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Population Dynamics of the Red Fox in Central Poland [1]

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The analysis of changes in the density of the red fox population over a period of several years showed a considerable stability of this population. The average density in winter was about 0.43 animal/km². A high reduction of foxes in winter (52%) seems to be mainly a result of hunting. In the population of adult foxes females prevailed. Litter size and the survival of cubs till the hunting season depended on the availability of small mammals (mainly rodents). The expected mean life span at birth (E_0) was low (0.84—0.91 year) as compared to populations subjected to lower hunting pressure. Only one fourth of foxes born survived to the age of 12 months.

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1. INTRODUCTION

The populations of red foxes *Vulpes vulpes* (Linnaeus, 1758) show a great variability of average litter size, proportion of reproductive females, mortality of young and adult foxes. In Poland the data on the variability of these parameters affecting the population size and its fluctuations are only fragmentary (Ryszkowski, Goszczyński & Truszkowski, 1973; Pielowski, 1976; Goszczyński, 1977). Such studies should be continued and extended for both better management of fox populations and a better undestanding of fox biology.

The present work was aimed at studying changes in the density of foxes over many years and at determining the basic demographic parameters of fox population.

2. STUDY AREA

Research was carried out near Rogów (51°48'N, 10°53'E) in central Poland in an area of 89.2 km². In this whole area the number of dens with young animals, the size of litters and the number of foxes killed were determined. The number of foxes living in one part of this area (about 21 km²) was estimated every winter, and in other parts the numbers were checked sporadically.

[1] Praca wykonana w ramach problemu RR.II.17. „Zasady gospodarowania populacjami ważnych gospodarczo gatunków zwierzyny"

The studied area was a mosaic of fields and forests. The latter formed isolated tracts and covered about 17% of the whole area. The forests were used by the foxes primarily as shelter and raising young animals, and less frequently as hunting territories (Goszczyński, 1985, 1989). Small fields, averaging 1 hectar in area, covered 72.3% of the territory, and buildings, roads and waste land, 5.7%. Small game was moderately numerous (Wasilewski, 1986a, b; Dudziński, 1988) and the density of rodents fluctuated only slightly (from several to several tens of animals/ha, (Goszczyński, 1985).

3. METHODS

3.1. Estimation of the Intensity of Area Searching by Foxes and Population Density in Winter

Changes in the intensity of penetration by foxes were recorded from the winter of 1979/1980 till the winter of 1987/1988 (except for one year) over an area of 21 km². The number of fox trails was counted on assessment lines, divided into 200 to 500 m long sectors. Due to varying lengths of the assessment lines an uniform index was introduced characterizing the intensity of area searching (A=number of trails intersected by 1000 m of the assessment line in 24 hours). If tracking was done 2-3 days after the last snowfall, the number of trails was divided by 2 or 3, respectively. The lines were evenly distributed over the whole area. In the calculation of the index of the seasonal intensity of area searching by foxes (mean value per each season of the year) the proportions of fields and forests in the area were considered. For the calculation of the density of foxes the formula by Priklonski (1965) was used:

$$\text{Density } (N/km^2) = \frac{A \times 1.57}{DMD}$$

where: DMD — daily movement distance (km).

On the basis of direct snow-tracking of foxes in this area it was found that DMD changed from one season to another only slightly, with a mean of 13.8 km (Goszczyński, 1989). This value was accepted for the calculation of population density. A total of about 140 daily assessment lines were analysed, with a total length of about 980 km.

Occasionally the intensity of area searching was checked in the remaining area for comparison with the results obtained in the smaller area under continuous observation.

3.2. Hunting Results. The Age and Sex of Killed Foxes

In Poland the fox hunting season lasts from September 1 to March 31, but in the studied area practically all hunting had been done between November and mid-March.

Information on the date of fox killing, sex and circumstances of shooting the animals was obtained from hunters and foresters. The skulls of foxes obtained from hunters were boiled, and teeth (upper and lower canines) were removed for age determination.

