

## Reproduction in European hare in a Danish farmland

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In order to assess the reasons for a 60% decline of the bag record of hares in Denmark during the last three decades, reproduction in *Lepus europaeus* Pallas, 1778 was studied in a location in Funen (Denmark) during April 1984 - March 1987. The breeding season was initiated around 1 January and lasted until September - October. In 1985 and 1986, 18.1% and 25.1% of the females delivered four litters, while three litters was maximum in 1984; but 13.6% - 21.4% of the females did not breed at all. The average number of litters produced per adult female was 1.93, 2.54, and 2.51 in 1984, 1985 and 1986, respectively; average litter sizes were 2.11, 2.33 and 2.06 in the survey years. For the whole study period, the average sizes of litters 1 - 4 were 1.51, 2.54, 2.53 and 1.71, respectively. During the shooting seasons the hare bags in the study area indicated 1.27, 1.64 and 1.01 young per female shot in 1984, 1985 and 1986, respectively. Postnatal mortality was calculated to be 68.0%, 72.3% and 80.6% in 1984, 1985 and 1986, respectively. The results indicate a relatively poor reproductive success due to a poor production of young and a high postnatal mortality. Shortage of sufficient nutrients in modern farming systems during the mid summer period may be a plausible explanation of these findings.

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### Introduction

In Denmark, the bag record of the European hare has declined from about 400,000 at the end of the 1950's to 160,000 today (Strandgaard and Asferg 1980, T. Asferg, unpubl.). Pegel (1986) adduced arguments that the reduced hare bag in Germany is due to an increased mortality of adults and juveniles during the breeding season.

Rieck (1956) concluded that fluctuations in the hare bag may be due to variable numbers of juvenile hares surviving until the shooting season. Pielowski (1976) found that the average number of young produced varies considerably in different years and this is strongly correlated with the percentage of juveniles in the late autumn population.

Tapper and Barnes (1986) found that landscape diversity has a causal effect on the numbers of hares in autumn, and that effects of modern farming methods could be responsible for a significant part of the decline in numbers of hares in Britain.

To be able to evaluate potential reasons for the decline in the Danish hare bag record, information on annual young production and postnatal mortality was needed. This paper presents data on breeding season, fertility, number of litters, litter size, annual productivity, and postnatal mortality of young in a Danish hare population.

### Material and methods

The study was carried out during April 1984 – March 1987 in an area of 525 ha south-east of Odense in the island of Funen, Denmark. The area consisted of arable land (53%); woods, hedgerows and coverts (19%); golf links, sports grounds and lawns (21%); buildings, parking grounds and path and road systems (7%).

Conventional farming practices were used for plant production in a farming system without animal husbandry; to protect and fertilize the crops, various chemicals were applied during the growing season. During the summer, lawns, sports grounds and parts of the golf links were mowed regularly. During the winter, sporadic felling of trees was carried out in the woods.

#### Weather conditions during the study period

Weather conditions were mostly quite normal for this part of Denmark. Only a single fact was notable during the study period: the summer of 1986 had periods of drought; June, July and September only had 2/3 of the standard mean rainfall of the period of 1931 – 1961, and August only half the standard mean amount (Fig. 1).

#### Sampling of hares

During the whole study period, 2 or 3 hares were shot almost every fortnight just after sunrise, on areas of low vegetation. Furthermore, around 1 November shootings were carried out during a whole day by 10 – 12 hunters; 36, 76 and 61 hares were bagged at these events in 1984, 1985 and 1986, respectively. During the study period, a total of 298 hares were bagged for examination (Table 1).

#### Age and sex of hares

The hares were classified as juveniles or adults; hares with an epiphyseal chondrosis (Stroh 1931) or a visible epiphysial line between the diaphysis and the distal epiphysis of ulna and radius – after the skin around the carpal joint was removed (Walhovd 1966) – were classified as juveniles.

The sex of the hares was determined from the external sexual organs (Rieck 1963) and checked on the internal sexual organs by evisceration.

