DANISH REVIEW OF GAME BIOLOGY Vol. 6 no. 5

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Introduction

From 1957 to 1970, the Game Biology Station has performed regular capture, marking, and release of hares on the Danish island of Illumø, which is situated in Helnæs Bay on the south-west coast of Funen.

The investigation has been concentrated on determination of population size and fluctuation, sex and age distribution, and mortality and reproduction. The objective of the investigation was to obtain more reliable and detailed results than those obtained from the Game Biology Station's studies based on the number of hares shot using the battue technique in different hunting areas, and from occasional studies of the hare populations of other small islands.

The project was initiated and run by JOHS. ANDERSEN, while most of the demographic treatment of the data has been carried out by F. ABILDGÅRD and O. BARNDORFF-NIELSEN.

Illumø island is 3½ km. long, 100–500 m. wide and its area is about 100 hectares (see Fig. 1). The soil is mostly fertile moraine. At least half of the island is farmed intensively with different cereals (especially barley), root crops such as sugar beet and swedes, grass, clover and lucerne. There are also meadows, used for grazing. Along the coastal slopes and stone dikes there are occasional thickets. The climate is that of the rest of Denmark, with averages of O° and 17° for the coolest (January) and warmest (July) months respectively. Precipitation along the SW coast of Funen is a little less than the average for the whole country (50-60 cm. and ca. 65 cm. annually respectively) (TRAP 1958 p. 66, Statistical Yearbook 1970 p. 4).

During the period of investigation no hares have been shot, but the oft-repeated captures have resulted in a certain amount of mortality, as accidents are unavoidable during the captures. There are no mammalian predators on the island.

The main feature of the Illumø island project is that it concerns a geographically limited and isolated population. Only during the exceptional conditions of winters of seafreezing (1963 and 1970) have hares been able to cross over to the mainland of Funen, a distance of 2 km., and the number of recoveries has shown that this migration only concerned a few individuals. The hare population of the island is high according to Danish standards, as on average there are about 200 individuals, i. e. a population density of 200 hares per. sq. km.

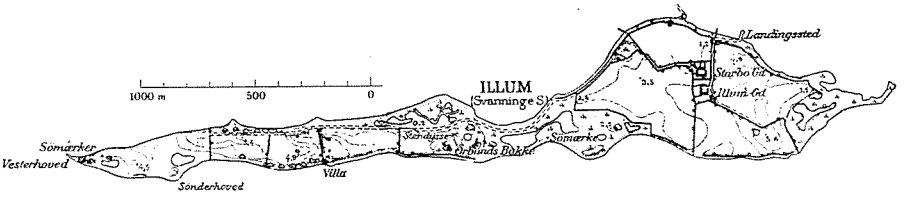


Fig. 1. Map of Illumø island.

Fig. 1. Kort der viser den langstrakte Illumø.

Capture technique

The hares were captured with nets. This cannot be done during the summer when crops such as barley are growing, but captures of as many hares as it was reasonably feasible to catch were carried out repeatedly during autumn, winter and spring.

The first autumn capture takes place about October 1st. By this time reproduction is completed, so that there is no more addition to the population in that year. At this time, the population is close to its annual maximum. The real maximum probably occurs earlier in the year, as some leverets die before the first capture in October.

The second capture takes place a week later, and two catches with a week's interval are made about December 1st, and in the spring, generally in March. In March the population is at its minimum size, due to the effects of autumn and winter mortality, and the fact that the production of young has not yet commenced. Table 1 gives the dates of captures.

The nets used resemble fish-nets, the mesh size being 7 cm. and the net height $1^1/_2$ m. The nets are erected vertically and hang quite loosely. They are placed across the narrow island in such a way as to divide it into 8 sections; this limits the distance over which the hares are driven.

A chain of beaters flush the hares. About 40 schoolchildren under the direction of adults traverse the short section 2-4 times, at a distance of $2^1/_2$–6 m. from

Fig. 2. Part of the chain of 40 schoolchildren who drive the hares from cover (Photo: Finn Christoffersen).

Fig. 2. En del af kæden af de 40 skolebørn, der driver harerne op.

Fig. 3. Two catchers removing hares from the net (Photo: FINN CHRISTOFFERSEN).

Fig. 3. To fangere tager harer ud af nettet.

each other (see Fig. 2). About 30 m. in front of the nets are the catchers, who are adults. Placed at a distance of 10–20 m. from each other, they are ready to drive the hares which pass them into the nets, where the hares are captured and seized by hand (see Fig. 3). The hares are placed in cotton bags and taken to a building in the middle of the island, where a special team note their weight, sex, and age. At the same time tags are also read, or placed on animals not previously caught. The metal tags are placed on the ear using pliers; as an extra precaution, a number is tatooed on the ear. At the end of the capture day the hares are released again.

The frequent repetitions of the captures imply that practically all hares are caught one or more times. Thus in the last capture in spring 96-100 % of the hares caught have been marked in earlier cap-

	Year *År*	.1	.2	.3	.4	.5	.6
1.	1957/58	25/9	7/10			8/3	13/3
2.	1958/59	26/9	6/10	27/11		12/2	19/2
3.	1959/60	24/9	6/10	1/12		14/3	21/3
4.	1960/61	29/9	8/10	26/11		28/2	4/3
5.	1961/62	26/9	3/10	25/11	4/12	28/2	7/3
6.	1962/63	5/10	9/10	5/12	8/12	10/4	17/4
7.	1963/64	5/10	9/10	6/12	11/12	4/3	11/3
8.	1964/65	7/10	10/10	5/12	12/12	20/3	24–26/3
9.	1965/66	12/10	19/10			11/3	18/3
10.	1966/67	6/10	18/10	6/12		11/4	
11.	1967/68			15/11	14/12	6/2	20/3
12.	1968/69	8/10	15/10	26/11	4/12	10/4	15/4
13.	1969/70	14/10		21/11		23/4	12/5
14.	1970			11/11	18–19/11		

Table 1. Dates of captures of hares on Illumø.
Tabel 1. Datoer for harefangster på Illumø.

tures. This result is the basis for presuming that all untagged animals in the following season are young hares. The validity of this assumption is supported by the fact that 98 % of the untagged animals in early October have an epiphysial knob on the ulna.

According to the calculations, there have been 1421 different hares on the island during the 14-year period of investigation, of which 1275 (89.7 %) have been captured. Many were re-captured 5-10 times.

Statistical estimation formulae

As mentioned above it is possible to state year-class and sex of each hare caught with practically full certainty. Every year-class of hares with the same sex may be considered as a population without increase and with decrease only due to death, either naturally or on capture.

Table 2 shows as an example the capture records for females born in year No. 9 (i.e. in summer 1965). Each row of the table gives the capture record of a hare using the following code (the different captures are represented by the successive columns in the table).

1: not caught in this capture, but later,

2: caught in this capture and in a (at least one) later capture,

3: caught in this capture, released, and not seen later,

4: caught and killed in this capture.

Thus the record 11214 means caught for the first time in the third capture (after birth), not caught in the fourth, but in the fifth capture, where the hare was killed off.

It may be of some immediate interest to estimate the size of the individual year-classes at the different captures. This is done on the basis of the following three numbers for each sub-population (year-class × sex) for each capture i, $i = 1, 2, \ldots, l$.

c_i: number of hares caught in capture i and in a later capture (number of "2" in the column for capture i in table 2),

v_i: number of hares caught, released alive, and not caught again (number of "3" in column i),

d_i: number of hares caught and killed off (number of "4")

(cf. table 2). It is useful furthermore to introduce the following three terms.

$$a_i = c_i + v_i + d_i \qquad i = 1, 2, \ldots, l$$

$$r_i = \sum_{j=i}^{l} (v_j + d_j) \qquad i = 1, 2, \ldots, l$$

$$b_i = r_i - a_i \qquad i = 1, 2, \ldots, l\,.$$

a_i is the total number of hares caught in capture i. r_i gives the so-called *registered population*, i.e. the number of hares which with certainty are known to be present at the time of capture i since they are caught in this capture or in a later one. b_i is the number of hares not caught in capture i but in a (at least one) later capture.

In most cases a good estimate N_i of the population size at capture i is obtained from the formula

$$(1) \qquad N_i = r_i + \frac{v_i\, b_i}{c_i}$$

If, however, it is known that there has been no mortality in the population between capture i and capture k ($k \geqslant i + 1$) apart from death on capture, $N_i, N_{i+1}, \ldots, N_k$ are determined as the numbers satisfying the system of equations

$$(2)\quad \begin{cases} N_{j+1} = N_j - d_j \quad j = i,\ i+1, \ldots, k-1 \\ \left(1 - \frac{a_i}{N_i}\right)\left(1 - \frac{a_{i+1}}{N_{i+1}}\right) \ldots \left(1 - \frac{a_k}{N_k}\right) \\ = \frac{N_i - r_i}{N_i} \cdot \frac{N_k - d_k}{N_k - d_k - r_{k+1}} \end{cases}$$

Under certain circumstances this formula also applies to recapture-experiments without this assumption as discussed in the following.

N_i may be regarded as the sum of the registered population r_i and a calculated unknown population U_i ($U_i \geqslant 0$)

$$N_i = r_i + U_i.$$

The calculation of r_i is merely a matter of stock-taking in the capture-records. In this sense one may claim that the error of N_i is connected solely with U_i.

The calculation of N_j, $j = i, \ldots, k$ according to (2) involves determination of the roots of a polynomial of degree $k - i + 1$, e.g. in N_i. It can be shown that this polynomial has one and only one root $N_i \geqslant r_i$. This means that there is always exactly one admissible solution of (2).

(1) may also be written on the form

$$(3)\qquad N_i = \frac{(a_i - d_i)r_{i+1}}{c_i} + d_i$$

which shows that (1) is a generalization of Petersen's formula to capture-chains with more than 2 captures[1] (in the case $l = 2$, $i = 1$ (3) is just Petersen's formula).

(2) was first given by Darroch for the case $d_i = \ldots = d_k = 0$.[2]

One can set up the following rules for the application of (1) and (2) to populations without influx.

(a) If $c_{i+1} = \ldots = c_k = 0$ apply (2) to $N_i, \ldots, N_k$ ($k \leqslant l - 1$),

(b) If $v_i = \ldots = v_{k-1} = 0$ apply (2) to $N_i, \ldots, N_k$,

(c) In all other cases N_i is calculated according to (1). It may hereby happen that $N_{i+1} > N_i - d_i$, being contrary to the assumption that the (sub-)population is never increasing. It is not yet finally clarified what one shall do in this situation. The following proposal, however, seems reasonable and is likely to be the right one. Apply (2) to obtain new estimates of $N_i, \ldots, N_k$ for all continuous chains of captures with $N_{j+1} \geqslant N_j - d_j$, $j = i, \ldots, k-1$. This may lead to $N_{i-1} - d_{i-1} < N_i$ or $N_k - d_k < N_{k+1}$. In this case (2) is repeated for $N_{i-1}, \ldots, N_k$ or $N_i, \ldots, N_{k+1}$ (or $N_{i-1}, \ldots, N_{k+1}$). Proceed in this way until $N_{j+1} \leqslant N_j - d_j$ for every $j = 1, 2, \ldots, l-2$.

