STUDIES ON THE EUROPEAN HARE XXIV.

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Dynamics and Production of the Hare Population in Poland

[With 18 Tables and 6 Figs.]

Over a period of five years, the following averages per 100 hectares were found in a population of hare: numbers born $\nu_r = 81$; elimination $E_N = 68$ ($E_J = 60$, $E_A = 8$); yield $Y = 14$; and in kg: production $P = 180$; elimination $E = 129$; yield $Y = 56$. Estimates for the whole of Poland are (in million individuals): $\nu_r = 6.6$; $E_N = 5.8$; and $Y = 0.8$. For a period of 12 years the yield varied in the neighbourhood of 0.8 million individuals and showed a slight upward trend. The age ratio $a = N_J : N_A$ varied within a wide range, but the average for one locality over several years and for some 16 different localities in Poland was ± 1.0. Mortality was for current year-borns for June to December 74 per cent, and for adults 30% in a year. Over a period of five years the mortality of current year-borns and the average numbers of adults were inversely related. For adults, mortality is in winter lower than in summer. Biomass is at its maximum in October and then declines. Average longevity is $t = 0.71$ year. Age structure: current and previous year-borns make up 78%, and all animals aged up to 3 years jointly make up 90% of the population. The turnover averages $\Theta = P : B = 1.3$ annually.

1. INTRODUCTION

Ample data concerning the ecology of the common or European hare (*Lepus europaeus* L i n n a e u s, 1758) have been collected in Poland, chiefly, on the initiative of the Hunting Section of Ecological Committee of the Polish Academy Sciences and Institute of Ecology. A large proportion of them have already been worked up and published by the Polish Academy of Sciences Institute of Ecology, the Polish Hunting Association's Research Station at Czempiń, near Poznań, and the Polish Academy of Sciences Mammals Research Institute at Białowieża; since they continue to be collected, a great many of them and sometimes highly interesting ones have accumulated in the institutions referred to and have not yet been published. Those that have been published seem to warrant:

(1) a tentative relatively accurate analysis of the numerical and biomass balance as well as production of the population in the Hunting Area of the Polish Hunting Association's Research Station for the period a few years; and

(2) a provisional and still rough analysis of the dynamics and production of Poland's hare population.

The empirical data in the present paper come from the material already published (see Table 1 and the bibliography). In addition, Dr. Z. P i e l o w s k i supplied data on the Czempiń population of autumn 1968 (with break-down for current year-borns and overwintereds) as well as that year's yield.

The dynamics of numbers and biomass of adult individuals (status during the open season, yield, and mortality of overwintereds) in Czempiń are based almost completely on highly accurate empirical data. Estimates of natality, mortality of the young ones, and productiion had to be based on calculations of the numbers born (ν_r), where in »averages for Poland« were not infrequently used. The analysis of this numerical dynamics and production of the Czempiń population served as a pattern for a similar analysis for the whole of Poland.

2. EMPIRICAL DATA AND THE PRINCIPLES OF THEIR PROCESSING

2.1. Numbers

Numbers and especially the standing crop of hares before the open season (hunting as well as live trapping) are the basic material. The size of the population before the open season (N) and after it (N') provide the basis for calculations of most of the other parameters of dynamics. Relevant data are still scant in Poland, but accurate ones are available for the hunting area of the Polish Hunting Association's Research Station in Czempiń for 1964—1968 (and they continue to be collected).

Also available are estimates arrived at by the method of strip censuses for the border areas at the edge of Kampinos Forest near Dziekanów (P i e l o w s k i, 1966) and for the hunting areas »Brody«, »Lutom« (both in Poznań province), and »Sokółka« (Białystok province) (J e z i e r s k i, 1968). Without suitable corrections, these data are much less accurate (P i e l o w s k i, 1962, 1966, 1969; R a j s k a, 1968) and have not been used in the present paper.

Estimates of population size based on the experience of hunters also are known for many areas, but they are unsuited for dynamics or production calculations.

All we have of country-wide data are only the annual yields for 1960 —1968 (A n d r z e j e w s k i, N o w a k & P i l i p i u k, 1968; A d r z e- j e w s k i & N o w a k, 1969; Statistical Yearbook, 1969).

Census data for the open season in Czempiń are highly accurate because they are based on the results of removal trapping in accurately known areas (A n d r z e j e w s k i & J e z i e r s k i, 1966; P i e l o w s k i, 1968) or of strip censuses, in which numbers were calculated by a method checked against the results of removal trapping on accurately known areas (P i e l o w s k i, 1968).

The procedure of removal trapping was as follows: a quadrat of an accurately known area, usually about 1 sq. km, was surrounded with nets and a group of drivers passed throught it back and forth four times disturbing the hares which then got caught in the nets. When the number of hares is recorded separately for each wave of drivers, the size of the population can be obtained from the regression line with great accuracy (A n d r z e j e w s k i & J e z i e r s k i, 1966). This is the most and very accurate method of calculating numbers before the yield (N). With the yield (Y) exactly known we can calculate $N' = N - Y$ the stock population which begins life and reproduction in the particular »hare« years and, together with the realized reproduction increase $N_{j(T)}$, gives the status of the stock populations before the open season of the particular year (also found empirically).

The »hare« year. The yield, as the result of shooting, is an integral element of the hare population dynamics. What remains after the open season overwinters and reproduces. This makes it appropriate to consider the end of the open season as the beginning of the hare year. The open season is in Poland from November 1 to January 10, and the yield is thus spread over a period of more than two months. It is convenient for the calculations to refer the whole yield to a single day. The middle of the open season falls roughly on December 6; however: (1) hare shooting is more comonly done when there is snow, i.e., rather in late December and the first decade of January, and (2) the average day of birth is about

June 15 (cf. 2.3.); hence it is more convenient for calculations and reasoning to divide the »hare year« exactly in half: from December 15 to June 15, and from June 15 to December 15.

Table 1.

Population numbers (individuals/100 ha — empirical data).
N — total, A — overwintereds, j — current yr borns.

Year	Category	$N'_T = N_{(T-1)} - Y_{(T-1)}$ N after hunting of previous yr (beginning of »hares yr«)	$N_T = N_{A(T)} + N_{j(T)}$ N before current yr's yield	$Y_{(T)}$ Yield	$N'_T = N_T - Y_{(T)}$ N beginning next yr	Reference
1962/3	N		66.3	24.3	42.0	Jezierski
	A		47.0	17.0	30.0	in litt.
	j		19.3	7.3	12.0	
1963/4	N	42.0	42.8	20.0	22.8	Andrzejewski and Jezierski, 1966
	A	30.0	27.6	12.9	14.7	Jezierski,
	j	12.0	15.2	7.1	8.1	in litt.
1964/5	N	22.8	29.3	11.3	18.0	Pielowski,
	A	14.7	12.0	4.6	7.4	1968
	j	8.1	17.3	6.7	10.6	
1965/6	N	18.0	46.0	13.3	32.7	,,
	A	7.4	12.3	3.5	8.8	
	j	10.6	33.7	9.8	23.9	
1966/7	N	32.7	46.7	14.0	32.7	,,
	A	8.8	27.0	8.1	18.9	
	j	23.9	19.7	5.9	13.8	
1967/8	N	32.7	46.7	12.0	34.7	Pielowski,
	A	18.9	28.0	7.1	20.9	pers. com-
	j	13.8	18.7	4.9	13.8	munication

The numbers of adults and juveniles in the yield have been calculated from $a = \frac{N_j}{N_A}$ and $Y_A = Y$: $(1 + a)$, with the same likelihood of being shot assumed for both age classes.

In work on the production and dynamics use was made of the empirical data (Table 1) from the papers by J e z i e r s k i (in litt.), A n d r z e j e w-s k i & J e z i e r s k i (1966), and P i e l o w s k i (1968), and — for 1968 — from a personal communication by Dr. Z. P i e l o w s k i, head of the Polish Hunting Association's Czempiń Research Station. Unless indicated differently, numbers are always relative to an area of 100 hectares. P i e-

l o w s k i's data (1968) referred to the size of the entire population of the hunting area of Polish Hunting Association's Czempiń Research Station. They were prorated on the 100 hectare basis by dividing them into the area under survey (i.e., 15,000 ha), woods included, because according to Dr. P i e l o w s k i these covered small areas surrounded by fields and used similarly by hares.

The point of departure was provided by the following empirical data (Table 1):

$N_{(T-1)}$ — population size before the yield (December 15) of the winter terminating the previous year of the research project, with break-down for

$N_{A(T-1)}$ — overwintereds from the previous and earlier years (before the yield) and

$N_{j(T-1)}$ — current year-borns before the yield,

$Y_{(T-1)}$ — the yield terminating the previous year;

N_T — the size of the stock population before the current year's open season, as made up of:

$N_{A(T)}$ — overwintereds (survivals until the open season from the previous and earlier years, i.e. from $N'_{(T-1)}$),

$N_{j(T)}$ — »realized increase« — current year-borns that have reached the open season (i.e., December 15 beginning the year under study),

Y_T — yield at the end (December 15 ending of the year under study).

By simple subtraction $N_{(T-1)} — Y_{(T-1)}$ we obtain the stock population $N'_{(T-1)}$, which lives, reproduces, and perishes in the year concerned.

