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STUDIES ON THE EUROPEAN HARE. XXXVI

Survival in Adult European Hares

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Broekhuizen S., 1979: Survival in adult European hares, Acta theriol., 24, 34: 465—473 [With 4 Tables & 1 Fig.].

The average annual survival rate of adult European hares (*Lepus europaeus* Pallas, 1778) in The Netherlands, determined as 0.34—0.38, was established by recoveries of hares which had been ear tagged in their adult phase, and by means of the ratio of first-year hares to older hares shot in December, assuming that survival in adult hares is independent of age. This rate was compared with data from literature. The survival rates from various European countries show a great variation. It is not clear whether hunting influences the average survival rates.

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I. INTRODUCTION

In relation to population dynamics of hares, it is important to know the survival rate of adult hares. Information about this is still scarce, most likely due to the fact that hares of different year classes cannot be easily distinguished in the field. Therefore, to determine the survival rate, hares were marked with ear tags, which is very labour intensive. In order to read these marks, the investigator either has to rely on hares being recaptured, or on the recovery of dead marked animals being reported. In practice, captures as well as recoveries are concentrated in the non-productive period, *i.e.* the end of autumn and the beginning of winter. In this period the conditions in the fields of the countryside are most suitable for catching hares and it is also the hunting period. This implies that the survival rate can only be determined for the whole reproductive season. Up to now it appears to be impossible to quantify the mortality in the course of the reproductive season.

We collected some data about the survival rate in Dutch hares from recoveries of tagged hares as well as by means of the ratio of first-year to older hares in the shooting bags during December. The results are compared with literature data from other European countries, which were obtained from different situations and by using different methods. These literature data will first be reviewed briefly.

II. REVIEW OF SURVIVAL DATA FROM LITERATURE

Information on the survival of adult hares has been obtained from a study of a population composed of hares of known age (Abildgård *et al.*, 1972), from the results of repeated recaptures of marked animals of known age (Pielowski, 1971 and 1975), from a study of the age composition of a random shooting (Frylestam & Von Schantz, 1977), and from reported recoveries by shooting of hares ear tagged as young (Rieck, 1955 and 1956).

1. Population of Known Age Composition

From the beginning of 1957 up to the end of 1970, more than 95% of the hare population of the Danish island Illumö was marked with numbered ear tags. Hence, unique data are available about the age composition of an entire population (Abildgård *et al.*, 1972). Since this investigation concerned an island situation, the influence of migration could be ignored, except perhaps one severe winter when the sea was frozen. It should be kept in mind that no predatory mammals occur on Illumö. There was no killing by hunting, but due to the capture

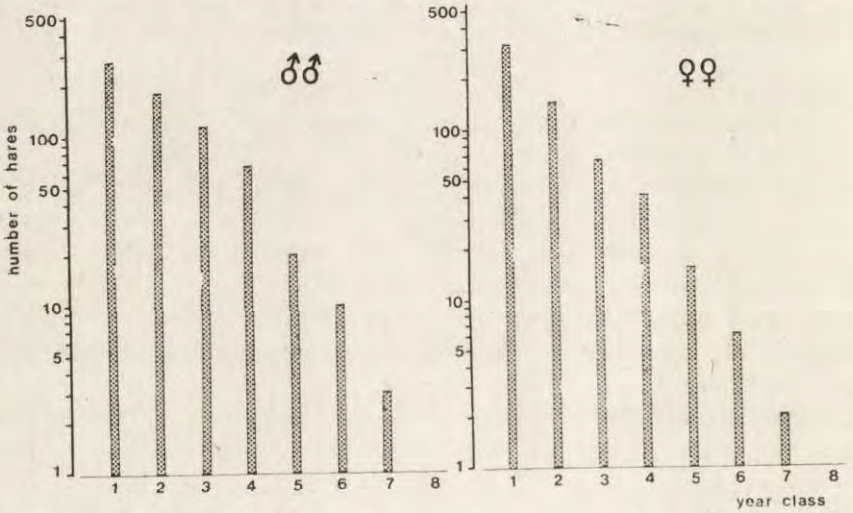

Fig. 1. Number of hares in the various year classes, present on the Danish isle Illumö in the first catches of November/December during the period 1962—1970 (after data from Abildgård *et al.*, 1972).

operations 2—3% died. During the study it became obvious that after 1962, unmarked adult hares were exceptions. The maximum age was 7 years. As can be expected, the mortality in young hares appeared to be notably higher than in adults. The average annual mortality rate in the adult females and males was 45 and 38% respectively.