Apart from the case $v_{l-1} = 0$ it is not possible to estimate N_l from a capture-recapture experiment.

If the purpose of a recapture-experiment is to study the dynamics of the population one is not primarily interested in the population sizes $N_1, \ldots, N_l$ but rather in the increase and decrease of the population. In the present study the former is elucidated by N_1 (the estimate of the initial population size) and the latter by the probabilities $\varphi_1, \varphi_2, \ldots, \varphi_{l-1}$ of survival from capture 1 to capture 2, from capture 2 to 3, etc.

The estimates N_i, $i = 1, \ldots, l-1$ above are just derived with regard to this posture of the problem. The basis of the derivation is a probability model, due essentially to Darroch[3], for the capture-records for a (sub-)population without influx, cf.[4]. This model depends on different parameters: the initial population size N_1, the survival frequencies $\varphi_1, \ldots, \varphi_{l-1}$, the capture frequencies $p_1, \ldots, p_l$, and the probabilities $\eta_1, \ldots, \eta_l$ for survival at each capture. With the proviso mentioned under (c) we can show that the maximum

1 Petersen, C. G. J. (1896): Rept. Danish Biol. Sta. for 1895, 6, 1–77.

2 Darroch, J. N. (1958): Biometrika 45, 343–359.

3 Darroch, J. N. (1959): Biometrika 46, 336–351.

4 Barndorff-Nielsen, O. (1972): Danish Rev. Game Biol. 6, No. 6.

Capture no.		9.1	9.2	9.5	9.6	10.1	10.2	10.3	10.5	11.3	11.4	11.5	11.6	12.1	12.2	12.3	12.4	12.5	12.6	13.1	13.3
Hare no.	2583	2	1	2	2	1	1	3													
	2587	2	1	1	2	2	2	2	2	1	1	1	1	1	1	2	2	2	2	3	
	2591	2	1	2	3																
	2593	2	1	2	2	2	1	1	2	2	1	1	3								
	2701	2	1	2	2	2	1	2	2	4											
	2703	2	1	2	2	1	2	2	4												
	2707	2	1	2	3																
	2711	2	3																		
	2715	2	3																		
	2721	2	1	2	2	2	2	2	1	1	2	1	2	1	1	3					
	2723	3																			
	2725	2	1	2	2	1	2	1	1	1	1	1	3								
	2727	2	3																		
	2729	2	2	2	2	2	1	1	1	2	2	2	2	2	2	2	1	2	2	1	3
	2733	1	2	2	2	1	2	3													
	2737	1	2	3																	
	2739	1	3																		
	2747	1	1	2	2	2	2	2	2	2	1	2	3								
	2753	1	1	2	3																
	2756	1	1	3																	
	2765	1	1	2	2	2	2	2	2	2	2	3									
	2767	1	1	2	2	2	3														
	2769	1	1	2	1	2	3														
	2773	1	1	2	3																
	2801	1	1	2	1	1	2	1	3												
	2805	1	1	2	1	1	2	3													
	2807	1	1	2	2	2	1	2	3												
	2809	1	1	2	2	2	1	3													
	2811	1	1	2	2	2	1	1	1	2	1	1	2	2	2	2	1	4			
	2818	1	1	1	2	1	1	2	3												
	2820	1	1	1	3																
	2822	1	1	1	2	1	2	3													
b_i	no. of "1"	18	24	4	3	8	8	5	4	3	5	5	1	2	2	0	2	0	0	1	0
c_i	no. of "2"	13	3	21	17	12	10	8	5	5	3	2	3	2	2	3	1	2	2	0	0
v_i	no. of "3"	1	4	2	5	0	2	5	3	0	0	1	3	0	0	1	0	0	0	1	1
d_i	no. of "4"	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0
a_i		14	7	23	22	12	12	13	9	6	3	3	6	2	2	4	1	3	2	1	1
r_i		32	31	27	25	20	20	18	13	9	8	8	7	4	4	4	3	3	2	2	1
N_i	1st stage	33	63.0	27.4	25.9	20.4	20.4	21.1	15.4	9.2	8.2	8.2	8.0	4.0	4.0	4.0	3.0	3.0	2.0	2.0	
N_i	new calculation	37	37.0			20.5	20.5	20.5													
φ_i	%		100.0	74.0	94.5	79.1	100.0	100.0	75.3	63.8	100.0	100.0	97.7	50.0	100.0	100.0	75.0	100.0	100.0	100.0	
p_i	%	37.8	18.9	84.0	85.0	58.6	58.6	63.5	58.4	65.3	36.7	36.7	75.0	50.0	50.0	100.0	33.3	100.0	100.0	50.0	
τ_{ii}	%	100.0	100.0	100.0	100.0	100.0	100.0	100.0	88.9	83.3	100.0	100.0	100.0	100.0	100.0	100.0	100.0	66.7	100.0	100.0	100.0

Table 2. Capture record of female hares born in the 9th year of study, and calculations of population size N_i, percentage of population captured p_i, survival between captures φ_i and survival at capture τ_{ii}.

Tabel 2. Fangststatistik for hunharer født i år 9 og beregning af bestandsstørrelsen N_i, fangstprocenten p_i, overlevelsen mellem fangsterne φ_i og overlevelsen ved fangst τ_{ii}.

likelihood estimators of these parameters are (cf. [4]).

$$(4)\quad \varphi_i = \frac{N_{i+1}}{N_i - d_i} \qquad i = 1, \ldots, l-2$$

$$(5)\quad p_i = \frac{a_i}{N_i} \qquad i = 1, \ldots, l$$

$$(6)\quad \eta_i = \frac{c_i + v_i}{a_i} \qquad a_i \neq 0, i = 1, \ldots, l.$$

It is seen that in all cases where N_i and N_{i+1} are calculated by means of (2) one has $\varphi_i = 1$.

Table 2 gives the estimates according to these formulae for the subpopulation considered.

The estimates of population size, survival frequency, etc. are bound up with two types of errors. The first one is the statistical error which is coined in the character of the estimators as stochastic variables. It is the tradition to describe this error in terms of some sort of standard deviation of the estimates. The utility of such error statements depends on what they are used for. It is difficult to imagine concrete, essential applications of error statements on the estimates of the population sizes. On the other hand there is an obvious need of comparisons of the estimates of the survival probabilities in different populations within the same time interval and of the survival probabilities for the same population in different time intervals (age intervals). There may also be interest in comparison of capture probabilities and of probabilities of survival on capture. These, however, are pure statistical test problems and there is not basis for presuming that they can be managed e. g. by means of asymptotic normal or χ^2-tests in sets of data like the present.

It has not yet been possible to develop correct tests of significance in the statistical model outlined above for the problems mentioned. In this situation it is recommendable instead to study and build the evaluation of the data directly on the statistical structure of the estimates.

The other type of error in the estimates of the parameters is connected with the assumptions under which they are derived. The construction of the statistical model is based on the following assumptions.

(i) hares being alive after capture i have the same probability φ_i of being alive at capture $i + 1$,
(ii) hares being alive at capture i have the same probability p_i of being caught,
(iii) hares being caught at capture i have the same probability η_i of being released alive.

A series of statistical problems is involved in checking these assumptions for a given set of data, and the possibilities of an effective direct control are strongly limited. Therefore, it is an important task for further work with the statistical model to investigate its sensitivity to departures from the homogeneity assumptions (i–iii).

It is our plan to elaborate on this point by means of numerical simulation starting from the primary data of the Illumø study. Furthermore, it is our plan to include an investigation of the statistical error of the estimates. By this it should be possible to obtain criteria for weighing the mutual importance of the two sources of error.

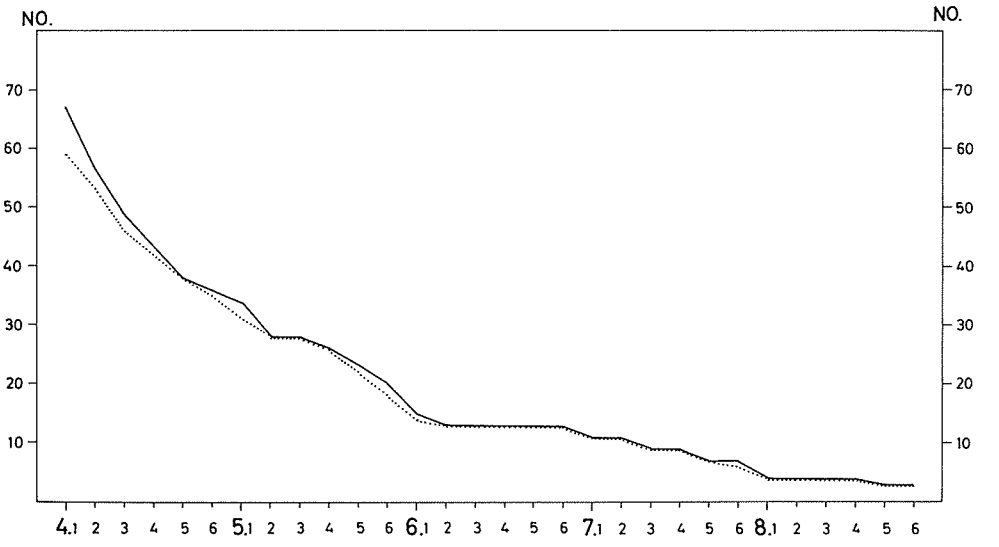


Fig. 4. Survival curve for males born in year no. 4 (1960). Lower line (dotted): the registered population (hares which have been caught at the capture considered or at later captures). Upperline: the estimated population. Note how close the two curves lie to each other.

Fig. 4. Overlevelseskurve for hanharer født i år 4 (1960). Nederst (stiplede linie) den sikre bestand (harer som er fanget ved den betragtede fangst eller senere). Øverst (optrukne linie) den beregnede bestand. Det bemærkes, hvor nær de to kurver ligger hinanden.

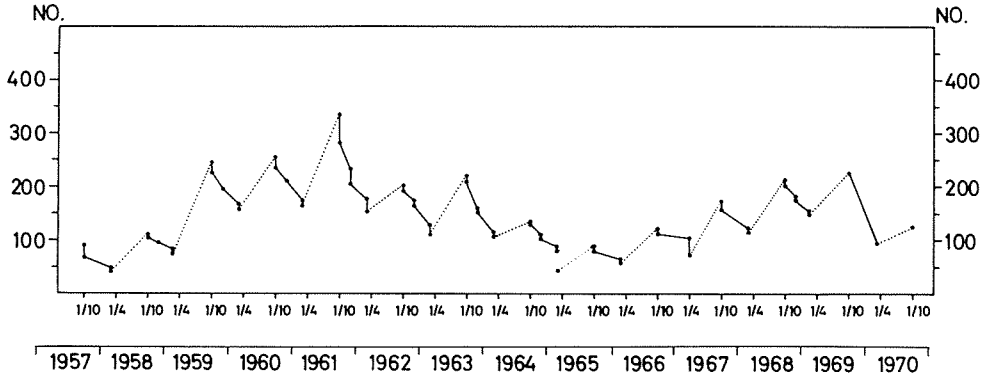


Fig. 5. Population size at each capture date, 1957-70.

