Climatic factors affecting a brown hare (*Lepus europaeus*) population

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Abstract: This study focuses on the possible effects of climatic factors and the frequency of flooding on variation in the size of a population of brown hare (*Lepus europaeus*) living on a salt marsh on the Wadden Sea island of Schiermonnikoog, the Netherlands. Between 1995 and 2003 an annual count was made each November in a 600 ha study area covering the eastern part of the island. Hare numbers and the change in hare numbers were correlated with a number of parameters, for rainfall, temperature and flooding. The number of hares negatively correlated with total rainfall and the number of months in which rainfall exceeded 100 mm. The change in hare numbers negatively correlated with the same two factors, as well as total rainfall in the reproductive period, the number of months in the reproductive period in which total rainfall exceeded 100 mm, and the number of days in a year that the sea level was > 200 cm above Normal Amsterdam Level. Temperature had no effect. Density independent factors appear to explain a substantial part of the variation found in hare numbers, but it is hypothesized that this variation is superimposed on a hare population that is also, in principle, regulated by density.

Key words: brown hare, *Lepus europaeus*, counts, population dynamics, climate, flooding, density independent factors.

Introduction

Densities of the brown hare (*Lepus europaeus*) vary enormously throughout its distribution range in Europe. The spring density can be as low as 3 hares/100 ha (e.g. Frylestam 1979, Pegel 1986, Panek & Kamieniarz 1999, Kilias & Ackermann 2001) and as high as 105 hares/100 ha (Pegel 1986). Low densities are generally attributed to present day intensive agricultural practices (little diversity in crops and habitats and intensive mechanisation), while high densities are associated with mild climates, nutrient rich soils and varied vegetation (Pielowski & Pucek 1976, Pegel 1986, Zörner 1996). Discounting long term changes, spring densities within any given area appear to be generally stable, with moderate to fairly large fluctu - tions around a long term mean. This suggests that hare populations are subject to some form of density dependent regulation and both Pegel (1986) and Frylestam (1979) have found strong evidence for this. Yearly variations, then, can be hypothesized to be primarily related to variations in the effects of density independent factors such as temperature, rainfall and disease.

Autumn density has also been used as an indicator of population size. Many authors have found a positive correlation between autumn density and temperature (Andersen 1952, Bresinski 1976, Spittler 1976, Eiberle 1984, Smith et al. 2005), and a negative one with rain in spring (Andersen 1952, Bresinski 1976, Spittler 1976, Smith et al. 2005). It is well known that rainfall can have a negative effect on juveniles in the early stages of their lives (Zörner 1996, Häcklander et al. 2002). During heavy rain leverets lie exposed to the elements and death by hypothermia poses a serious risk. In some areas, such as on the island of Schiermonnikoog, one of the Dutch Frysian islands in the Wadden Sea and the location of the field work on which this paper is based, strong winds regularly occur. Long wet spells, such as the storms that occur in November, might also increase the mortality rate of adult hares, through increasing the incidence of parasites. In 1995 we inspected 25 hares that were shot during the last permitted hunt and found almost all of them to be carrying at least two types of parasites; most commonly long worms, pseudotuberculosis and coccidiosis (van Wieren, unpublished data). Although many parasites can be found in clinically healthy hares, it is suspected that wet conditions favour their incidence, especially of coccidiosis, increasing mortality rates (Barré et al. 1977, Eiberle 1984, Zörner 1996). The stochastic effects of disease have never been quantified

In this study we focus on a hare population living on the salt marsh of the island of Schiermonnikoog. Although this population lives in a natural environment with no human influence and is almost free of predators, autumn densities can vary considerably. We hypothesize that this variation is mainly due to density independent factors. The most important of these is thought to be irregular flooding of the salt marsh during the hares' reproductive period. Such floods are caused by the combined effects of a high tide together with strong (north) westerly winds. We assume that leveret mortality on the salt marsh during the suckling period can be very high when these floods occur, especially when the whole salt marsh is flooded. Our central research question therefore is: to what extent can variations in the incidence of flooding, as well as temperature and rainfall, explain variations in autumn hare densities on this salt marsh.

Study area

The island of Schiermonnikoog is situated ca. 5 km north of the coast of the Netherlands. The study area lies on the eastern part of the island, and consists of about 600 ha of mainly salt marsh, with sand dunes in the north. Mammalian predators are absent, except for a few feral cats. Potential avian predators include marsh harrier (*Circus aeruginosus*) and common buzzard (*Buteo buteo*). Hares were introduced on the island in 1896 and subject to hunting until 1995, when hunting was banned as the study area had become a national park. Average autumn density of hares during the study period (1995-2003) was 80/100 ha.