The age of the foxes was determined by two methods. Young animals differed from the old ones in the width of tooth canal. For this purpose, the width of the upper or lower canine tooth, and the width of dental canal were measured at the widest part of the dental root. The canal-width measurement was taken after cutting-off half of the tooth in the sagittal plane with a carborundum saw-blade disc (Fig. 1). The measurements were taken with sliding calipers with accuracy to 0.1 mm. The ratio of the canal width to tooth width changes with age (in young foxes at the beginning of the hunting season it was about 60% and at the end of the season about 40%) and in old animals the canal may be completely absent. In the case of tooth fracture the process of canal obliteration is inhibited (this was observed earlier by Grue & Jensen, 1976) and in such cases measurements were carried out on another (healthy) tooth. No significant differences were found between the measurements of the upper and lower canine teeth but upper canines, being less curved than the lower ones, are easier for cutting. The method described here was nearly identical to that used by Yves *et al.* (1986) for determination of the age of coyotes, and very similar to the method described by Jensen who used X-ray films instead of cutting of teeth (Grue & Jensen, 1976).

In some doubtful cases (*e.g.* in young foxes killed at the end of the hunting season when the dental canal is fairly narrow) and also for estimation of the age of the animals older than 1 year the method of grinding was used. This method is less labourious than the histological method and gives the same results (Yves *et al.*, 1986). The teeth ground in the sagittal plane were placed under stereoscopic microscope (magnification from 24 to 100 times) and the lines of annual increments in the cement were counted near the root papilla. Age was determined for 113 killed foxes (61 males and 52 females).

3.3. Assessment of the Number of Litters and the Number of Cubs in a Litter

In the observed area cubs were usually born at the end of March and the beginning of April, but sometimes they occurred also late in April. At the beginning of spring fox dens occupied by foxes were found over the whole area (89.2 km^2), and the numbers of cubs leaving the dens were counted. While counting, an attempt was made to observe the den sufficiently long to count all cubs. If there was any doubt, counting was repeated. Data were available on 34 litters but in only 27 cases it was accepted that the observation gave the actual number of cubs.

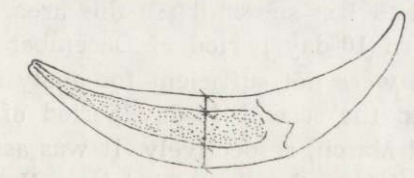

Fig 1. Measurements taken on width of a canine tooth root and width of a dental canal.

4. RESULTS

4.1. Reduction of the Number of Foxes in Winter

On the basis of the data from the whole observation period the indices of area searching intensity by the foxes were calculated per 10-day periods. The distance of the 24-hour wandering of foxes did not vary significantly during the winter, and its average value (13.8 km) was accepted for calculation of the density of the population of foxes in various 10-day periods. The winter data from tracking on the assessment lines was collected from November 20 to March 20 which corresponded

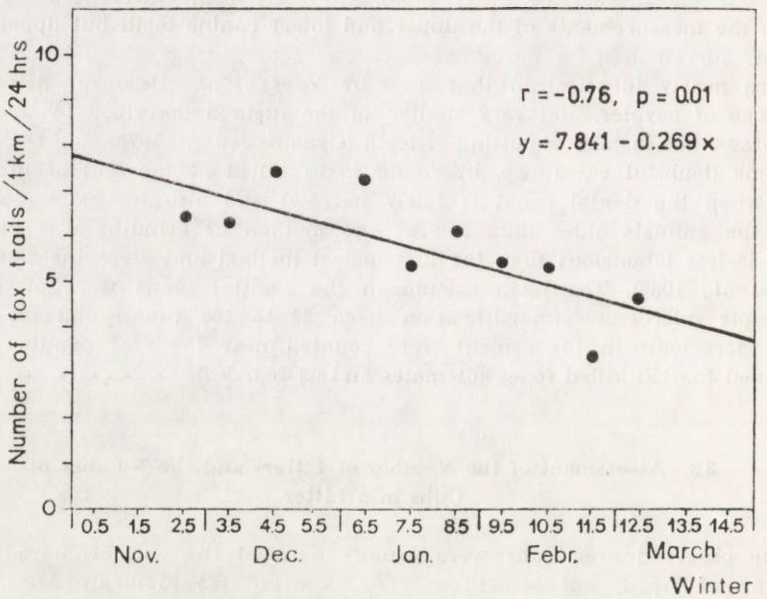

Fig 2. Changes in the intensity of area searching by foxes during winter season. (A — number of fox trails per 1 km of assessment line per 24 hours. The numbers 0.5, 1.5, 2.5 *etc.* on axis of abscissa are the middles of successive decades).