Fig. 5. Bestandsstørrelsen på alle fangsttidspunkter fra 1957 til 1970.

Population size and structure

THE SIZE OF THE POPULATION

As a result of the large number of hares caught each year, only a very few hares remain unmarked. On average, the registered population is 90 % of the calculated population (see Fig. 4).

N_i is an estimate of population size at capture i. Table 3 and Fig. 5 give the estimated values of N per capture, for a total of 67 captures. All the peaks of the curve are the October populations, and the lowest points are the spring populations.

From the beginning of the investigation, the population size shows an increasing trend to a maximum in October 1961 of 339 individuals. After this there has been a decreasing trend until autumn 1964 when there were 135 individuals. In spring 1965, 43 hares were removed after the last capture, and the remaining spring population consisted of 20 male and 20 female hares. After this regulation, the population increased slowly to

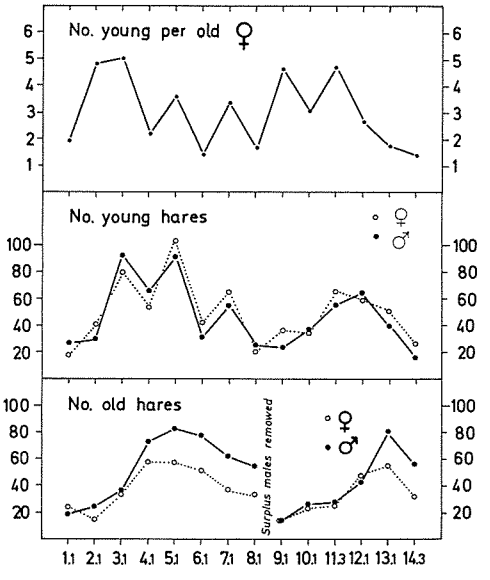


Fig. 6. Upper: No. of young hares per old female in autumn.
Middle: No. of males and females in the young hare population.
Lower: No. of males and females in the older hare population.

Fig. 6. Øverst: antal ungharer pr. gammel hun om efteråret.
I midten: antal af ♂ og ♀ blandt ungharerne.
Nederst: antal af ♂ og ♀ blandt de gamle harer.

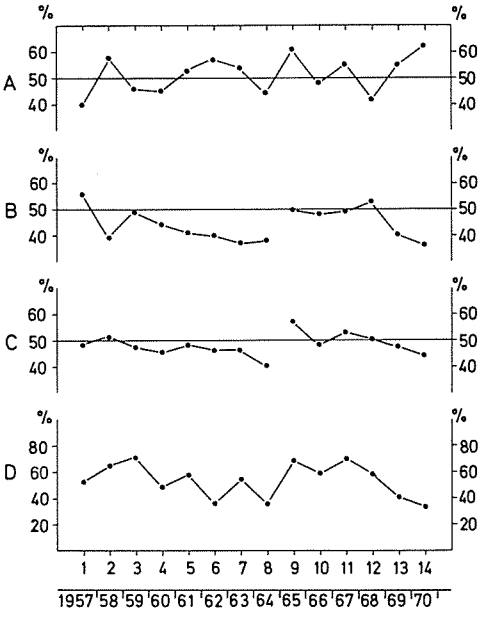


Fig. 7. The population structure at the first capture, approx. October 1.
A. percentage of females in young hares.
B. percentage of females in old hares.
C. percentage of females in the total population.
D. percentage of young hares in the total population.

Fig. 7. Bestandens struktur ved 1. fangst (ca. 1. oktober).
A. procenten af hunharer blandt ungharerne.
B. procenten af hunharer blandt de gamle harer.
C. procenten af hunharer i hele bestanden.
D. ungharernes procentvise andel af bestanden.

		♂ Males N_i															♀ Females N_i															Total
		Year class															Year class															
		<1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	total	<1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	total	♂ + ♀
Year	Capture																																
1957/58	1.1	19	28														47	24	19														43	90
	2	18	24														42	17	10														27	69
	5	13	14														27	14	7														21	48
	6	13	14														27	12	7														19	46
1958/59	2.1	12	12	31													55	10	5	42													57	112
	2	11	11	29													51	10	5	38													53	104
	3	10	10	26													46	10	5	32													47	93
	5	9	10	25													44	8	5	26													39	83
	6	8	10	21													39	8	5	25													38	77
1959/60	3.1	8	9	20	94												131	8	5	22	81												116	247
	2	8	9	20	86												123	8	5	22	69												104	227
	3	8	9	15	72												104	7	5	18	62												92	196
	5	6	8	12	64												90	5	4	13	54												76	166
	6	6	6	12	63												87	4	4	11	53												72	159
1960/61	4.1	5	6	10	52	67											140	3	4	9	42	55											113	253
	2	5	6	10	47	57											125	3	4	9	39	54											109	234
	3	5	6	10	43	49											113	3	4	9	38	44											98	211
	5	4	5	9	35	38											91	2	4	6	30	41											83	174
	6	4	5	7	34	36											86	2	4	6	29	37											78	164
1961/62	5.1	3	5	7	34	34	93										176	2	3	6	21	26	105										163	339
	2	3	3	7	28	28	75										144	2	3	6	21	25	81										138	282
	3	2	3	6	23	28	63										125	2	2	6	21	22	55										108	233
	4	2	3	6	23	26	62										122	1	2	1	19	22	40										85	207
	5	2	2	4	21	23	52										104	1	2	1	18	16	36										74	178
	6	2	2	2	19	20	48										93		2	1	13	16	30										62	155
1962/63	6.1	1	2	2	18	15	40	32									110		2	1	13	12	24	43									95	205
	2	1		2	18	13	37	31									102		2	1	13	10	23	43									92	194
	3	1		2	18	13	36	23									93		2	1	13	10	22	34									82	175
	4	1		2	18	13	32	23									89		2	1	12	10	20	34									79	168
	5	1		2	7	13	32	17									72		2	1	12	6	19	18									58	130
	6	1		2	7	13	30	15									68		1	1	6	6	13	15									42	110

1963/64	7.1	2	6	11	30	13	56								118	1	1	4	6	10	15	66								103	221
	2	2	6	11	27	13	54								113	1	1	4	6	8	14	63								97	210
	3	2	6	9	25	12	39								93	1	1	4	5	8	13	37								69	162
	4	2	6	9	25	12	35								89	1	1	4	5	8	10	32								61	150
	5	2	6	7	22	11	19								67		1	2	5	8	10	23								49	116
	6	1	6	7	22	10	18								64			1	5	6	9	22								43	107
1964/65	8.1	1	5	4	19	9	17	26							81			1	5	6	6	15	21							54	135
	2	1	5	4	19	9	17	25							80			1	5	6	4	15	20							51	131
	3	1	5	4	15	9	17	19							70			1	5	4	4	13	13							40	110
	4	1	5	4	15	8	15	17							65			1	5	4	4	13	13							40	105
	5	1	5	3	14	8	13	14							58				5	4	3	11	9							32	90
	6	1	5	3	14	8	12	12							55				1	4	3	11	8							27	82
1965/66	9.1					1	5	8	24						38				1	1	3	5	4	37						51	89
	2					1	5	6	19						31				1	1	3	5	2	37						49	80
	5					1	5	3	19						28				1	1	2	5	2	27						38	66
	6					1	5	3	19						28				1		2	3	2	25						33	61
1966/67	10.1					1	5	3	17	38					64				1		1	2		20	35					59	123
	2					1	5	2	17	37					62				1			2		20	33					56	118
	3					1	4	2	17	30					54				1			2		20	29					52	106
	5					1	4	1	9	21					36							2		15	21					38	74
1967/68	11.3					1	3	1	6	16	56				83							2		9	15	66				92	175
	4					1	3	1	6	14	55				80							2		8	15	53				78	158
	5					1	3	1	5	12	37				59							2		8	12	43				65	124
	6					1	2	1	5	7	36				52							2		8	11	40				61	113
1968/69	12.1					1	1	1	2	7	30	65			107							2		4	9	32	60			107	214
	2					1	1	1	2	7	30	65			107							2		4	9	27	55			97	204
	3					1	1	1	2	7	28	53			93							2		4	9	27	47			89	182
	4					1	1	1	2	7	28	53			93							1		3	9	27	47			87	180
	5						1	1	1	7	26	45			81							1		3	9	24	38			75	156
	6						1	1	1	7	25	43			78							1		2	9	24	36			72	150
1969/70	13.1						1	1	1	7	24	41	43		118							1		2	8	18	24	53		106	224
	3							1	1	6	24	41	38		111									1	6	18	23	52		100	211
	5									2	12	31	15		60									1	2	12	13	15		43	103
	6									2	12	31	13		58									1	2	8	12	14		37	95
1970/71	14.3									2	12	31	13	16	74										2	7	8	13	26	56	130

Table 3. Estimates of the size of year-classes of males and females and of the total population, at each capture from 1957–1970.
Tabel 3. Beregnet størrelse af hver årgang, hanner og hunner og af hele bestanden ved hver fangst fra 1957–1970.

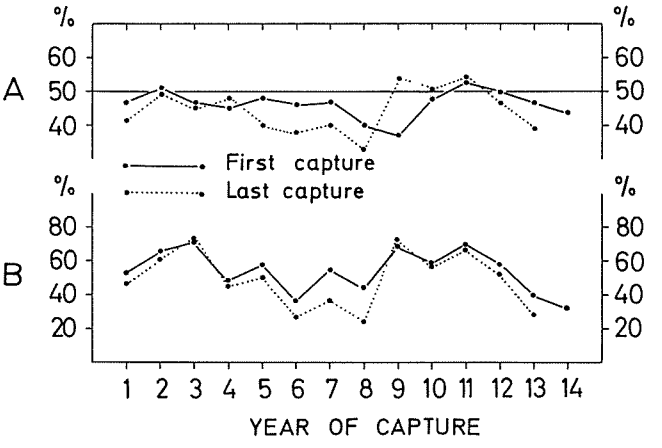


Fig. 8. Changes in the population structure during autumn and winter.
A. the percentage of females in the total population at the first and last capture of the year.
B. the proportion of young hares in the total population at the first and last capture of the year.

Fig. 8. Ændringer i bestandens struktur i løbet af efterår og vinter.
A. procenten af hunharer i hele bestanden ved første fangst og sidste fangst i året.
B. ungharernes andel af den samlede bestand ved første fangst og sidste fangst i året.