#### Production of young

Adult female hares were examined for pregnancy, the number and stage of development of embryos or fetuses in the uterus, and the number of corpora lutea in the ovaries were determined. Furthermore, the uterine horns were examined for presence of placental scars.

The internal uterine wall has a lengthwise folded structure in female hares shot in the breeding season. This folded structure is interrupted at places, where a placenta has been established. During November – December, it often found that the uterine wall is thin and lacks the folded structure of the internal parts. In these uteri no placental scars can be detected. It seems that the internal part

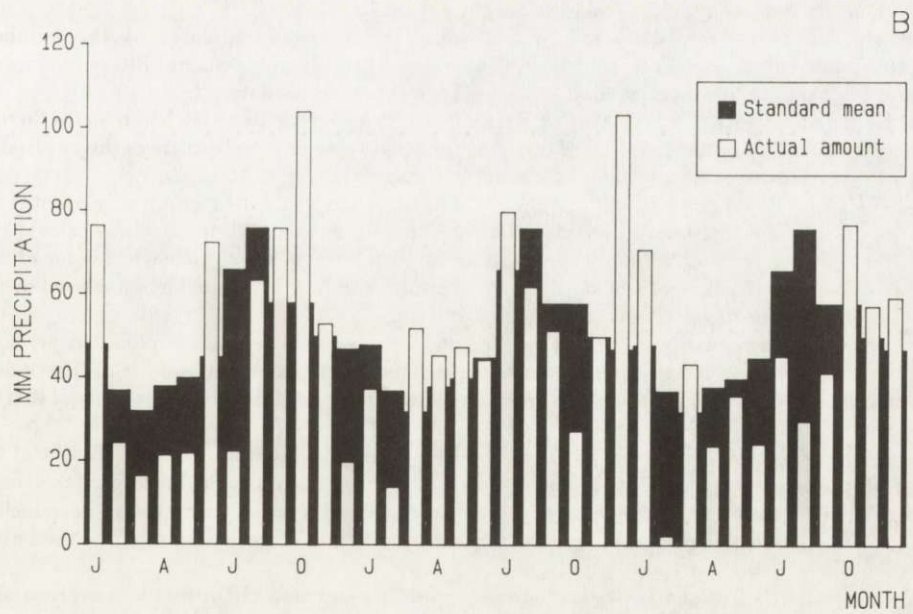
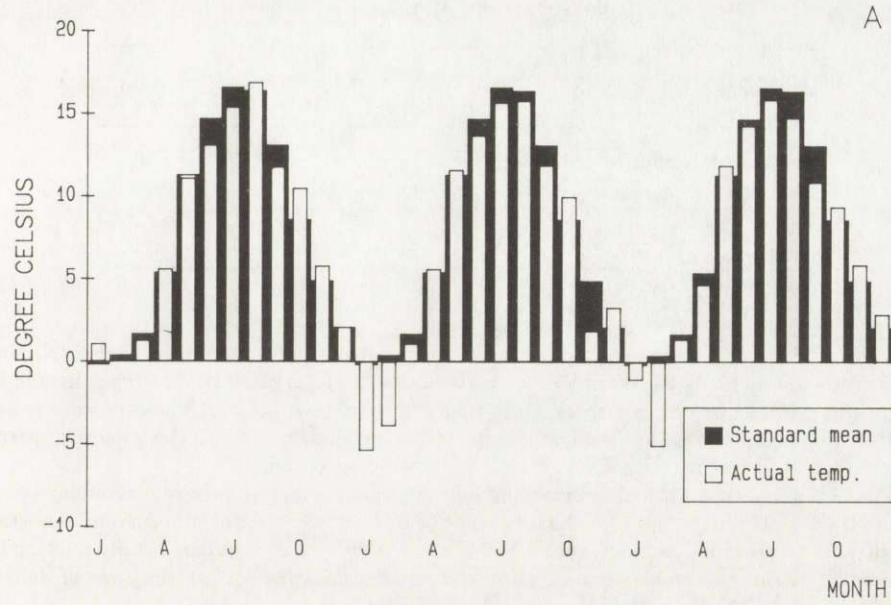


Fig. 1. Meteorological conditions in the study area during January 1984 – December 1986 obtained from the National Meteorological Office ("Weekly Reports"). A: The actual average temperature of the period and the standard mean temperature of 1931 – 1961 on a monthly basis. B: The actual mean precipitation of the period and the standard mean rainfall of 1931 – 1961 on a monthly basis.