Material and methods

Hare counts

Between 1995 and 2003, a count of hares was made each November. The counts started about 2-3 hours before low tide. At the onset of the count the observers formed a line across the width of the whole island at the most westerly boundary of the study area and slowly moved eastwards across the island, driving out the hares by making noise (figure 1). Each counter only counted the hares that passed him on the right, crossing the line of counters. On the shores of the Wadden Sea, the North Sea, and the eastern end of the island the hares were counted by experienced counters who counted the hares passing along the outward boundaries of the line. The number of counters varied from 34 to 48 (average 37). At its widest the observed area was 3000 m, giving an average maximum distance between counters of 81 m. The number of counters was not corrected for a number of reasons. Firstly because in the part of the transect where the distance between counters was largest, the density of hares was very low (Kuijper 2004). Secondly because where the number of hares started to increase (Kuijper 2004) the width of the vegetated part of the island was less than 1800 m, decreasing the maximum width to an acceptable maximum of 50 m, which decreased more further to the east. Finally, because on average more than 20 % of hares are counted by only two counters (those going out to the shore and the sand flats at the end of the island). These three reasons are likely to make intra-count variation between counters highly variable and possibly as variable as the inter-count variation between counters.

Environmental data

The Vrije Universiteit, Amsterdam, collects temperature and rainfall data for the island and

Figure 1. A line of counters during a hare count. *Photograph: Sipke E. van Wieren.*

Table 1. Data collected on dependent and independent variables during the study period 1995-2003. Year = November previous year-October that year; Number = total number of hares counted; N(jx-(jx-1)) = change in hare numbers in two successive years jx and (jx-1); mmtot = yearly total rainfall in mm; mmtot(3-10) = total rainfall in the period March-October; mmtot(11-2) = total rainfall in the period November-February; n>100mm = total number of months in which total rainfall exceeded 100 mm; n>100mm(3-10) = total number of months in the period March-October in which total rainfall exceeded 100 mm; Tm(5-9) = average maximum temperature in the period May-October (all temperature measurements in °C); Tm(3-5) = average maximum temperature in the period March-May; Tm(4) = average daily maximum temperature in April; Tm(5) = average daily maximum temperature in May; n>180cm = number of days in year that the sea level equalled or exceeded +180 cm NAP (Normal Amsterdam Level); n>180cm(4-9) = number of days in the period April-September that the water level equalled or exceeded +180 cm NAP; n>200 = number of days in year that the water level equalled or exceeded +200 cm NAP; n>200cm(4-9) = number of days in the period April-September that the water level equalled or exceeded +200 cm NAP.

Year	1996	1997	1998	2000	1999	2001	2002	2003
Number	550	596	445	479	500	379	320	553
N(jx-(jx-1))	250	46	-151	34	21	-121	-59	233
mmtot	509	682	862	725	801	837	974	748
mmtot(3-10)	376	457	683	459	444	613	571	507
mmtot(11-2)	133	225	176	266	357	248	403	273
n>100mm	0	1	3	0	2	2	4	0
n>100mm(3-10)	0	0	3	0	1	2	1	0
Tm(5-9)	17.7	19.8	18.4	19.4	18.7	18.7	19.6	20.7
Tm(3-5)	9.5	11.9	12.7	12.6	13.3	11.1	12.9	13.8
Tm(4)	11.8	10.5	12.1	12.4	13.3	11	12.5	13.8
Tm(5)	12.4	15.9	16.4	15.9	17.6	15.5	16.4	16.4
n>180cm	8	14	17	14	21	8	21	6
n>180cm(4-9)	1	5	2	0	0	3	0	1
n>200cm	4	6	13	7	11	6	10	3
n>200cm(4-9)	0	2	1	0	0	1	0	1

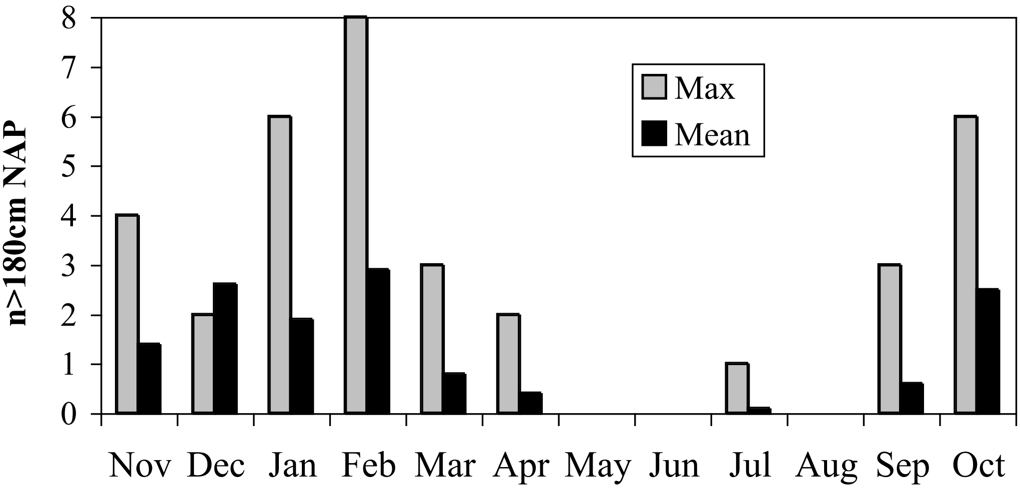

Figure 2. Mean and maximum number of inundations per month of the salt marsh of the island of Schiermonnikoog (1995-2003).

