

Population dynamics of the European hare *Lepus europaeus* Pallas, 1778 in Central Poland

Michał WASILEWSKI

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Density, sex and age distribution, recruitment rate and mortality in hares within the hunting grounds of Central Poland were analyzed. Density estimates were made in spring and autumn by a transect census method. Age was determined by a method using lens dry mass. Hares were shot during five hunting seasons ($n = 754$). Sex was determined on the spot. In autumn, the population ranged from 25 to 30 hares per 100 hectares. The recruitment rate was very low, 0.5 to 1.0 juvenile per female and this greatly affected the autumn population density ($r = 0.65$). The mortality of the adults between spring and autumn ranged between 36 and 15 per cent greatly affecting the density of this age group ($r = 0.75$) prior to the hunting season. A slight surplus of females was observed in adults. The proportion between sexes did not change significantly during the study. Adult hares from two types of habitat showed various patterns of reproduction and mortality.

Warsaw Agricultural University, Department of Wildlife Management, Rakowiecka 26/30, 02-528 Warsaw, Poland

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Introduction

In the late 1970s a decline in hare numbers occurred, reaching the lowest level ever recorded in Poland (Pielowski 1984). To counteract this adverse trend a series of administrative decisions were taken. The size of the hunting ground areas during the hunting season was reduced and some ways of hunting hares were abolished. These remedies only cured the symptoms, without understanding the causes of the decline. It is surprising that this happened to a game species whose biology, ecology and game management were thought to be known (Pielowski and Raczyński 1976).

The aim of this study was to estimate the population status of hares in Central Poland and to analyze some parameters of the population dynamics which might exert a major influence upon changes in abundance.

Study area

The study was carried out in 1985–89 in the location situated near Rogów (51°48' N, 10°53' E) and covered an area of about 75 square kilometers. The study area is a mosaic of fields and forested areas (80 and

Table 1. Characteristics of analyzed habitats.

Type of habitat	Area, km ²	Fraction of area forested	Predator density*
Field (2)	28.5	3.0	+
Field-forest (3)	46.7	20.0	+++

* Acc. to Goszczyński (1985).

(2), (3) – the number of study plots in the selected habitats.

20 per cent respectively). The habitats (similar to hunting grounds) under study differed in the percentage of forested areas, the density of predators, and the proportion of the two principal types of habitats: field and field-forest (Table 1). The agricultural sector there is dominated by small farms supplying variable production to local markets. The fields are usually small, about one hectare on average. The following bird game species occur in the study area: the pheasant *Phasianus colchicus* (Linnaeus, 1758) (Wasilewski 1986a) and the partridge *Perdix perdix* (Linnaeus, 1758) (Dudziński 1988). The carnivores are mostly represented by the fox *Vulpes vulpes* (Linnaeus, 1758) and two species of martens: *Martes martes* (Linnaeus, 1758) and *Martes foina* (Erxleben, 1777) (Goszczyński 1985). The main species of birds of prey are the buzzard *Buteo buteo* (Linnaeus, 1758) and the goshawks *Accipiter gentilis* (Linnaeus, 1758) (Goszczyński and Piłatowski 1986).

Methods

Density estimates

Density estimates of hares in the open field were made twice a year, during spring (March) and in autumn (November) by a transect census method (Pielowski 1969). The total transect length was 56 kilometers, and covered 10 per cent of the study area, excluding woodlands.

Hare population density in the open areas was assumed to be identical with the density in the forested areas. Density was calculated according to the formula:

$$\text{Density (N per 100 ha)} = \text{Nh/Nkm} \times 10$$

where: Nh – the number of hares in transects, Nkm – length of transects in kilometers.

Sex and age distribution

Age was determined from the lens dry mass. The lenses were collected from hares obtained in the study area in December. The excised eye-balls were preserved in 10% solution of formaldehyde. Later the lenses were rinsed in distilled water and dried at 80°C to a constant weight. Lenses weighing up to 275 mg were assumed to be from animals in their first year as distinct from older animals (Bujalska *et al.* 1965). In total, 754 individuals were aged. Sex was determined by examining the genitalia. The sex ratio in the class of animals older than one year enabled the estimation of the number of potentially reproductive females.

Birth rate and mortality estimates

Natality and mortality were estimated on the basis of the annual balance of numbers. The annual balance was obtained from: (1) the number of individuals in the breeding stock (*Dsp*), (2) the number of females at reproductive age (*Df*), (3) the number of newborn (*Ny*), (4) the rate of recruitment of juveniles per female (*Rr*), (5) the mortality of young during the reproductive period (*My*), (6) the mortality of adults during the reproductive period (*Ma*), (7) the population age distribution in autumn (*Fa*), (8) the autumn density (*Da*), and (9) winter losses (*Wl*). These parameters were obtained in the following way:

D_{sp} and D_a were determined on the basis of the transect census results.

