolds and Tapper, 1995).

Goszczyński and Wasilewski (1992) performed a research on fox predation on brown hare in central Poland (89,2 km²). This research measured the amount of foxes in certain areas with the amount of hares in these same areas (both including new recruitment). The hare mortality in the spring, summer and first half of autumn could be accounted for 20% by foxes (45 % adults and 20% young). In the last half of the autumn and the winter season a 53% of the mortality of hares are caused by red fox (all adult hares). The total annual hares present in the research area were 8464 individuals. The annual mortality of hare was 6610. Total annual mortality caused by the red fox was 1522 hares; 23% of the total mortality.

As seen in figure 15, most young hares are taken by foxes in spring and summer, with respectively 511 and 457 animals being eaten. Adult hares seem to be more vulnerable to predation in mainly spring and winter, with respectively 103 and 147 animals being taken by foxes. It can be calculated that, according to figure 15 a breeding pair would consume approximately 31 adult hares per year in central Poland (when 2 leverets are counted as 1 adult). This would be in coherence with the estimation of the Game Conservancy in the UK and with the findings from figure 12. On average a pair of red foxes would consume 13 young hares and 2,5 adults in spring, 14,5 young hares and 1,5 adults in summer, 7 young hares and 2 adults in Autumn, and 7 adults in winter.

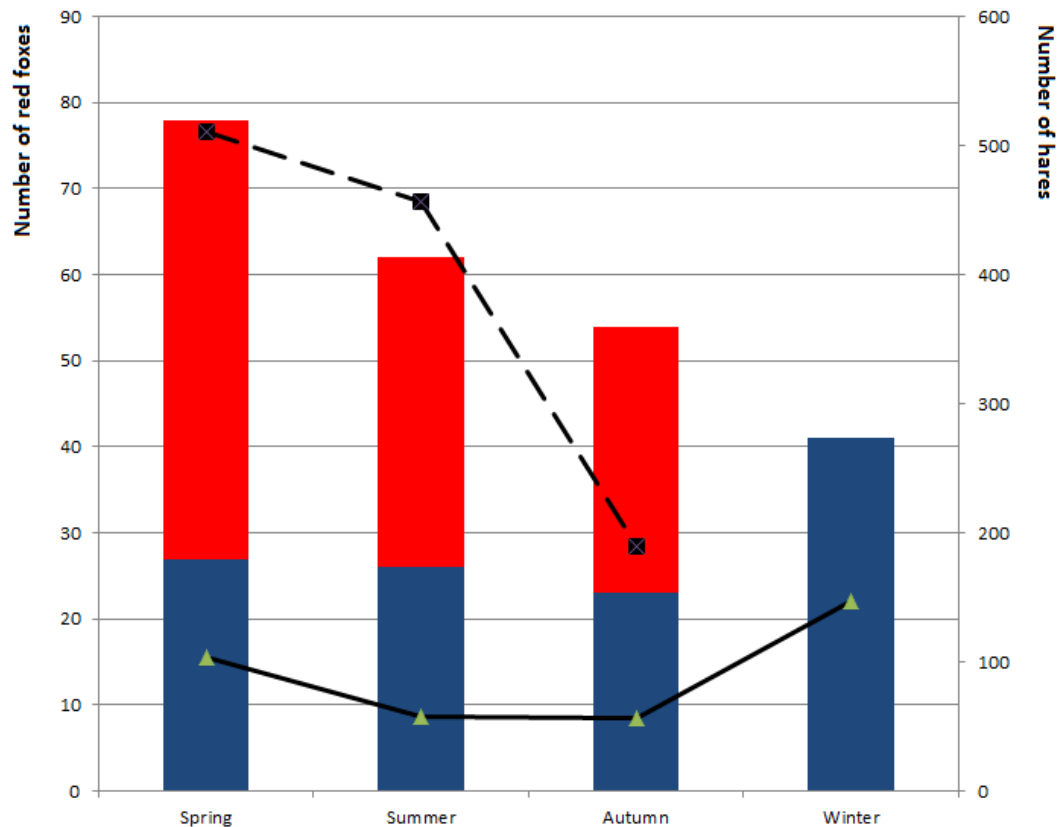


Fig. 15: The bars show the total number of red foxes. The blue parts of the bars represent the amount of adult foxes, the red parts represent the total amount of young red foxes (born in April in total study area of 89,2 km²). The young are counted as mature when they reach winter. The dashed line describes the number of young hares (bodyweight below the adult weight of approximately 4 kg) taken by red foxes. The solid line gives the number of adult hares taken by red foxes (data obtained from Goszczyński and Wasilewski (1992)).

3.2.4 Effects of predation pressure

Next to the direct predation (killing) of predators, predation pressure might also play a role in the life of the brown hare. An important aspect to measure the impact of predation on a prey population, is by understanding numerical and functional responses of the predators to the prey density (Krebs, 2013). The response of predators to different prey densities depends on the feeding behaviour of individual predators (functional response) and the response of the predator population through reproduction, immigration, and emigration (numerical response) (Solomon, 1949). The numerical response can be defined as the trend of predator numbers against prey density. As prey density increases, more predators will survive and reproduce. Effects of both survival and fecundity result in an increase of the predator population, which in turn eats more prey (Sinclair et al., 2006). The functional response is defined as the relationship between predation rate (number of prey eaten per predator per unit time) and prey density (Solomon, 1949). As mentioned before in the text, red foxes do not rely heavily on brown hare, given their range of alternative prey (Cowan, 2004; Dell'Arte et al., 2007). Red foxes increase their search activity with increasing hare density. Mortality first increases with prey increasing density, and then declines as the predators reach their maximum food intake capacity (Holling, 1959).

Since the 1970's red fox numbers are increasing in the habitat of the brown hare, which probably means that predation pressure is also increasing. Hares, as well as red foxes, prefer edge habitats and both species rest and forage in the same areas (Goszczyński and Wasilewski, 1992;

Panek and Bresiński, 2002). This increased predation pressure most likely occurs in the period where red fox reproduce. The food intake of a vixen during gestation (beginning of February – end of March) increases approximately by one fourth, and during lactation (April) her food requirement doubles. This increase of food intake by the vixen together with growing young (May- November) means that red foxes will have higher energetic needs. This would mean that predation pressure is much higher during this period. However, there is no real proof that brown hares change their behaviour or forage in habitats with lower predator densities during these periods of higher fox densities. No study has been found on the effects of predation pressure on brown hares in Europe.

Apparently, snowshoe hares undergo a period of stress when the predator response is at a high level. This stress causes higher level of free cortisol, reduced testosterone response, reduced body-mass in the winter and reduced leukocyte counts. This concludes that predation pressure can result in the reduced reproduction causing a decline in the snowshoe hare population (Boonstra et al., 1998). Because the snowshoe hare is a similar species, it can be expected that the effects of predation pressure are partly the same for brown hare. However, the snowshoe hare lives in a different habitat and has to deal with other predators than the brown hare does.

3.3 Energetics

A research of Hewson and Taylor (1975) on the reproductive system of the brown hare and the length of the breeding season in Scotland showed that over 13 years, the breeding season sometimes lasted from early January until the end of December. On average, breeding began in early February and lasted until the end of October. The levels of pregnancy rose from 11% in January to over 90% in April and May and declined to 11% in November. The average litter size in Scotland increased from 2.0 in January to a peak of 3.2 in April/May and then declined steadily to 1.8 in December. In figure 16 an overview is given of the proportion of hares pregnant in each season in north-east Scotland during the period of 1961-1972. Similar results were found in Poland, Russia, Australia, Canada and New Zealand (Flux, 1965). Poor weather conditions shortened the breeding season significantly, especially in autumn. This research showed that in these 13 years the shortest breeding season was almost twice as short as the longest.

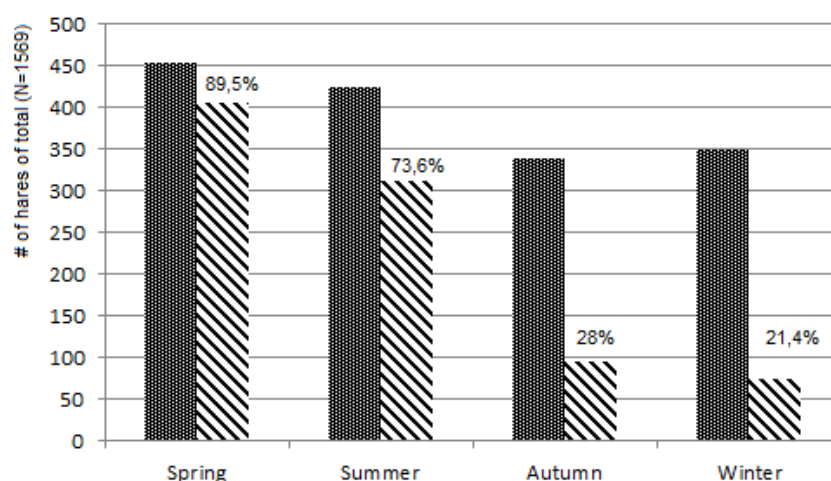


Fig. 16: Number of female hares in different season during the period 1961-1972 in North-East Scotland, (N) = 1569. The black bars represent the total number of females in the area, the black-white striped bars with corresponding numbers represent number of females pregnant in each season. The percentages that are given in the figure show the % of females pregnant during each season (data obtained from Hewson and Taylor, 1975).

3.3.1 Energetic costs of reproduction

A research of Valencak et al. (2009) states that brown hares in Europe have high energetic costs of reproduction, mainly due to precocial, rapidly growing young that rely largely on energy-rich milk. Peak rates of energy assimilation at a high litter size of 3 young have been estimated to range above five times Resting Metabolic Rate (almost similar to Basal Metabolic Rate: From here on referred to as: RMR) (Hammond and Diamond, 1997; Hackländer et al., 2002b). On the costs of lactation of female hares, several researches have been conducted. These were laboratory researches where females were placed in exhibits. In the first two researches that are discussed, three times a year a male was placed for a period of two days in the spring, summer and autumn (Valencak et al., 2009). Three leverets per nest were necessary to measure similarly obtained energy amounts by females and young as well as the energy output through milk. Leverets were added to nests which did not have enough young (Valencak et al., 2009; Valencak et al., 2010).