Similarly, with the current year's yield ($Y_{(T)}$) known, we have: $N'_{(T)} = N_T—Y_{(T)}$, the stock population for the coming year (the starting numbers of the »hare« year and at the same time the calendar year analyzed).

Assuming the same likelihood of yield for the overwintereds N_A and the current year-borns $N_{j(T)}$ that have survived until the open season we

can calculate: $N'_A = N' : (a + 1) = N' : \left(\dfrac{N_j}{N_A} + 1\right)$, i.e., the numbers of the

overwintereds (from the previous and the earlier years) of the stock po-

pulation after the yield, where a is the age ratio for $N \left(a = \dfrac{N_j}{N_A}\right)$, N_j and

N_A are the numbers of the young ones and overwintereds before the yield (empirical data), and also $N'_j = N' — N'_A$, i.e., the young ones that have survived the open season and remained in the stock population (Table 1).

2.2. Mortality of Adults

Given the size of a population at two or more consecutive years it is possible to arrive at qualitatively completely new data through the intro-

duction of the parameter of time. It becomes possible to calculate the mortality for the stock population considered.

From $N'_{(T-1)}$, the size of the stock population after the yield that marks the beginning of the hare years (December 15), and $N_{A(T)}$, the numbers of overwintereds before the next yield, i.e., after one year (December 15 of the calendar year), which is what remains of $N'_{(T-1)}$ after one year, we can easily and very accurately calculate the natural elimination of overwintereds for the particular year:

$$E_{NA} = N'_{(T-1)} - N_{A(T)}, \text{ where}$$

E_{NA} stands for natural elimination in terms of individuals (cf. Fig. 4).

Table 2.

Mortality of adults (overwintereds) in Czempiń (individuals/100 ha).

	$N'_{(T)}$*) N in stock population (basic stock) after yield (Dec. 15 — ending yr)	$N_{A(T)}$*) Overwintereds surviving until next yield (Dec.-15 — ending yr)	$E_A = N'_{(T)} - N_{(AT)}$ (natural elimination)	$m_A = \dfrac{E_A}{N'_{(T)}}$	$m_A' = \dfrac{E_A}{N_A \cdot T}$	$m_A'' = \dfrac{E_A + v}{N'}$ Total elimination
1964	42.0	27.6	14.4	.34	.0011	.65
1966	22.8	12.0	10.8	.47	.0008	.67
1966	18.0	12.3	5.7	.32	.0010	.51
1967	32.7	27.0	5.7	.17	.0005	.42
1968	32.7	28.0	4.7	.14	.0004	.36
Average	—29.6	—21.4	—8.3	.29	.0008	.53
Average for Poland (in thousands)	2400	1600	800	.33		.66

*) Empirical data from Table 1.

From this we can calculate mortality. For calculations it is conveniently expressed as the proportion (or percentage) of those that have perished in the given years in relation to the point of departure $N'_{(T-1)}$:

$$m_A = \frac{E_{NA}}{N'_{(T-1)}} = \frac{N_{(T-1)} - N_{A(T)}}{N'_{(T-1)}}$$

When so calculated, mortality enables us to calculate from the known population size for a particular year the natural elimination by simple multiplication: $E_N = N_{(T-1)} \cdot m_A$. Elimination thus understood was used by A n d r z e j e w s k i & J e z i e r s k i (1966) in the equation for permissible yields.

With data as accurate as those for the Czempiń population, it also is possible to calculate mortality per average adult individual per year:

$$\overline{m} = \frac{E_A}{\overline{N}_A} = \frac{2\,E_A}{N'_{(T-1)} + N_{A(T)}}$$

as well as the average daily mortality of adults:

$$m'_A = \frac{E_A}{\overline{N}_A \cdot T}$$

or, finally, the complete elimination of adults, including yield:

$$m'' = \frac{E_A + Y}{N'}$$

In calculating the dynamics of numbers country-wide, the only possible procedure is to adopt arbitrarily some average mortality. For Poland it was put at 33 per cent. The only empirical guideline was the fact that in Czempiń the average mortality recorded over a period of five years was roughly 30%, and wildlife is better looked after in Poznań province than on average elsewhere in the country. We obviously realize that data collected over a period of five years and for a single locality only are inadequate as a basis, and are thus only a rough estimate for Poland.

2.3. Number Born (ν_r)

At the present stage of research, only rough estimates of hare natality are possible. In this the data reported by R a c z y ń s k i (1964) were used. Between December 1958 and February 1960 he examined 269 adult females, i.e., from 8 to 27 a month, and reported for particular months (1) the size of the litter (number of young ones per gravid female), and (2) the percentage of gravid females. With these data as the basis, he calculated (l.c.) that the average female produces annually 7.82 young ones. In the present analyses the average number of young ones produced annually by an average female was calculated with the aid of P e t r u s e-w i c z's (1968) simplified formula, namely: (1) at the time of growing numbers of gravid females, the numbers born (ν_r) were described by the equation:

$$\nu_r = \frac{\overline{N}_{p(T)} \cdot T}{t_p} - \frac{\Delta N_{p(T)}}{2} \cdot L$$

was used, where L is the size of the litter in a given month, tp is the time of gestation, put at 42 days, T is the time interval for which the numbers born were calculated (1 month $=$ 30 days), N_p is the percentage of gravid females in the particular month, and ΔN_p is the increase in N_p for the particular month (L, N_p etc. after R a c z y ń s k i, 1964).

The number of individual-days for the gravid females $(\overline{N}_p \cdot T)$ for the month was arrived at by calculating the area for the particular month under Raczyński's curve of the percentage of gravid females (1964) (Figure 1) [1]. Namely, starting from $\left[\dfrac{N_{p(T)} \cdot T}{2} - \dfrac{\varDelta N}{2}\right] L$ the following equation was obtained for each month:

$$\nu_r = \left[\frac{(N_{p\,T-1} + N_{p\,T}) \cdot 15}{2 \cdot t_p} + \frac{(N_{p\,(T)} + N_{p\,(T+1)}) \cdot 15}{2 \cdot t_p} - \frac{\varDelta N_p}{4}\right] \cdot L;$$
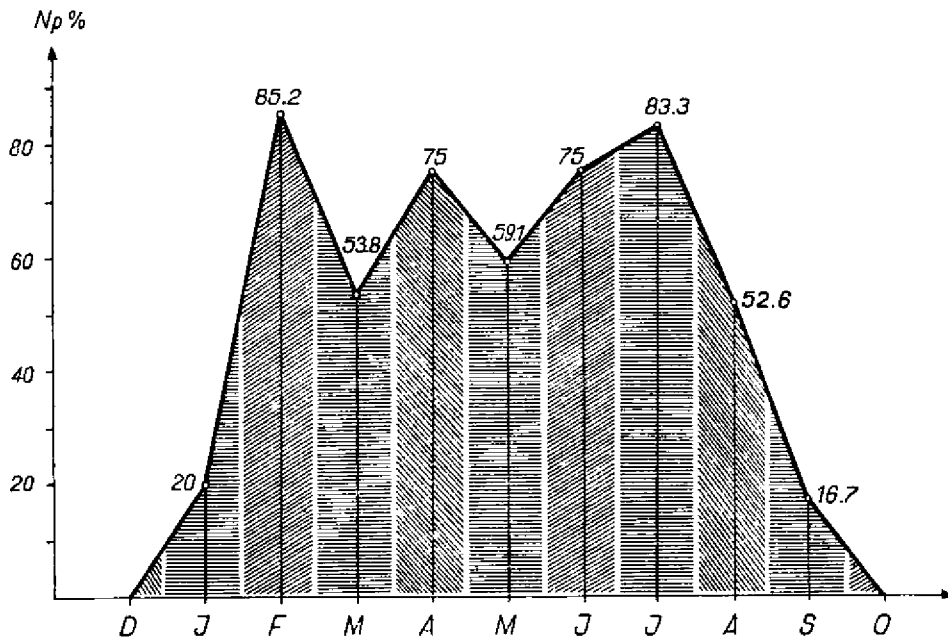
Fig. 1. The percentage of gravid females, annually.

where $N_{p(T)}$ is the number of gravid females in the month considered, $N_{p(T+1)}$ that number in the next month, L the size of litters in the month considered, 15 the number of days preceding and following the month

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[1] The accurate figures both of the percentage of gravid females and the young ones produced by an average female in a particular month were obtained directly from Dr. R a c z y ń s k i, because readings from the graph would necessarily give only approximate values.

considered, and ΔN_p the increase in N_p in the month before and the one after the month considered. On transformation, this equation gave:

$$\nu_r = \left\{\left[N_{p(T-1)} + 2N_{p(T)} + N_{p(T+1)}\right]\cdot\frac{15}{84} - \Delta N_p\right\}L.$$

This equation gave 7.4 young ones produced by an average female in the population (Table 3), which is $L = 3.7$ per individual per year (assuming a sex ratio of 1:1).

In calculating the numbers born (ν_r) for the year, this figure $L = 3.7$ was multiplied by the number of individuals capable of reproduction. Of data relating to the number of individuals capable of reproducing, the

Table 3.