Ma was calculated by subtracting autumn (D_a) and spring (D_{sp}) densities.

The number of adults surviving till the beginning of the hunting season was estimated on the basis of the size of this age group in the autumn population.

D_f was calculated by taking into account the mortality level among adults and the fraction of this age group in the autumn population. The female/male ratio was assumed to be constant between spring and autumn.

N_y was determined by assuming after Raczyński (1964) and Pielowski (1976), a constant litter size for condition prevailing in Poland, i.e. 7.4 young born to one female during one breeding season.

R_r defined as birth rate per female minus juvenile mortality till autumn was calculated as an autumn ratio of the number of the young, born this particular year to the number of potentially reproductive females.

My was calculated by subtracting the number of young surviving till autumn from the number of hares born.

Wl , i.e. the number of individuals shot and natural reduction combined was calculated by subtracting the numbers in the autumn season, and the numbers of breeding stock in the next spring.

The parameters of the annual balance of numbers were estimated in the whole study area and in the each of the five habitats (similar to hunting grounds) it comprised.

Table 2. Hare population density changes (individ./100 hectares).

Year	Season*	Density	SD
1985	Sp	—	
	A	31.4	5.4
1986	Sp	27.2	4.9
	A	29.3	5.1
1987	Sp	24.8	4.0
	A	24.6	5.0
1988	Sp	20.8	4.8
	A	29.1	4.7
1989	Sp	25.3	5.6
	A	30.8	4.6

* Sp – spring, A – autumn, — not estimated.

Table 3. Hare age distribution (%). Age class fraction showed significant differences in subsequent years ($\chi^2 = 12.31$, $0.025 > p > 0.01$).

Year	N	Juv.	Ad.
1985	224	32.1	67.9
1986	200	34.5	65.5
1987	155	21.3	78.7
1988	175	39.4	60.6
1989	158	34.2	65.8

Table 4. Sex distribution of adults.

Year	N	Females : Males
1985	147	1.01
1986	135	1.33
1987	147	1.13
1988	133	1.29
1989	140	1.09

Results

Density changes

The data on hare density during the study showed insignificant fluctuations which ranged from 25 to 30 individuals. In 1987 autumn numbers were the same as in the preceding spring. In 1986, 1988 and 1989 autumn numbers were slightly higher than preceding spring numbers (Table 2). The differences were statistically insignificant.

Age and sex distribution

The proportion of hares less than one year old, in the autumn population varied between years, ranging from 20 – 40% per cent (Table 3). These differences were statistically significant ($\chi^2 = 12.31$; $0.025 > p > 0.01$). This indicates variable survival of the young before autumn.

Within young animals (lens mass below 275 mg) it was found, that the individuals with lens mass of 180 – 260 mg dominated. On average their share in this class was 80 per cent (Fig. 1). Among individuals older than one year, hares with lens mass 300 – 380 mg dominated, making up 70 – 80% (Fig. 1). The fraction of hares with lens mass above 400 mg was very small and made up only several per cent (Fig. 1).