Table 1. Number of hares shot within and outside the soothing seasons (1 October – 18 December) during April 1984 – March 1987.

Time	Year				Total
	1984	1985	1986	1987	
January – September	25	32	32	7	96
October – December	44	92	66	–	202
Total	69	124	98	7	298

of the uterine wall is regenerated, and by that scars from the previous season vanish (K. Hansen, unpubl.). Thus the number of scars in the uterus indicates the total number of young delivered by the female in the previous breeding season, which ended a short time before. The scars were separated in distinct groups according to size and pigmentation (Frylestam 1980). The grouping permitted identification of different litters delivered within the breeding season.

The data were worked up to determine the following parameters of hare reproduction:

Onset and length of the breeding season were determined from the stage of development of fetuses and the number of litters already born by pregnant females. By relating length and weight to age of embryos or fetuses (Broekhuizen and Martinet 1979), the time of delivery of young was calculated for each pregnant female hare investigated.

The breeding season was defined to begin when pregnancy was first observed among females and to end when the last young had passed the suckling stage.

Number of litters delivered by individual females was expressed by the number of distinctive groups of placental scars in the uterine horns. The average number of litters produced per female in the population was calculated for each of the three study years.

Adult females which were shot after the period for delivering the first litter in the breeding season were classed to be unproductive if they had the lengthwise folded structure of the internal part of the uterine horns without any signs of placental scars.

Litter size was expressed by the number of scars in each distinctive group of placental scars and/or by the number of fetuses in pregnant hares. The average annual litter size was calculated for each of the study years. Furthermore, average size for each litter in the chronological order of litters delivered during the breeding seasons in each of the study years was calculated and analysed by using ANOVA and pooled-variance *t* tests.

Potential production of young was defined as the number of young produced per female hare if she gave birth to litters of mean sizes and delivered the maximum number of litters during the breeding season. This calculation was made to allow comparison between the results of this work and most of the data already published.

Real production of young was calculated for each breeding season as the product of mean number of litters delivered per female and the annual average litter size of the respective years. By this calculation, both unproductive females and females delivering one or more litters were included. Thus, the calculated value of real production of young represents the population and is the basis for calculation of postnatal mortality.

Distribution of young production was based on estimated birth time and average size of the corresponding litter in the chronological order of litters delivered during the breeding season. On a weekly basis, the number of births was multiplied by the average litter size of the respective litters. The results are presented as an average of the three study seasons.

Preimplantation mortality was expressed by the difference between numbers of ovulations in the ovaries and numbers of implantations in the uterus of pregnant females.

Postnatal mortality was estimated from the number of young per adult female in the bag around 1 November and the real production of young per female in the previous breeding season. It was assumed that the age distribution in the bag record reflects that of the study area population. The mortality rate of adult females during the breeding season was unknown and is left out of consideration in this paper.

## Results

### Age and sex of sampled hares

A total of 207 adult and 91 juvenile hares were shot (Table 2). Juveniles made up 31.8%, 41.3% and 40.9% of the October – November bag in 1984, 1985 and 1986, respectively.

Table 2. Age and sex composition of the 298 hares shot for examination during April 1984 – March 1987.

Age and sex	Year				Total
	1984	1985	1986	1987	
Adult male	29	44	24	3	100
Adult female	21	40	43	3	107
Juvenile male	11	13	14	1	39
Juvenile female	8	27	17	0	52

Juveniles found to have a reliable sign of epiphyseal chondrosis (Stroh 1931) made 60.0%, 51.4% and 69.6% of the juveniles identified in 1984, 1985 and 1986, respectively.