Numbers born, by month by 100 females (= 200 population members).
R a c z y ń s k i's (1964) empirical L and N_p served to calculate after P e t r u s e-
w i c z (1968) the numbers born in particular months from the equations:

$$\nu_r = \frac{\overline{N_p}T \cdot L}{t_p}\text{during } N_p \text{ decline, and } \nu_r = \left(\frac{\overline{N_p}T}{t_p} - \frac{\Delta N_p T}{2}\right)L \text{ during } N_p \text{ rise; } \overline{N_p} -$$

average number of gravid females in a given month; T — 30 days; t_p — gestation =
= 42 days; ΔN — increase in N in a given month.

Months	$N_p \%$ Pregnant femalesin 200 individuals	L Litter size	ν_r N of born/100 ♀
I	20	0.1	0
II	85.2	1.3	35.3
III	53.8	2.4	102.1
IV	75	3.6	149.9
V	59.1	1.9	83.4
VI	75	1.7	78.5
VII	8?.3	2.9	146.3
VIII	52.6	2.5	91.6
IX	16.7	3.5	53.7
Total			740.8

following were available: (1) $N'_{(T-1)}$, the starting level of the population, i.e., per December 15 (the beginning of the hare year), and (2) $N_{A(T)}$, the number of all overwintereds individuals that have survived until the end of the hare year. If used as the basis, $N'_{(T-1)}$ would afford an exaggerated number of all overwintered individuals that have survived until the end ducing. If the basis is $N_{A(T)}$, i.e., the level at the end of the year — as in A n d r z e j e w s k i & J e z i e r s k i's celculations (1966) — the numbers born would be too low, because a certain number of females reproduce before they are eliminated. Consequently, the reproducing population was assumed as $N_{A(T)} + \frac{1}{4} E_{A(T)}$, on the assumption that (1) one-half of

the eliminated individuals (E) perish before the breeding season (in winter), and (2) that of the one-half that survive the winter into the breeding season one-half will and the other one-half will not reproduce before elimination. Consequently, one-quarter of the eliminated individuals are likely to reproduce before elimination, and the reproductive stock was assumed as $\nu_{RS} = N_{A(T)} + \frac{1}{4} E_{A(T)}$.

It should be noted that the numbers born (Table 3) represent merely a rough estimate. The basic figure is the numbers born per individual per year $L = 3.7$ — which (1) was calculated only for one province (Poznań) and for a single year (December 1958 to February 1960), with the litter size calculated for some months from as few as six or seven gravid females, which is certainly not enough and that is probably the reason of the large and irregular fluctuations of L. The same can be said of the number of gravid females. Moreover, the number of individual-days, i.e., the multiplier for L, is calculated on certain assumption (see above), and these, although very likely, are only assumptions. As the result, we have to assume that the numbers born per capita in a population are constant, which is not very likely to be so.

Being a physiological and specific value, the average litter size may be supposed to be more or less constant. The percentage of gravid females, on the other hand, which is ecologically determined, is likely to vary within a considerable range, and the number of young ones produced by a statistical individual may therefore depart considerably from the value $L = 3.7$. Hence, more accurate knowledge of the dynamics of Poland's hare population requires that the studies be repeated covering a more ample material and a wider geographical range. A project of this kind is certainly difficult to organize (a suitably large material is not easily available all year round), but the problem is important.

2.4. Mortality and Survivorship of Current-year Born

With regard to the Czempiń population we have empirical and very reliable data on how many of young ones born in a given year survived until the time of yield (ca. December 15), which is the realized increase (natality) $N_{j(T)}$ according to A n d r z e j e w s k i & J e z i e r s k i (1966). This is extremely important in practical as well as theoretical respects. From the practical point of view it is about one-half of the hares available for shooting.

Furthermore, the age ratio score $a = \frac{N_{j(T)}}{N_{A(T)}}$ is a value involved in the equation defining the yield permissible without overexploitation (A n- d r z e j e w s k i & J e z i e r s k i, 1966). This equation, which tells us how

large a part of a population can be remove while ensuring that its level
will next year equal that before the yield, is:

$$Y = N_T \frac{(1+a)\,(1-m_A)-1}{(1+a)\,(1-m_A)} \text{ or } y = \frac{Y}{N_T} = \frac{(1+a)\,(1-m_A)-1}{(1+a)\,(1-m_A)}$$

From the point of view of theoretical research, realized increase $(N_{j(T)})$
enables us to determine the mortality and mortality rate of young ones,
which is essential for calculations of production. Realized increase and
its index $a = N_{j(T)} : N_{A(T)}$ are therefore very important quantities. The
index is not unduly difficult to determine; it is enough to find by Stroh's
method [2] the number of young and old animals in any sufficiently large
number of hares in autumn, and it will be given by the age structure as
$a = N_{j(T)} : N_{p(T)}$.

Table 4.

Age ratio $a = \dfrac{N_j}{N_A}$ in Czempiń in the open season.

Year	'57	'58	'59	'60	'61	'62	'63	'64	'65*	'66*	'67*	'68**	a
a	1.0	0.9	1.6	0.5	1.2	0.6	0.4	0.6	1.4	2.7	0.7	0.7	1.008

* Calculated from P i e l o w s k i's data (1968), ** Acc. to P i e l o w s k i (pers.
comm.). The remaining figures calculated after A n d r z e j e w s k i & J e z i e r s k i
(1966).

In Poland, we already have a considerable volume of relevant data. We
have empirical and highly accurate values for $a = N_j : N_A$ for Czempiń
for a period of 11 years (Table 4) as well as values based on large figures
for various other parts of Poland (Table 5). They are absolutely fit to be
used for calculating with adequate reliability the mortality of grown
(overwintereds) hares for Czempiń with the aid of the concrete empirical
value of realized increase found for a particular year. It also is possible
to calculate the average age ratio $(a = N_j : N_A)$ for Poland. But although
it is based country-wide on very large material, it refers outside Czem-
piń to 1957 and 1958 only. It is very necessary to collect more data in

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[2] Identification of young ones by Stroh's method has been strongly criticized and
continues to be so (B u j a l s k a et al., 1965; A n d r z e j e w s k i & P u c e k, 1965).
The criticims, however, have failed to demonstrate the error to be unidirectional.
And if errors are not unidirectional, they are bound to offset each other where
adequately large numbers are involved. The method of Stroh gains much in accuracy
when the skin is slit open to expose the leg examined. Furthermore, it is more
accurate earlier in the season (in November than in December, i.e., when the ani-
mals are one month younger (P i e l o w s k i, 1962; A n d r z e j e w s k i & P u c e k,
1965). And therefore we take from P i e l o w s k i's data (1962) only those for Nov-
ember, and ignore the December ones.

autumn, during the open season, and from a large number of regions. It could be done by individual Hunting Circles, or by the provincial organs of the Polish Hunting Association.

The weighted mean of all these data is $a = 0.97$ (≈ 1) (Table 5). Between regions, the values vary from 0.4 to 2.7, which is a very wide range.

With the numbers born available as a rough estimate country-wide and a concrete empirical value for Czempiń and with the country-wide average realized increase (if $a = 1$, the population is composed in equal parts of current year-borns and overwintereds), it is possible to calculate the

Table 5.

Age ratio (a) in the open season ($\pm$ December 15).

Region	Year	$N = N_j + N_A$	$N_{j(T)}$	$a = \dfrac{N_j}{N_A}$	Reference
Poznań province	1957	6420	3323	1.1	Jezierski, 1959
Moszna (Opole province)	1957	1163	677	1.4	„
Czempiń (Poznań province)	1957	2203	1081	1.0	„
Provinces of Wrocław, Lublin, Kraków, Warszawa, Szczecin, Olsztyn	1958	3740	1621	0.8	Pielowski, 1962
Provinces of Poznań, Wrocław, Szczecin, Gdańsk, Opole, Kraków, Warszawa, Lublin, Łódź, Olsztyn	1961	7344	3378	0.9	„
Czempiń (Poznań province)	1958–63	7502	3334	0.8	Andrzejewski & Jezierski, 1966
„ „	1964	3823	2003	1.1	
„ „	1965	1700	1003	1.4	Pielowski, 1968
„ „	1966	2000	1460	2.7	„
„ „	1967	2100	865	0.7	„
„ „	1968	1800	741	0.7	Pielowski, pers. comm.
Total and average		39795	19486	0.97	

natural elimination of young individuals ($E_j = \nu_r - N_{j(T)}$) and their mortality. The latter can be calculated in relation to the numbers born ($m_j - E_j : \nu_r$). Assumming that from birth until winter they are eliminated at a constant rate (in proportion to density), their instant mean mortality rate can be calculated from the equation $N_{j(T)} = \nu_r \cdot e^{-\mu T}$ (T being half a year, because the average date of birth is June 15, and the date of the yield is December 15).