Table 2. Simple correlations (Pearson) between the number of hares counted and the change in hare numbers in two successive years, and a selection of independent variables. * = $P<0.05$, ** = $P<0.01$. For legend see table 1.

	Number	n(jx-(jx-1))
Year	-0.48	-0.11
n(jx-(jx-1))	0.70*	1.00
mmtot	-0.80*	-0.73*
mmtot(3-10)	-0.65	-0.79*
mmtot(11-12)	-0.50	-0.24
n>100mm	-0.77*	-0.78*
n>100mm(3-10)	-0.59	-0.82**
Tm(5-9)	0.13	0.18
Tm(3-5)	-0.14	-0.24
Tm(4)	-0.01	0.33
Tm(5(	-0.24	-0.48
n>180cm	-0.39	-0.54
n>180cm(4-9)	0.33	-0.18
n>200cm	-0.49	-0.75*
n>200cm(4-9)	0.37	-0.14

their database was used in the analysis. Data on sea-levels were provided by the Ministry of Transport, Public Works, and Water Management (www.waterbase.nl) in cm (relative to NAP -Normal Amsterdam Level). The independent variables derived from these databases are given in table 1. When the sea level reaches 180 cm above NAP, most of the salt mash is flooded; at 200 cm above NAP, the whole salt marsh, and the lower parts of the sand dunes, are flooded. These variables are thought to particularly have an effect on juvenile mortality. However, as the timing and length of the reproductive period are not precisely known, there is some degree of arbitrariness in the time specificity of some of the variables chosen (for a list of the variables used and their meaning, see table 1). It is thought that the whole reproductive season runs from March to October, hence the variables mmtot (3-10) and n>100mm (3-10) are used. Most leverets are probably born between April and October (van Wieren, unpublished data), and hence the variables n>180cm(4-9) and n>200cm(4-9) are used to catch major catastrophic events in this period. The Tm variables try to capture the effects of average maximum summer temperatures, Tm(5-9), spring, Tm(3-5), and the months when the growing season on the salt marsh starts: April, early start, Tm(4), and May, late start, Tm(5).

Data analysis

This large number of (partially auto-correlated) variables warrants a cautious approach. First, simple correlations (Pearson) between dependent and independent variables were calculated. Thereafter only those variables, which were significantl , and best correlated in their class (temperature, rainfall, flooding), were used in a stepwise multiple regression analysis. All the variables used in this analysis were normally distributed.

In 1995, 300 hares were counted. This count was held immediately after the last hunting season, a year in which hunting was almost twice as intensive as normal. For this reason this data was excluded from further analysis regarding numbers, but not for the analysis related to changes in numbers, since the production of leverets can be expected to be a significant factor in the net change in numbers from one year to the next.

Results

The number of hares counted in the period 1996-2003 varied from 320 to 596 (table 1), with an average of 429. Fluctuations in numbers were quite large, with 1996 and 2003 standing out as good years and 1998 and 2001 as years with a substantial net decrease in hare numbers. Rainfall, temperature and flooding data for the study period are given in table 1. Total yearly rainfall varied from 509 to 974 mm. In all years the salt marsh was flooded a number of times, with many more inundations in the winter period than in the breeding season (table 1, figure 2), although some inundations did occur in the breeding season, notably in 1997. Correlations between numbers and yearly change in numbers, and the independent variables are given in table 2. Neither the number, nor the change in numbers were correlated with year. The number of hares correlated negatively with total yearly rainfall and the number of months when total rainfall exceeded 100 mm. The change in hare numbers correlated negatively with total rainfall, the number of months in which total rainfall exceeded 100 mm, the total number of months in the reproductive period in which total rainfall exceeded 100 mm, and the number of days in a year when inundations above 200 cm NAP occurred. Regression analysis with variable selection showed that the number of hares was most closely related to total rainfall:

Number = - 0.536 (mmtot) + 888.8 (r^2=0.64, P<0.05)

For a stepwise regression on changes in hare numbers, the total number of months in the reproductive period in which total rainfall exceeded 100 mm and the number of days in a year when inundations above 200 cm NAP occurred were selected. This procedure only selected the rainfall variable in the model:

Change in hare numbers = - 107.5 (n>100mm (3-10)) + 125.7 (r^2=0.67, P<0.05)

Discussion

The autumn density of the hare population on this island (ca. 70 hares/100 ha) is high compared to populations of hares studied on mainland Europe (e.g. Panek & Kamieniarz 1999, Kilias & Ackermann 2001) and is comparable with the population density on two other Wadden Sea islands: Föhr (Pegel 1986) and Ven (Frylestam 1979). These islands share some important characteristics: an absence of main predators, of heavy traffic, and a low levels of human use. On the island of Schiermonnikoog the hares live in a natural environment and are protected from hunting.

