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STUDIES ON THE EUROPEAN HARE. XXXIII

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Embryo Counts and Length of the Breeding Season in European Hares in Scotland from 1960—1972

[With 5 Tables]

Pregnant hares were found in 7—12 but more usually in 8—11 months each year. The incidence of pregnancy rose from 11% in January to over 90% in April and May, then declined to 11% in November. Embryo counts varied from means of 2.0 in January to a maximum of 3.2 in May, and remained at 2.0 or over until October. On average breeding began about 4 February and ended on 19 October; long breeding seasons finished late but did not start early. Big litters in the main breeding season (March-August) were correlated with temperature in January-August and January-March, and the incidence of pregnancy with annual mean temperature. Late breeding was correlated with warm weather during the last four months of the year.

I. INTRODUCTION

F l u x (1965), who reviewed the literature on reproduction of European hares, pointed out that their breeding season lasts a similar time in New Zealand, Australia, Scotland, Canada, Russia and Poland. However all these studies were short, for three years or less, and they showed little variation between years.

This paper describes a small study of breeding in European hares *Lepus capensis* L i n n a e u s, 1758 (= *L. europaeus*) in northeast Scotland over 13 years, compares breeding in Scotland with data from Poland where R a c z y ń s k i (1964) did a detailed study, and examines weather factors which may be related to variations in breeding.

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II. THE STUDY AREA

The study area comprised about 2000 ha between 120 and 300 m altitude, mostly above 180 m. About 960 ha was coniferous woodland, much of it about 10 years old or less, and about 600 ha was farmland used for stock-raising and arable crops. The remaining ground consisted of heather *Calluna vulgaris* moorland and rough pasture. The cultivated ground was worked on a seven-year rotation so that at any time 1/7 had turnips, 2/7 oats, and 4/7 temporary grass.

Hares fed on the farmland and mainly at night. During the day they moved to thick cover, on average about 1.7 km from the feeding grounds (Hewson & Taylor, 1968).

III. METHODS

Hares were treated as pests by the Forestry Commission and were killed by shooting and snaring throughout the year. One of us opened about 10 females in the field each month and counted the embryos. No further examination of the material was possible. As this method does not detect the earliest stages of pregnancy, the estimates of litter size and duration of breeding are probably on the low side. However, in Mountain hares *L. timidus* placental swellings 25 mm in diameter contained embryos only 2—3 mm long (Hewson, unpublished). According to Bookhout's (1964) key to embryo development of Snowshoe hares *L. americanus* these might have been about nine days old. If embryonic development in European hares is like this, we may have missed only a small proportion of the pregnancies. Between January 1961 and December 1972, 1569 hares were examined of which 890 were pregnant. A further 95 hares containing 70 litters were examined in 1960 but a full record was not kept of the total number of non-pregnant females examined in that year.

Table 1

Proportion of hares pregnant in each month 1961—1972 in north-east Scotland (total number — 1569) and in 1959 in Poland (Raczyński, 1964).

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Females examined in Scotland											
117	124	152	151	152	150	144	130	119	113	108	109
Percentage pregnant											
11.1	46.8	82.9	94.0	92.1	80.7	80.6	57.7	43.7	27.4	11.1	3.7
Females examined in Poland											
25	27	26	20	22	8	12	19	12	16	13	12
Percentage pregnant											
20.0	85.2	53.8	75.0	59.1	75.0	83.3	52.6	16.7	—	—	—

IV. RESULTS

Incidence of Pregnancy and Duration of Breeding

Pregnant females were found in every month of the year, but December pregnancies only in 1967 and 1971. The breeding season lasted longer in Scotland than in Poland and had a more pronounced spring-summer peak (Table 1). Also, variations from month to month in the proportion of hares pregnant appeared to be less than in Poland.

More than half the hares from March to July were pregnant, and in most years in August also. This March—August period is obviously the main breeding season and it has been used to compare incidence of pregnancy and litter size in different years. The proportion of females pregnant in this period varied from 68% in 1962 to 100% in 1967 (Table 2).