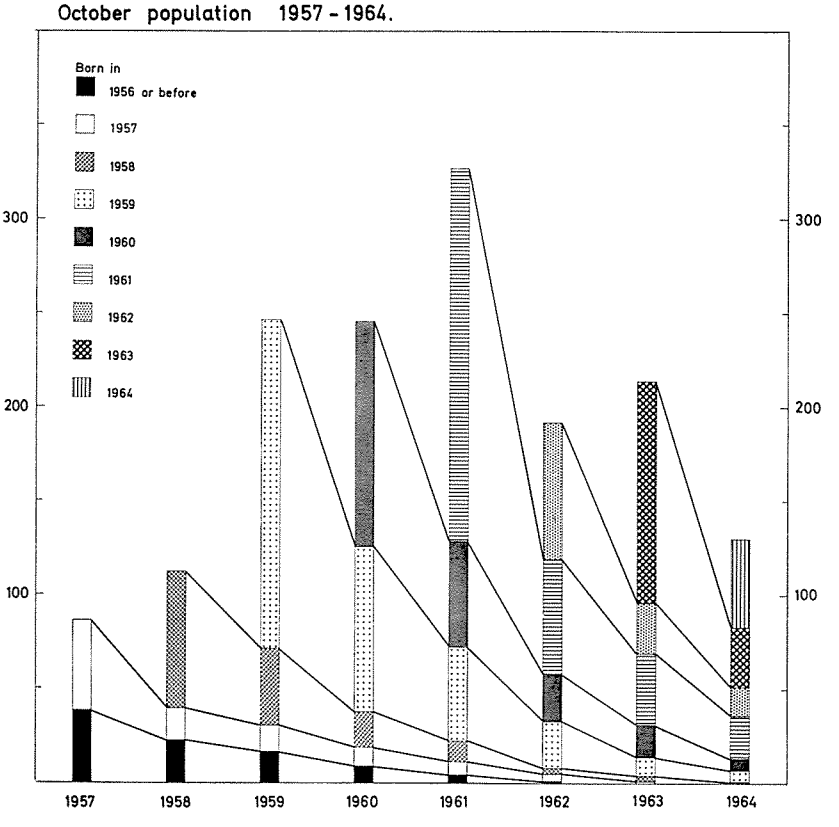


Fig. 9a.
The age-class distribution in the population 1957-1964.

Fig. 9a.
Bestandens aldersmæssige struktur 1957-1964.

224 hares by autumn 1969. In autumn 1970 the population had again fallen to 130 individuals after a very long and cold winter.

Table 4 gives a summary of the population structure at the first capture of the year, and Fig. 6 shows the distribution of the sexes in old and young animals. It appears that the two sexes are equally represented in young animals. Among the estimated influx of 1378 individuals from 1957–1970, 48.5 % were males and 51.5 % were females. However, males are in majority in older animals. Equal numbers of the sexes were achieved by drastic reduction of the population at the last capture in the 8th year of study, but the sexual balance again appears to be developing towards a majority of males in the 13th and 14th year.

The distribution of the sexes can also be shown as a proportion (Fig. 7). The figure shows the same as the previous one; an equal distribution of the sexes in young hares, and an unequal distribution in older hares. If the two groups are taken as a whole, the inequality becomes less obvious, and the percentage of females in the population is then 48.1 % on average in the 13 autumn captures.

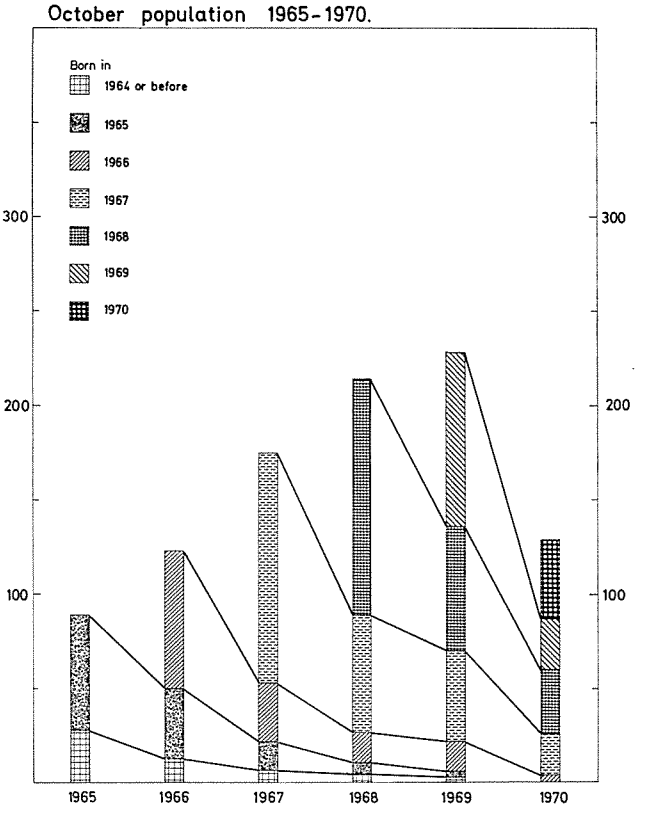


Fig. 9b. The age-class distribution of the population 1965-1970.

Fig. 9b. Bestandens aldersmæssige struktur 1965-1970.

Date *Dato*	Young (<1 year) *Unge* ♂	♀	♀+♂	♀+♂/♀+ %	Old *Gamle* ♂	♀	♀+♂	♀+♂/♀+ %	Total *Ialt* ♂	♀	♀+♂	♀+♂/♀+ %	Young /total %	Young /old ♀
1. 25/9 1957	28	19	47	40.4	19	24	43	55.8	47	43	90	47.8	52.2	1.96
2. 26/9 1958	31	42	73	57.5	24	15	39	38.5	55	57	112	50.9	65.2	4.87
3. 24/9 1959	94	81	175	46.3	37	35	72	48.6	131	116	247	47.0	70.9	5.00
4. 29/9 1960	67	55	122	45.1	73	58	131	44.3	140	113	253	44.7	48.2	2.10
5. 26/9 1961	93	105	198	53.0	83	58	141	41.1	176	163	339	48.1	58.4	3.41
6. 5/10 1962	32	43	75	57.3	78	52	130	40.0	110	95	205	46.3	36.6	1.44
7. 5/10 1963	56	66	122	54.1	62	37	99	37.4	118	103	221	46.6	55.2	3.30
8. 7/10 1964	26	21	47	44.7	55	33	88	37.5	81	54	135	40.0	34.8	1.42
9. 12/10 1965	24	37	61	60.7	14	14	28	50.0	38	51	89	57.3	68.5	4.36
10. 6/10 1966	38	35	73	47.9	26	24	50	48.0	64	59	123	48.0	59.3	3.04
11. 15/11 1967	56	66	122	54.1	27	26	53	49.1	83	92	175	52.6	69.7	4.69
12. 8/10 1968	65	60	125	48.0	42	47	89	52.8	107	107	214	50.0	58.4	2.66
13. 14/10 1969	43	53	96	55.2	75	53	128	41.4	118	106	224	47.3	42.9	1.81
14. 11/11 1970	16	26	42	61.9	58	30	88	34.1	74	56	130	43.1	32.3	1.40
Total young hares (<1-year): *Unge harer (<1 år) ialt:*	669	709	1378	51.5										

Table 4. The estimated population size at the first autumnal capture of each year. Percentage of females among young and old hares, percentage of youngs and number of youngs per old female.

Tabel 4. Den beregnede bestandsstørrelse ved første efterårsfangst hvert år. Procenten af hunharer blandt unge og gamle harer, procenten af ungharer og antal unger pr. gammel hun.

Date *Dato*	Young (< 1 year) *Unge* ♂	♀	♀+♂	♀+♂/♀+ %	Old *Gamle* ♂	♀	♀+♂	♀+♂/♀+ %	Total *Ialt* ♂	♀	♀+♂	♀+♂/♀+ %	Young/total %
1. 13/3 1958	14	7	21	33.3	13	12	25	48.0	27	19	46	41.3	45.7
2. 19/2 1959	21	25	46	54.3	18	13	31	41.9	39	38	77	49.4	59.7
3. 21/3 1960	63	53	116	45.7	24	19	43	44.2	87	72	159	45.3	73.0
4. 4/3 1961	36	37	73	50.7	50	41	91	45.1	86	78	164	47.6	44.5
5. 7/3 1962	48	30	78	38.5	45	32	77	41.6	93	62	155	40.0	50.3
6. 17/4 1963	15	15	30	50.0	53	27	80	33.8	68	42	110	38.2	27.3
7. 11/3 1964	18	22	40	55.0	46	21	67	31.3	64	43	107	40.2	37.4
8. 24-26/3 1965	12	8	20	40.0	43	19	62	30.6	55	27	82	32.9	24.4
9. 18/3 1966	19	25	44	56.8	9	8	17	47.1	28	33	61	54.1	72.1
10. 11/4 1967	21	21	42	50.0	15	17	32	53.1	36	38	74	51.4	56.8
11. 20/3 1968	36	40	76	52.6	16	21	37	56.8	52	61	113	54.0	67.3
12. 15/4 1969	43	36	79	45.6	35	36	71	50.7	78	72	150	48.0	52.7
13. 12/5 1970	13	14	27	51.9	45	23	68	33.8	58	37	95	38.9	28.4

Table 5. The estimated population size at the last spring capture of each year (see also Table 4).

Tabel 5. Den beregnede bestandsstørrelse ved den sidste forårsfangst hvert år (se også Tabel 4).

THE AGE STRUCTURE OF THE POPULATION

In the column diagram (Fig. 9, p. 14-15), a column describes the age structure of the population for each year. The upper section of the columns represents the young hares of the year. It is possible to follow the presence of a particular group of young hares in the population through time; for example, in 1958 the number of young hares was 73 individuals and in the following year 1959 there were 42 remaining, and so on for 1960-1964.

The young hares of 1959 numbered 175, and were very strongly represented in the following years. It is evident that some hares may reach an age of 6-7 years, and that in 1963 and 1964 the population contained 7 generations.

There is a break in the curve between 1964 and 1965. This is due to the removal of a part of the population in the spring of 1965, as mentioned p. 11.

Capture frequency

The capture frequency or capture percentage of a capture describes the proportion of the population caught.

The capture frequencies for the two sexes have been compared but no systematic differences were discovered (cfr. Table 6).

Figure 10 gives a comparison of the capture percentages of two age groups at different times of the year. It appears that it is more difficult to capture young hares in the autumn captures. Accordingly it has been observed in the field that it is not easy to flush young hares from cover. In October they are at most 4-6 months old, and many are younger. In the spring captures the opposite tendency is evident; there is a higher capture percentage for young hares than for older ones. The explanation for this may be that young hares have less well-established territories than older ones. There is no difference between the capture frequencies of 1- and 2-year old hares, but the results (Table 7) indicate that the capture frequency of hares which are 3 years or more is slightly less than that of younger hares.

Altogether, there are no great differences in the capture frequencies of different age-groups, but there is variation within the year. The capture percentage each year (Table 8) is lowest at the two captures early in October. This is due to there being good cover available for the hares, in grass and swedes, at this time of year. As a result the capture percentage is on average less than 50 %. At the December captures there is less cover and the capture likelihood is better; the capture percentage is then about 50 %. In the spring, at captures 5 and 6, grassy vegetation is at a minimum, and the other fields have been ploughed, giving the hares very little cover; the capture percentage is then in the region of 65-70 %.