3.3.2 Energy expenditure of females, males and young hares

When the litter weight increases, milk production of lactating females does not increase as fast as the body weights of the young (Hackländer et al., 2002a; Hackländer et al., 2002b). These findings suggest that female hares, like other mammals, may face a physiological limit of energy throughput during peak lactation. In order to fulfill in the needs of the young, hares build up fat stores during winter, and may even partly restore fat depots during the non-reproductive period or during gestation in the breeding season. Individuals with the greatest amounts of stored fat have the highest reproductive success (Marboutin et al., 2003; Valencak et al., 2009; Vaughan et al., 2011).

The results of Valencak et al. (2009) gives a clear view on what seems to be the most expensive period of the female brown hare, which is the period of lactating. In figure 17 the results are shown with the MEI of female lactating hares and their milk energy output (both including peaks). Peak levels of MEI and milk energy output give a better view on the absolute range of these costs for short periods of time. The lowest periods of MEI are based on female nonparous MEI. The peaks of MEI in spring, summer and autumn are respectively: 5,7, 5,5 and 6,2 times RMR. Valencak et al. (2010) even showed that when laboratory female lactating hares, which are kept at a temperature of 5 °C, the peak level of MEI may go up to 7,3 times RMR (litter size N = 3).

Male brown hares do not share the same life cycle of the females considering the nursing of their offspring. Unlike females, male hares are not involved in the nursing process of the young. This means that their energy expenditure should be significantly lower. However, it is known that male brown hare do have a larger range of distribution (Broekhuizen, 1979). This is considered as a factor that may ensure that the general energy expenditure throughout the year is higher than that of the female. Males will probably be more active at the end of winter, spring and summer when reproduction occurs (Tapper and Yalden, 2010). Given that males are probably more active during the three reproductive periods throughout the year; the energy expenditure will show a peak level.

For the energy expenditure of young hares (after weaning) the MEI increases with time. According to Hackländer et al. (2002b), the MEI of leverets in the last week of lactation is about 785 kJ. Broekhuizen (1979) found that young hares reach their mature bodyweight at six months of age (approximately 3,55 kg). It is assumed that a young hare will increase its MEI until it reaches the MEI of a nonparous female (1325 kJ per day) (Hackländer et al., 2002a).

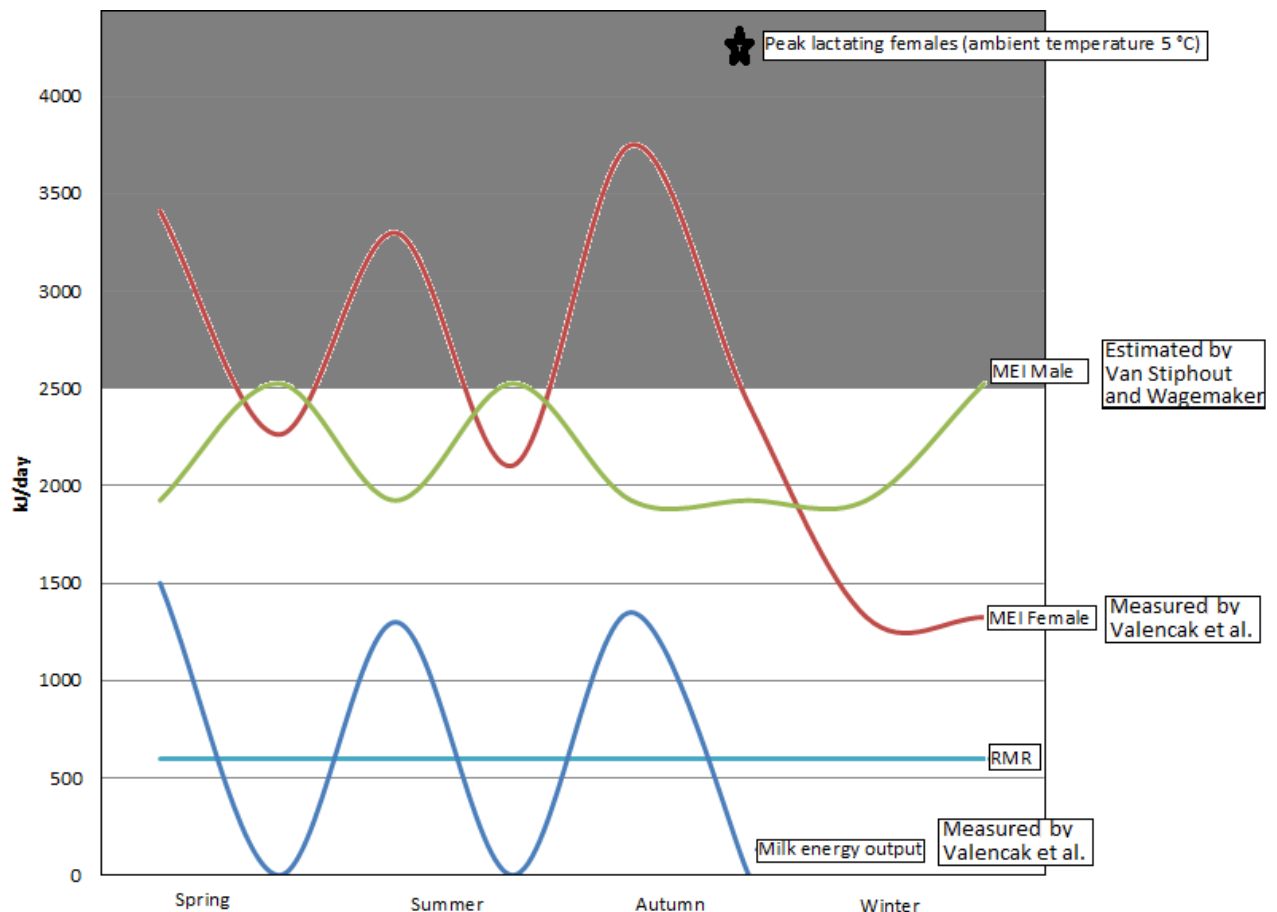


Fig. 17: Energetic model of the female brown hare whilst lactating for nests of 3 leverets (at beginning of spring, summer and autumn). The upper red line gives the peaks of MEI, the blue line gives the peak milk energy output per season (lactating period of 5 weeks). The green line shows peak MEI levels of males. Numbers are from laboratory studies with ambient temperatures that varied between 8 and 25 °C. The peak MEI of lactating females on lower temperatures (in graph 5 °C) is given as a single point in the graph. The grey area on top shows the boundary of 5 RMR and above (data obtained from Valencak et al., 2009 and Valencak et al., 2010).

3.3.3 The role of ambient temperature on energy expenditure

The ambient temperature plays a major role in the energy expenditure of the female hare during lactation. A research conducted by Valencak et al., (2010) on captive breeding hares (with *ad libitum* food availability) in three different groups. One group was kept on room temperature (both females and young), one group on cold a temperature (also both female and young) and one group was kept on room temperature (female) and cold temperature (young). This research showed that female lactating hares kept on low temperatures (5 ± 2 °C) had a mean energy intake of $3735,62 \pm 132,86$ kJ/day with a peak of $4375,35 \pm 177,8$ kJ/day. Lactating hares kept on room temperature (22 ± 2 °C) had a mean energy intake of $2897,86 \pm 119,42$ kJ/day with a peak of $3563,46 \pm 220,15$ kJ/day. The last group where the females were kept on room temperature and their young on cold temperatures, the female had a mean MEI of $3668,7 \pm 93,1$ with a peak of $4080,65 \pm 120,05$ kJ per day. The group kept with only the leverets on low temperature and the group with both females and leverets kept at low temperature showed a greater amount of milk energy output (MEO) than the group on room temperature (females and leverets). The difference in temperature made females give different amounts of average milk energy output. The differences between mothers and leverets kept on room temperature went up to 17,6% (both cold) and 27,3%

(only young cold) more milk energy output to their young. Results from this research are also given in figure 18.

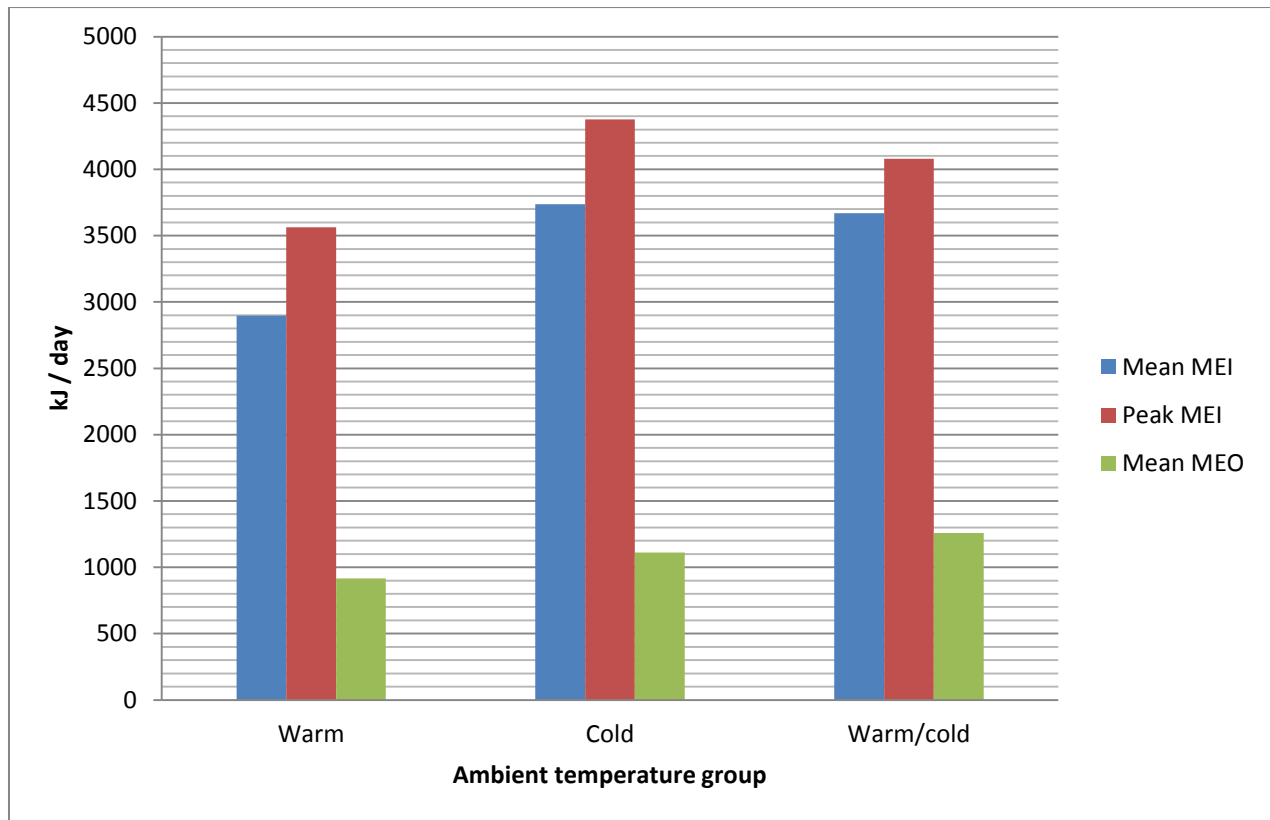


Fig 18: energy expenses by lactating females and leverets kept on different ambient temperatures. Warm = both females and leverets at 22 ± 2 °C, Cold = both females and leverets at 5 ± 2 °C and Warm/cold = females at 22 ± 2 °C and leverets at 5 ± 2 °C. Litter size (N) = 3 (data obtained from Valencak et al., 2010).