### Breeding season

In the second half of November and the first half of December, all females investigated had thin uterine walls missing the internal folded structure. In the second half of October, the first female of this category was found, and females showing degeneration of the uterine wall made up 4.8% of the females shot in this period. After mid January all females were found to have the more thick-walled uterine horns with the internal lengthwise folded structure. None of the female hares investigated from mid January to mid October showed signs of regenerating processes in the uterine walls.

Pregnant females were recorded from the beginning of February to the end of August. Embryos or fetuses were found in 23 of the 33 females shot during this period.

An estimate of the delivery time for the pregnant hares indicated that the first young were born in the middle of February and the last ones by the end of September (Fig. 2).

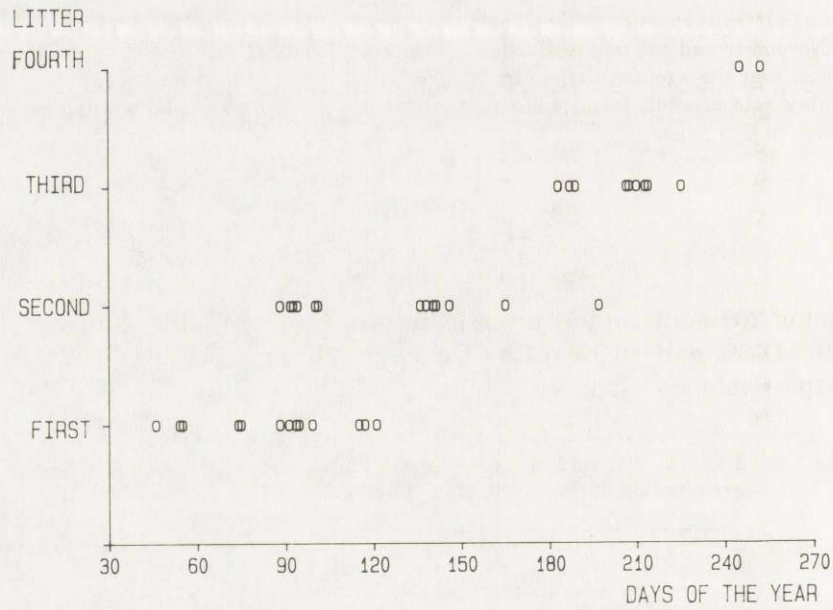


Fig. 2. Estimated birth days for litters (N = 29) recorded in pregnant females shot during April 1984 - March 1987. The dates of birth are classified according to litter number of the breeding season in which they would have been born.

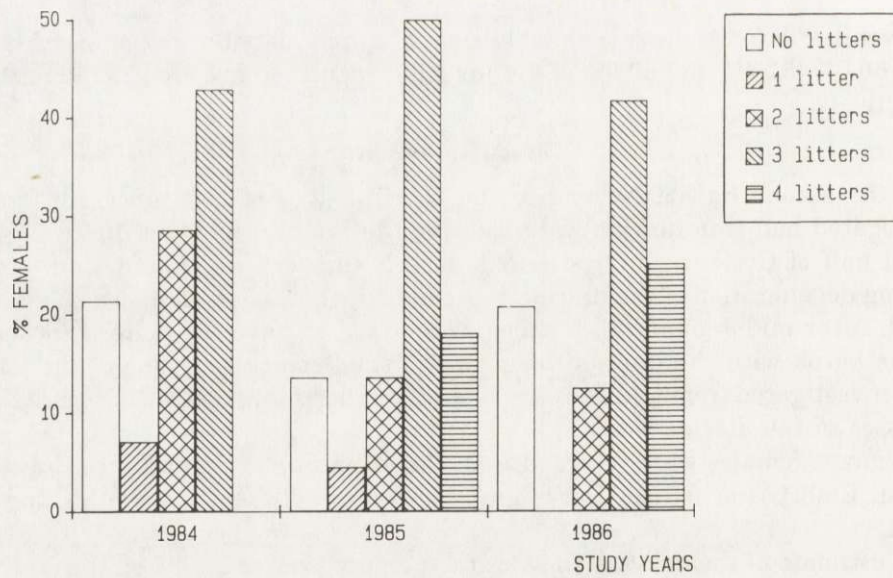


Fig. 3. Relative distribution of female hares based on number of litters delivered in the breeding seasons 1984 (N = 14), 1985 (N = 22) and 1986 (N = 24).