Table 2

Incidence of pregnancy in hares in north-east Scotland.

Year	Whole year		March–August	
	No. examined	% pregnant	No. examined	% pregnant
1961	114	64.9	74	79.7
1962	91	42.9	53	67.9
1963	123	52.0	61	83.6
1964	121	52.9	61	83.6
1965	133	40.6	65	75.4
1966	134	44.8	72	79.2
1967	133	79.0	72	100.0
1968	164	61.6	95	81.1
1969	171	59.1	108	82.4
1970	150	55.3	88	80.7
1971	149	65.8	85	81.2
1972	86	54.7	45	88.9

Table 3

Duration of the breeding season from first to last pregnancy in hares in north-east Scotland.

Year	Date of first pregnancy	Date of last pregnancy	Duration of breeding (days)
1960	Jan. 20	Oct. 7	260
1961	Jan. 19	Sept. 27	251
1962	Feb. 5	Aug. 1	176
1963	Jan. 31	Oct. 22	264
1964	Feb. 3	Nov. 4	274
1965	Feb. 25	Sept. 24	211
1966	Feb. 28	Sept. 15	199
1967	Feb. 6	Dec. 12	309
1968	Jan. 29	Nov. 27	302
1969	Jan. 27	Oct. 22	268
1970	Feb. 9	Oct. 21	254
1971	Jan. 20	Dec. 30	344
1972	Feb. 21	Oct. 30	251

The onset of pregnancy varied less than its ending. The first pregnant hares were found from 19 January to 28 February, averaging 4 February but the dates of last pregnancies varied between 1 August and 30 December averaging 19 October (Table 3). Long breeding seasons finished late but did not begin particularly early. Although Raczyński (1964)

considered that variation in the length of the breeding season was linked with an early start, he gave no data to support this. Years with the longest breeding seasons, 1967 and 1971, also had a high incidence of pregnancy between March and August.

Litter Size

Mean litter size in Poland (2.8) was marginally higher over the whole year than in Scotland (2.7) (Table 4), but the incidence of pregnancy and litter size varied less throughout the year in Scotland. Litter size in Scotland increased from 2.0 in January to a peak of 3.2 in May and then declined steadily to 1.8 in December. Litters of three predominated in the main breeding season and litters of two during the rest of the year. An-

Table 4

Number of embryos in European hares during each month in north-east Scotland 1960—1972 and in Poland, New Zealand and U.S.S.R.

Month	Scotland							Mean litter size in		
	Number of embryos					No. of litters	Litter size	Poland	New Zealand	U.S.S.R.
	1	2	3	4	5					
Jan.	2	**10**	2			14	2.00	1.00	2.8	1.7
Feb.	8	**35**	15	1		59	2.15	1.43	2.3	
March	4	47	**71**	15		137	2.71	2.64	2.7	
Apr.	1	34	**76**	41	1	153	3.05	4.00	2.0	3.5
May	2	28	**62**	59	4	155	3.23	3.46	—	
June	7	39	**53**	33		132	2.85	3.17	1.0	
July	10	45	**47**	20		122	2.63	3.50	1.1	3.7
Aug.	12	**40**	28	3		83	2.27	2.90	1.2	
Sept.	14	**29**	11	2		56	2.02	3.50	2.3	
Oct.	7	**18**	8			33	2.03	—	2.5	3.0
Nov.	4	**6**	2			12	1.83	—	2.8	
Dec.	1	**3**				4	1.75	—	2.6	
	72	334	375	174	5	960	2.69	2.76	2.21 *	

Modal class shown in heavy type.

* After taking resorption of embryos into account (20% over the whole breeding season).

nual mean litter size in the four countries for which data are available varied from 2.2 in New Zealand to a maximum of 2.8 in Poland. There were big differences between years. In 1967, litter size was the biggest for the whole period 1960—1972 in 8 months out of the 11 in which hares bred; and 1971 produced the largest litters in two of the remaining three months. Mean litter size from March — August was significantly higher ($P<0.001$) in the main breeding season in 1967 than in any other year (Table 5).