The distribution among the different year classes of the hares, examined during the first winter captures (November or December) of the years 1962—1970 is shown in Fig. 1, which was composed after data presented by Abildgård *et al.* (1972). The numbers are plotted on a log-scale. As the tops of the columns

representing the numbers of females nearly fit to a straight line, the mortality rate in the females appears to be independent of age. In the males the annual mortality rate during their first three years is lower than in females. A b i l d g å r d *et al.* (1972) reported that particularly in years of high density and in the periods of decrease afterwards, the mortality in males was lower than in females.

2. Recaptures of Hares Tagged as Young

The survival of hares can be investigated by means of repeated recaptures of marked animals of known age. The age of hares can only be reliably estimated in the young; therefore, it is necessary to mark the leverets. The most extensive study using this method was carried out near Czempiń in the province of Poznań in Western Poland (P i e l o w s k i, 1971 and 1975). The young hares found in the field were ear tagged and released. During the winter about 30% of the

Table 1

Life table for the hare population near Czempiń, based on data from P i e l o w s k i (1975).

Age (years)	l_x	d_x	q_x
0—1	1.000	0.500	0.500
1—2	0.500	0.278	0.556
2—3	0.222	0.086	0.387
3—4	0.136	0.062	0.456
4—5	0.074	0.024	0.324
5—6	0.050	0.015	0.300
6—7	0.035	0.011	0.314
>7	0.024	0.024	1.000
Total	2.041	1.000	
$\bar{q}$ (1—7)			0.489

l_x — proportion of animals that survived to the year class x; d_x — difference between two succeeding values of l_x; q_x — mortality rate of the year class x ($q_x = d_x/l_x$).

population was caught, and exported, except the marked animals which were released again. In this way data were collected about the number of young surviving the different year classes. From these data I have constructed a life table (Table 1). The average annual mortality rate was calculated as $\bar{q}_x = \Sigma d_x / \Sigma l_x$. and turned out to be 0.49 over the first 7 years.

Since we consider the survival rate in adult hares, it is to be noted that in the life table the age class of 0—1 year is included. As capturing took place in winter time, one would expect most of the hares caught to be older than 4 months, since the majority of the young born in late summer and autumn die before the winter, due to parasitic infections such as coccidiosis and strongylosis. Assuming that the survival of young hares of five months and older does not differ from that of adults, all hares of five months and over have been considered as »adults«.

The oldest hare recaptured in the Czempiń area was at least 12.5 years old. However, the proportion of hares older than 7 years was small (2.4%). All hares older than 6 years proved to be females.

3. Age Composition of a Random Shooting

From hares killed at a shooting session, an impression can be gained of the age composition of the population. A disadvantage of this method is that it is hardly possible to be sure about the nonselectiveness of the shooting. By using the number of periosteal growth lines in the lower jaw as a criterion for age, Frylestam & Von Schantz (1977) determined the age composition of a sample of 39 hares shot from an area in South Sweden. The number of hares (l) belonging to the different year classes was determined; the differences between the l-values of succeeding year classes (d) indicate the annual mortality. Although the sample may be too small to be representative for the population, I constructed a »life table«, and from this the average annual mortality rate was calculated to be 0.49. It should be noted that also in this case the first-year-hares have been included as »adults«.

4. Recoveries from Shooting of Hares Tagged as Young

Recoveries of marked hares are mostly obtained from shot or dead animals. Data from the latter are so scarce, that they cannot be discussed separately.

Table 2

Life table based on recoveries from ear tagged hares, collected by Rieck (1955, 1956).

Age (years)	d	l	l_x	d_x	q_x
0—1	81	130	1.000	0.623	0.623
1—2	29	49	0.377	0.223	0.618
2—3	8	20	0.154	0.061	0.396
3—4	7	12	0.092	0.054	0.587
4—5	1	5	0.038	0.008	0.210
5—6		4	0.031	0.023	0.742
6—7	0	1	0.008	0.000	
7—8	1	1	0.008	0.008	1.000
Total	130	222	1.708	1.000	
q_x					0.585

Rieck (1955 and 1956) collected recoveries of shot hares and I assembled them in a life table (Table 2). The first-year-hares shot during the hunting seasons are again considered as »adults«.