Capture no. *Fangst nr.*	♂			♀			♂+♀		
	a_i	N_i	p_i %	a_i	N_i	p_i %	a_i	N_i	p_i %
5.1	50	93.00	54	34	105.00	32	84	198.00	42
.2	34	75.48	45	28	81.33	34	62	156.81	40
.3	39	63.57	61	24	55.63	43	63	119.20	53
.4	41	62.57	66	22	40.89	54	63	103.46	61
.5	40	52.94	76	27	36.90	73	67	89.84	75
.6	32	48.12	67	23	30.76	75	55	78.88	70
6.1	14	40.00	35	9	24.75	36	23	64.75	36
.2	15	37.73	40	11	23.22	47	26	60.95	43
.3	15	36.73	41	11	22.00	50	26	58.73	44
.4	18	32.23	56	11	20.38	54	29	52.61	55
.5	19	32.23	59	8	19.38	41	27	51.61	52
.6	18	30.84	58	6	13.50	44	24	44.34	54

Table 6. An example of the calculation of capture frequency p_i of males and females in the 5th year-class. (a_i = no. captured, N_i = estimated population size).

Tabel 6. Et eksempel på beregning af fangsthyppigheden p_i for hanner og hunner af 5. årgang (a_i = antal fanget, N_i = beregnet bestandsstørrelse).

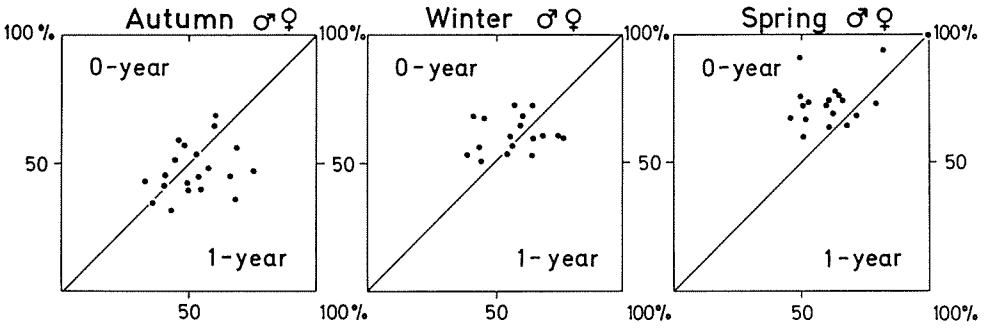


Fig. 10. The relationship between the capture frequency for 0-year-old and 1-year-old hares.

Fig. 10. Relationen mellem fangsthyppigheden for 0-årige og for 1-årige.

♂ + ♀	Age class *Aldersklasse* 0–year			1–year			2–year			≧ 3–year		
	a_i	N_i	p_i %	a_i	N_i	p_i %	a_i	N_i	p_i %	a_i	N_i	p_i %
1.1	31	47.00	66									
2	27	35.13	77									
5	17	21.15	80									
6	16	21.15	76									
2.1	34	73.00	47	13	17.12	76						
2	24	67.15	36	11	16.12	68						
3	40	58.93	68	7	15.08	46						
5	38	51.53	74	12	15.08	80						
6	32	46.43	69	7	15.08	46						
3.1	78	175.00	45	23	42.61	54	10	14.07	71	7	8,32	
2	70	155.71	45	28	42.61	66	7	14.07	50	10	8,32	
3	99	134.70	73	22	33.76	65	10	14.07	71	7	8.32	
5	89	119.58	74	16	26.51	60	7	12.50	56	8	6.43	
6	90	116.99	77	12	24.18	50	4	10.34	39	10	6.43	
4.1	53	122.00	43	47	94.19	50	11	19.94	55	8	18.66	43
2	51	111.67	46	36	87.18	41	7	19.42	36	5	18.66	27
3	65	93.76	69	50	82.43	61	6	19.42	31	7	18.66	38
5	52	79.71	65	45	65.87	68	12	15.40	78	6	16.10	37
6	51	74.30	69	46	63.92	72	12	13.04	92	9	16.10	56
5.1	84	198.00	42	25	60.86	41	23	55.41	42	5	27.12	18
2	62	156.81	40	30	54.30	55	24	49.43	49	14	24.67	57
3	63	119.20	53	33	51.08	65	29	44.57	65	8	21.22	38
4	63	103.46	61	37	49.04	75	21	42.13	50	11	16.22	68
5	67	89.84	75	27	40.21	67	27	39.78	68	6	13.00	46
6	55	78.88	70	23	36.39	63	26	32.40	80	5	9.00	
6.1	26	75.00	35	23	64.75	36	11	28.10	39	11	39.02	28
2	24	74.00	32	26	60.95	43	5	23.59	21	8	37.02	22
3	33	57.84	57	26	58.73	44	9	23.59	38	9	37.02	24
4	31	57.84	54	29	52.61	55	15	23.59	64	11	36.23	30
5	24	35.82	67	27	51.61	52	15	19.02	79	11	25.47	43
6	23	30.64	75	24	44.34	54	15	19.02	79	10	18.25	55
7.1	64	122.00	52	13	28.77	45	22	41.51	53	18	31.89	56
2	47	117.00	40	14	27.95	50	12	36.12	33	12	31.89	38
3	53	77.23	69	11	26.07	42	21	34.19	61	11	28.71	38
4	37	68.48	54	9	23.24	39	11	34.19	32	16	28.71	56
5	39	42.25	92	11	21.93	50	20	31.01	64	15	23.26	64
6	25	41.01	61	10	19.50	51	13	28.68	45	10	20.26	49
8.1	28	47.00	60	15	32.82	46	7	15.85	44	16	41.43	39
2	31	45.00	69	20	32.82	61	5	13.18	38	16	41.29	39
3	20	33.07	60	20	30.56	65	10	13.18	76	11	35.51	31
4	19	30.98	61	20	29.09	69	8	12.00	67	17	35.51	48
5	22	23.14	95	20	24.09	83	7	11.22	62	18	32.00	56
6	20	20.00	100	23	23.00	100	10	11.22	89	27	28.00	96

Table 7. Capture frequencies per age class. Symbols as in table 6.
Tabel 7. Fangsthyppigheder pr. aldersklasse. Symbolerne som i tabel 6.

Continued *(fortsættes)* p. 20

♂ + ♀	0–year			1–year			2–year			≧ 3–year		
	a_i	N_i	p_i %	a_i	N_i	p_i %	a_i	N_i	p_i %	a_i	N_i	p_i %
9.1	26	61.00	43	4	12.00	33	4	10.70	37	2	6.22	
2	11	56.08	20	3	8.00		3	10.70	28	1	6.22	
5	40	46.46	86	3	5.22		6	10.70	56	2	5.00	
6	35	44.96	78	3	5.22		5	8.03		2	4.00	
10.1	35	73.00	48	22	37.66	58	2	3.22		3	11.03	27
2	40	70.00	57	18	37.66	48	0	2.00		6	9.03	
3	43	59.23	73	22	37.66	58	2	2.00		5	8.07	
5	28	43.08	65	15	24.40	61	1	1.00		6	7.07	
11.3	70	122.00	57	18	31.58	57	6	15.44	39	4	7.00	
4	65	108.21	60	23	29.92	77	8	14.44	55	6	7.00	
5	64	81.37	79	16	25.43	63	6	13.19	45	4	7.00	
6	59	76.86	77	12	18.50	65	11	13.00	85	4	6.00	
12.1	70	125.00	56	43	62.66	69	8	16.01	50	5	9.00	
2	64	120.00	53	30	57.86	52	9	16.01	56	8	9.00	
3	62	101.13	61	32	55.88	57	10	16.01	62	9	11.00	82
4	52	100.86	52	25	55.88	45	7	16.01	44	4	9.00	
5	61	83.88	73	32	50.54	63	10	16.01	62	6	7.00	
6	58	80.00	73	27	49.47	55	14	16.01	87	4	6.00	
13.1	49	96.00	51	36	65.67	55	16	42.49	38	9	21.00	43
3	60	90.25	66	40	64.61	62	24	42.49	56	9	15.00	60
5	27	30.34	89	27	44.72	60	15	24.17	62	3	5.00	
6	19	27.88	68	29	43.58	67	17	20.34	84	4	5.00	
14.3	22	42.00	52	20	26.73	75	11	39.01	28	11	23.17	47

Table 7. Continued. Capture frequencies per age class. Symbols as in table 6.

Tabel 7. Fortsat. Fangsthyppigheder pr. aldersklasse. Symbolerne som i tabel 6.

	Autumn *Efterår*		Winter *Vinter*		Spring *Forår*	
Year	Capture .1	.2	.3	.4	.5	.6
1.	55.6	61.3			84.4	76.6
2.	55.1	45.9	62.4		71.2	63.1
3.	47.6	50.3	69.8		70.8	71.8
4.	46.7	41.8	59.7		64.9	70.5
5.	40.1	45.6	55.1	63.2	69.7	69.6
6.	34.3	32.2	43.5	50.5	58.4	64.1
7.	52.2	39.9	57.8	47.2	71.8	53.0
8.	48.1	54.4	54.3	59.5	74.1	98.4
9.	40.0	22.2			75.7	72.3
10.	49.6	53.9	67.3		66.2	
11.			56.2	63.9	70.9	75.2
12.	58.7	54.2	61.4	48.4	69.2	68.0
13.	48.9		62.6		69.1	71.3
14.			48.9			

Table 8. Capture frequencies of the total population.

Tabel 8. Fangstprocenterne for totalpopulationen.

Capture mortality

Due to accidents at the time of capture, an artificial mortality is induced. In general, 2-3 % of the individuals taken at a capture are injured and must be killed off. As the population is subjected to repeated captures, the number killed in this way must be considered specially and not included with natural mortality. Through the years, 161 hares have been killed off, of which 78 were males and 83 females. The majority were young or 1-year old hares. Not included with these are 43 hares killed off in spring 1965 in the population reduction mentioned previously.

Natural mortality

Each year, a large number of hares die from natural causes. Some of the dead hares are found by people on the island, but the majority disappear without trace.

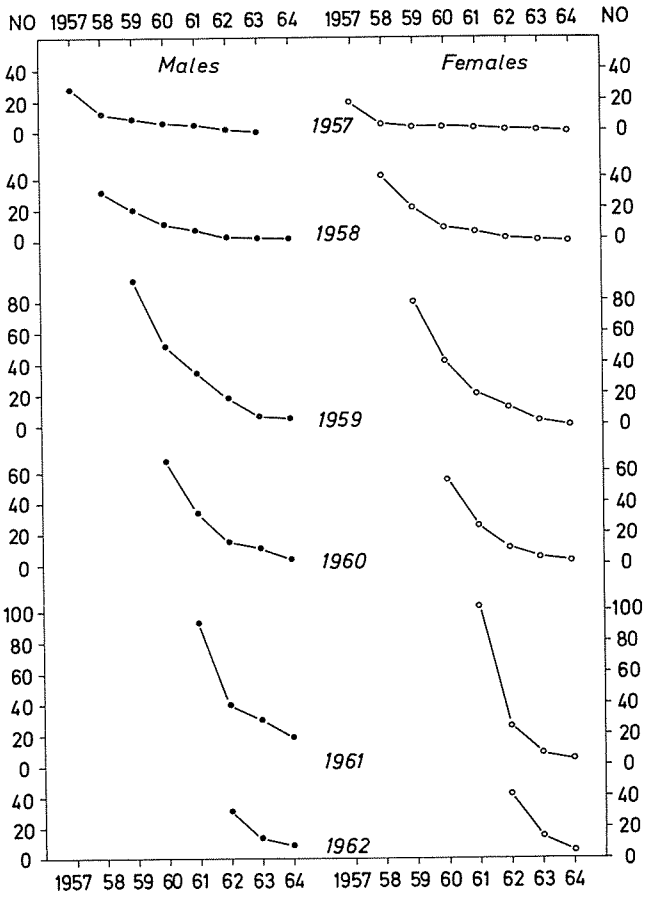


Fig. 11. Mortality curves for males and females of each generation.