roughly to the first and last snowfalls in this area. Since the data collected during the third 10-day period of December and the second 10--day period of March were not sufficient for analysis, they were pooled with data gathered in the second 10-day period of December and the first 10-day period of March, respectively. It was assumed that the data obtained were representative for the period from November 1 to April 1. The density of the fox population decreased during the winter (Fig. 2) and the reduction of the population was calculated on the basis of regression. The density of the population at the beginning of winter was calculated, based on the data shown in Fig. 2, as 0.89 animal per 1 km^2, and at the end of this season it was 0.43/km^2. The reduction during 5 months was 52%.

Control tracking over the remaining area showed that the population density was about 45% lower. This agreed with the estimations of the number of litters in these areas in spring (mean annual value 0.171 and 0.094 dens with young animals per 1 km^2). On the basis of these data the average abundance of foxes in the whole area of 89.2 km^2 over the study period was estimated. On November 1 it was 52.2 animals, and on April 1 it was 25.1 animals. According to the official statistics 48% (13 animals) of foxes lost in the winter are killed by hunters.

4.2. Density Variations in Winter

The annual calculations of the intensity of area searching by foxes demonstrated a low variability of this parameter. The population density calculated on this basis ranged from 0.48 to 0.91 animals/km^2 (Table 1). The mean density was 0.71 ind./km^2 which was the value approximating the density estimate based on the reduction rate in the winter (0.66 ind./km^2 on January 15). The highest values of the index of area searching and thus of population density were recorded in the winters of 1981/1982 and 1986/1987 after high summer and autumn densities of field voles *Microtus arvalis* (Pallas, 1779) and in 1983/1984, bank voles *Clethrionomys glareolus* (Schreber, 1780) in the forests. A statistically significant correlation ($r = -0.73$; $0.05 > p > 0.01$) was found between the proportion of small mammals (mainly rodents) in the food of foxes in the autumn-winter and the density of this carnivore (Table 1).

No significant correlation was found between the average litter size in spring and the density of the fox populations in winter ($r = -0.38$, $p > 0.1$). Therefore it was checked whether the availability of small mammals affected the survival of young foxes to the winter. Since the size of the sample (killed animals) was not large, and not all winters were represented by sufficiently large samples, the material was divided into two groups. The first group included those seasons in which the proportion of small mammals in the fox diet did not exceed 40% by weight, and the second group included the seasons with the proportion of small mammals in the food of foxes exceeding 40%. In these groups the proportion of young animals in the whole number of killed foxes was calculated. In group I young foxes accounted for 46.5% (N=58)

Table 1

Intensity of penetration by foxes and density of these predators assessed by winter tracking.

Analysed seasons	Total length of assessment lines (km)	Number of fox trails/ 1 km assessment line (A)	Density (N/km²)	Proportion of small mammals in fox diet [1]
1979/1980	155.7	6.4	0.73	24.4
1980/1981	152.3	4.2	0.48	32.4
1981/1982	83.8	8.0	0.91	64.7
1982/1983	no data	no data	no data	15.1
1983/1984	60.3	7.9	0.90	51.3
1984/1985	238.1	4.8	0.55	15.3
1985/1986	119.1	6.0	0.68	44.0
1986/1987	96 0	8.0	0.91	40.8
1987/1988	72.1	4.7	0.53	29.3
Total	978.0			
Mean		6.25	0.71	
S. D.		1.59	0.18	

[1] mean weight percentage of small mammals in the food consumed by foxes in the autumn and winter seasons (Goszczyński, 1986, and Goszczyński — unpublished data)

and in group II — 65.5% (N=55). The difference between these values was statistically significant ($d=2.03$; $0.05>p>0.02$). This indicates that the survival of cubs till the hunting season depends on the abundance of this food.