Table 2 shows, like Table 1, no significant difference in mortality rate between first-year and second-year-hares. The mean annual mortality rate was 0.58, and the oldest hare recovered was 7 years of age.

Calculating the mean annual mortality rate, mortality was assumed to be independent of age. In contrast to the mortality among the adult females of Illumö (section II.1), there is no basis here for this assumption, because the numbers recovered at older ages are too small to demonstrate any significance between differences. Furthermore, the recoveries collected by Rieck were mainly from shot hares (91.5%). Since it is unlikely that such a high proportion of the population dies through hunting, the rate of recovery in shot hares must be

much higher than in hares died by other causes. Since the calculation is only based on recoveries from shootings, it is important to know whether hunting is age-dependent, especially within the mature section of the population. Unfortunately no sufficient information is available about this. Rieck (1967) compared the bag of a drive from November with that of a succeeding drive over just the same area one month later. There was no significant difference between the proportion of first-year-hares from November (76%) and that from December (72%) ($\chi^2=2.03$; $P>0.05$); this implies that the chance of being shot on drives for first-year-hares and older ones is about the same. So it may be assumed that mortality caused by shooting is not dependent on age. An effect of senescence may be neglected.

III. RESULTS OF OWN INVESTIGATIONS IN THE NETHERLANDS

1. Recoveries from Shootings of Hares Tagged as Adult

For several years hares were caught and ear tagged in The Netherlands at the end of the shooting season and just afterwards. These hares were released partly in the same area and partly in other fields. Some of them were recovered, mainly because they were shot. To calculate the survival rate of these hares, we used only recoveries from animals which were estimated to be at least 5 months old, when they were

Table 3

Recoveries from Dutch ear tagged hares, marked at the age of 5 months or older. Recoveries from shootings only (n=418).

Year of marking	Number marked	Time between marking and recovering (years) 0—1	1—2	2—3	3—4	4—5	5—6	6—7	7—8	8—9	9—10
1968	1	1	0	0	0	0	0	0	0	0	0
1970	2	0	0	0	0	0	0	0	0		
1971	74	9	0	1	0	1	0	0			
1972	48	4	1	1	0	0	0				
1973	95	11	5	2	0	0					
1974	177	18	8	0	2						
1975	7	1	0	0							
1976	3	1	0								
1977	11	1									

caught. The estimation was done by the stage of ossification of the distal epiphyseal knob of the ulna (Broekhuizen & Maaskamp, 1979). Only the recoveries from shoots were used. Although it was not confirmed, it was assumed that the recovery rate was the same in the various fields. It was assumed also, that every year a similar proportion was shot and the survival rate of tagged hares of at least 5 months old was independent of age and calendar year. Taking all these

assumptions into account, the survival rate was calculated by applying a model given by C a v é (1977) [1] (Table 3).

The survival rate was found to be 0.34 (S.D.: 0.10) and the recovery rate 0.163 (S.D.: 0.018). The differences between the observation and the expectation from Cavé's model may be due to chance ($\chi^2=3.23$; $\nu=5$; $P=0.34$), so there are no reasons to reject the assumptions of the model. Comparing the mortality rate in the first year with that of the succeeding years, there is no significant difference, so the assumption of mortality being independent of age in hares of 5 months and older can be maintained.

2. Recruitment in Stable Populations

When a population is stable in the long term, the average number of mature animals dying per year must be equal to the average number of yearlings joining the reproductive part of the population. In that situation the percentage of first-year-hares at the start of the reproductive season (recruitment) equals the annual mortality rate in the older hares, provided that in the latter mortality is age-independent. On those conditions the mortality rate in adult hares can be obtained from the recruitment.

Hunting statistics show that the level of the hare populations may fluctuate. A d a m c z e w s k a - A n d r z e j e w s k a & S z a n i a w s k i (1972), P e p i n (1974) and M ö l l e r (1975) showed that also the proportion of first-year-hares can vary considerably, not only year by year but also between different areas in one year. Since in The Netherlands the reproductive season starts at the end of December (B r o e k h u i z e n, in prep.), the percentage of first-year-hares shot in December can be used as a measure of the recruitment. However, this percentage has to be obtained from data collected during several years from several areas, assuming that hunting does not affect the age composition of the population.