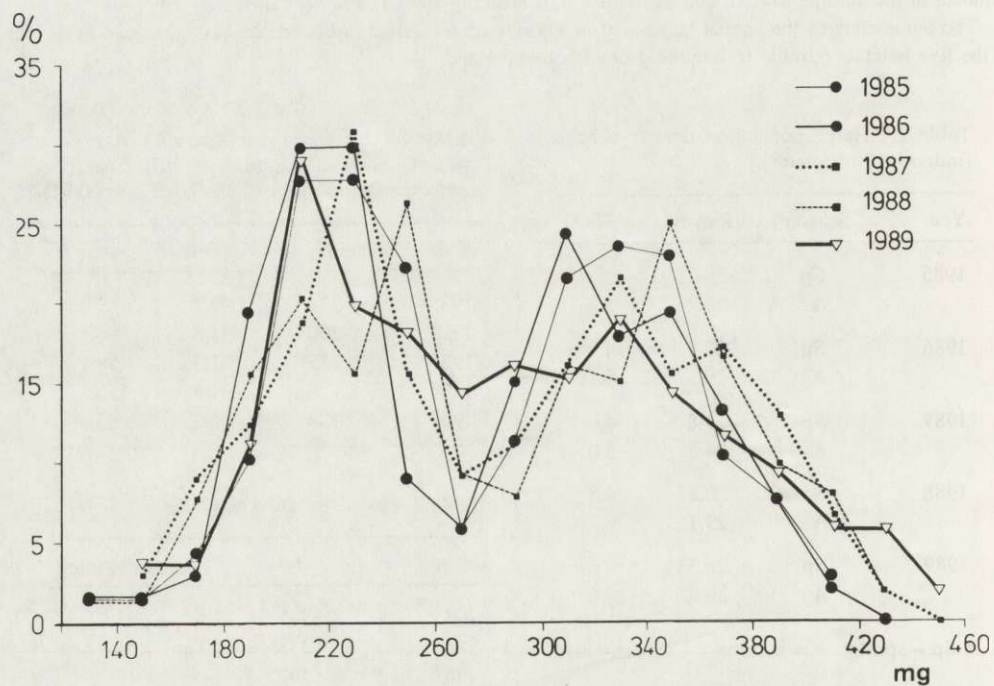


Fig. 1. The proportions of hares of different lens mass in the autumn population.

While comparing lens weight from hares bagged in the experimental area with those obtained by Broekhuizen (1971) we found that 4 to *ca* 8 months old as well as those younger than 3 years predominated among one year old and older individuals. The results showed that the mean length of life in the population under study is very short as compared to e.g. physiological longevity of hares (Pielowski 1971). No differences in lens weight distribution pattern was observed between years (Fig. 1).

During the study a total of 702 adults (about 140 each year) were sexed. The sex ratios each year ranged between 1.01 and 1.33 in favor of females (Table 4). The proportion between sexes did not change significantly during the study.

Annual number balance

When analyzing the parameters used to calculate the annual balance of numbers in the population, it was observed that during the study, 60 to 85 per cent of adult hares survived from spring until the hunting season (Table 5). This mortality significantly affected the autumn abundance of this age group ($r = -0.75$, $0.05 > p > 0.01$) (Fig. 2).

In the four years of the study recruitment was only 0.94, 0.46, 1.06 and 0.87 young per female (Table 5). This was very low when compared to recruitment recorded in Poland in earlier studies (Jeziarski 1965). The level of recruitment was different under study, and it was found that it affected significantly the autumn density ($r = 0.65$, $0.05 > p > 0.01$) (Fig. 3).

Table 5. Annual number balance (1 – density individ./100 ha; 2 – specific indices, in %; × – not estimated).

Characteristics of the population	1986		1987		1988		1989	
	1	2	1	2	1	2	1	2
Breeding stock (<i>Dsp</i>)	27.2	–	24.8	–	20.8	–	25.3	–
Mortality of adults during reproductions (<i>Ma</i>)	9.8	36.0	5.6	22.6	3.2	15.4	4.8	19.0
Females entering reproduction (<i>Df</i>)	12.7	57.0	11.7	53.1	10.8	56.4	11.9	51.8
Number of the newborn (<i>Ny</i>)	94.0	7.4/♀	86.6	7.4/♀	79.9	7.4/♀	88.1	7.4/♀
Recruitment rate (<i>Rr</i>)	11.9	0.94/♀	5.4	0.46/♀	11.5	1.06/♀	10.3	0.87/♀
Mortality of the young (<i>My</i>)	82.1	87.3	81.2	93.8	68.4	85.6	77.8	88.3
Population in autumn: (<i>Da</i>)	29.3	–	24.6	–	29.1	–	30.8	–
– young	11.9	40.6	5.4	21.8	11.5	39.4	10.3	33.5
– adults	17.4	59.4	19.2	78.2	17.6	60.6	20.5	66.5
Winter losses (<i>Wl</i>)	4.5	15.4	3.8	15.4	3.8	13.1	×	×

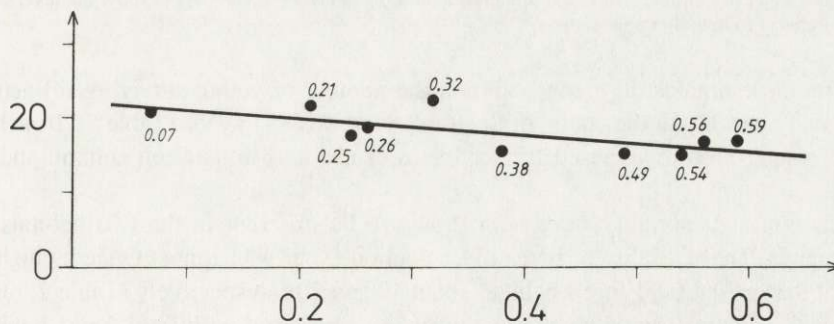


Fig. 2. Relationship between mortality of adults (x) and their autumn density (y). ● – spots show mortality within five hunting grounds during the study.