2.5. Individual Growth Curve

We still have exceptionally few data on the individual growth curve of hares. It has been prepared under experimental conditions of animals kept in cages (P i l a r s k a, 1969) on the basis of frequent and accurate measurements extending over a period of 270 days since birth but involving a relatively scant material (12 individuals). When the experimental data were compared with the weight of wild animals, the former proved to be distinctly lower at the age of 100—270 days. With ad-hoc data on the weight of hares in the field (Warsaw area) available to us, we tried to extrapolate the laboratory curve (Fig. 2) to the average weight of an adult hare in the province of Poznań (P i e l o w s k i, 1962).
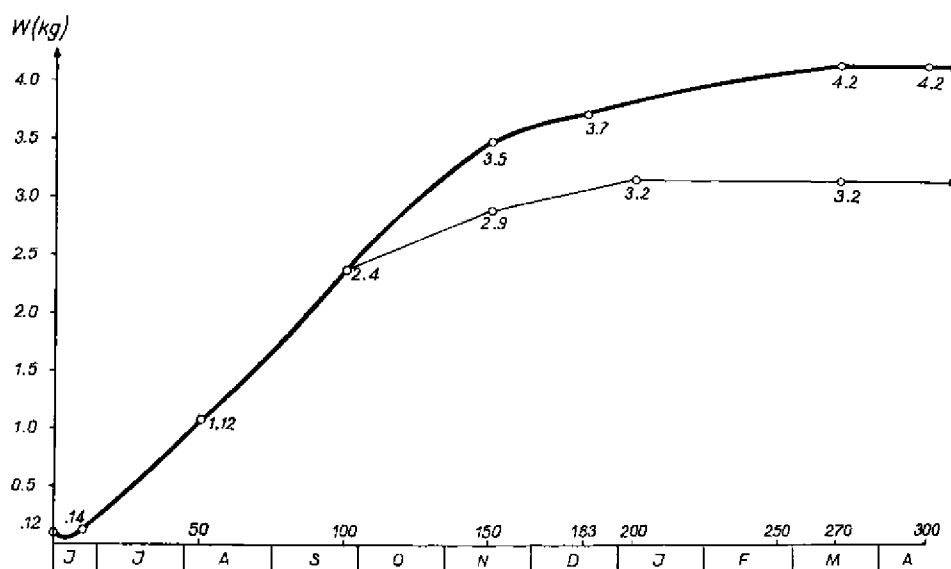

Fig. 2. Individual growth curve (bottom line: laboratory data).

An analysis of the resulting individual growth curve showed the rate of growth to be inconstant. For hares aged up to 100 days, the curve may be written:

$W_t = 0.45 \ t^2 — 2.53 \ t + 121.2$, whereas from that age onwards it corresponds to the equation $W_t = -6753 + 2006 \ ln \ t$, where W_t is the weight in grams at the age t, and t the age in days.

But it needs to be born in mind that this individual growth curve is an extrapolation based on laboratory data. Its calculation on the basis of field data remains still to be done.

3. ANALYSIS OF DYNAMICS OF NUMBERS

3.1. Population Dynamics, Realized Increase, and Mortality of Adults (Czempiń)

From certain points of view it is useful to consider separately the dynamic of the grown part of the population, i.e., to take as the point of departure its size in the open season. This is the size which is the most interesting from the point of view of shooting. Furthermore, its analysis is easier because it can be based on accurate empirical data, whereas all our knowledge about the number of born and what happens to them until the time of the yield is based on computations.
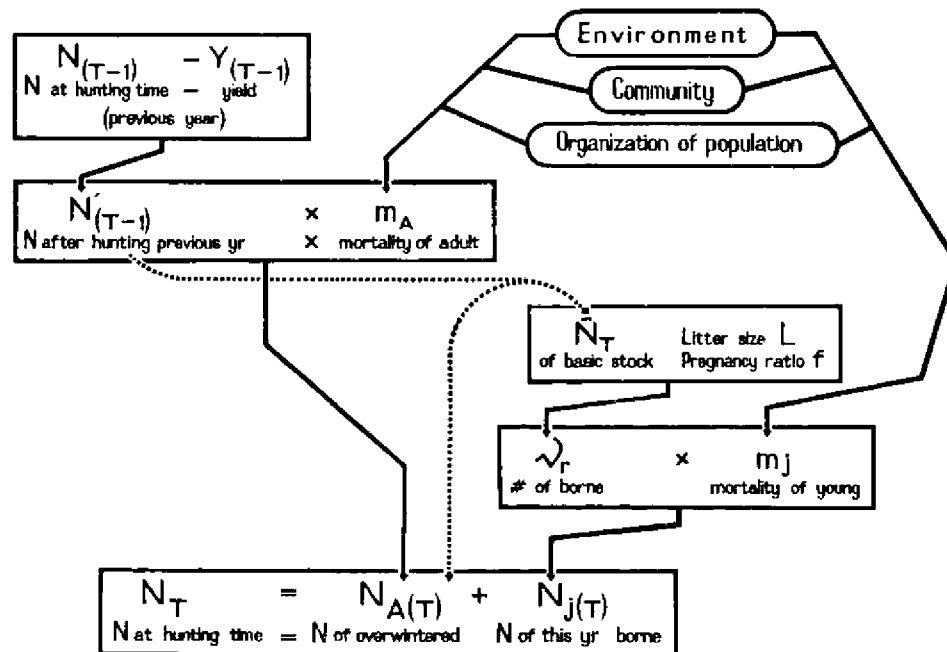

Fig. 3. Factors which determine the number of individuals at the time of the open season (N_T). Explanations in the text.

The number of hares in the open season is the sum of the overwintereds $(N_{A(T)})$ that have survived until their next autumn and the realized increase $(N_{j(T)})$, i.e., current year-borns that have survived until the open season $(N_T = N_{j(T)} + N_{A(T)})$.

The number of overwintereds $(N_{A(T)})$, on the other hand, is a derivative of the size of the basic stock $(N'_{(T-1)})$ at the beginning of the year and the mortality of adults (m_A), because $N_{A(T)} = N'_{(T-1)} \cdot m_A$. And the size of the basic stock is, in turn, the size of the stock population at the beginn-

ing of the year, i.e., $N_{(T-1)}$, less the previous year's yield: $N'_{(T-1)} = \nu_{(T-1)}$ — $Y_{(T-1)}$ (Fig. 3).

Next, the realized increase (natality) $N_{j(T)}$ is derived from number of born individuals and the mortality of young ones (μ) until the open season, where the number of born depends on the number L of young ones produced per average adult individual in the population, which in our calculations has been assumed as constant and equal to 3.7 (see 2.3), on the number of adults, the sex ratio, and the percentage of gravid females (Fig. 3).
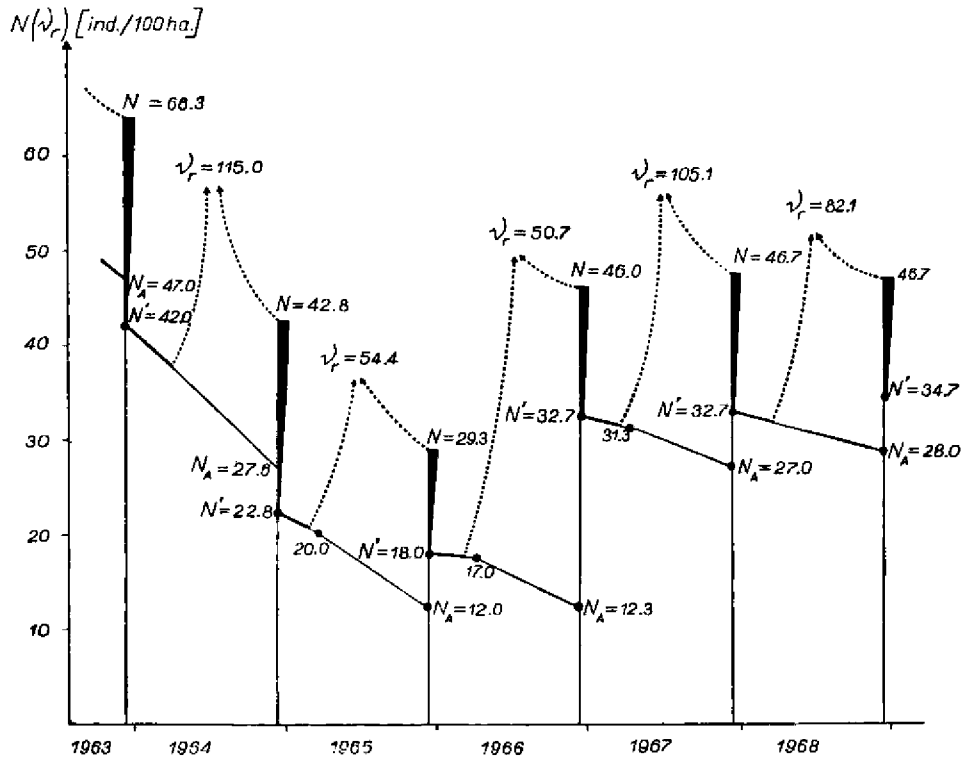
Fig. 4. Dynamics of numbers (Czempiń).
Dark wedges: yield date (open season); N: numbers before yield (open season); N': numbers after yield (open season); N_A: numbers of overwintereds before yield (open season); ν_r: number born, assigned arbitrarily to the mean date of birth (June 15). All data per 100 hectares.

For Czempiń we have for a period six years highly reliable empirical data on the population size before the time of the yield (N_T) and the yield (Y) (Table 1). This enables us to plot the dynamic of the shootable (grown) part of the population for a period of five years (Fig. 4). By

discriminating current year-borns from all overwintereds we can very accurately determine the mortality of adults:

$$m_A = \frac{N_{(T-1)} - Y_{(T-1)} - N_{A(T)}}{N_{(T-1)} - Y_{(T-1)}} = \frac{N'_{(T-1)} - N_{A(T)}}{N'_{(T-1)}} = \frac{E}{N'_{(T)}} \text{(see 2.2 and Table 2).}$$

The first conclusion suggested by an analysis of population dynamic for five years is that all the ecological parameters (mortality m_A; yield Y, and the realized increase (N_j or a) which determine the numbers of adults vary greatly between different years. Thus, mortality of adults ranged from $m_A = 0.14$ to $m_A = 0.47$ (Table 2), the yield index (y) from 0.26 to 0.47, and the realized increase (N_j) from 15.2 to 33.7 individuals per 100 ha (Table 1), or, when expressed by the score $a = N_j : N_A$, from 0.4 to 2.7 (Table 4 and Table 5).