Table 3. Mean size of litter 1 – 4 in the breeding seasons of 1984, 1985 and 1986 ( $\bar{x}$  = mean value, SD = standard deviation, OR = observed range of litter sizes, N = number of litters in the samples).

Year		Litter			
		1	2	3	4
1984	$\bar{x}$	1.636	2.385	2.418	–
	SD	0.924	0.768	0.669	–
	OR	1–3	1–4	1–3	–
	N	11	13	12	–
1985	$\bar{x}$	1.600	2.571	2.667	2.000
	SD	0.565	1.168	1.017	0.756
	OR	1–3	1–5	1–5	1–3
	N	25	28	21	8
1986	$\bar{x}$	1.370	2.567	2.458	1.444
	SD	0.565	0.935	1.179	0.527
	OR	1–3	1–4	1–5	1–2
	N	27	30	24	9

Table 4. Test results of pooled-variance *t*-test of the hypothesis: the mean size of first, second, third and fourth litter equal each other. The significance level is based on a two-tailed test on the difference in means.

Litters tested	<i>t</i> value	df	<i>p</i>
1 versus 2	– 6.98	132	0.000
1 versus 3	– 6.60	118	0.000
1 versus 4	– 1.11	78	0.271
2 versus 3	0.05	126	0.960
2 versus 4	3.24	86	0.002
3 versus 4	3.11	72	0.003

The number of female hares with milk in the mammary glands was 9.1%, 19.0 and 18.5% around 1 November in 1984, 1985 and 1986, respectively.

#### Number of litters

The most reproductively active females delivered four litters in 1985 and 1986, while three litters was maximum in 1984 (Fig. 3). No indication of reproductive activity was found for 21.4%, 13.6% and 20.8% of the females shot during the breeding seasons of 1984, 1985 and 1986, respectively.

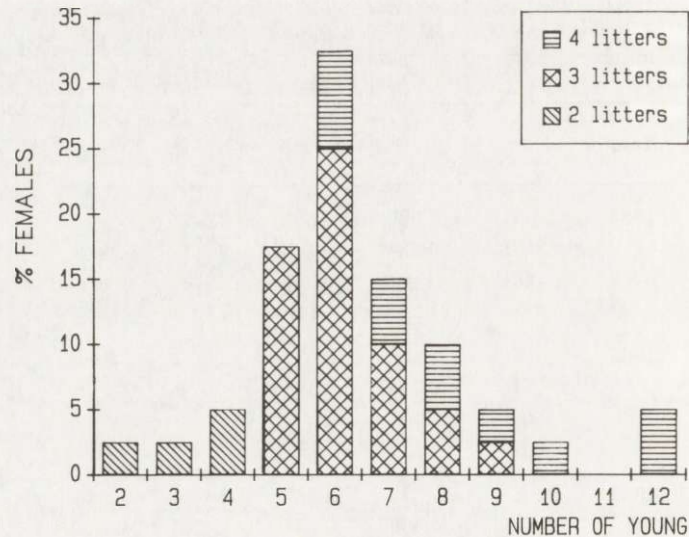


Fig. 4. Proportional distribution of adult females according to total number of young delivered during April 1984 - March 1987. The contribution from females which delivered two litters ( $N = 4$ ), three litters ( $N = 27$ ) and four litters ( $N = 11$ ) is indicated by different hatching of the bars.

The average number of litters produced per female hare - including unproductive females - was 1.93 ( $SD = 1.29$ ,  $N = 13$ ), 2.54 ( $SD = 1.26$ ,  $N = 21$ ) and 2.51 ( $SD = 1.55$ ,  $N = 27$ ) in 1984, 1985 and 1986, respectively.

The young of the first litter were born during the weeks 7 - 18, those of the second litter during weeks 13 - 27, those of the third litter during weeks 24 - 39, and those of the fourth litter during weeks 35 - 41.