Factors Related to Reproduction

Records were available from the weather station at Dyce (58 m), 60 km away from the study area. For each year of the study monthly and annual mean temperatures and amount of rainfall were available, and we compared these recent data with the long-term mean annual values of temperature from 1931—60 and of rainfall from 1916—1950.

Mean litter size in the main breeding season from March to August was correlated with temperature during January to August ($r = 0.71$, $P<0.01$). It was also correlated, but less strongly, with temperature during the first three months of the year, before new plant growth would be expected ($r = 0.62$, $P<0.02$). The incidence of pregnancy in the main breeding season was not significantly correlated with Jan.—Aug. temperature ($r = 0.55$, $P<0.1$), but the incidence of pregnancy throughout the whole

Table 5

Litter size of European hares in north-east Scotland, during their main breeding season from March-August.

Year	Number of litters	Mean litter size ± 95 % confidence limits
1960	62	2.84±0.71
1961	59	2.78±0.71
1962	36	2.67±0.88
1963	51	2.55±0.71
1964	51	2.82±0.76
1965	49	2.59±0.73
1966	57	2.88±0.74
1967	72	3.28±0.76
1968	77	2.69±0.61
1969	89	2.84±0.59
1970	71	2.83±0.67
1971	69	3.03±0.71
1972	39	2.95±0.92

year was correlated with annual mean temperature ($r = 0.75$, $P<0.01$). Unlike litter size, the incidence of pregnancy was not correlated with temperature during the first three months.

Long breeding seasons occurred due to breeding continuing longer than usual into the autumn, although there was a fairly sharp tailing off after September. Breeding after the end of August was correlated with mean temperature during the last four months of the year ($r = 0.69$, $P<0.01$). Duration of breeding tended to be associated with big litter size, and with a high incidence of pregnancy during the main season in some years, but these correlations were not significant.

Neither the incidence of pregnancy nor litter size in the main breeding

season was correlated with differences from long-term average rainfall over the first three or the first eight months of the year. Also the duration of breeding was not correlated with annual mean rainfall.

V. DISCUSSION

The present study suggests that, whatever factor is involved it affects the incidence of pregnancy, litter size, and the duration of the breeding season; in other words the hare's total reproductive performance in that year. In 1967, the incidence of pregnancy was the highest, mean litter size largest, and the duration of breeding the second longest. Moreover Mountain hares on a study area 8 km away bred more successfully in 1967 than in any year from 1956 to 1969 (Hewson, 1974). As the gestation period (50 days) and duration of breeding differ from those of the European hare, as does the food (mainly heather), the weather factor involved appeared to be having a general, widespread, influence rather than being confined only to the breeding habits of European hares. As there were no major changes in farming practice which might affect hare reproduction via food supply, the likeliest variable between years in weather.

European hares and Mountain hares in Scotland both start breeding before there is any substantial new growth of herbage, although this may be available for the weaned young. The onset of breeding may be influenced by factors which inhibit courtship, such as rain or high winds, but this kind of behaviour has been little studied. European hares were most prolific after high ambient temperatures in the first three months of the year, with a breeding season featuring big litters and a high incidence of pregnancy, and breeding continuing into the autumn. This suggests that hares started to breed when in good physiological condition, arising perhaps from lack of stress caused by bad weather, and subsequently maintained this condition. Myrcha (1968) found that a decrease of 1°C in air temperature caused a big increase in the food intake of captive European hares and wild hares would perhaps have difficulty in getting extra food in late winter. The link between a warm autumn and continued breeding influenced by a better food supply is more obvious.

In New Zealand, Flux (1967) found a significant correlation whereby European hares started breeding earlier in the two preceding months were warmer than usual. Litter size of Mountain hares in north-east Scotland during the early part of the year was negatively correlated with air frost, and the size of late litters positively correlated with rainfall (Hewson, 1970). Meslow & Keith (1971) examined possible correlations between breeding in five populations of Snowshoe hares and 12 weather factors. Lower temperatures in the 250 days before mid-February, and deeper snow, were followed by larger litters in spring; deep-

er snow may have enabled hares to feed on twigs which they could not otherwise have reached. Breeding began earlier if there were fewer clouds in mid-winter, possibly due to a photoperiodic effect.