Leverets kept on low temperatures with their mother kept on room temperature ate significantly more solid food than the room temperature kept leverets. Groups of leverets, with mothers kept on low temperatures, only ate slightly more solid food. Mean birth masses of the different groups of leverets were: $124,3 \pm 3,4$ g ($N=36$), $112 \pm 4,4$ g ($N=24$) and $127,6 \pm 3,2$ g ($N=27$) for warm groups, cold groups and warm/cold groups, respectively. Differences in birth mass were significant. The mass gain weight between birth and weaning (after 5 weeks) amounted to 533,3, 546,4 and 640,8g for warm groups, cold groups and warm/cold groups, respectively. These results were not significant, so ambient temperature did not affect leveret growth in this experimental set up (with *ad libitum* food availability). Average temperatures per season in the Netherlands are 9,5, 17, 10,6 and 3,4°C in spring, summer, autumn and winter, respectively (Weerstatistieken.nl, 2013). The temperature of 5 ± 2 °C will probably be an extreme (if constant) in a natural setting of breeding hares in the Netherlands. However, it can be said that average temperatures in spring and autumn makes energy needs of leverets (and adults) higher.

3.3.4 Energetic costs of lactation

Over the course of the breeding season the amount of milk production remains constant but fat content of the milk decreases. Hence, total energy transfer to young decreases significantly in autumn. This indicates that fat reserves are gradually depleted over the breeding season. Stored fat allows female hares to down regulate energy intake and expenditure early in the breeding season,

whereas late breeding forces them to reach peak energy intake levels. Energy demand for lactating females is highest between the second and fifth week of lactation, with a peak in the fourth week. Juveniles in autumn compensate for lower milk quality by increasing solid food intake in the last phase of lactation (week 3-4). This compensatory increase in energy intake can be limited by the quality or quantity of natural food sources, as well as increased predation risk. This makes that litters born late in the season do in fact experience disadvantages due to impaired milk energy uptake (Hackländer et al., 2002a; Marboutin et al. 2003; Valencak et al., 2009).

As can be seen in figure 19, Valencak et al. (2009) showed that milk fat partially originated from maternal fat stores, particularly in spring. The peak sustained energy assimilation rates of lactating females were significantly higher in autumn, due to increased rates of food intake. This research also suggests that in hares, peak energy turnover during lactation varies with the availability of fat reserves. When energy reserves are high, sustained metabolic rate in lactating hares is down-regulated strongly, which points to a trade-off between cost and benefits of maximum energy turnover. Female hares use their own body fat reserves to cover the high energetic costs of reproduction early in the year, and raise their energy or food intake when facing high energy demands. The major benefit of the fat reserves early in the year may be the reduction of predation risk by avoiding intensive foraging (Jönsson, 1997).

Hackländer et al. (2002b) conducted a research on captive brown hare juveniles with respect to food intake, growth and thermoregulation. For this study 491 leverets out of 213 nests were analysed. Precocial young need more energy than altricial because they need to maintain their body temperature themselves while altricial young use the body warmth of their parent(s) and have insulated nests. Precocial young, like the brown hare, do have the ability to evade predators and are less relying on their parents (Pagel and Harvey, 1988).

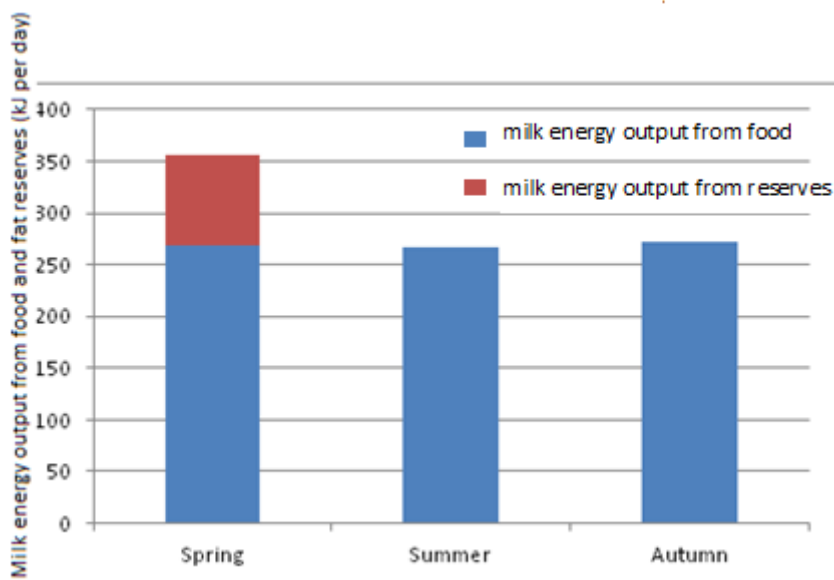


Fig. 19: Energy budgets of lactating females. Numbers are given as a mean from 50 lactation periods in 28 females. ($\text{kJ kg}^{-1} \text{d}^{-1}$). Blue bars represent the milk energy output from food; the red bars represent the milk energy output from reserves stored during winter (data obtained from Valencak et al, 2009).

3.3.5 Energy intake of young hares

Milk was the main energy resource for the leverets and this was on average five times larger than the contribution of the energy intake by solid food. The amount of energy digested from milk

was relying on the litter size. Litters of one leveret received significantly more energy from milk than two or three leverets per litter. Digestion efficiency of milk was $99.35 \pm 0.09\%$, so (total) milk energy obtained and milk energy output were more or less the same. From the second week on, leverets are able to digest solid food. In the article an example was given for the third week where the amount of kJ per day from digested energy from solid food. Litter sizes of one, two and three digested, respectively, $22,29 \pm 5,9$ kJ, $54,49 \pm 21,4$ kJ and $92,01$ kJ from solid food (Hackländer et al., 2002b). Amounts of digested kJ's from milk and milk energy output per litter size are shown in figure 20.

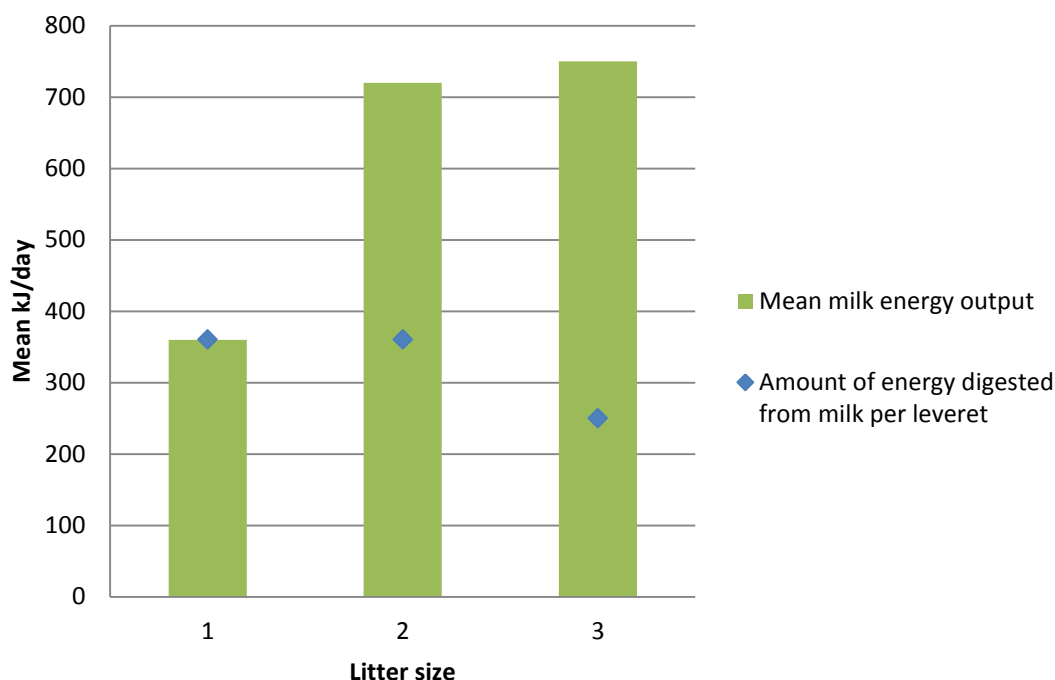


Fig. 20: Differences per litter size. Mean amount of milk energy output of lactating females and the digested energy from milk during the lactation period per leveret. No peaks of milk energy output were added to this graph because of insufficient data (data obtained from Hackländer et al., 2002b).

About 20% of the leverets were stillbirths or died during lactation, mainly due to infectious diseases. The mortality rate increased with litter size at birth. Birth weight was also relying on litter size where singletons weighed, on average 123 grams and quintuplets weighed 95 grams. In litters without losses of leverets, the average bodyweight 8,5-folded after 35 days (weaning). The average litter size between November and March was one or two leverets. In the period of April until the end of October the average litter size was between two and three leverets.