Table 6.

Abundance of overwintereds versus realized reproduction.

$N'_{(T-1)}$ — standing crop at beginning of year, $\overline{N}_A$ — average abundance $\overline{N}_A =$
$= [N'_{(T-1)} + N_{A(T)}] : 2$, $a = N_j : N_A$, N_j — realized reproduction; N', $\overline{N}_A$ and N_j —
numbers per 100 ha.

Year	'64	'67	'68	'65	'66
$N'_{(T-1)}$	42	32.7	32.7	22.8	18
N_A	←—— 34.8	29.9	25.4	17.4	16.7
a	0.6	0.7	0.7	1.4	2.7 ——→
N_j	15.2 ——→	19.7	18.7	17.3	33.7 ——→

But, high variability apart, the average index of realized increase (natality) is $a = 1.06$, i.e., even as a five-year average, aprroaches the 1.008 which we obtain for a 13-year period for Czempiń (Table 4), and the 0.97 which we obtain from a large material from various years and parts of the country (Table 5). It seems that even with large differences between particular years for a given place and between different places for a given year we may assume the country-wide average and the average for a particular place for several years to be $a = N_j : N_A \approx 1$ without the risk of an unduly large error.

The relation between realized increase and the numbers of over-wintereds (grown) also is interesting; this relation is inverse, and very strictly so (Table 6). The realized increase is lowest when numbers of grown are highest ($N' = 42$, and $N_A = 35$), and highest ($N_j = 33.7$) when numbers of grown are lowest ($N' = 18$, and $N_A = 16.7$); and in years

when numbers of grown (overwintered) are about average (23—33), realized increase varies within a fairly narrow range (17.3—19.7), the variations being probably not statistically significant (the material available does not admit of statistical analysis and determination of standard deviation). Five years is indeed too little for inverse correlation to be established as statistically significant, but enough to show the trend. If this trend proved to be a more general rule, the mortality of young ones could be presumed to depend not only on environmental conditions (such as a year's atmospheric conditions, predators, etc.) but also the density of the reproducing population (i.e., the adult part of the population), meaning that when the adult part of the population is at a high level, it is little supplemented by realized increase. And this entails further consequences: the population is capable of being more intensively exploited, because when its adult part is at a low level. The elimination of current year-borns also is low, which helps to bring the population size by the time of the open season (end of the hare years) to the previous year's level. This thesis obviously calls for confirmation in a larger material.

Table 7.

Winter versus summer mortality of adults. Winter: December — March (3 months); summer: March — December (9 months).
Mortality rate per month $m = (N_o — N_T) : N_o \cdot T$; T — in months. Data from Fig. 4 after P i e l o w s k i, 1968).

Period	Winter 1964/5	Summer 1965	Winter 1965/6	Summer 1966	Winter 1966/7	Summer 1967	Winter Summer Average
Mortality	·041	·044	·019	·032	·014	·015	·024 ·033

It derives some support from the fact that on average, for large areas and major periods of time, the index of natural increase $a = N_j : N_A$ is constant and equals unity.

P i e l o w s k i (1968) reports very interesting findings concerning the mortality of the grown part of a population: he found it to be lower in winter than in the vegetative season. P i e l o w s k i (1968) reports the standing crop for spring (end of March) and the open season (assumed as December 15 on average). This, together with A n d r z e j e w s k i & J e z i e r s k i's data (1966), makes it possible to plot for a period of three years the dynamics of the grown part of a population with clear consideration of winter and the vegetative season. The curve reflecting the changes in the numbers of adults is at the same time the survival curve of the adult part of the population, because after the realized increase becomes added to the population, the basic stock only decreases, it is the

year's cohort as it were (see Fig. 4). And these data, in their turn, enable us to calculate the monthly mortality rate for the three winter months (end of December until end of March) and for the nine months of the vegetative season for three consecutive years.

The resulting data (Table 7) show that although in some years mortality may be higher in winter than in the summer of some other year, it is nevertheless: (1) as a three-year average distinctly lower in winter, and (2) in any particular year, whether considered to begin with winter or with summer, lower in the winter months than in the summer. The difference is sometimes very slight, but it is there. This is remarkable also because hunters and biologists of the shooting sport are more or less unanimous in regarding March as the hardest month for hares in our climite (frequent ice-crusts over the snow and the difficulty or even impossibility of reaching food), yet March is among the three winter months in which average mortality is below that of the summer months.

This squares very well with observations concerning the mortality and survivorship of *Clethrionomys glareolus* (S c h r e b e r, 1780) (G l i w i c z *et al.*, 1968), which also show a distinctly higher mortality in summer.

3.2. Natality and Mortality of Current Year-borns

With the fecundity of an average female calculated as above at 7.4 young ones annually (3.7 per average individual at the sex ratio $s = N\female :$ $N\male \approx 1$), we can calculate the numbers born by a population. We have no empirical data and cannot calculate the theoretical numbers of young ones for the different parts (months) of the vegetative season. All we can do is assign the numbers born (ν_r) to the mean date of births (June 15). Consequently, we have in the plot of the dynamics of numbers (Fig. 4) two categories of data: (1) the number of adults at the mean data of yield (December 15), before the yield (N), and after the yield (N'). These are concrete standing crops; and (2) the summed up number of those born, arbitrarily assigned to the mean date of birth (June 15).

The number of born vary within the wide range of 51 to 115 individuals per 100 ha (Table 8, Fig. 4). The mortality of young ones has an even wider range of variations. With the date of birth assumed arbitrarily as June 15 (the number of births being the same before that date and after it — Table 3) and the elimination of young ones assumed as exponential, the mortality of current year-borns until the time of the yield (ca. December 15) may be seen to be very high, viz., $0.002 \leqslant \mu \leqslant 0.011$, the five--year average being $\mu = 0.007$ (Table 8). It is much higher than the comparable indices for adults (Tables 2 and 8). The annual mortality of the stock population averages 29% of the initial level, whereas for the young

ones it averages for one-half year 74%, rising in some years as high as 86%.

This extraordinarily high mortality of young ones underscores the problem of the realized increase. While in the open season it accounts for roughly one-half of shootable animals on average, it amounts in terms of

Table 8.

Number of young produced and their mortality until their first open season. $N_{j\,T}$ — number of juveniles by the end of the year, before the yield (realized increase: $E_j = \nu_r - N_{(T)}$ — natural elimination (see Table 2) during the year; ν_r, $N_{j(T)}$, and E_j — numbers per 100 ha. Juvenile mortality is calculated for half a year (June 15 until December 15). Averages for Poland calculated, with assumption: $a = 1.0$, $m_A = 0.33$ and $y = 0.25$.

Year	ν_r	$N_{j(T)}$	$E_j = \nu_r - N_{j(T)}$	$m_j = E_{j(T)} \cdot \nu_r$	$\mu = \dfrac{ln\nu - lnN_{j(T)}}{183}$	$m'_j = E_{j(T)} \cdot N_j \cdot T = \dfrac{E \cdot 2}{\nu_r + N_{j(T)} \cdot 183}$
1964	114.7	15.2	99.5	0.86	0.011	0.008
1965	54.4	17.3	37.1	0.68	0.006	0.006
1966	50.7	33.7	17.0	0.34	0.002	0.002
1967	105.1	19.7	85.4	0.82	0.009	0.008
1968	82.1	18.7	63.4	0.77	0.008	0.007
Average for Czampiń	81.4	20.3	60.5	0.074	0.007	0.006
Average for Poland (in thousands)	6600	1600	5000	0.76	0.008	0.007

those born to barely some 25%. A higher survivorship of current year-borns would eminently raise the level of the population at the time of the open season and would thus make a higher yield possible. Since $N_j = (1-m_j)$. ν_r, a reduction of the mortality of young ones by „k" would make the realized increase equal to $(1-m_j+k)$, and $\nu_r = N_j + \nu_r \cdot k$; in per cent,

the growth of the basic stock would be $X = \dfrac{k \cdot \nu_r}{N_T} \cdot 100$. Under the conditions in Czempiń, a 1% decline in the mortality of current year-borns would increase the population size by 2% or more.