The study revealed that density independent factors do seem to influence the population size and density. However, no effect was found for temperature, contrary to a number of authors who have identified a positive correlation between temperature in the reproductive season and autumn density (Andersen 1952, Bresinski 1976, Spittler 1976, Eiberle 1984). Flux (1967) found that cold springs led to females starting their breeding later, producing fewer litters and having fewer young per litter. There was a weak negative correlation of May temperatures on the change in hare numbers (r=-0.48), but this relation was not significant. Possibly, the relative small differences between summer and winter temperatures in this maritime climate may explain the lack of a temperature effect. Rainfall had the most effect on variations in hare numbers. Hare numbers were affected by yearly total rainfall and the number of months with rainfall above 100 mm, but the change in numbers was also negatively related to total rainfall in the reproductive season, as has been found by other authors (see introduction).

All variables related to the flooding of the salt marsh correlated negatively with the change in hare numbers, but this was only significant with regard to the frequency of floods above 200 cm NAP. Contrary to expectations, there was no noticeable effect from spring/summer inundations. Thus, extreme high tides do have an effect and we suspect that these effects might be greater than detected in these calculations. This is because we only have autumn counts and there are no available data to allow a more detailed analysis of the effect of calamities, such as a flood, and because we do not know when the precise peak in reproduction occurs. Although hares can breed throughout most of the year (Zörner 1996), the period March-May is considered the most important for increases in hare populations (Hewson 1964, Pegel 1986). While we have seen juvenile hares as early as February we think that the peak breeding season on the salt marsh will not be before April, as the growing season starts late in this rather cold and wet environment. Various authors have reported the strong effect of short periods of bad weather when the young are being suckled (Martinet & Moret 1971, Tournut 1971, Spittler 1976, Hackländer et al. 2002) and a single flood may have occurred at such a time but gone undetected in this study. Although most inundations of the salt marsh happen outside the breeding season (figure 2), some do occur in that period, although they are infrequent. To demonstrate the potential (joint) effects of a number of variables on the change in hare numbers the two good years, 1995 and 1996, can be compared with the two bad years, 2002 and 2003 (table 1). Higher values for all factors were recorded in the two years which saw the strongest net decrease in hare numbers.

From the above it is clear that rainfall and floo - ing do affect the hare population on the island of Schiermonnikoog. It is likely that the irregular strong winds, and parasites, both of which occur in conjunction with wet periods, are additional factors which contribute to the wide variations in hare density. The operation of these density independent factors, appear to act as primary controls on the population, before it reaches limits set by the availability of food. A preliminary study estimated that there is enough food in the study area in early spring for about 1500 hares (van Wieren, unpublished data). As most hare populations in Europe seem to be regulated by density dependent factors (cf. Frylestam 1979, Pegel 1989), we conclude that this island population can persist under high levels of stochasticity.

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Samenvatting

De invloed van klimaatfactoren op een hazenpopulatie ***(Lepus europaeus)***

Deze studie richt zich op de mogelijke effecten van klimaatfactoren en overstromingsfrequentie op de variatie in de omvang van een hazenpopulatie (*Lepus europaeus*) op de kwelder van het waddeneiland Schiermonnikoog. Van 1995 tot 2003 werden in november hazen geteld in het meest oostelijke deel van het eiland (600 ha). Het aantal hazen en de verandering in het aantal hazen werden gecorreleerd met een aantal neerslag-, temperatuur-, en overstromingsparameters. Het aantal hazen was negatief gecorreleerd met de totale jaarlijkse neerslag en met het aantal maanden waarin de neerslag groter was dan 100 mm. De jaarlijkse verandering in het aantal hazen was negatief gecorreleerd met de totale neerslag, het aantal maanden waarin de neerslag groter was dan 100 mm, de totale neerslag in de voortplantingsperiode, het aantal maanden in de voortplantingsperiode waarin de neerslag groter was dan 100 mm, en het aantal dagen in het jaar waarin het zeeniveau hoger kwam dan 200 cm boven NAP. Temperatuur had geen aantoonbaar effect op de hazenpopulatie. Dichtheidsonafhankelijke factoren verklaarden een substantieel deel van de gevonden variatie in het aantal hazen en we kunnen concluderen dat deze hazenpopulatie zich weet te handhaven onder overheersende stochastische processen.

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