3.3.6 Influence of high- and low fat diet on lactating hares

Hackländer et al. (2002a) conducted a research on breeding brown hares. The goal of this research was to discover what influence high-fat and low-fat diets had on the lactation quality of the does and what were the consequences of this quality on the leverets. Some important aspects of this research are that leverets of does which are set on a low-fat diet are more relying on gaining extra bodyweight by eating more solid food. This was because these does had a lower quality in milk than the high-fat diet does. The two different types of diet did not have any influence on the average litter size or had an effect on body weight at birth of the leverets (130 ± 4 grams for low-fat diet, 131 ± 4

grams for high-fat diet), nor had any effect on the average body weight at weaning ($1,096 \pm 42$ grams, $1,043 \pm 35$ grams). Further, a difference between parous and nonparous is given, whereas the nonparous females ate about 55% less food than the average parenting female (Hackländer et al., 2002a).

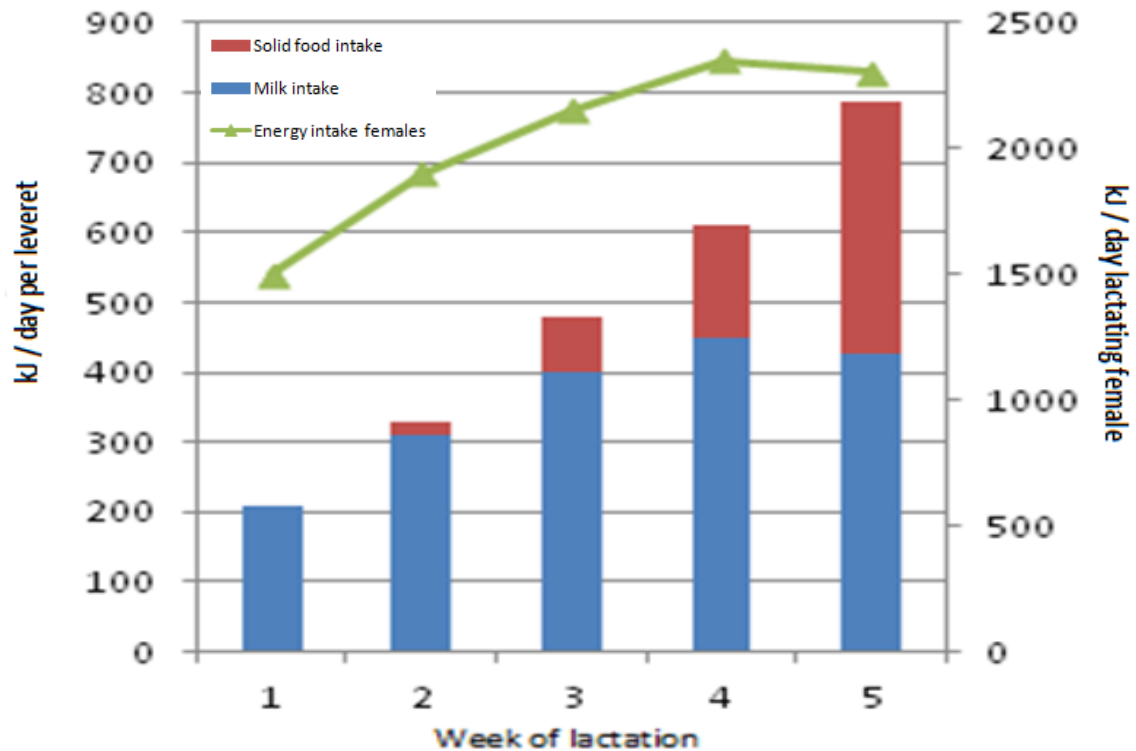


Fig. 21: The blue bars describe the amount of kJ obtained from milk per leveret per day and the red bars show the amount of kJ obtained per day from solid food. The green line shows the MEI per day for lactating females (ambient temperature 10-20 °C, $N = 491$ leverets out of 213 litters, litter sizes: (N) = 1-3 (data obtained from Hackländer et al., 2002b).

In figure 21 description is given how leverets obtain their energy from milk and solid food throughout the lactation period of 5 weeks when the solid food (for both lactating female and leverets) is low-fat containing. It appears that leverets are well capable to replace milk energy with energy digested from solid food. The low-fat diet is taken because this is thought to be the most natural diet.

4. Discussion

This research focuses on the impact of predation (and predation pressure) on brown hares in a multi predator environment, in relation to the seasonal energy requirement of hares. The aim of this research is to give an insight in the crucial moments for the brown hare within a year and broaden the knowledge about the role of the main predators on hare population. The results were divided in ecological niche, predation, and energy. We combined the different results and will show in this chapter how these factors alone, or in combination, can cause crucial periods for brown hares (male/ female/ leverets) during different seasons.

Smith et al. (2004) suggests that hares select a variety of habitats for both feeding and resting throughout the year, as found by Tapper and Barnes (1986). When habitats were suitable for both, hares often used the same one for feeding and resting, as found by Reitz and Léonard (1994) and Marboutin and Aebischer (1996). McLaren et al. (1997) found that hare population density in pasture landscapes in the UK is very low compared to arable landscapes in spring and autumn. Tapper and Barnes (1986) also found lower hare densities in pasture landscapes than in mixed and arable habitats, also mixed habitats had lower hare densities than arable habitats (Pépin, 1985, 1987; Marboutin and Aebischer, 1996). This variation in density with habitat type throughout Europe was also found by Smith et al. (2005). The difference in hare density could be caused by the fact that mixed- and pasture landscapes have higher predator numbers. Also hares in pasture areas probably spend more energy on foraging and are unable to maintain body condition as well as hares from arable areas.

Jensen (2009) found that brown hares rely heavily on habitat quality during the breeding period. Females in heterogeneous habitats are likely to produce more litters, larger litters and/or larger off-spring at birth. This was also found by Vaughan and Keith (1981). Frylestam (1980b) found that lighter hares produced fewer litters, and similarly, Jennings et al. (2006) found poor body condition and lower reproductive output in hares in pasture areas compared to arable areas. This is also in accordance with the results of Goszczyński and Wasilewski (1992), who found that hares from pasture areas are generally smaller, lighter and have less fat than those from arable areas. Frylestam (1980b) noted that hares living in low landscape-diversity areas had higher mortality rates and lower body weights than hares living in more diversified landscapes, and that lighter hares produced fewer litters.

Multiple studies show that hares prefer edge habitats and especially edges toward tree stands (Tapper and Barnes, 1986; Pépin, 1989; Goszczyński and Wasilewski, 1992; Reynolds and Tapper, 1995; Roedenbeck and Voser, 2008; Tapper and Yalden, 2010). Bresinski (1983) noted that few hares lived in fields close to woods, and showed that hares used woods as sheltering areas. Jensen (2009) states that the mean condition of female hares in Denmark was positively affected by the coverage of grass-leys and the amount of edge habitat towards tree-stands in the sampling area. During the main part of the breeding season, hares select habitat structures that provide more cover from predators and unfavourable weather conditions (Tapper and Parsons 1984; Smith et al., 2004; Jennings et al., 2006). These studies emphasize that woodlands provide protection from predators (for adults and their young) as well as shelter from the weather, and that hares on open ground near woods would be more vulnerable to avian and mammalian predators. However, since the fox is acknowledged the main predator of adult and young hares it is difficult to see how this behaviour could reduce fox predation. This is because the preferred habitat of the red fox is mixed field-forest habitats (Pielowski, 1976; Goszczyński, 1985).

The main predator of the brown hare in Europe is generally acknowledged to be the red fox.

This research therefore mainly focused on the effects of red fox predation on brown hare populations. But it has to be mentioned that in Europe, besides the red fox, hares also have to deal with predation from other mammalian predators such as the stoat, the wolf, and the lynx. And avian predators the buzzard, tawny owl and the goshawk (Pielowski, 1976; Von Schantz, 1980; Erlinge et al., 1984; Goszczyński and Wasilewski, 1992; Reynolds and Tapper, 1995; Jensen, 2009). Next to red foxes which increased in numbers in the past decades, the buzzard and the goshawk increased in population numbers as well. Also the distribution of natural predators of the brown hare changed throughout the years in the Netherlands. We believe that factors like these all influence the predation pressure on the brown hare, without knowing the exact numbers of individuals taken by avian predators.

Studies of Panek et al. (2006) and Lindström (1994) show that red fox predation is a crucial factor in limiting the numbers of brown hares. This is also in accordance with the results of Jensen (2009), who stated that brown hare population in Denmark has increased coherently with the outbreak of mange that eradicated the fox here in the 1980's. An interesting fact found by Marboutin and Hansen (1998) was that the survival rate of males and females without mammalian predation were respectively 0.50-0.61 and 0.44-0.56. This is interesting because Jensen (2009) found survival rates of 0.40 for males, and 0.57 for females in an area with predation. This would mean that males have a 10- 21% higher survival rate in an area without predators than in an area with predators. This is probably because male hares move more between habitats.

Schmidt et al. (2004) concluded that the decline of Danish European brown hare populations can mainly be attributed to predation by red fox, but the development in agricultural land-use during the last 45 years have also affected the European brown hare numbers negatively. Excellent experimental studies of a broad range of species have confirmed that risk effects on prey demography, density and dynamics can be large, sometimes even exceeding direct effects. If risk effects are not considered explicitly, it seems likely that they will go undetected or be attributed to processes other than predation, particularly when risk effects reduce reproduction. Creel and Christiansen (2008) showed that predation risk has a great influence on elk (*Cervus canadensis*) reproduction. The presence of wolves showed to be a significant factor on calf recruitment. The amount of calves taken by direct predation by these wolves appeared to be 2-3 times lower than the effect of predation risk on reproduction. The adult elks showed a decrease in reproduction with the presence of predators. We believe that predation risk for the brown hare is on its high in the course of spring and summer when the mammalian and avian predators reproduce and population numbers increase. Since the 1960s red foxes have expanded their natural habitat (forest) to more agricultural landscapes. Around the 1970's, 43% of breeding sites in western Poland were found in farmland, although no breeding dens located in crops had been recorded at that time (Pielowski, 1976). By the end of the 1990's, the searching intensity of farmland by foxes was independent on the distance from forest, and the proportion of breeding sites located outside of forests almost doubled (Goszczyński and Wasilewski, 1992). Panek and Bresiński (2002) found 83% of fox dens in farmland. Red fox and brown hare now share the same areas for both resting and foraging/feeding. So it can be stated that predation, together with a decline in landscape diversity, cause crucial periods for the brown hare.