Flux showed that the important variable on any one area is not absolute temperature but the difference from the long term average, a difference which may be relatively small. European hares start to breed during January in the northern hemisphere, and during July in the southern hemisphere, at mean temperatures varying from −3°C to 7°C (Flux, 1967). The correlation between an earlier onset of breeding in New Zealand and warm weather may be due to earlier growth of vegetation there, and would not therefore be expected in Scotland. In north-east Scotland, Mountain hares bred earlier on a moor with much young, nutritious heather than on a moor a few km away with little young heather, which again suggests that the level of nutrition may be important, even before any new plant growth occurs (Hewson, 1970).

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REFERENCES

1. Bookhout T. A., 1964: Prenatal development of snowshoe hares. J. Wildl. Mgmt., *28:* 338—345.
2. Flux J. E. C., 1965: Timing of the breeding season in the hare *Lepus europaeus* Pallas and rabbit *Oryctolagus cuniculus*. Mammalia, *29:* 557—562.
3. Flux J. E. C., 1967: Reproduction and body weights of the hare *Lepus europaeus* Pallas in New Zealand. N.Z. Jl. Sci., *10:* 357—401.
4. Hewson R. & Taylor M., 1968: Movements of European hares in an upland area of Scotland. Acta theriol., *13:* 31—34.
5. Hewson R., 1970: Variation in reproduction and shooting bags of mountain hares on two moors in north-east Scotland. J. appl. Ecol., *7:* 243—252.
6. Hewson R., 1974: Population changes and grazing preferences of mountain hares *Lepus timidus* L. in north-east Scotland. M. Sc. thesis, Aberdeen University.
7. Kolosov A. M., 1941: The reproductive biology of the hare *Lepus europaeus* Pallas. Zool. Ž., *20:* 154—172.
8. Meslow E. C. & Keith L. B., 1971: A correlation analysis of weather versus snowshoe hare population parameters. J. Wildl. Mgmt, *35:* 1—15.
9. Myrcha A., 1968: Winter food intake in European hare *Lepus europaeus* Pallas, in experimental conditions. Acta theriol., *13:* 453—459.
10. Raczyński, J., 1964: Studies on the European hare. V. Reproduction. Acta theriol., *9*: 305—352.

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ILOŚĆ EMBRIONÓW I DŁUGOŚĆ SEZONU ROZRODU U ZAJĄCA SZARAKA W SZKOCJI, W LATACH 1960—1972

Streszczenie

Ciężarne samice zająca szaraka znajdowano padłe przez 7 do 12 miesięcy każdego roku. Zwykle jednak okres rozrodu wynosi od 8 do 11 miesięcy roku (Tabela 1). Ilość ciężarnych samic w stosunku do wszystkich zbadanych samic wynosi 11% w styczniu a w kwietniu i maju aż 90%, po czym zniża się ponownie do 11% w listopadzie (Tabela 2). Liczba embrionów waha się od 2,0 w styczniu do 3,2 w maju, by następnie znów zniżyć się do około 2,0 w październiku (Tabela 4). Sezon rozrodu zaczyna się średnio w dniu 4 lutego i kończy się 19 października; dłuższe sezony kończą się później, ale nie rozpoczynają się wcześniej (Tabela 3). Wielkość miotu różni się nieco, zależnie od roku w którym czynione były obserwacje (Tabela 5). W okresie od marca do sierpnia wysoka liczebność miotów skorelowana jest z temperaturą w okresie styczeń — sierpień i styczeń — marzec. Natomiast procentowy udział samic ciężarnych w populacji zależy od średniej temperatury roku. Przedłużenie rozrodu powodowane było ciepłą pogodą panującą w ciągu czterech końcowych miesięcy roku.