#### Litter size

The largest litters held 5 young each and were observed in 7 of the 208 litters investigated. They all occurred in the second or the third litter of the breeding season. The largest first and fourth litter held 3 young (Table 3).

The average size of the first, second, third and fourth litters did not differ significantly from year to year (ANOVA,  $p = 0.391$ ). The first and fourth litters were significantly smaller than the second and third litters ( $p < 0.1$ ) (Table 4).

The average annual litter sizes were 2.11 ( $SD = 0.82$ ,  $N = 36$ ), 2.33 ( $SD = 1.03$ ,  $N = 82$ ) and 2.06 ( $SD = 1.03$ ,  $N = 90$ ) in 1984, 1985 and 1986, respectively.

#### Annual production of young

Females delivering only one litter within a breeding season gave birth to only one or two young. Females delivering two, three or four litters gave birth to 2 - 4 young, 5 - 9 young or 6 - 12 young, respectively (Fig. 4).



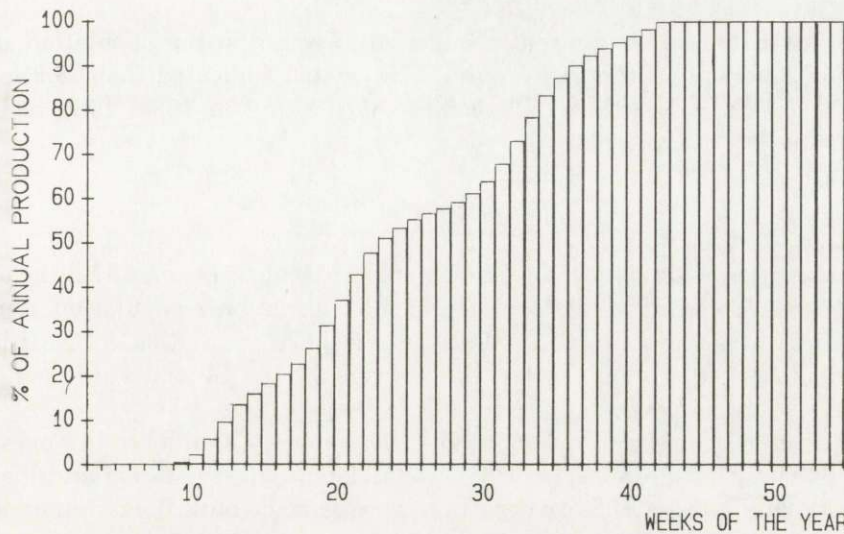


Fig. 5. Mean distribution of the annual production of young in 1984 – 1986. The relative production is calculated on a weekly basis and cumulated over the breeding season. Around 20 May (week 21) half of the annual production is delivered.

The average potential production of young per adult female was calculated to be 6.34, 8.78 and 7.90 in 1984, 1985 and 1986, respectively.

The average real production of young per adult female was calculated to be 4.08, 5.92 and 5.16 in 1984, 1985 and 1986, respectively.

#### Annual distribution of young production

The greatest birth rate was found in week 19, where 5.8% of the annual production was delivered. Birth rate peaks were also found in the weeks 10 and 31 (3.9% and 5.5% of the annual production, respectively). These peaks reflect the main production of the first, second and third litter (Fig. 5).

Calculated on the basis of all three breeding seasons, 21.7%, 36.3%, 37.3% and 4.7% of the annual production of young were delivered in the first, second, third and fourth litter, respectively.

#### Preimplantation mortality

The number of embryos or fetuses made up 90.9%, 93.5% and 77.8% of the number of eggs released from the ovaries in 1984, 1985 and 1986, respectively.

In 1984 and 1985 it was only in the period June – August that the number of corpora lutea in the ovaries was higher than the number of embryos or fetuses in the uterine horns. In 1986, the number of ovulations was higher than the number of embryos or fetuses among 62% of the pregnant females; the phenomenon was observed during the whole breeding season, and the largest number occurred in July and August.