3.3. Longevity and Age Structure

Given the size of the population for six consecutive years and the ability to discriminate between current year-borns and overwintereds in the autumn, we are in a position to arrive at qualitatively new ecological parameters, because we may introduce the time factor in the analysis. This enables us to determine the mortality and survivorship of individual age groups (cohorts), their longevity (average, maximum, and ecological), and also the population's age structure (cf. 2.2, Fig. 4, and Table 2). On the assumption that mortality is for all overwintereds the same irrespective of the cohort to which they belong and equals the over-all mortality of overwintereds in a particular year, it is possible to calculate how many
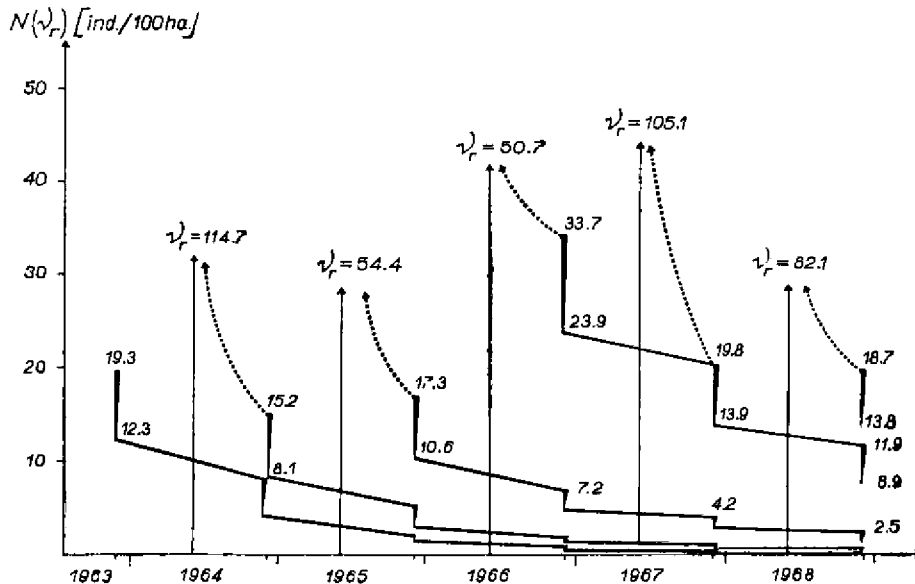

Fig. 5. Survivorship curve for annual cohorts.
v_r: number of current year-borns; first figure: realized increase (natality); second figure of current year-borns after the yield (open season). Vertical wedge: yield.

(or what percentage) of a particular cohort will survive until the second, third, fourth, etc. year. This assumption is a very probable one because there seems to be nothing to suggest that three, four, and five-year old hares differ in mortality, the physiological age of death (about 10—12 years) being still far off, five-year old hares are still in the »prime of life«.

We are in position to follow the fate of the 1963 and 1964 cohorts until their sixth and fifth year of life respectively, and that of the 1965 cohort until its fourth year. The data available (Table 9 and Fig. 5) show that

there are barely 0.4—0.5 hares per 100 ha in their fifth year of life (completing in autumn 4.5 on average), and only juch 0.2 six-year old ones per 100 ha.

The results are similar when we extrapolate the survivorship of the 1965 age group into the fifth and sixth year of life, with mortality and yield assumed at the levels of the six-year averages. Consequently, this may be presumed to be the probable efective ecological longevity of

Table 9.

Survival of annual cohorts in Czempiń.

N — numbers before yield; N' — numbers after yield; $y = \dfrac{N'-N}{N'}$ (proportion in yield); $m_A = \dfrac{N_T - N_A\,(T+1)}{N_T}$ (proportion in natural elimination).

Born in:			Before 1963	1963	1964	1965	1966	1967	1968
Number born			?	?	114.7=755%	54.4=314%	50.7=150%	105.1=533%	82.1=439%
1963	N	y=.37	47.0 100%	19.3 100%					
	N'		29.7 63%	12.3 63%					
		m_A=.34							
1964	N	y=.47	19.5 42%	8.1 42%	15.2 100%				
	N'		10.4 22%	4.3 22%	8.1 53%				
		m_A=.47							
1965	N	y=.39	5.5 12%	2.3 12%	4.2 28%	17.3 100%			
	N'		3.3 7%	1.4 7%	2.7 17%	10.6 61%			
		m_A=.32							
1966	N	y=.29	2.3 5%	0.9 5%	1.9 12%	7.2 41%	33.7 100%		
	N'		1.7 3%	0.6 3%	1.3 9%	5.2 29%	23.9 71%		
		m_A=.17							
1967	N	y=.30	1.4 3%	0.5 3%	1.1 7%	4.2 25%	19.8 62%	19.7 100%	
	N'		0.9 2%	0.4 2%	0.8 5%	2.9 18%	13.9 43%	13.8 70%	
		m_A=.14							
1968	N	y=.26	0.8 2%	0.3 2%	0.6 5%	2.5 14%	11.9 35%	11.9 60%	18.7 100%
	N'		0.6 1%	0.2 1%	0.5 3.0%	1.9 10%	8.9 26%	8.8 45%	13.8 74%

hares. The physiological longevity is believed to be about 10—12 years. According to Dr. P i e l o w s k i (pers. comm.) one individual marked in Czempiń was caught 13 years later in good condition. This would suggest a physiological longevity of more than 13 years, but only occasional individuals are aged upwards of five to six years, and their density is one per 200—400 hectares, which is of no consequence either in practice (shooting) or in ecology (density, reproduction).

Table 10.

Average length of life (in years) of hares born in different years. Counted from birth and, separately, from first autumn (i.e., grown life time).

Born in:		1963	1964	1965	1966	1967	1968	Average
From birth to first yield		?	0.17	0.20	0.23	0.17	0.19	0.19
From first yield	to	1.24	1.07	1 50	1.92	—	—	1.43
From birth	death	?	0.31	0.65	1.18	—	—	0.71

Table 11.

Age structure (in per cents) of Czempiń population in the open season (December 15). Total number before yield in each year treated as 100%.

Year of birth		1963	1964	1965	1966	1967	1968
Total number before yield		66.3	42.8	29.3	46.0	46.7	46.7
Age class (mean age in years)	Current yr-borns (0.5)	29	35	59	73	42	40
	Second yr-old (1.5)		19	14	16	43	25
	Third yr-old (2.5)		?	8	4	9	25
	Fourth yr-old (3.5)		?	?	2	2	5
	Fifths yr-old (4.5)		?	?	?	1	2
	Sixths yr-old (5.5)		?	?	?	?	1
Age unknown, born before 1963		71	46	19	5	3	1
Average age (in years)		?	?	± 1.7	± 1.0	1.4	1.6

The mean ecological longevity of hare is surprisingly low. What may interest us is: (1) the mean longevity of young ones to the time of the first open season; (2) the mean longevity of adults (from their first open season until death); or (3) the full mean longevity (from birth until death). In the present calculations the assumption was that a cohort ceased to exist when its density dropped below 0.3 individual per 100 hectares. The 1965 and 1966 cohorts could be followed only for four or three years respectively. Their survivorship was extended to subsequent years by

assuming the six-year average annual yield ($\bar{y}$ = 0.35) and the five-year average mortality ($\overline{m_A}$ = 0.29), i.e., the averages in Table 9. Longevity was then calculated accordingly.

The results (Table 10) give the full ecological longevity (from birth until the extinction of the entire cohort) as t = 0.71 year (from 0.31 to 1.18 year), the average longevity of adults as 1.43 year, and the average longevity of young ones as barely 0.19 year (0.17 to 0.23 year).

This remarkably low ecological longevity is determined primarily by the extraordinarily high mortality of the young ones. As has already been said, barely 26% on average survive half a year (Table 8), and of these an average of 35% is shot in Czempiń during the first open season (Table 7), so that only 17% really survived beyond the first half a year; for 1964 the figure was even lower, only 8%. The average longevity of a cohort (or age group) also depends on the absolute realized increase the higher it is (the more have survived until the first open season) the greater the likelihood of their longer survivorship.

Table 12.

Age structure at the end of year (± December 15) in per cent of total N.

Year	'65	'66	'67	'68	Average
Less than 1 yr old	59	73	42	40	53
1 and 2 yrs old	73	89	85	65	78
1, 2 and 3 yrs old	81	93	94	90	90
Older than 3 yars	19	7	6	10	10

The data available have made it possible to determine the population age structure in particular years and the average for the period under study (Table 11). What strikes the eye is the remarkably young age of the population. Cohorts of the current and the previous year, i.e., individuals averaging 0.5 year and 1.5 year in autumn make up 78% of the population (Table 12), and all those aged up to three years make up 90% which leaves for all the older ones (aged 4 years and more) only 10%.

3.4. Mortality and Yield

We may be interested to know how many (what percentage) of a particular cohort can be harvested by man in the course of its lifetime and how much is lost to man through natural mortality. In this analysis the

point of departure may be either the number of born or the realized increase.

Of the total number born only an average of 25% is harvested by man (Table 13). This is the consequence of the extraordinarily high natural mortality of the young ones.

The natural mortality of the adult part of the population is different. With the realized increase (N_j) as the starting point, i.e., the number of individuals before the open season, on calculating the total yield and total elimination (until extinction of the cohort), we may note that the yield harvested by man exceeds natural mortality, because it averages 64% (Table 13). Country-wide, mortality has been assumed as an average 33%, which is more than the yield estimated above as 25%, and yet the

Table 13.

Elimination versus yield of different year cohorts, during total life of cohort.

Year		1963	1964	1965	1966	Avg.
Number of born v_r (= 100%)		?	114.7	54.4	50.7	73.3
Yield	in per cent	—	8	21	45	25
Elimination	of v_r	—	92	79	55	75
Realized reproduction N_j (= 100%)		19.3	15.2	17.3	33.7	21.6
Yield	in per cent	63	62	65	67	64
Elimination	of N_j	37	38	35	33	36

sum total of the bag exceeds the number of all naturally eliminated individuals. This is so because in a cohort's first autumn, i.e., at the time when this cohort accounts for the largest number of grown individuals, these individuals become the object of shooting. Hence, even as a lower percentage, but calculated from a higher base figure, the yield obtained from a cohort in the course of its life-time exceeds natural mortality.