4.3. Analysis of Killed Animals

In the group of 113 animals obtained for estimation of age, the male/ /female ratio was 1.17:1 but the predominance of males was not significant statistically ($\chi^2=0.72$; $p>0.5$). Besides these data, additional information on the sex of killed foxes was obtained from hunters and foresters in the study area. Since these data were not obtained randomly (*e.g.* only certain hunters were interviewed) it was difficult to estimate on this basis the sex proportion among the killed animals, but they were used for analysis how various types of hunting affect the male/ /female ratio and how this ratio changed in the winter. It was found that battue hunting frequently in the observed area caused a selective killing of males (Table 2). On the other hand during accidental encounters with foxes and during hunting at the dens the male/female ratio was similar (Table 2). Thus, the proportion of males among the killed

Table 2

Effect of hunting method on the male: female ratio in the total kill.

Hunting method	N foxes killed	Proportion of males	χ^2	p
Battue hunting (1)	86	64.0	6.70	<0.01
Accidental encounter with fox (2)	16	43.8		
Hunting at dens (3)	18	44.4		
(2) + (3)	34	44.1	0.47	NS

foxes depended on the intensity of battue hunting and, as a rule, in the observed area more male foxes were killed. Moreover, it was demonstrated that as winter progressed the male/female ratio was approaching (Table 3).

Table 3

Changes of the male: female ratio during the winter season.

Period	N foxes killed	Proportion of males	χ^2	p
1 Nov — 15 Dec	48	64.6	4.08	<0.05
16 Dec — 31 Jan	58	65.5	5.59	<0.02
1 Feb — 15 March	41	46.3	0.22	NS

Since fox shooting is organized in autumn and winter and the young foxes are born in early spring the shot animals belong to age groups: 0.5-1, 1.5-2, 2.5-3... years. The proportion of young animals among the shot males was 59%, an that of young females, 52%. The oldest male belonged to the age group 4.5-5 years and the oldest female was shot at the age of 6.5-7 years.

4.4. Reproduction

The litter size, as revealed by occasional autopsies of pregnant females killed in March, was 5.5. In the entire study area the average number of dens with young animals recorded in one season was 10 (S.D. = 1.6). The number of dens varied from 8 to 12. It was therefore rather stable and no correlation was found between it and the density of small mammals. On the basis of observations at dens the average number of cubs was estimated at 3.8 per den. In various years the number of young foxes varied from 2.7 to 4.5. No sufficient data on the composition of fox diet in spring was available, but a comparison of the proportion of small mammals in the food of foxes in winter (that is at the time immediately preceding births) and the number of cubs demonstrated a significant correlation between these parameters ($r=0.70$; $0.05>p>0.02$; Fig. 3).

4.5. Age and Sex Composition of the Fox Population

Hunting and mortality resulting from wound are important components of the total mortality of foxes in the study area. Moreover, shooting may selectively affect animals in different age groups. For this reason, the sample of carcasses was treated as a sample of the dying animals. Since the collected material was too small for analysis of changes in the age pattern from one year to another, it was divided into two groups. The first group was comprised of 5 seasons (1979—1983) and the second group, 4 seasons (1984—1987). On the basis of data obtained in the sample of animals killed the number of foxes surviving to the beginning of each age class was estimated (Table 4)

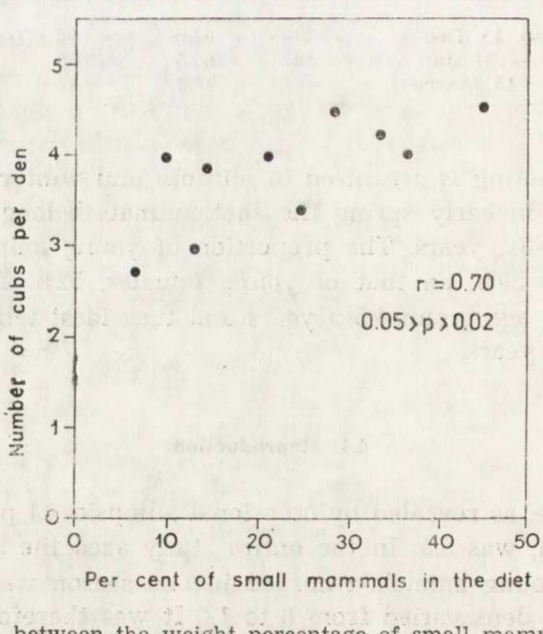

Fig 3. Correlation between the weight percentage of small mammals in the winter diet of foxes and the mean number of cubs per litter in different years of the study period.