#### Postnatal mortality

Calculations based on the real production of young in the population and the number of juveniles in the bag around 1 November indicated that 68.9%, 72.3% and 80.6% of the young had died before the hunting in 1984, 1985 and 1986, respectively.

#### Discussion

In comparison with a previous Danish study (Abildgård *et al.* 1972) the present study shows a lower juvenile proportion in the autumn hare population. Abildgård *et al.* (1972) found that around 1 October the hare population in the island of Illumø held 32.4 – 70.9% juveniles; the average for the 14-year study period was 53.8%.

The juvenile proportion in 1985 and 1986 was very similar to the ones found in German hunting grounds in Schleswig-Holstein, Hesse, Rheinland-Pfalz and Bavaria during 1981 – 1983, where the average of juveniles was reported to be 43% (Pegel 1986).

According to Rieck (1956), years with high bag records of hares hold relatively high shares of juveniles. This tendency was observed for the breeding season 1985, but not for 1986; although the bag was greater than in 1984 juveniles made up a higher proportion in 1984 than in 1986.

#### Young production

The dates of birth of young suggest that the first females were fertilized during the beginning of January. When a suckling period of about one month is added for the last litter of the season (Schneider 1978), the breeding season runs from early January to the end of October. These findings are similar to what was found in Scania, southern Sweden (Frylestam 1980), Poland (Raczyński 1964) and East Germany (Möller 1976).

Only few females were pregnant from the beginning of January. The majority of females became pregnant during the second half of January. Only a minority of females delivered young during September; most of the females gave birth to their last young in August.

In 1984, the breeding season ended nearly a month earlier than in the two following seasons; no birth was observed after the end of August and no fourth litters were delivered. These results were confirmed by the fact that a much higher proportion of females had milk in the mammary glands around 1 November in 1985 and 1986 than in 1984. Furthermore, the results agree very well with findings from East Germany, where Möller (1971) found that about 30% of the female hares were still lactating by 1 November.

The birth rate peaks indicate a tendency towards synchronism in delivering time within each of the four litters of the breeding season. The birth of the first litter peaked in mid March and the second litter about 8 weeks later. The period

Table 5. Annual maximal number of litters, average litter size and production of young per adult female in various parts of Europe. \*) females producing 3 – 4 litters. (Figures in brackets give the largest number of young found in a litter of the referred study).

Country	Maximal number of litters	Annual average litter size	Annual production per female	Reference
Denmark	3 – 4	2.1 – 2.3 (5)	4.1 – 5.9 (6.3 – 8.8)*	This study
Sweden	3 – 4	2.5 – 3.2 (5)	6.8 – 8.9	Frylestam (1980)
U.S.S.R. (north)	2 – 3	2.5	7	Kolosov and Bakeev (1947)
Netherlands	4 – 5	2.7 (5)	11	Broekhuizen and Maaskamp (1981)
France	4 – 5	2.5	9.4 – 11.3	Pépin (1989)
West Germany	3 – 4	2.3	9	Rieck (1956)
East Germany	3 – 4	1.7 – 2.8 (5)	3.2 – 11.0	Möller (1976)
Poland	3 – 4	2.0 – 2.8 (6)	6.5 – 9.0	Pielowski (1976)
Czechoslovakia	4 – 5	2.8	13.0	Velek and Semizorova (1976)
Yugoslavia	4 – 5	1.6 – 2.0 (6)	7.8 – 10.0	Stane (1956)
U.S.S.R. (south)	3 – 4	2.5	10	Kolosov and Bakeev (1947)

between the second and the third litter was considerably longer than between first and second litter, as the third litter did not peak until around 1 August. The fourth litter was delivered about 8 weeks after the third. Previous studies in West Germany (Rieck 1956) and Poland (Raczyński 1964) reported that the first two litters of the breeding season were delivered with an interval of about 8 weeks; later litters had longer intervals.

The average annual litter sizes of this study are low compared to those of other European studies (Table 5). Litter sizes found in Poland during 1966-1973 (Pielowski 1976) varied between 2.02 and 2.80, which means that the average years in the Danish study are equal only to the poorest years in Poland.