Fig. 11. Dødelighedskurver for de enkelte generationer af ♂ og ♀.

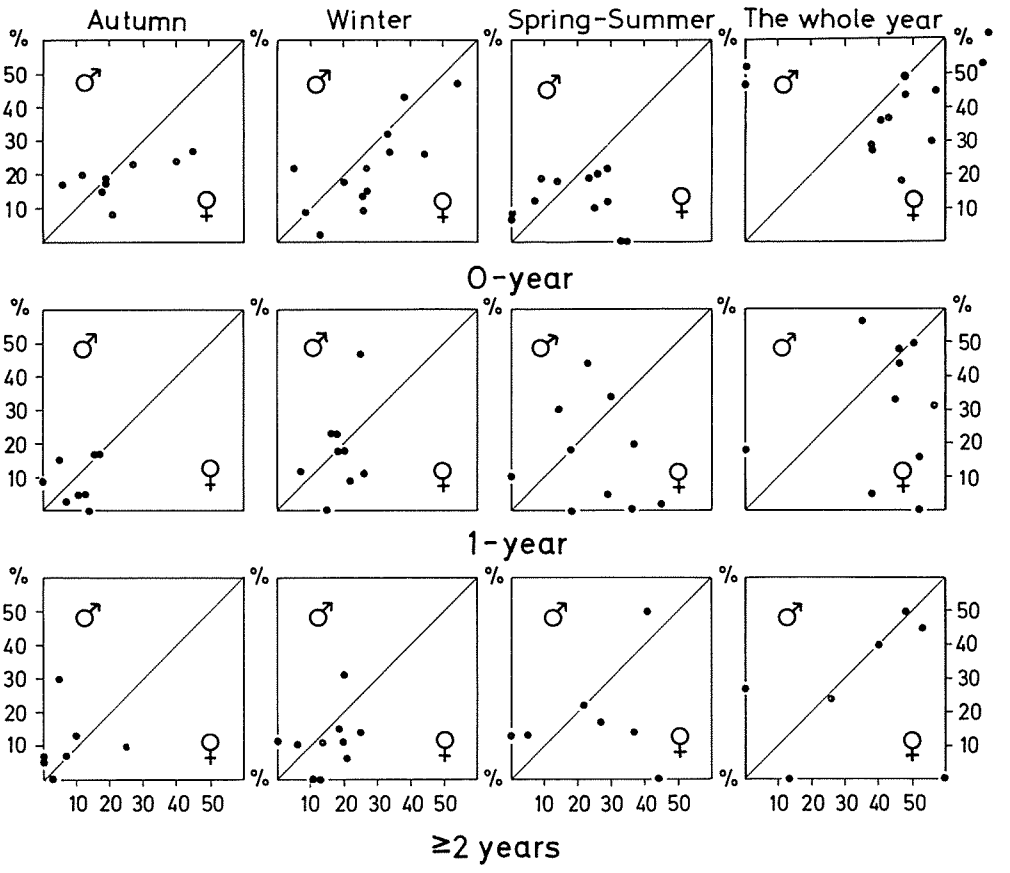


Fig. 12. The relationship between the mortality for the two sexes.

Fig. 12. Relationen mellem dødeligheden for de to køn.

The dead hares found have almost always a disease of some form or other, most commonly coccidiosis or a trichostrongyle attack, and cases of pseudotuberculosis, abcess disease, pasteurellosis and amylodosis occur, but no disease on the island has been of epidemic character.

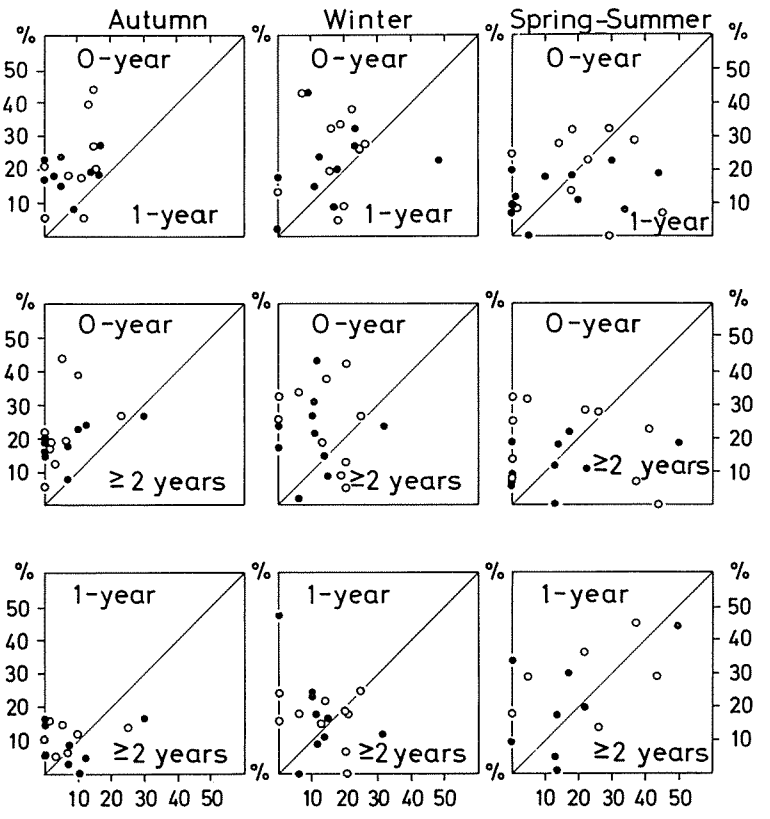
The survival frequency from capture i to capture i + 1 is calculated from:

$$\varphi_i = \frac{N_{i+1}}{N_i - d_i}$$

that is, the proportion of the population size at capture i + 1 to that at capture i from which the hares killed off in the latter capture have been subtracted. The survival frequency from capture i to capture i + 2 is calculated as the product of survival from i to i + 1 and i + 1 to i + 2. Mortality is calculated as 1 – survival frequency. The mode of calculation is shown in Table 9 and the first three examples in it.

Fig. 13. The relationship between the mortality in different age classes.
● ♂ ○ ♀

Fig. 13. Relationen mellem dødeligheden for forskellige aldersklasser.
● ♂ ○ ♀



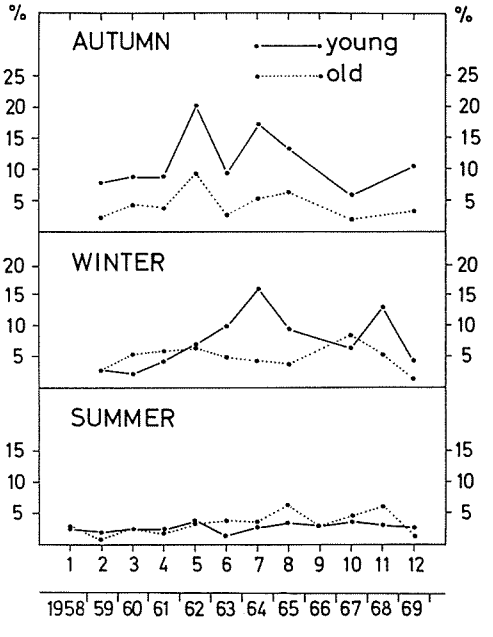


Fig. 14. The average monthly mortality in young and old hares in autumn, winter and summer.

Fig. 14. Gennemsnitlig månedsdødelighed hos ungharer og gamle harer efterår, vinter og sommer.

Firstly, the relationship between mortality and sex, age and season is analysed.

A diagrammatic comparison of the calculated percentage mortalities of males and females in autumn, winter, and spring is given in Fig. 12. Considering the mortality for young hares (0-year old), 1-year and ⩾ 2-year hares in the above periods, it is evident that there is a marked tendency towards greater mortality in females than in males in young hares. This difference is not confined to the reproduction period, but can be observed in each of the periods considered.

For 1-year olds there is a similar difference, but much less marked than in the young hares. In ⩾ 2-year old hares there is only a slight difference in mortality between the two sexes.

Mortality is also related to the age of the hare. In a comparison of the percentage mortalities of young hares, 1-year olds, and ⩾ 2-year olds in the same periods as above (cf. Fig. 13), the most striking fact is a clear tendency towards greater mortality in young hares than in 1-year olds, in the autumn. In the winter the same difference occurs to a lesser extent, and it disappears completely in the spring and the summer period. A comparison of mortality in 1- and ⩾ 2-year old hares shows a similar trend in autumn and winter, although to a smaller extent.

The frequency of mortality $1-\varphi_i$ depends on the length of the period observed, as well as on sex and age. In comparing mortality at different times of year, or in different years, it is convenient to be able to refer to periods of equal length. It has been decided in this study to calculate a mortality intensity as "average monthly mortality" 1-f, using the formula

$$f = \varphi^{\frac{1}{g}}$$

where g is the length of the period measured as months of 30 days, φ the survival frequency for g days and f the average monthly survival frequency, cf. Table 9, example 4.

Table 10 gives the calculated average monthly mortalities. For perspicuity differentiation is only made between young and old (i. e. 0-year and 1-year hares).

The monthly mortality in young hares is on average 10-11 % in autumn, 8-9 % in winter and 2-3 % in summer with considerable variation from year to year. In old hares the mortality is on average 4-5 % without clear differences between the seasons.

Fig. 14 illustrates the variation from year to year of the seasonal mortalities for young and old hares in table 10. In the autumn there is a surprising accordance between the fluctuations for the two age-groups. The interpretation of this is that the variation in the autumnal mortality must be due to fluctuations in environmental conditions. It is on this background astonishing that the winter mortality seems to vary independently in the two age-groups. In spring and summer the mortality is almost constant from year to year.

Capture no. *Fangst nr.*	♂				♀				♂ + ♀			
	N_i	d_i	φ_i %	φ_i %	N_i	d_i	φ_i %	φ_i %	N^i	d_i	φ_i %	φ_i %
5.1	93.00	3			105.00	1			198.00	4		
			83.87				78.20				80.83	
5.2	75.48	2		72.56	81.33	3		55.54	156.81	5		63.47
			86.51				71.02				78.52	
5.3	63.57	1			55.63	2			119.20	3		
			100.00				76.24				89.04	
5.4	62.57	0		84.61	40.89	2		72.34	103.46	2		78.84
			84.61				94.88				88.55	
5.5	52.94	0			36.90	1			89.84	1		
			90.90				85.68				88.79	
5.6	48.12	1		77.17	30.76	1		71.26	78.88	2		74.78
			84.89				83.17				84.22	
6.1	40.00	1			24.75	0			64.75	1		

Example 1: Survival frequency of 0-year old hares of both sexes from capture 5.1 to capture 5.2

$$= \frac{156.81}{198.00-4} = 0.8083;\ \text{mortality} = 1-0.8083 = 0.1917 = 19.17\ \%$$

Example 2: Survival frequency of 0-year old male hares from capture 5.1. to capture 5.3.