Besides predation, infectious diseases such as the European brown hare syndrome virus, pseudotuberculosis, pasteurellosis and coccidiosis are present in many European brown hare populations (Jensen, 2009). Juveniles probably become susceptible to EBHS after losing their protective maternally derived antibodies (Duff et al., 1997) with disease outbreaks killing most hares

between September and December. The general view is that diseases can have a significant influence on hare populations, particularly when they occur as local epidemics. However, Haerer et al. (2001) concluded that diseases were not responsible for the decline of brown hare populations in Switzerland. Similarly, Frölich et al. (1996) found that compared to red foxes, infectious diseases seemed to play a minor role in the dynamics of European brown hare populations in Germany. Young hares are most vulnerable for EBHS after weaning and losing their protective maternally derived antibody which kills most hares in autumn. Coccidiosis is enhanced by cold and wet weather (Edwards et al, 2000) and so we believe that a crucial period may occur in autumn.

Culling is also mentioned as a possible cause for the decline in hare populations. A research of Pépin (1989) showed that hare populations are resilient to heavy hunting pressure of between 40-50% of the population during autumn when juvenile: adult ratios were between 1.2-2.5 prior to hunting. This resilience depends mostly on high juvenile productivity. General quotas are set to ensure that hunting does not over exploit the hare population. Edwards et al. (2000) found that if these quotas are not fixed, overshooting could be an additional factor in the decline of the brown hare population. In the Netherlands, culling occurs in the autumn and winter. We believe that culling is not a crucial factor on brown hare as a population. When quotas are met, shooting should not have a crucial influence on hare population dynamics. It may even increase the survival rate of the remaining population through the winter.

Literature on brown hare energetics is mainly focused on lactation. We believe that reproduction is an important factor to find the critical periods of these animals. Females reach critical energy expenditures to raise their young. Reproducing females are generally acknowledged to be a key factor in the maintaining of the hare populations. According to the found results we conclude that the crucial periods for lactation occur in summer and autumn. The female spends her body reserves on her first litter, no body fat reserves are left for the second and third and ambient temperatures drop. The lack of body fat reserves and colder temperatures means an increase in foraging behaviour resulting in an increase of predation risk (Hackländer et al., 2002b; Valencak et al., 2009). We believe that average nest sizes decrease at the end of the breeding season so reproduction energetic may be reduced. This may also be the reason less females reproduce in autumn next to spring and summer.

Due to a lack of information about the energy expenditure of male brown hares, information of the females was used to make an estimation of the MEI throughout the year. We believe that male activity rises in great amounts in the breeding periods. We believe that these breeding periods create critical periods, based on energetics, for the males. However, no sufficient information is available on this subject. Therefore we will not include the male hare in the end model.

Similar to data on male hares, information was missing on young hares (after weaning) on energy expenditures. Our results do show that ambient temperature does play an important role to in the energetics of leverets. This mainly has to do with the maintenance of body temperature. The probable cause why female hares with the highest amount of stored fat have the highest reproductive success (Marboutin et al., 2003; Valencak et al., 2009; Vaughan et al., 2011) is because the milk of the first litter contains extra energy from the stored fat reserves. Leverets of these nests are not obligated to forage large amounts of solid food at a younger age to make up for the missing energy from their mother. We believe that the crucial periods for young hares occur during weaning. Especially in summer and autumn weaning will be more crucial when milk is of lower quality and ambient temperatures drop.

All crucial periods of the female brown hare that we found are shown in the end model; figure 22.

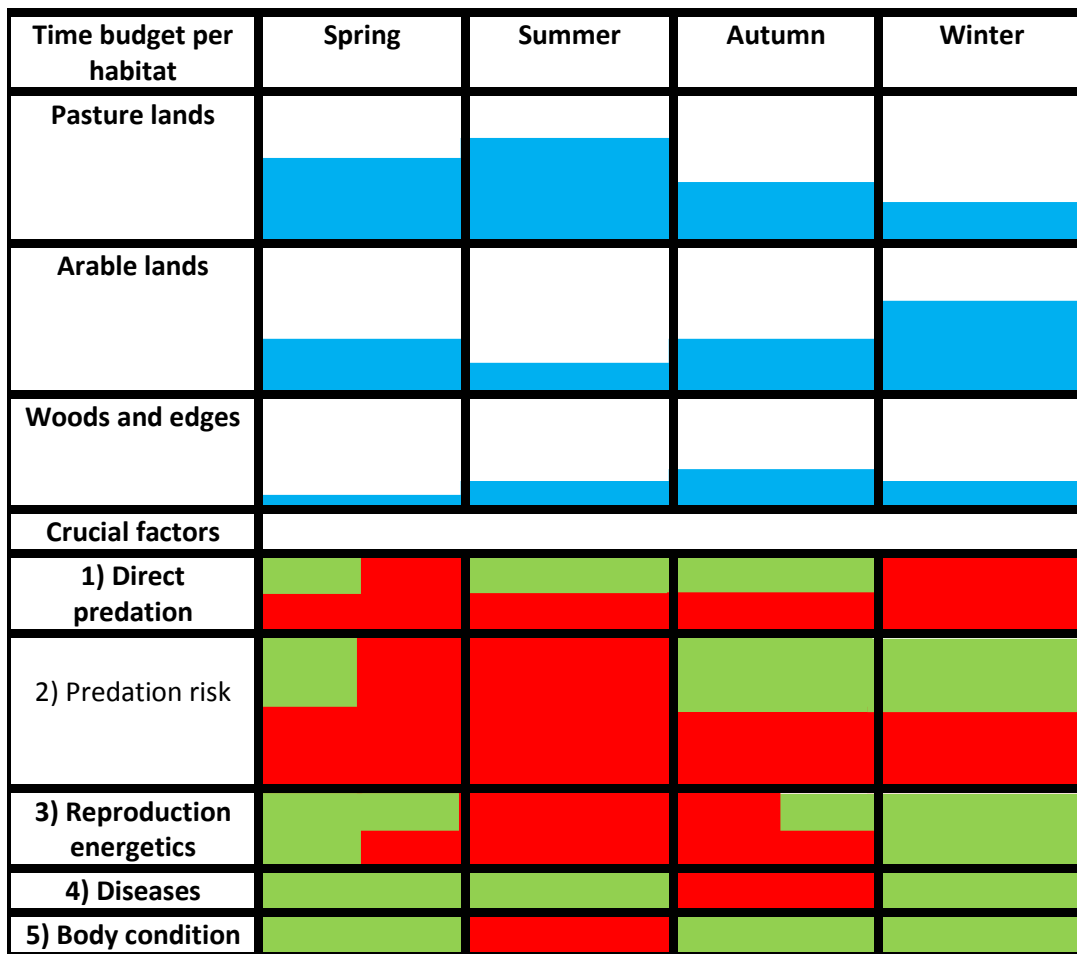


Fig. 22.:Crucial periods of the female brown hare. The factors are given that cause crucial periods for a female brown hare during the year. The blue squares show the habitat choice in Europe throughout the year with time budget of a brown hare in different habitats (in percentages). The red squares show the crucial periods of different factors during the four seasons on female brown hares. The size of the red squares show the extent of that certain factor in the particular season.

1) Direct predation increases during spring by high energy needs of parenting predators and increase of the predator population. Brown hares face their crucial periods concerning direct predation in spring, summer and winter.

2) Predation risk increases simultaneously with direct predation. Predation risk is counted as twice the value of direct predation. Predation risk increases when mammalian and avian predators increase their energetic needs, population number (reproduction) and distribution through their habitat by foraging. The effect of predation pressure causes brown hares to face crucial periods in spring and summer.

3) The costs of reproduction start off low in spring when female body fat reserves are used for covering up a part of these costs. Later on the breeding season; in summer and autumn female hares need to forage more intensively to cover her costs for breeding. At the end of autumn her energy costs drop when litter sizes decrease or no reproduction occurs.

4) Diseases mainly occur in autumn when weather conditions become unsuitable and high population densities.

5) Body conditions may be affected by high energetic costs as reproduction, but also food availability is an important factor in this.

Hares change their distribution throughout the year (also see figure 22); that is if they have the opportunity to do so. The intensification of agriculture causes an increasing loss of habitat heterogeneity. The loss of heterogeneity means that distances between habitats get bigger and it gets more and more difficult for brown hares to switch between different landscapes. Our research

shows that if brown hares are restricted to one particular habitat, it could have tremendous effects on the dynamics of this species. It is found that hares in arable areas may face a food shortage in summer when crops mature. Hares living in mainly pasture areas are unable to maintain a healthy body condition, have lower reproductive rates, and are less protected from unfavorable weather conditions and predators. This all results in low survival and reproductive rates and high mortality in these populations. We can conclude that brown hares have an impeccable need for habitat heterogeneity, and that with a modification of agriculture the crucial periods for brown hares will become increasingly difficult to overcome.

5. Recommendations

- There seems to be a link between landscape diversity and the population dynamics of hares, and we believe more studies are needed on the influence of predation and food availability, and its effect on energy, fecundity, fertility, reproductive success and survival.
- The effects of the other predators are significantly smaller than that of the red fox and are often not taken into account in studies on predation on the brown hare, therefore it is not known what the precise effects of total predation on brown hare populations are and more research has to be done on this subject.
- It seems that red fox have a significant influence on the adult male hares. Until now we found no exact reason for this phenomenon, but it could be explained by the fact that males move more between habitats and therefore are an easier prey for predators such as the red fox. More research may be performed on this subject for a better insight on male mortality.
- The red fox has significantly increased in the habitat of the brown hare, and the proportion of breeding sites located in farmlands outside of forests almost doubled since the 1970's. No literature is found about the increase of the red fox in brown hare habitat since the 1990's, so it might be possible that during the last 15 years the proportion of brown hare in the diet of red fox has increased and more research has to be done on this subject.
- No information is available about the impact of predation pressure of red fox on brown hare dynamics. Because brown hares and red fox share the same habitat for both resting as feeding, it seem that brown hares do not show a change in behaviour (or anti-predator response), in contrast to the snowshoe hare. More research has to be done on this subject.
- Due to a lack of information about the energy expenditure of male brown hares, information of the females was used to make an estimation of the MEI throughout the year. We believe that male activity should rise during the breeding periods. We believe that these breeding periods create critical periods, based on energetics, for the males. However, no sufficient data is available about this subject, and more research has to be done.