The age structure of the studied population in years 1979—1983 and 1984—1987 was estimated separately, and found to be similar. Slight differences were found in the age class of young foxes and those aged over 4.5 years (Fig. 4).

Since size and age composition of the studied population seemed to be stable over many years, the specific mortality index (q_x) was calculated for different age groups of both sexes. The survival of young males was higher than that of young females, whereas the mortality of adult animals of both sexes was almost equal (Table 5).

In spring, on April 1, the average number of foxes in the whole studied area was estimated as 25.1 (Chapter 4.1.). Since the survival

Table 4

Comparison of survival rates of foxes in two consecutive study periods. d_x was estimated on the basis of age distribution of killed animals.

Age class	1979-83		1984-87	
yrs.	l_x	d_x	l_x	d_x
0.5—1	53	32	60	31
1.5—2	21	7	29	15
2.5—3	14	10	14	6
3.5—4	4	2	8	6
4.5—5	2	2	2	0
5.5—6			2	1
6.5—7			1	1
Total	94	53	116	60

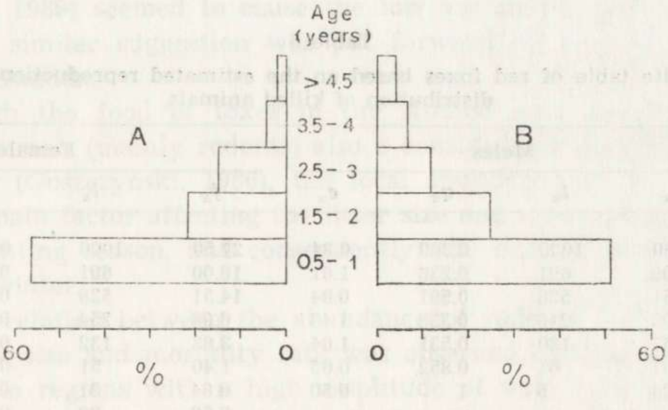

Fig 4. Age structure of the population in winter season (A — period 1979—1983, B — period 1984—1987).

of young males was lower than that of young females (Table 5), and the maximal age found in the group of males was lower than that of females, it may be expected that among 25.1 animals recorded in spring, females prevailed. To calculate their proportion, it was assumed that there was a 1:1 ratio of young males to young females at the beginning of the hunting season, and that the mortality in winter in various age groups agreed with the calculated values of q_x. Following these assumptions 11.4 males and 13.7 females could be expected on April 1. The number of young male foxes (and females) at the beginning of the hunting season was estimated at 14.5.

Data on sex ratio, age-specific mortality, and reproduction were used for construction of the life table of the studied population (Table 6). The data in the table show that about 22% of males and about 25% of females have a chance to survive to the age of 12 months. The survival

Table 5

Age-specific mortality of males and females of red fox. d_x was estimated on the basis of age distribution of killed animals.

Age class	Males				Females			
yrs.	l_x	d_x	q_x		l_x	d_x	q_x	
0.5—1	61	36	0.590	0.52	52	27	0.519	0.51
1.5—2	25	10	0.400		25	12	0.480	
2.5—3	15	8	0.533		13	8	0.615	
3.5—4	7	6	0.857		5	2	0.400	
4.5—5	1	1	1		3	1	0.333	
5.5—6					1	1	1	
6.5—7					2	1	0.500	

Table 6

Composite life table of red foxes based on the estimated reproduction and the age distribution of killed animals.

Age	Males				Females			
yrs.	f_x	l_x	q_x	e_x	f_x	l_x	q_x	e_x
0	27.50	1000	0.309	0.84	27.50	1000	0.309	0.91
0.167	19.00	691	0.236	1.01	19.00	691	0.236	1.11
0.5	14.51	528	0.591	0.94	14.51	528	0.519	1.07
1	5.95	216	0.398	1.43	6.98	254	0.480	1.46
2	3.57	130	0.531	1.04	3.63	132	0.614	1.35
3	1.67	61	0.852	0.65	1.40	51	0.392	1.70
4	0.24	9	1	0.50	0.84	31	0.355	1.47
5					0.56	20	0.500	1.00
6					0.28	10	1	0.50

rate of adult foxes (older than 1 year) was estimated as 48-49%. The expected life span at birth (E_0) was only 0.84 year for males and 0.91 year for females.