Investigation of the eye lens weight of 4801 hares collected every year in December from shooting bags during the years 1967—1975 in 24 different areas, showed that 62% of the hares were first-year animals. We defined hares as first-year when their eye lens fixed in formalin 10% and dried at 80°C, was less than 280 mg in weight (B r o e k h u i z e n & M a a s k a m p, 1979). At an average recruitment of 62%, therefore, the average survival rate in hares older than one year should be 0.38.

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[1] I am greatly indebted to Dr A. J. Cavé for conducting the computation.

IV. DISCUSSION

The average survival rate in adult hares from The Netherlands as obtained by recoveries from hares ear tagged as adult (0.34), corresponds, notwithstanding the presuppositions, very well with that obtained from the mean recruitment just before the beginning of the reproductive season (0.38). Therefore, the survival rate in adult hares from The Netherlands is set at approximately 0.35.

Comparing this figure with the survival rate of males (0.62) and females (0.55) calculated by Abildgård *et al.* (1972) in the unexploited population from Illumö, and that (0.51) found by Pielowski (1975) in an unexploited part of a population near Czempiń, the survival rate we found in The Netherlands is remarkably low. The difference is

Table 4

Data from the literature about the percentage of hares older than one year, found in shooting bags.

Country	Years	Numbers examined	% ad.	Author
G.D.R., N part	1965—1972	6287	74	Möller, 1975
G.D.R., S.E. part	1965—1972	10976	65	„
G.D.R., S.W. part	1965—1972	16687	54	„
Poland, 5 provinces	1966—1970	24595	52	Adamczewska-Andrzejewska & Szaniawski, 1972
Poland, prov. Poznań	1966—1970	7762	54	„
The Netherlands	1967—1975	4801	38	Own data
Switzerland	1967, Oct.-Nov.	414	47	Wandeler & Huber, 1969
Denmark	1963, Dec.	146	35	Walhovd, 1966
France, Provins	1971—1972	435	26	Pepin, 1974
F.R.G., Biebesheim	1964, Nov.	798	24	Rieck, 1967
F.R.G., Biebesheim	1964, Dec.	402	28	„

unlikely only to be the result of the exploitation of the Dutch hares by hunting. During the period 1966—1970, Adamczewska-Andrzejewska & Szaniawski(1972) found 54% adults in shooting bags from the Polish province of Poznań (where Czempiń is also located). During the same period, they found 52% adult hares in their total material from 5 provinces. When these populations are supposed to be stable, the survival rates were respectively 0.54 and 0.52. This shows that survival in exploited populations may have the same high value as in unexploited populations, and it suggests that the exploitation is counterbalanced by compensatory mortality.

In the period 1965—1972, Möller (1975) found in the south-west, south-east and northern parts of the G.D.R. 53, 65 and 74% respectively,

adult hares in shooting bags. This also indicates survival rates which are not lower than found in Illumö and Czempiń. It is not reported whether hunting in Poland and the G.D.R. influenced the age composition. It is premature, therefore, to conclude that shooting does not affect the survival rate of adult hares. Sufficient information on the ecological conditions in the various areas is also lacking. Data about the percentage of adult hares in shooting bags obtained from short-term investigations in different European countries (Table 4), indicate that also lower survival rates in adult hares occur in exploited populations. Due to the different ecological conditions and the incidental character of these samples, it is not possible to evaluate the differences.

From the average survival rate in adult hares from The Netherlands, set at 0.35, the average expectation of further life can be calculated by the formula $(2—m)/2m$, where m is the annual mortality rate (Lack, 1954). So the expectation of further life found for a Dutch adult hare is about one year (1.04).

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PRZEŻYWALNOŚĆ DOROSŁYCH ZAJĘCY SZARAKÓW

Streszczenie

Średnią roczną przeżywalność dorosłych zajęcy szaraków (*Lepus europaeus* Pallas, 1778) określono w Holandii na 0,34—0,38. Podstawą do wyliczenia było znakowanie (Tabela 3) oraz analiza stosunku ilościowego osobników tegorocznych do starszych strzelanych w grudniu — przy założeniu, że przeżywalność dorosłych jest niezależna od wieku. Uzyskane wyniki porównano z danymi literaturowymi, które mówią o dużym zróżnicowaniu przeżywalności w różnych krajach Europy (Tabele 1, 2, 4, Ryc. 1). Nie jest jasne czy fakt polowania na danym terenie wpływa istotnie na średnie wskaźniki przeżywalności.