6. References

Scientific literature

- Andersen J. (1957). Studies in Danish Hare-Populations.I. Population fluctuations. *Danish Review of Game Biology*, 3: 85-131.
- Baarda, D.B., de Goede, M.P.M. (2006). *Basisboek Methoden en Technieken*. Noordhoff Uitgevers, Groningen, Netherlands.
- Benton, T.G., Vickery, J.A., Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18: 182–188.
- Bertóti, I. (1975). The effect of modern corn production system on hare production (in Hungarian). *A Vadgazdalkodás Fejlesztése*, 15: 33–41.
- Boonstra, R., Hik, D., Singleton, G. R., Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecology Monographs*, 79(5) 371–394.
- Bresinski, W. (1983). The effect of some habitat factors on the spatial distribution of a hare population during the winter. *Acta Theriologica*, 28-29: 435-441.
- Broekhuizen, S. (1979). Survival in Adult European Hares. *Acta Theriologica*, 24: 465-473.
- Broekhuizen, S. (1982). *Studies on the population ecology of hares in the Netherlands*. Research Institute for Nature Management, Arnhem, Netherlands.
- Broekhuizen, S. (1992). *Vos (Vulpes vulpes) Arias van de Nederlandse zoogdieren*. Stichting Uitgeverij van de Koninklijke Nederlandse Natuurhistorie Vereniging, Utrecht, The Netherlands.
- Broekhuizen, S., Maaskamp, F. (1980). Behaviour of does and leverets of the European hare (*Lepus europaeus*) whilst nursing. *Journal of Zoology*, 191: 487-501.
- Broekhuizen, S., Maaskamp, F. (1981). Annual production of young in European hares (*Lepus europaeus*) in the Netherlands. *Journal of Zoology*, 193: 499-516.
- Broekhuizen, S. and Maaskamp, F. (1982). Movement, home range and clustering in the European hare (*Lepus europaeus* Pallas) in the Netherlands. *Zeitschrift für Säugetierkunde*, 47: 22-32.
- Campbell, N.A., Reece, J.B., Urry, L.A., Cain, M.L., Wasserman, S.A., Minorsky, P.V., Jackson, R.B. (2008). *Biology*. Pearson Education, San Francisco, USA.
- Chapuis J.L. (1990). Comparison of the diets of two sympatric lagomorphs, *Lepus europaeus* (Pallas) and *Oryctolagus cuniculus* (L.) in an agroecosystem of the Ile-de-France. *Zeitschrift für Säugetierkunde*, 55:176–185.
- Chautan, M., Pontier, D., Artois, M. (1998). Role of rabies in recent demographic changes in Red Fox (*Vulpes vulpes*) populations in Europe. *Mammalia*, 64: 291-410.
- Cowan, D. (2004). An overview of the current status and protection of the Brown Hare (*Lepus europaeus*) in the UK. *European Wildlife Division*.

- Creel, S., Christianson, D. (2008). Relationships between direct predation and risk effects. *Department of Ecology*, 23: 194-201.
- Dell'Arte, G. L., Laaksonen, T., Norrdahl, K., Korpimäki, E. (2007). Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta oecologica*, 31:276-281.
- Duff, J.P., Whitwell, K., Chasey, D., (1997). The emergence and epidemiology of European brown hare syndrome in the UK. *Symposium of Calciviruses*, 4: 176–181.
- Edwards P.J., Fletcher M.R., Berny P. (2000). Review of the factors affecting the decline of the European brown hare, *Lepus europaeus* and the use of wildlife incident data to evaluate the significance of paraquat. *Agricultural Ecosystem Environment*, 79: 95–103.
- Erlinge, S., Goransson, G., Hogstedt, G., Jansson, G., Liberg, O., Loman, J., Nillson, I.N., Schantz, T., Sylven, M. (1984). Can vertebrate predators regulate their prey? *The American Naturalist*, 123: 125-133.
- Flux, J.E.C (1965). Timing of the breeding season in the hare *Lepus europaeus* and rabbit *Oryctolagus cuniculus*. 29: 31-34.
- Frölich, K., Meyer, H.H.D., Pielowski, Z., Ronsholt, L., Seck-Lanzendorf, S.V., Stolte, M. (1996). European brown hare syndrome in free-ranging hares in Poland. *Journal of Wildlife Diseases*, 32: 280–285.
- Frylestam, B. (1976). Effects of cattle-grazing and harvesting of hay on density and distribution of an European hare population. *Ecology and Management of European Hare Populations*: 199-204.
- Frylestam, B. (1980a). Utilization of farmland habitats by European hares (*Lepus europaeus*) in southern Sweden. *Viltrevy*, 11: 271–284.
- Frylestam, B. (1980b). Growth and body weight of European hares in Southern Sweden. *Holarctic Ecology*, 3: 81-86.
- Frylestam, B. (1986). Agricultural land use effect on the winter diet of Brown hare (*Lepus europaeus*) in Southern Sweden. *Mammalian Review*, 16:157–161.
- Gavier-Widen, D., Morner, T. (1993). Descriptive epizootiological study of European brown hare syndrome in Sweden. *Journal of Wildlife Diseases*, 29: 15–20.
- Goszczyński J. 1985. The effect of structural differentiation of ecological landscape on the predator-prey interaction. *Rozprawy Naukowe Monografie*, 46: 1-80.
- Goszczyński, J., Wasilewski, M. (1992). Predation of foxes on hare populations in central Poland. *Acta Theriologica*, 37: 329-338.
- Hackländer, K., Tataruch, F., Ruf, T. (2002a). The effect of dietary fat content on lactation energetics in the European hare (*Lepus europaeus*). *Physiological and Biochemical Zoology*, 75: 19-28.

- Hackländer, K., Tataruch, F., Ruf, T. (2002b). Postnatal development and thermoregulation in the presocial European hare (*Lepus europaeus*). *Journal of Comparative Physiology Biochemical Systematic and Environmental Physiology*, 172: 183-190.
- Haerer G., Nicolet J., Bacciarini L., Gottstein B., Giacometti M. (2001). Causes of death, zoonoses, and reproduction in the European brown hare in Switzerland. *Schweizer Archiv für Tierheilkunde*, 143: 193–201.
- Hammond, K. A., Diamond, J. (1997). Maximal sustained energy budgets in humans and animals. *Nature*, 386: 457-462.
- Hewson, R., Taylor, M. (1975). Embryo counts and length of breeding season in European hares in Scotland from 1960- 1972. *Acta Theriologica*, 20: 247-254.
- Hik, D.S. (1995). Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. *Wildlife Research*, 22: 115-129.
- Hodges, K.E., Sinclair, A.R.E. 2003. Does predation risk cause snowshoe hares to modify their diets? *Canadian Journal of Zoology*, 81: 1973-1985.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91: 385-398.
- Hutchings, M.R., Harris, S. (1996). *The Current Status of the Brown Hare (Lepus europaeus) in Britain*. Joint Nature Conservation Committee, Peterborough, UK.
- Jennings, N., Smith, R.K. Hackländer, K., Harris, S., White, P.L.C. (2006). Variation in demography, condition and dietary quality of hares *Lepus europaeus* from high density and low-density populations. *Wildlife Biology*, 12(2): 179-189.
- Jensen, T. L. (2009). *Identifying causes of population decline of the brown hare (Lepus europaeus) in agricultural landscapes in Denmark*. National Environmental Research Institute, Aarhus University, Denmark.
- Jeschke, J.M., Kopp, M., Tollrian, R. (2002). Predator functional response: Discriminating between handling and digesting prey. *Ecological Monographs*, 72: 95-112.
- Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78: 57-66.
- Krebs, C. J. (2013). *Population Fluctuations in Rodents*. The University of Chicago Press, Chicago, USA.
- Kurki, S., Nikula, A., Helle, P., Lindén, H. 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology*, 67: 874-886.
- Lamarque, F., Barratt, J., Moutou, F. (1996). Principle diagnoses for determining causes of mortality in the European hare (*Lepus europaeus*) found dead in France between 1986 and 1994. *Game Wildlife*, 13: 53–72.

- Lincoln, G. (1974). Reproduction and March madness in the Brown hare (*Lepus europaeus*). *Journal of Zoology*, 174: 1-14.
- Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.A., Martinsson, B., Sköld, K., Swenson, J.E. (1994). Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. *Ecology*, 75: 1042-1049.
- Marboutin, E., Aebischer, N.J. (1996). Does harvesting arable crops influence the behaviour of the European hare *Lepus europaeus*? *Wildlife Biology*, 2: 83–91.
- Marboutin, E., Bray, Y., Peroux, R., Mauvy, B. and Lartiges, A. (2003). Population dynamics in European hare: breeding parameters and sustainable harvest rates. *Journal of Applied Ecology*, 40: 580-591.
- Marboutin, E., Hansen, K. (1998). Survival rates in a non-harvested brown hare population. *The Journal of Wildlife Management*, 62: 772-779.
- Macdonald, D.W. (1987). *Running with the fox*. Unwin-Hyman, London, UK.
- McLaren, G.W. (1996) *Resource limitation in brown hare (Lepus europaeus) populations*. Thesis. University of Bristol, UK.
- McLaren, G.W., Hutchings, M.R., Harris, S. (1997). Why are brown hares (*Lepus europaeus*) rare in pastoral landscapes in Great Britain? *Gibier Faune Sauvage*, 14: 335–348.
- Nyenhuis H. (1995). Der Einfluss des Wetters auf die Besatzschwankungen des Feldhasen (*Lepus europaeus* P.). *Zeitschrift für Jagdwissenschaft*, 41: 182–187.
- Pagel, M.D., Harvey, P.H. (1988) How mammals produce large-brained offspring. *Evolution* 42:948–957.
- 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: 345-349.
- Panek M. and Bresínski W. 2002. Red fox *Vulpes vulpes* density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. *Acta Theriologica*, 47: 433–442.
- Panek, M., Kamieniarz, R., Bresinski, W. (2006). The experimental removal of red foxes *Vulpes vulpes* on spring density of brown hares *Lepus europaeus* in Western Poland. *Acta Theriologica*, 51: 187-193.
- Pépin, D. (1985). Spring density and daytime distribution of the European hare in relation to habitat in an open field agro system, *Zeitschrift für Säugetierkunde*, 51: 79–86.
- Pépin, D. (1987). Dynamics of a heavily exploited population of brown hare in a large scale farming area. *Journal of Applied Ecology*, 24: 725-734.
- Pépin, D. (1989). Variation in survival of brown hare (*Lepus europaeus*) leverets from different farmland areas in Paris basin. *Journal of Applied Ecology*, 26: 13–23.