$= 0.8387 \times 0.8651 = 0.7256$; mortality $= 1-0.7256 = 0.2744 = 27.44\ \%$

Example 3: Survival frequency of 0-year old female hares for a complete year (from capture 5.1 to capture 6.1)

$= 0.7820 \times 0.7102 \times 0.7624 \times 0.9488 \times 0.8568 \times 0.8317 = 0.2863$

or $0.5554 \times 0.7234 \times 0.7126 = 0.2863$;

yearly mortality $= 1-0.2863 = 0.7137 = 71.37\ \%$

Example 4: Average monthly survival of 0-year old hares of both sexes from capture 5.1 to capture 5.3 (as captures took place on 26/9 and 25/11, there is an interval of 60 days).

$= 0.6347^{30/60} = 0.6347^{0.5}$; $\log 0.6347^{0.5} = 0.5 \times \log 0.6347 =$

$0.5 \times (0.8026-1) = -0.0987 = 0.9013-1$; antilog $(0.9013-1) = 0.7967$;

Average monthly mortality $1-0.7967 = 0.2033 = 20.33\ \%$

Table 9. Calculation of survival rates φ and mortalities 1-φ in the 5th yearclass (N_i = estimated population size, d_i = no. killed on capture).

Tabel 9. Beregning af overlevelsesprocenter φ og dødelighed 1-φ for årgang 5 (N_i = beregnet bestandsstørrelse, d_i = antal dræbt ved fangst).

	No. of days *Antal dage*			0-year ♂			0-year ♀			≧ 1-year ♂			≧ 1-year ♀		
	.1–.3	.3–.5	.5–.1	.1–.3	.3–.5	.5–.1	.1–.3	.3–.5	.5–.1	.1–.3	.3–.5	.5–.1	.1–.3	.3–.5	.5–.1
1957/58: 1.	(164)		202	(11.18)		1.10	(13.17)		.						
1958/59: 2.	62	77	229	4.10	0.61	2.67	10.86	5.36	1.24	4.64	0.00	1.37			
1959/60: 3.	63	104	199	9.38	2.73	2.97	9.50	2.77	2.24	4.23	5.03	2.59	5.42	6.14	2.59
1960/61: 4.	58	94	210	10.79	7.59	0.00	6.81	1.68	5.49	5.40	5.34	1.25	2.62	6.45	3.50
1961/62: 5.	60	95	219	14.82	5.14	3.49	25.47	9.71	4.54	13.24	4.25	3.62	4.93	8.62	3.17
1962/63: 6.	61	126	178	9.42	6.47	2.20	9.70	12.77	1.23	3.78	3.62	1.12	3.47	3.68	8.51
1963/64: 7.	62	89	217	12.84	17.56	1.56	21.76	14.92	4.59	5.47	3.83	3.34	5.59	6.42	4.39
1964/65: 8.	59	105	206	12.56	8.63	1.16	14.78	11.23		3.64	4.48	7.82	10.81	3.69	6.42
1965/66: 9.	(150)		209	(1.89)		1.49	(5.84)		4.09	(6.62)			(4.92)		8.98
1966/67: 10.	61	126	(218)	8.58	6.14	(3.05)	2.85	6.92	(4.07)	4.14	10.72	(3.94)	0.00	5.91	(5.12)
1967/68: 11.		83	245		12.77	2.52		13.27	3.17		6.95	7.46		3.55	4.55
1968/69: 12.	49	135	187	10.19	2.65	1.37	11.53	4.76	5.94	2.63	1.60	.94	5.38	2.54	3.35
1969/70: 13.	38	153	(202)	7.13	15.70	(2.26)	.00	21.46	(1.48)	1.15	8.48	(.00)	4.57	9.97	(6.89)
Average *Gennemsnit*				9.98	7.82	1.87	11.33	9.53	3.61	4.83	4.94	3.28	4.75	5.70	5.05

Table 10. The estimated monthly percentage mortality, 1957–1969. (Numbers in brackets refer to results either from captures .1–.5 or from .5–.3).
Tabel 10. Den beregnede månedlige dødelighed i procent 1957–1969. (Tal i parentes refererer til perioderne .1–.5 eller .5–.3).

The total average yearly mortality (Table 11 and Fig. 15) from October to October is 46 % for all hares, but different within the different groups:

Young females: average yearly mortality is 56 %

Young males: average yearly mortality is 44 %

Older females: average yearly mortality is 45 %

Older males: average yearly mortality is 38 %.

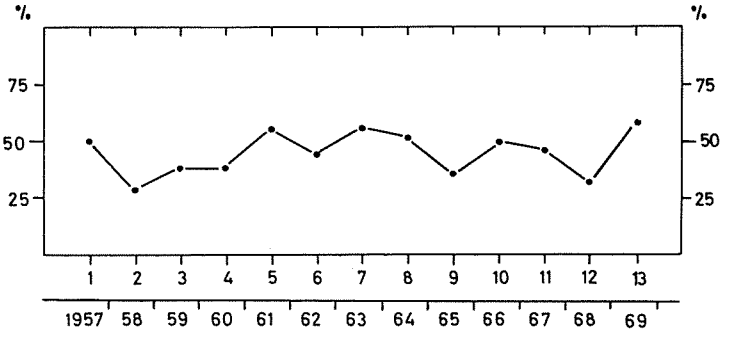


Fig. 15. The yearly mortality (from October to October) of the total population.

Fig. 15. Årsdødelighed (fra oktober til oktober) for totalpopulationen.

Year of study	0-year old *0 år gamle* ♂	0-year old *0 år gamle* ♀	⩾ *1-year old* ⩾ *1 år gamle* ♂	⩾ *1-year old* ⩾ *1 år gamle* ♀	Total *Ialt*
1.– 2.	51.5	67.4	32.8	50.6	50.5
2.– 3.	26.5	37.8	23.0	13.9	28.2
3.– 4.	39.5	36.7	35.8	40.0	38.1
4.– 5.	37.4	44.3	30.7	39.8	37.4
5.– 6.	52.6	71.4	49.6	46.6	56.5
6.– 7.	45.9	57.4	30.4	53.1	44.4
7.– 8.	62.1	73.4	38.0	46.9	55.5
8.– 9.	48.3	71.9	53.6	55.6	52.9
9.–10.	18.1	44.7	29.0	51.0	36.6
10.–11.	49.0	48.4	57.4	47.2	50.5
11.–12.	44.3	48.1	56.5	38.1	46.8
12.–13.	31.8	55.1	16.1	34.2	35.6
13.–14.	67.3	73.6	37.3	65.9	58.4
Average *Gennemsnit*	44.2	56.2	37.7	44.8	45.5

Table 11. The total yearly mortality between the first autumnal captures of subsequent years.

Tabel 11. Den samlede årlige dødelighed fra første efterårsfangst til første efterårsfangst.

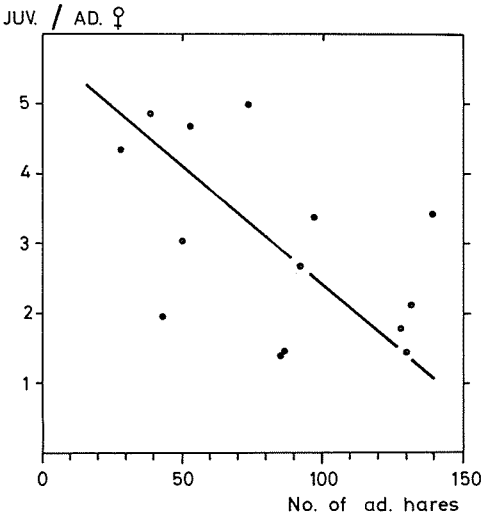


Fig. 16. The no. of young hares per old female at first autumnal capture in relation to the no. of old hares.

Fig. 16. Antal ungharer pr. gammel hun ved første efterårsfangst i forhold til bestandsstørrelsen af gamle harer.

Reproduction

No studies have been made on the island of the number of embryos per female, and neither has any information been obtained on the size of the litter or the number of litters per year. However, from the capture-recapture experiments described, an idea of breeding is obtained by considering how many young hares produced in spring and summer are present in the autumnal captures.

Calculation of the size of the proportion of young hares in the total population of late September or early October reveals that the percentage varies from 32-71 %; on average the percentage of young is 53, Table 4 and Fig. 7 bottom.

Table 4 furthermore gives the number of young per old female in autumn. The figures vary from 1.40 (in 1970) to 5.00 (in 1959), and the average per year is about 3 (Fig. 6). If, as shown in Fig. 16, the number of young per old female at the first autumn capture is compared with the number of old hares in the preceding spring, it appears that the greatest number of young per old female occurs when population density is low, and the least number of young per old female occurs at high population densities.

This was one of the reasons for the reduction of the population in spring 1965, allowing only 20 hares of each sex to remain. It was wished to find out whether a thinning-out in the population – in this case from 83 to 40 – would result in more young the following autumn. In autumn 1965 there were 4.69 young per old female, and in the following years 4.04 and 4.69 young. As mentioned previously, the other reason was the desire to re-establish an equal sexual distribution. The population reduction carried out was intended to place the population under conditions similar to those at the beginning of the study.

Dansk resumé

Bestanden af hare *(Lepus europaeus* PALLAS) på Illumø, Danmark
Analyse af materialet fra 1957–1970

1) I årene 1957–1970 gennemførte Vildtbiologisk Station fangst, mærkning og genudsætning af harer *(Lepus europaeus)* på øen Illumø ved Fyn, Danmark. Undersøgelsens formål har været at bestemme bestandsstørrelsen og dennes variation, køns- og aldersfordelingen samt dødelighеds- og reproduktionsforhold.

2) Øen (se Fig. 1) omfatter ca. 100 hektar, hvoraf halvdelen dyrkes med almindelige markafgrøder, mens resten er strandenge med kreaturgræsning. Bestanden af harer er efter danske forhold ret stor, gennemsnitlig 200 individer pr. kvadratkilometer.

3) Harerne drives i net opstillet tværs over den smalle ø (se Fig. 2 og 3). Fangster er gennemført efterår, vinter og forår.

Bestandsopgørelsen er baseret på fangst, mærkning og genudsætning, og genfangst. Med ca. en uges mellemrum er der foretaget to fangster omkring 1. oktober, to omkring 1. december, samt to om foråret (oftest i marts). Fangstdatoer fremgår af Tabel 1.

Ved forårsfangsterne er næsten 100 % af de fangne harer mærket ved fangster tidligere i sæsonen. I tabellerne er de enkelte fangster betegnet med tal, f. eks. 2.3 (andet fangstår, tredje fangst).