We may also be interested to know the whole of a population's losses, i.e., elimination plus yield $(E + Y)$. The grown part of the population considered (Czempiń) sustains an annual loss of about 60% of its level (Table 2). The analysis shows that then the total annual loss is about two--thirds of the size (1964 and 1965, Table 2), the population has a negative balance $(\Delta N = N_T - N_{(T-1)} < 0)$ and diminishes in size.

3.5. Population Numerical Balance

The data available make it possible to draw up a balance for the population in terms of individuals for a five-year period (Table 14, Fig. 4).

The measure of the stability of a population is the difference in size at intervals of exactly one year. If $\Delta N = N_T - N_0 \approx 0$, the population is stable. As was to be expected, ΔN was not infrequently far from zero (Table 14, Fig. 4). The Czempiń population diminished between 1963/64 and 1965/66. In 1964 it was almost halved. This may be attributed to

Table 14.

Yearly income and outcome of individuals (per 100 ha).

Year	'64	'65	'66	.67	'68	Avg.	Poland (thousands)
Basic stock after yield $N'_T = N_{(T\text{-}1)} - Y_{T\text{-}1}$	42.0	22.8	18.0	32.7	32.7	29.6	2400
Natural elimination E_A	14.4	10.8	5.7	5.7	4.7	8.2	800
Adults at end of yr $N_A = N' - E_A$	27.6	12.0	12.3	27.0	28.0	21.4	1600
Born ν_r	114.7	54.4	50.7	105.1	82.1	81.4	6600
Elimination per yr E_j	99.5	37.1	17.0	85.4	63.4	60.5	5000
Realized reproduction $N_j = \nu_c - E_j$	15.2	17.3	33.7	19.7	18.7	20.9	1600
N before yield $N = N_A + N_j$	42.8	29.3	'46.0	46.7	46.7	42.3	3200
Yield Y	20.0	11.3	13.3	14.0	12.0	14.1	800
Basic stock for next yr $N'_{(T\text{-}1)} = N - Y$	22.8	18.0	32.7	32.7	34.7	28.2	2400
$\Delta N = N'_{(T+1)} - N'_T$	−19.2	− 4.2	+14.7	0.0	+ 2.0	− 1.4	0

a coincidence of overexploitation ($y_{64} = 0.47$ — Table 9) with a very high mortality of grown animals in 1964 ($m_A = 0.47$. Between 1964 and 1965 this reduced the population by some 30% (Table 14). In other years the total annual loss (yield + mortality of overwintereds) amounted to 38— 58% (average 53%). A high realized increase in a single years (1966) was enough to offset the 1963—1965 reduction in size.

But even for as little as five years, the average change in size approaches zero, being $\Delta N = - 1.4/100$ ha, which means that the population was stable at the level of 30 individuals per hectare after the shoot-

ing, or 42 individuals per 100 hectares before the open season, i.e., at the end of a hare years (Table 14).

The average six-year annual balance for the Czempiń population may be written as follows:

$$\begin{array}{ccc}
\text{gain} & \text{loss} & \text{balance} \\
v_r - & (E_j + E_0 + Y) & = \varDelta B \\
81.5 - & (60.5 + 8.2 + 14.1) & = -1.4
\end{array}$$

4. HARE NUMBERS IN POLAND

Hunters are generally agreed on putting the mortality of the adult hare population at between 25 and 40% of the initial population. For the Czempiń population the five-year average was $m_A = 0.29$ (Table 2). In Poznań province, game management standards are rather high, and especially Czempiń, as a research centre, may be presumed to save an average mortality somewhat below the national average. It therefore seems that mortality of one-third of the basic population as a country-wide average will be close to reality, and any rate safe, because it may be expected to be in fact a little lower.

All we know about the numbers of hares is only the annual yield, namely:

(1) the average annual yield for the past six years, which was about 800,000 (A n d r z e j e w s k i, N o w a k & P i l i p i u k, 1969; Statistical Yearbook, 1969), and

(2) data indicating that the annual yield varies within a rather narrow range and shows no definite trend in the course of the past fifteen years or so (which means that it is roughly constant).

When (1) the constancy of the absolute country-wide yield ($y \approx 800,000$) is assumed to be the result of the constancy of the over-all annual percentage of hares shot, and (2) the adult mortality is taken to be $m_A = 0.33$ in agreement with the previous reasoning, then, with (3) the national average $a = N_j$ ($N_A \approx 1.0$) obtained from the large empirical material, we find from A n d r z e j e w s k i and J e z i e r s k i's (1966) equation:

$$y = \frac{(1 + a)(1 - m_A) - 1}{(1 + a)(1 - m_A)} \approx 0.25$$

With $Y = 800,000$, the equation $Y = N \dfrac{(1+a)(1 - m_A) - 1}{(1+a)(1 - m_A)} = N \cdot 0.25$

gives us as the average for Poland:

$N = 800,000 : 0.25 = 3,200,000$ hares at the time of the open season (roughly December).

The balance in terms of individuals is reproduced in Table 14. It needs to be stressed that all the figures represent only rough estimates.

5. BIOMASS BALANCE AND PRODUCTION

5.1. Biomass Dynamics

Under the conditions existing in Poland, the hare grows about 270 days (see 2.5, Fig. 2). The open season falls on the interval of 160—210 days of current year-borns, which therefore keep growing during the open season (C a b o ń - R a c z y ń s k a, 1964; P i e l o w s k i, 1968; Fig. 2). Their weight, therefore, averages at the beginning of the open season (November 1) some 3.2 kg, and by the end of it (December 10) some 3.8 about 3.7 kg.

Table 15.

Balance of biomass.

B'_T — biomass after yield (beginning of hare year); P — production; E — elimination; B_T — standing crop before yield; Y — yield in the year considered; B'_T — stock population (basic stock) for next year.

Data for Czempiń population expressed in kg/100 ha.

Year	B_T	$+$ P	$-$ E	$=$ B_T	B_T $-$ Y	$=$ B'_{T+1}	$B'_{T+1}-B_T=\Delta B$
1964	170	206	200	176	18	92	—78
1965	92	132	110	114	44	70	—22
1966	70	164	58	176	51	125	+55
1967	125	217	156	186	56	130	+ 5
1968	130	177	120	187	48	139	+ 8
Average	117	179	129	167	56	111	— 6
Poland thousand tons	9.5	14.8	11.6	12.7	3.2	9.5	0

The population biomass is the result of the simultaneous processes of reproduction, growth, and elimination of individuals. Hares born the previous year go on growing until about March; their weight gain obeys the equation $W_{t\,(g)} = -6753 + 2006 + \ln t$ (see 2.5.), and they are eliminated at the rate m_A (Table 2). Individuals aged two or more years do not grow but only drop out. The result is that from December to March the biomass of a population declines. From March onwards until the open season all overwintereds have a constant weight, which averages 4,200 g. Their numbers decline, and so does, therefore, the biomass of this part of the population. The five-year average of this decline is 35 kg/100 ha/yr.

Current year-borns grow over the first 100 days of life (until the end of September on average) at the rate $W_{t\,(g)} = 0.45\,t^2 - 25.3\,t + 121$ (cf. 2.5.) and disappear at a rate which is exponential (assumption) and varies between different years (Table 8).

When past the age of 100 days (from the beginning of October), the young ones grow much more slowly ($W_{t\,(g)} = -6753 + 2006\,\ln t$). Con-

sequently, the biomass of current year-borns can be described by the equation: $B_t = N_0 \cdot e^{-\mu t}(-6753 + 2006 \ln t)$. Hence, in four out of the five years the population's weight gain from October onwards does not offset the loss of biomass due to mortality. As the result, the biomass attains maximum at the beginning of October or there abouts and then declines (Fig. 6). Only in 1966, with its exceptionally low mortality of young ones, did the population biomass grow until December to peak out in the open season (Fig. 6).
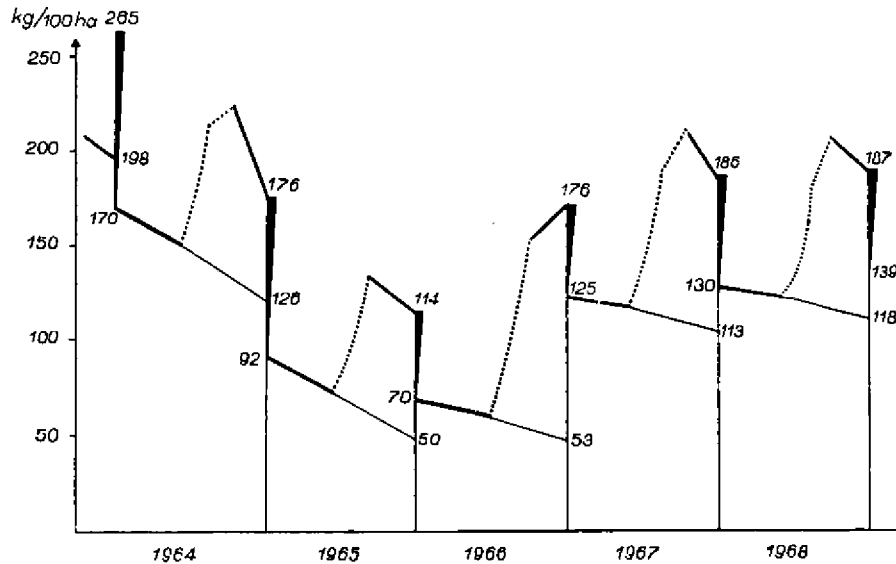

Fig. 6. Dynamics of biomass of the population in Czempiń.