- Petrak, M. (1990). Einflüsse landwirtschaftlicher Nutzung auf die Population des Feldhasen (*Lepus europaeus*). *Verhandlungen der Gesellschaft für Ökologie*, 19: 88–97.
- Petrov, P. (1976) Über den Hasenbestand in Bulgarien. *Ecology and Management of European Hare Populations*: 1–2.
- Petrov, P. and Dragoev, P., 1962: Untersuchung mancher Besonderheiten über die Vermehrung des Feldhasen (*Lepus europaeus* Pallas) in Bulgarien. *Bulgarian Institute of Zoology*, 10: 143-168.
- Pielowski Z. (1976). The role of foxes in the reduction of the European hare populations. *Ecology and management of European hare populations*: 135 - 148.
- Pielowski Z. and Raczyński J. 1976. Ecological conditions and rational management of hare populations. *Ecology and management of European hare populations*: 269 - 286.
- 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: 143–157.
- Reynolds, J.C., Tapper, S.C. (1995). The ecology of the red fox (*Vulpes vulpes*) in relation to small game in rural southern England. *Wildlife Biology* 1: 105-119.
- Roedenbeck, I.A. and Voser, P. (2008). Effects of roads on spatial distribution, abundance and mortality of brown hare (*Lepus europaeus*) in Switzerland. *European Journal Wildlife Res.* 54: 425-437.
- Schantz von, T. (1980). Prey consumption of a red fox population in southern Sweden. *Symposium on Behaviour and Ecology*, 18: 53- 64.
- Schmidt, N.M., Asferg, T., Forchhammer, M.C. (2004). Long-terms patterns in European brown hare population dynamics in Denmark: effects of agriculture, predation and climate. *BMC Ecology*, 4: 15.
- Sinclair, A.R.E., Fryxell, J.M., Caughley, G. (2006). *Wildlife ecology, conservation, and management*. Blackwell Science, Malden, USA.
- Smith, R.K., Vaughan, N.J., Robinson, A., Harris, S. (2004). Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? *Journal Applied Ecology*. 41, 1092-1102.
- Smith, R.K., Jennings, N.V., Harris, S. (2005). 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: 1-24.
- Solomon, M. E. (1949). The natural control of animal populations. *Journal of Animal Ecology*, 18: 1–35.
- 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: 39–52.
- Tapper, S. C., Parsons, N. (1984). The changing status of the Brown hare (*Lepus capensis* L.) in Britain. *Mammalian Review*, 14: 57-70.

- Tapper, C., Reynolds, J.C. (1995). Predation of foxes (*Vulpus vulpus*) on Brown hare (*Lepus europaeus*) in central southern England, and its potential on annual population growth. *Wildlife Biology*, 1: 145- 158.
- Tapper, S., Yalden, D.W. (2010). *The Brown Hare*. The Mammal Society, Southampton, UK.
- Valencak, T.G., Tataruch, F., Ruf, T. (2009). Peak energy turnover in lactating European hares: the role of fat reserves. *Experimental Biology*, 212: 231-237.
- Valencak, T. G., Hackländer, K. and Ruf, T. (2010). Peak energy turnover in lactating European hares: a test of the heat dissipation limitation hypothesis. *The Journal of Experimental Biology* 213: 2832-2839.
- Vaughan M.R., Keith L.B. (1981). Demographic response of experimental snowshoe hare populations to overwinter food shortage. *Journal of Wildlife Management*, 45: 354-380.
- Vaughan, T. A., Ryan, J. M., Czaplewski, N. J. (2011). *Mammalogy*. Jones and Bartlett Publishers, Sudbury, Massachusetts, USA.
- Voigt, D.R., Novak, M., Baker, J.A., Obbard, B. (1987). Red fox. Wild furbearer management and conservation in North America. *Ministry of Natural Resources*: 378-392.
- Webbon, C.C., Baker, P.J., Harris, S. (2004): Faecal density counts for monitoring changes in red fox numbers in rural Britain. *Journal of Applied Ecology*, 41: 768-779.
- Wilson, D.E., Mittermeier, R.A. eds. (2009). *Handbook of the Mammals of the World*. Vol. 1. Carnivores. Lynx Edicions, Barcelona, Spain.

Websites

- Biology-online (2013). Ecological niche. Available on: http://www.biology-online.org/dictionary/Ecological_Niche [Visited on 24-05-2013].
- European hare (*Lepus europaeus*) (2013), Available on: http://animaldiversity.ummz.umich.edu/accounts/Lepus_europaeus/. [Visited on 13-05-2013].
- Game Wildlife and Conservation Trust, Brown hare (*Lepus europaeus*). Available on: http://www.gwct.org.uk/research_surveys/wildlife_surveys_and_ngc/national_gamebag_census_ngc/mammals_comprehensive_trends_new/2927.asp. [Visited on 10-10-2013].
- Game Wildlife and Conservation Trust, Red fox (*Vulpes vulpes*). Available on: http://www.gwct.org.uk/research_surveys/wildlife_surveys_and_ngc/national_gamebag_census_ngc/mammals_comprehensive_trends_new/3133.asp. [Visited on 10-10-2013].
- IUCN (2013). IUCN Red List *Lepus europaeus*. Available on: <http://www.iucnredlist.org/details/41280/0> [Visited on 24-06-2013].
- KNMI (2013). Season dates. Available on : <http://www.knmi.nl/cms/content/33516/seizoensdata>. [Visited on 11-09-2013].

- NEM (2013). NEM (VZZ, SOVON and CBS), Aantalsontwikkeling dagactieve zoogdieren, 1994-2010.
Available on: <http://www.compendiumvoordeleefomgeving.nl/indicatoren/nl1424-Aantalsontwikkeling-van-zoogdieren>. [Visited on 24-06-2013].
- PBL (2008). Available on: www.milieuennatuurcompendium.nl. PBL, CBS, and WUR Wageningen.
[Visited on 11-06-2013].
- Weerstatistieken (2013). Average temperatures per season, The Netherlands.
<http://www.weerstatistieken.nl>. [Visited on 09-10-2013].

Appendices

Appendix I

Life table of brown hare in an arable landscape(based on survival rates by Petrov and Dragoev, 1962; Pielowski and Raczynski, 1976; Broekhuizen, 1979; Frylestam, 1980b; Pépin, 1989; Jensen, 2009).

With lx showing proportion of original cohort surviving (starts with 1000 females in year 0), sx shows survival rate per year, mx shows number of surviving offspring per female per year, and the last column shows total number of surviving offspring per year (with a total of 1276,5 females after 8 years).

Age	lx	sx	mx	# offspring	# female off-spring
0	1.000	0.37	0	0	0
1	0.370	0.57	3	1110	555
2	0.211	0.57	3	633	316,5
3	0.120	0.57	3	360	180
4	0.069	0.57	3	207	103,5
5	0.039	0.57	3	117	58,5
6	0.022	0.57	3	66	33
7	0.013	0.57	3	39	19,5
8	0.007	0.57	3	21	10,5
Total:				2553	1276,5

Appendix II

Life table of brown hare in a mixed landscape (based on survival rates by Petrov and Dragoev, 1962; Pielowski and Raczynski, 1976; Broekhuizen, 1979; Frylestam, 1980b; Pépin, 1989; Jensen, 2009).

With l_x showing proportion of original cohort surviving (starts with 1000 females in year 0), s_x shows survival rate per year, m_x shows number of surviving offspring per female per year, and the last column shows total number of surviving offspring per year (with a total of 795 females after 8 years).

Age	l_x	s_x	m_x	# offspring	# female off-spring
0	1.000	0.23	0	0	0
1	0.230	0.57	3	690	345
2	0.131	0.57	3	393	196,5
3	0.075	0.57	3	225	112,5
4	0.043	0.57	3	129	64,5
5	0.024	0.57	3	72	36
6	0.014	0.57	3	42	21
7	0.008	0.57	3	24	12
8	0.005	0.57	3	15	7,5
Total:				1590	795

Appendix III

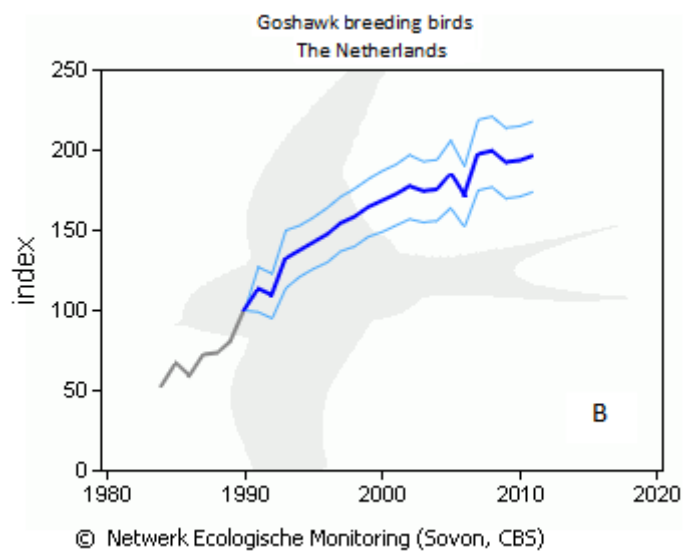
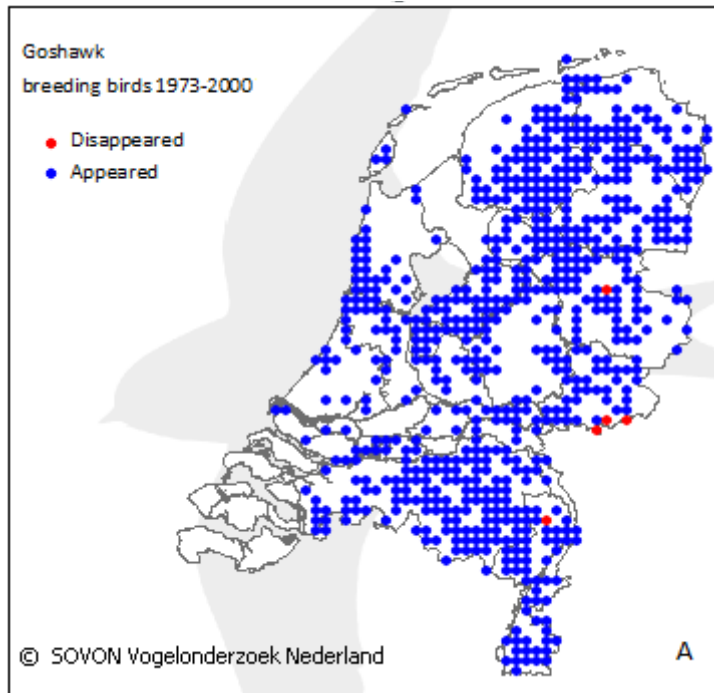
Life table of brown hare in a mainly pasture landscape (based on survival rates by Petrov and Dragoev, 1962; Pielowski and Raczynski, 1976; Broekhuizen, 1979; Frylestam, 1980b; Pépin, 1989; Jensen, 2009). With l_x showing proportion of original cohort surviving (starts with 1000 females in year 0), s_x shows survival rate per year, m_x shows number of surviving offspring per female per year, and the last column shows total number of surviving offspring per year (with a total of 621 females after 8 years).