Table 6. Annual number balance in analyzed hunting grounds (mean values for 1986 – 1989), (1 – density individ./100 hectares; 2 – specific indices, in %).

Characteristics of the population	Field		Field-forest	
	1	2	1	2
Breeding stock (<i>Dsp</i>)	27.5	–	26.1	–
Mortality of adults during reproduction (<i>Ma</i>)	11.2	40.9	5.9	22.6
Females entering reproduction (<i>Df</i>)	11.8	53.1	12.4	52.8
Number of the newborn (<i>Ny</i>)	87.3	7.4/♀	91.8	7.4/♀
Recruitment rate (<i>Rr</i>)	11.7	0.99/♀	8.6	0.69/♀
Mortality of the young (<i>My</i>)	75.6	86.6	83.2	90.6
Population in autumn: (<i>Da</i>)	28.0	–	28.8	–
– young	11.7	41.8	8.6	29.9
– adults	16.3	58.2	20.2	70.1

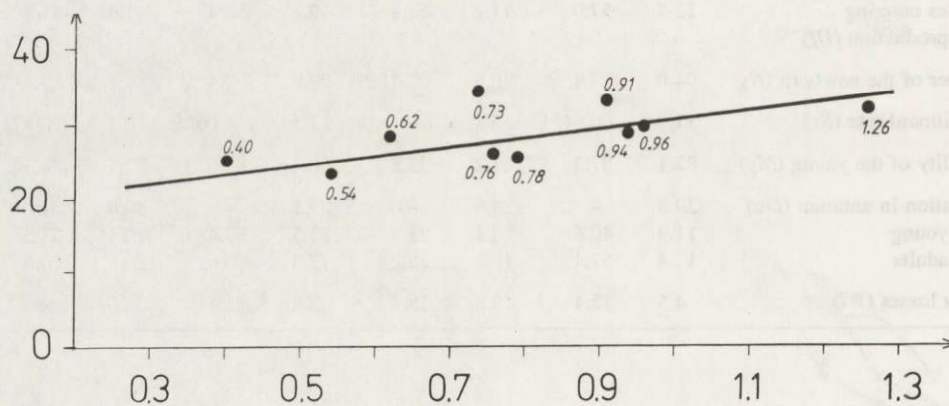


Fig. 3. Relationship between the recruitment rate (x) and autumn density (y). ● – spots show the level of natality within five hunting grounds during the study.

Based on the estimates of young born and the number of young surviving till autumn, it was found that mortality of the young in Central Poland was 85 to 95% (Table 5). Both hunting and natural winter mortality caused further losses of about 15% between autumn and spring (Table 5).

Reproduction and mortality were both shown to be different in the two habitats of the hunting grounds. The mortality of hares older than one year was almost twice as high in the field habitat than in the field-forest habitat, about 40 and 20% respectively (Table 2, 6). In the field habitat the level of recruitment was higher in comparison with field-forest habitat, i.e. 1.0 and 0.7 juvenile per female, respectively (Table 2, 6). Consequently, the spring and autumn numbers are similar in both habitats (Table 6).

Discussion

As shown by Wasilewski (1986b, and unpubl.) long term fluctuations of hare numbers during the last 25 years in other areas in Poland were similar to changes in numbers recorded in our study area. It seems, therefore, that the results presented here reflect the situation of hare population in the whole country.

The parameters which limit the growth in abundance of hares in Central Poland, were the high mortality of breeding stock between spring and autumn and the very low recruitment rate of young. The mortality of adult hares during their breeding in the study area was twice as high in field habitat when compared to field-forest habitat. It can be assumed (Bresiński and Chlewski 1976, Bresiński 1983) that seasonal migration of hares from fields to forest are possible in annual cycle. Such migrations of hares inhabiting the field-forest habitat reduce the mortality of adult individuals caused by such negative factors as agricultural practices (Kałuziński and Pielowski 1976, Durdik 1981), use of chemicals (Pav and Zahradnikova 1987, Paukert 1988), weather conditions (Eiberle 1983). On the other hand in the field-forest mosaic higher predator pressure was observed (Goszczyński 1985). It seems that the population using the two components of their habitat (field and forest), have a typically lower mortality of adults and lower recruitment rate, which finally causes the population levels in the two kinds of habitats to be fairly similar.

Age structure of the population, estimated as a proportion of individuals with different lens masses was similar in subsequent years. However, different mortality of adult hares and similar fraction of hares with certain lenses mass during the study support indirectly hypothesis that survivorship is independent of age. This fact is supported by results of previous investigation (Frylestam 1979, Kovacs 1983).

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