På grund af den store fangsteffektivitet vil alle de umærkede harer, som fanges i en efterårs- og vintersæson, være unger fra sommerens produktion. 98 % af disse umærkede dyr havde epifyseknop på ulna først i oktober.

4) I undersøgelsesperioden har den »sikre bestand« af ungharer og gamle (d. v. s. antallet af individer, som fanges ved den betragtede fangst eller senere) været 1275, mens den »beregnede bestand« har været 1421 individer. Statistisk usikkerhed knytter sig kun til den »ukendte bestand« (d. v. s. individer, der aldrig har været fanget), som udgør 10 % af den beregnede bestand. Metoden til beregning af bestanden er beskrevet side 7. Tabel 2 giver et eksempel på bestandsberegningen og Fig. 4 viser overlevelseskurverne for den sikre bestand og for den beregnede bestand af en årgang.

Bestandsstørrelsen N_i for hver fangstdato i undersøgelsesperioden er beregnet ved addition af de beregnede tal for hver aldersgruppe (Tabel 3 og Fig. 5).

I 1957/58 var bestanden på 90 individer. Herefter steg den til et maksimum på 339 individer i 1961. Derefter dalede bestanden atter indtil 1964, da der var 135 harer. I foråret 1965 fjernedes efter sidste fangst 43 harer, og tilbage i undersøgelsesområdet var 20 hanner og 20 hunner. Derefter steg antallet til 224 i efteråret 1969. Tabel 4 og Fig. 9 viser bestandens størrelse ved første fangst i de enkelte år.

5) Blandt unge harer er der næsten lige mange hanner og hunner (se Fig. 6 midterste kurve). Blandt gamle harer er der flest hanner (Fig. 6 nederste kurve). Ved reduktionen af bestanden i 1965 blev der igen oprettet ligevægt imellem kønnene, men efter 4-5 år var der atter overvægt af hanner (se også Fig. 7). Ungharernes andel i bestanden varierer fra 32 % til 71 % (se Fig. 7 D). Hunnernes andel af bestanden (Fig. 8 A) og ungeprocenten (Fig. 8 B) daler fra første til sidste fangst (oktober-marts).

Fig. 9 viser efterårsbestanden i de enkelte år, idet søjlerne er inddelt i overensstemmelse med de enkelte generationers (årganges) andel af den samlede bestand. Den øverste sektion af kurven angiver årets ungebestand.

6) Fangstprocenten (den del af bestanden, som fanges ved en fangst) er ens for hanner og hunner. Unge harer har om efteråret en lidt lavere fangstprocent end gamle harer. Omvendt forholder det sig om foråret. Harer, som er 3 år eller mere, synes vanskeligere at fange end de 1-2-årige dyr. Fangstprocenten er lavere om efteråret (bedre dækning) end om foråret. Fig. 10 viser sammenhængen mellem fangstprocent for 0-årige og 1-årige harer på forskellige årstider (se også Tabel 7 og 8).

7) Under fangsterne sker uheld, så harer må aflives. Dette regnes ikke med i den naturlige dødelighed. Den naturlige dødelighed er for alle kategorier af harer for alle årene i gennemsnit 46 %, men varierer meget de forskellige år og efter køn og alder.

Tabel 9 viser, hvorledes dødeligheden beregnes. Tabel 10 viser dødeligheden beregnet for hver måned. Dødeligheden er størst om efteråret, især hos unge harer (10-11 % pr. måned). I vintermånederne har ungharerne en dødelighed på 8-9 % pr. måned. Både efterår og vinter er dødeligheden større hos hunner end hos hanner. Forår og sommer er dødeligheden kun 3-5 % pr. måned. Fig. 12 viser dødeligheden på forskellige årstider og hos forskellige aldersklasser hos ♂ og ♀ i forhold til hinanden. Fig. 13 viser dødelighed hos 0-årige, 1-årige og 2-årige eller

ældre i forhold til hinanden. Fig. 14 viser gennemsnitlig månedsdødelighed hos ungharer og gamle harer efterår, vinter og sommer. Fig. 15 viser årsdødeligheden (fra oktober til oktober) for totalpopulationen.

Den gennemsnitlige årsdødelighed beregnet fra oktober til oktober (se Tabel 11) er for

unge	♀	56 %
unge	♂	44 %
gamle	♀	45 %
gamle	♂	38 %

8) Ungeprocenten ved første efterårsfangst (efter en dødelighed af ukendt størrelse blandt killingerne i perioden fra fødslen til ca. 1. oktober) varierer mellem 32 % og 71 % (gennemsnit 53 %) (Fig. 7 D). Antallet af unger pr. gammel hun varierer fra 1,40 (1970) til 5,00 (1959) (gennemsnit ca. 3,0) (se Fig. 6 øverst). Det største antal unger pr. gammel hun synes at forekomme i år med små totalbestande (se Fig. 16). Efter reduktionen af bestanden i 1965 var der det følgende efterår 4,69 unger pr. gammel hun.

Резюме на русском языке:

Состав зайца *(Lepus europaeus* PALLAS*)* на острове Иллумё, Дания. Отчет о материале с 1957 по 1970 г.

1) С 1957 по 1970 г., Станция Исследования Биологии Дичи проводила ловлю, пометку и выпуск на свободу зайцев *(Lepus europaeus)* на острове Иллумё вблизи острова Фюн, Дания. Целью исследования являлось определение численности состава и её изменений, распределения по полу и возрасту, и получение данных о смертности и продукции.

2) Остров (см. фиг. 1) охватывает прибл. 100 га. Половина этой площади состоит из обычных полевых культур, а остальная часть из прибрежных лугов, служащих пастбищами для скота. По датскому масштабу состав зайцев довольно велик, средним числом около 200 особей.

3) Зайцев загоняют в сети, расставленные поперек узкого острова (см. фиг. 2 и 3). Ловли проводились осенью, зимой и весной.

Определение состава основано на ловле, пометке, выпуске на свободу и повторной ловле. С интервалами по прибл. одной неделе проводились две ловли около 1-го октября, две около 1-го декабря, и две весной (как правило: в марте). Даты ловли указаны в табл. 1.

При весенних ловлях почти 100 % пойманных зайцев заранее помечены на ловлях предыдущей части сезона. В таблицах, отдельные ловли обозначены цифрами, напр. 2.3 (второй год ловли, третья ловля).

Вследствие высокой эффективности ловли, все непомеченные зайцы, пойманные в течение осеннего и зимнего сезонов, являются зайчатами продукции прошедшего лета. 98 % этих непомеченных зайцев в начале октября имели эпифизные шишки на *ulna*.

4) В течение периода исследования, »достоверный состав« молодых и старых зайцев (т. е. число пойманных, разных особей) составлял 1275, между тем как »вычисленный состав« был 1421 особей. Статистическая неуверенность играет роль только при определении »неизвестного состава« (т. е. не пойманных особей), составляющего 10 % вычисленного состава. Способ вычисления состава описан на стр. 7 В качестве примера соотношения между вычислен-

ным и достоверным составом, см. фиг. 4 и табл. 2.

Состав (N_i) за каждую дату ловли в течение периода исследования получен сложением вычисленных количеств каждой возрастной группы (табл. 3 и фиг. 5).

В 1957/58 г. состав был 90 особей. Затем он возрос до максимума 339 особей в 1961 г. После этого, состав снова уменьшился до 1964 г., в котором он состоял из 135 зайцев. Весной 1965 г. после последней ловли было удалено 43 зайца, и в районе исследования осталось 20 самцов и 20 самок. После этого, число повысилось до 224 к осени 1969 г. Табл. 4 и фиг. 9 показывают состав во время первой ловли каждого отдельного года.

5) Среди молодых зайцев число самцов и самок приблизительно одинаково, а именно 48,5% и 51,5% (см. среднюю кривую на (фиг. 6), Среди старых зайцев, большинство составляют самцы (фиг. 6, нижняя кривая).

Благодаря сокращению состава в 1965 г. равновесие между полами было восстановлено, но по истечении 4–5 лет опять установился перевес самцов (см. также фиг. 7). Состав молодых зайцев колеблется от 32% до 71% (см. фиг. 7D). Доля самок в составе (фиг. 8 A) и процент зайчат (фиг. 8 B) уменьшается от первой до последней ловли (от октября до марта).

Фиг. 9 показывает осенний состав отдельных годов, причем столбы разделены соответственно долям, составляемым отдельными поколениями (по годам рождения). Число зайчат, рожденных в том-же году, составляет верхнюю часть столба.

6) Кривые на фиг. 11 показывают число оставшихся в живых ♂ и ♀ каждого поколения. Проценты поимки (та часть состава, которую удается поймать во время одной ловли) одинаковы у самцов и самок. Процент поимки молодых зайцев осенью немного ниже, чем у старых зайцев. Весной это соотношение противоположное. Кажется, что зайцев трехлетнего и более старых возрастов ловить труднее, чем одно- и двухлетних. Осенью, процент поимки ниже, чем весной (зайцам легче скрываться). Фиг. 10 показывает взаимоотношение процентов поимки 0-летних и 1-летних зайцев в разные времена года (см. также табл. 7 и 8). Табл. 6 показывает частоту поимки зайцев пятого разряда по возрасту.

7) При ловлях бывают несчастные случаи, вследствие которых зайцев приходится убивать. Это не включено в естественную смертность. Для зайцев всех категорий за все годы, смертность в среднем составляет 46%, но сильно колеблется с года на год, а также по полу и возрасту.

В табл. 9 показано, как вычисляется смертность. Табл. 10 показывает смертность, вычисленную за каждый месяц. Смертность наиболее высока осенью, в особенности у молодых зайцев (10–11% за месяц). В зимние месяцы, смертность молодых зайцев составляет 8–9% за месяц. Как осенью, так и зимой, смертность более высока у самок, чем у самцов. Весной и летом, смертность составляет только 3–5% за месяц. Фиг. 12 показывает взаимоотношение смертности ♂ и ♀ в разные времена года и у разных разрядов по возрасту. Фиг. 13 показывает смертность у 0-летних, 1-летних, 2-летних и более старых зайцев по сравнению между ними. Фиг. 14 показывает среднюю месячную смертность молодых и старых зайцев осенью, зимой и весной. Фиг. 15 показывает годовую смертность (от октября до октября) общего состава.

Средняя годовая смертность, вычисленная от октября до октября (см. табл. 11) составляет:

у молодых	♀	56%
у молодых	♂	44%
у старых	♀	45%
у старых	♂	38%

8) Процент зайчат при первой осенней ловле (после смертности неизвестной величины у зайчат в течение периода от их рождения до прибл. 1-го октября) колеблется от 32% до 71% (в среднем 53%) (фиг. 7 D). Число зайчат за старую самку колеблется от 1,40 (1970) до 5,00 (1959), в среднем прибл. 3,0 (см. верхнюю часть фиг. 6). Повидимому, наибольшее число зайчат за старую самку встречается в тех годах, в которых общий состав невелик (см. фиг. 16). После сокращения состава в 1965 г., число зайчат за старую самку следующей осенью составляло 4,69.

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