Age	l_x	s_x	m_x	# offspring	# female off-spring
0	1.000	0.18	0	0	0
1	0.180	0.57	3	540	270
2	0.103	0.57	3	309	154,5
3	0.058	0.57	3	174	87
4	0.033	0.57	3	99	49,5
5	0.019	0.57	3	57	28,5
6	0.011	0.57	3	33	16,5
7	0.006	0.57	3	18	9
8	0.004	0.57	3	12	6
Total:				1242	621

Appendix IV

A: Distribution of the goshawk (*Accipiter gentilis*) in the Netherlands from 1973 to 2000.

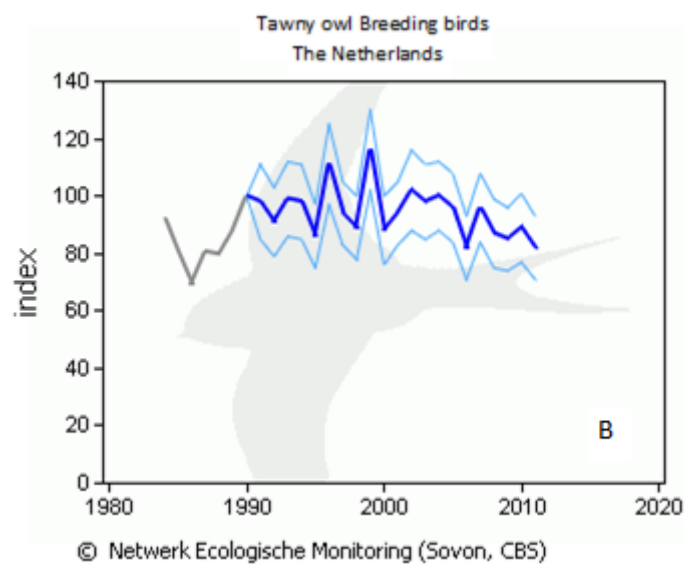
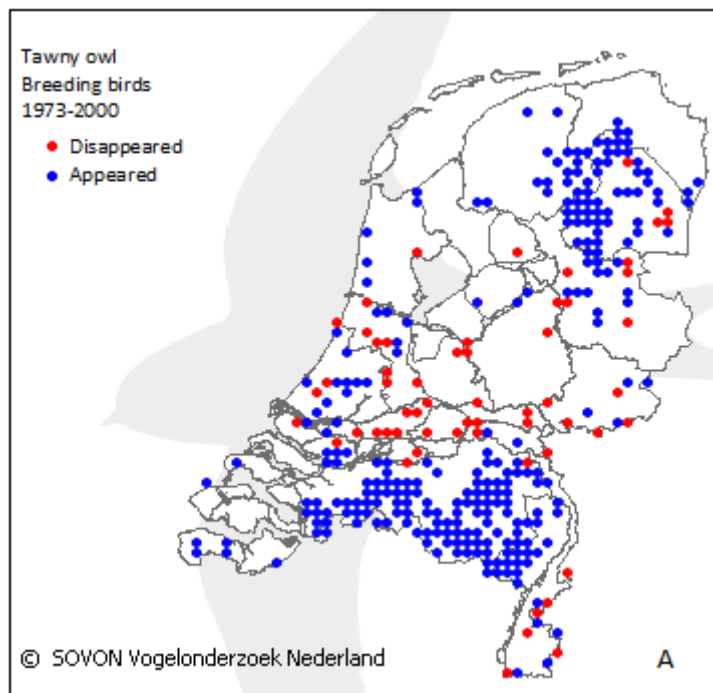
B: Population numbers index of the goshawk (*Accipiter gentilis*) in the Netherlands from 1990 to 2010.



Appendix V

A: Distribution of the tawny owl (*Strix aluco*) in the Netherlands from 1973 to 2000.

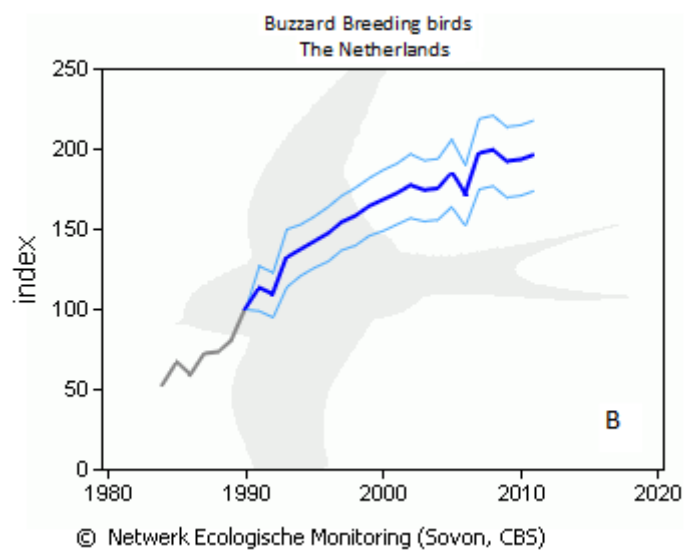
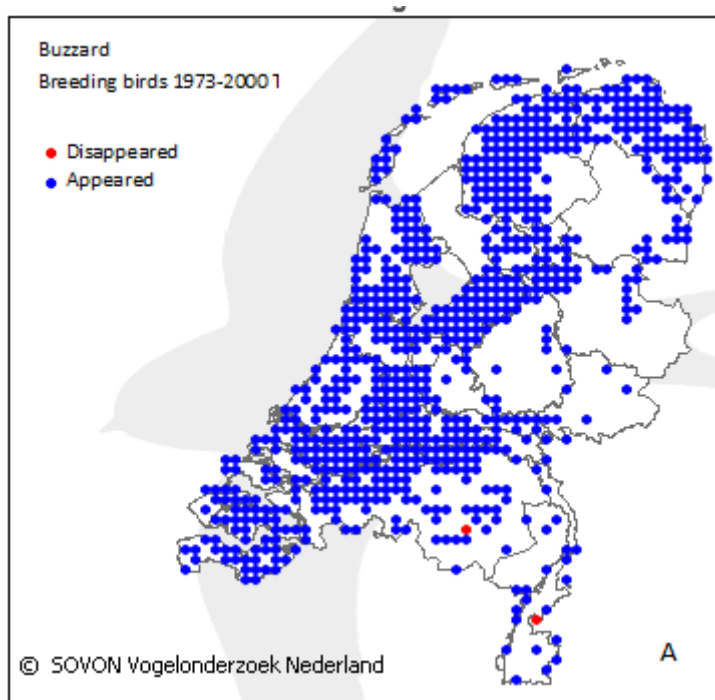
B: Population numbers index of the tawny owl (*Strix aluco*) in the Netherlands from 1990 to 2010.



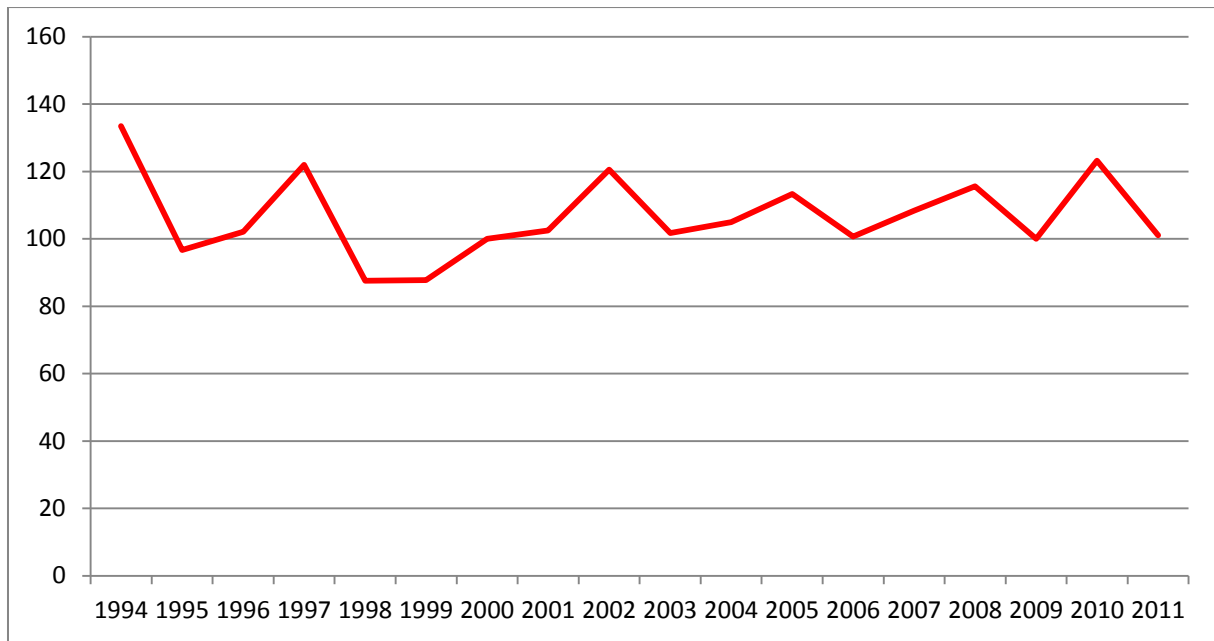
Appendix VI

A: Distribution of the buzzard (*Buteo buteo*) in the Netherlands from 1973 to 2000.

B: Population numbers index of the buzzard (*Buteo buteo*) in the Netherlands from 1990 to 2010.



Appendix VII



Red fox population index (NEM, 2013).