Vertical wedge: yield; figures at the top: biomass of the population before the yield (open season); figures left of the vertical age limit line: biomass of the population after the yield (open season); figures right of the vertical age limit (year) line: biomass of overwintereds before the yield (open season). All figures in kg/100 ha.

These results appear to indicate that, being unable to reduce the mortality of young ones by some special measures, we would have a larger yield in terms of biomass if the open season started earlier. The size of individuals would be indeed smaller, but so many more could be shot without detriment to the population that in terms of weight the yield would be larger. This again raises the problem of the mortality of young ones in all its acuteness.

Before the date of the yield (about December 15), the population biomass averaged in the five years 167 kg/100 ha (from 114 kg to 186 kg per 100 hectares — Table 15, Fig. 6). The average annual yield was 56 kg/

/100 ha, and the biomass of the basic population at the hare year beginning therefore averaged in the five years 117 kg/100 ha (from 70 kg to 170 kg per 100 ha; Table 15).

5.2. Production and Elimination

Production was calculated from the growth-survivorship curve (Ness and Dougal's method, see: Petrusewicz & Macfadyen, 1970).

Current year-borns are responsible for far the largest part of production. Previous year-borns gain each an average 0.5 kg in weight and add barely 6.8 kg per 100 ha, which is 4% of the annual production total (Table 16). The five-year production average was 179 kg/100 ha (from 132 kg to 217 kg per 100 ha).

Much the bigger part of production is eliminated, an average of 129 kg/100 ha (Table 15), which amounts to 70% of the total (Table 15 and 16). An average 56 kg/100 ha is left for the yield, which is 30% of the

Table 16.

Biomass inflow and outflow in per cent of production.
Values of P expressed in kg/100 ha and treated as 100%.

		1964	1965	1966	1967	1968	Avg.	Poland (tons)
	P	206.0	131.8	163.9	217.0	176.7	179.1	14 800
$P=P_A+P_j$	P_A	3	3	3	5	4	4	5
	P_j	97	97	97	95	96	96	95
$P=$ $(E+Y)+\Delta B$	E	99	83	35	72	68	71	78
	Y	39	33	31	26	27	31	22
	ΔB	—38	—16	34	2	5	—2	0

total production. In particular years the total of the loss in biomass (elimination + yield) is not always balanced by production; we have both positive and negative ΔB (Table 15), but even over as little as five years theses changes in biomass (ΔB) approach zero, amounting to 6 kg/100 ha.

Hare production in Poland is estimated at 14,800 matric tons, of which 3,200 tons is accounted for by the yield (Table 15).

It is interesting to compare it with the production of other animal species. We have in this country data on the production of Clethrionomys glareolus (Petrusewicz et al., 1968) which, in terms of live weight, amounts to $P = 0.286$ g/m²/yr. This comparison shows the production of hare to be very clearly less at $P = 0.189$ g/m²/yr (from 0.132 g to 0.206 g/m²/yr).

The caloric value of the biomass of hare is known only for December (M y r c h a, 1968). It is 1.874 kcal/g. With this as the basis, the five-year average of the production of the Czempiń population would be $P = 0.354$ kcal/m²/yr (0.332 kcal to 0.206 kcal/m²/yr).

There are still no data on the daily consumption or respiration of hare. Calculations have been made only of the ecological parameter of individual-days or biomass-days of a hare population per 100 hectares (Table 17), which tells us how many individuals (or grams) and of what size group (or age group) were present in the population per unit area, *i.e.*, the number of individuals or the quantity in terms of biomass which consumed, assimilated, etc. on the area of 100 ha in a year.

Table 17.

Biomass-days and individual-days per year for different age (weight) classes.

Weight (kg), Age (days)		.1—1.1 0—50	1.1—2.4 50—100	2.4—3.7 100—183	3.7—4.2 183	Total per yr
Biomass-days 100 kg · days/100 ha	1964	19.1	41.4	61.3	531.7	654
	1965	11.2	29.2	56.3	265.5	362
	1966	12 3	37.8	93.2	230.2	373
	1967	19.0	44.4	72.8	452.3	588
	1968	15.4	37.3	65.2	462.1	580
	Mean	15.4	38.0	69.8	388.3	511
Individual-days per 100 ha	1964	4 530	2 608	2 150	12 702	21 990
	1965	2 368	1 755	1 990	6 370	12 483
	1966	2 415	2 188	3 228	5 330	13 361
	1967	4 303	2 743	2 568	10 895	20 509
	1968	3 423	2 285	2 279	11 078	19 065
	Mean	3 407 8	2 315.8	2 443.0	9 315.0	17 482

Production due to reproduction (P_r) is hard to determine for the hare, because it is not well known how long a young one lives at the expense of the mother. At any rate it does briefly, because it is precocial. Biomass of new born (P_b) is not very large and averages over the five-year period some 10 kg/100 ha/yr, which is not quite 6% of production. With *Clethrionomys* and laboratory mice it was about 15%.

6. TURNOVER

The data available make it possible to determine the turnover of numbers and of biomass for the Czempiń population. The former is defined as the ratio of the number of discrete individuals that were present in the population during the year under study, *i.e.*, $\nu = N_0 + \nu_r$ (with immigration assumed as equal to emigration) to average numbers in that

year $\Theta_N = \nu : N$ (P e t r u s e w i c z, 1966). For the five-year period it averaged 2.3, and varied as little as form 1.9 to 2.6 (see Table 18).

The turnover of biomass, $\Theta = P : B$ averaged over the five years 1.3,

Table 18.

Turnover of numbers and biomass.

($\overline{N}$, ν, P, and $\overline{B}$ per 100 ha per yr), N was calculated by relating the number of young ones to the entire year ($N = \overline{N} \cdot T/363$).

	1964	1965	1966	1967	1968	Mean
$\overline{N}$	34.8	17.5	15.2	30.4	30.4	25.5
$\nu = N_o + \nu_r$	157.0	77.3	68.7	137.8	114.8	111.1
$\Theta_N = \nu : N$	2.6	2.3	1.9	2.5	2.2	2.3
$\overline{B}$	179.1	99.2	103.3	161.2	158.9	140.3
P	206.0	131.8	163.9	217.0	176.7	179.1
$\Theta = P : B$	1.2	1.3	1.6	1.3	1.7	1.3

which means that a little more than the entire average biomass existing in the area is exchanged annually. The variations in biomass turnover are very slight and within the range of 1.1—1.6.

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DYNAMIKA I PRODUKCJA POPULACJI ZAJĄCA W POLSCE

Streszczenie

Dane empiryczne (Tabela 1) wraz z procentem samic ciężarnych (Fig. 1) pozwalły wyliczyć, że populacja zająca szaraka w Czempiniu rodzi rocznie średnio 81 osobrików per 100 ha (Tabela 3). Śmiertelność wszystkich przezimków populacji w Czenpiniu wynosiła 29% (Tabela 2). Stwierdzono, że stosunek tegorocznych do przezimków silnie się waha, ale już średnia z lat 5-ciu dla tej samej miejscowości oraz średnia z różnych miejscowości dla danego roku zbliża się do 1.0 (Tabele 4, 5).

Stwierdzono, że zrealizowany przyrost (liczebność tegorocznych w okresie polowania) jest odwrotnie proporcjonalny do stanu przezimków (Tabela 6).

Śmiertelność tegorocznych jest wyraźnie większa niż przezimków (Tabele 2 i 8). Śmiertelność przezimków jest niższa zimą niż latem (Tabela 7). Wyliczono, że osobników starszych niż 5 lat, jest mniej niż 1/200 ha, czyli że praktycznie nie mają znaczenia ani w rozrodzie ani jako obiekt łowny (Tabele 9, 11, 12). Znaleziono osobnika znakowanego 13 letniego, lecz średnia długość życia zająca wynosi 0,7 roku (Tabela 10).

Średnio za 5 lat pozyskanie wynosi zaledwie 25% urodzonych, eliminacja naturalna zaś 75% (Tabela 13).

Posiadając krzywą wzrostu osobniczego (Fig. 2), dynamikę liczebności (Fig. 4) i przeżywalność (Fig. 5), obliczono bilans populacji w osobnikach (Tabela 14) i w biomasie (Tabele 15, 16 i 17) oraz wykreślono dynamikę biomasy (Fig. 6). Stwierdzono, że ok. 95% produkcji przypada na tegoroczne, oraz że już w ciągu 5 lat, mimo wahań w poszczególnych latach, średnio produkcja równała się eliminacji.

Oszacowano pogłowie zająca w Polsce w okresie polowań na ok. 3200 tys. sztuk, pozyskanie 800 tys., stado podstawowe (stan po polowaniu) na ok. 2400 tys. sztuk (Tabela 14).

Turnower osobniczy wynosi ok. 2.3 a biomasy ok. 1.9 rocznie (Tabela 15).