However, most other studies are based on countings of fetuses in pregnant females; when using this procedure on the present material, the average litter size is 2.64 for 23 pregnant hares shot during the whole study period. This result may indicate that some placental scars have been overlooked and that the average annual litter sizes may be a little higher than observed; nevertheless, Frylestam (1980) had higher litter sizes by using the same procedure.

The study area is not typical for direct comparisons with other results of this sort in Europe; but the hare population of the study area forages in the fields in the same way as reported from a typical Danish farmland (Hansen *et al.* 1989).

#### Reproductive success

The total number of young produced by females delivering three or four litters was the same as in Scania (Frylestam 1980) and in Poland (Pielowski 1976). This number, however, is a potential production of young, but does not represent the

whole population, because unproductive females and females delivering only one or two litters lowered the average number of young produced per female. The real production of young was only about 2/3 of the potential production. The production of young may fluctuate very much from year to year because of differences in the proportion of breeding females (Möller 1971).

Reduced fertility by preimplantation mortality during periods within the breeding season may contribute to reduced production, too (Szederjei 1959, Raczyński 1964, Möller 1971). The reduced fertility in the summer of 1986 may have been caused mainly by the dry summer, as it obviously led to insufficient growth conditions for hare food items (Hansen, in press).

In all three breeding seasons of the present study, the number of juveniles per female in the bag was lower than the average (1.76) found by Pielowski (1981) in a Polish farmland study. Furthermore, the proportion of juveniles only reached the lowest levels found by Frylestam (1980) in Scania and by Abildgård *et al.* (1972) on the Danish island of Illumø. According to Pielowski (1976), the percentage of juveniles in the population in the late autumn is correlated to a high degree with average number produced per female in the same year; it means that low levels of juveniles in autumn may indicate a poor breeding success in the present study.

The postnatal mortality was not higher than reported in several other studies; in Poland in the 1960s, Petruszewicz (1970) found mortality rates reaching 84% in some years. In the mid 1970s, the postnatal mortality in Scania was about 80% (Frylestam 1980).

No papers on postnatal mortality – with the exception of the results published by Möller (1971) – seem to consider the possibility of unproductive females in the hare populations. Therefore, previous publications on postnatal mortality are mainly based on estimates which this publication defines as potential young production. Calculating postnatal mortality from the potential young production, the mortality was found to be 79.9%, 81.3% and 87.2% in 1984, 1985 and 1986, respectively. Comparing these results to findings on postnatal mortality by Petruszewicz (1970), Frylestam (1980), Pielowski (1981) and Pegel (1986) it is concluded that the postnatal mortality found in the present study is among the highest found so far.

The reason why 1985 was the most successful year – with the highest proportion of juveniles in the study area bag – seems to be the good growing conditions for the vegetation during spring and summer, followed by an autumn with a relatively small amount of precipitation. The higher weight of juveniles in 1985 compared to 1984 and 1986 (Hansen 1991) seems to be a consequence of the growing conditions of the year, and thus stresses the above explanation.

A low production of green herbaceous plants within the hares' home range may influence lactating females and growing young in a negative way. Especially, the high postnatal mortality found in 1986 compared to the two previous years of study may be a direct effect of malnutrition. The results of a parallel running

study on preferred food items of hares indicated that the amount of food of sufficient quality might be very low during the summer period before the harvest of ripe crops. In this period hares living near golf links and lawns changed from feeding on crops in the fields to feed on green plants of the mowed areas of golf links, sports grounds and lawns (K. Hansen, in press).

Intensively farmed areas with only cereals and seed crops are poor in green herbs of high nutritive values and quantities of water. In the period 1958 – 1988 the number of hares bagged in Denmark is reduced by 60.4% and in the same period, the total area covered by roughage crops is reduced by 47.0%. I think that the changes in agriculture from producing various roughage to feed a miscellaneous livestock to produce cereals and seed crops in larger fields may be responsible for a significant part of the decline in numbers of hares bagged in Denmark during the last three decades. Further investigations are needed to certify this hypothesis.

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