5. DISCUSSION

The density of the fox population in central Poland is rather low in comparison with West Europe (Lloyd *et al.*, 1976), and particularly with suburban areas and towns in Great Britain (Harris, 1981; Harris & Smith, 1987). Densities similar to or lower than that described here are known from neighbouring countries, *e.g.* the GDR (0.65 foxes per km^2 reported by Stubbe, 1980), Sweden (0.2 — 0.4 per km^2 — Lindström, 1982), the USSR (Byelorussia: 0.2 foxes per km^2 — Gavrin & Krapivnyj, 1965), and also from other parts of Poland (Pielowski, 1976; Goszczyński, 1977; Fedyk *et al.*, 1984).

From year to year the density of the fox population in the studied area persisted at a stable and rather even level. This was due, probably, to a permanent division of the space available between several fox families, and also to the balance between birth rates and losses caused by hunting. In the studied area for several years no cases of rabies among foxes have been observed. It is known that this disease may strongly affect fox population size. Besides that, in central Poland outbreaks of field voles have not been observed. Therefore the food availability has been here much more stable from year to year than in western and northern Poland, where there are cyclic vole populations (Goszczyński, 1986).

The stability of spatial distribution of foxes over the study area (Goszczyński, 1989) seemed to cause the low variability in the number of litters. A similar suggestion was put forward by Lindström (1982) in southern Sweden.

Although the food of foxes in the studied area contained, besides small mammals (mainly rodents) also a considerable proportion of hares and birds (Goszczyński, 1986), the local abundance of small mammals was the main factor affecting the litter size and survival of young foxes to the hunting season, and consequently, the density of the fox population in winter.

The correlation between the abundance of rodents and the ovulation rate, litter size and mortality rate was observed by other authors, particularly in regions with a high amplitude of vole cycles, where these rodents were the main food of foxes (Heptner & Naumov, 1967; Englund, 1970; Lindström, 1982).

The analysis of life tables shows that in the studied population the survival rate of young foxes in the first year of life was very low, whereas the survival rate of adult animals (48—49% yearly) was at a level similar to that found in other countries (Harris, 1977; Lloyd, 1980; Lindström, 1982; Harris & Smith, 1987 and others). The maximum life span (4.75 — 6.75 years) was lower than that noted in other populations (Englund, 1980; Maekawa *et al.*, 1980; Lindström, 1982). Similarly, the life span expected at birth (E_0) is low in relation to the populations subjected to lower hunting pressure.

The number of foxes killed each year in the studied area was not related to the population density ($r = -0.19$, $p > 0.1$) and depended on the number of licences granted to hunters. According to official data the losses caused by hunting accounted for half the total mortality in winter. This is, doubtlessly, an underestimation, since part of the foxes died from wounds, and some were killed by poachers. Apart from hunting, a small proportion of the foxes disappearing during winter might have been killed by dogs, and some foxes might have died of diseases, such as mange (among the killed foxes, some were infected with mites, *Sarcoptes scabiei*). It seems, however, that most foxes were killed by hunters.

In all, in the studied area more male foxes were killed. The frequently used mode of hunting with battue seems to have a selective effect on the males which are more active and less frequently remain in dens. On the basis of analyses of the killed animals it was found that in the adult population of foxes (aged 1 year or more) males accounted for about 45.5% and it seems that this was mostly due to hunting. Yoneda & Maekawa (1982), who analysed the effect of hunting on age structure and survival rates of foxes showed also a lower proportion of males in the populations exposed to greater hunting pressure.

A comparison of two numbers: the number of dens occupied by fox families (10) and the number of males and females known to be alive at the beginning of breeding season (11.4 and 13.7 respectively), indicated that in spring the majority of family groups consisted of one female and one male. Thus, reproductive success and growth rate of the population in the study area depended on the survival of males up to April 1.

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DYNAMIKA POPULACJI LISÓW W ŚRODKOWEJ POLSCE

Streszczenie

Na podstawie tropień zimowych prowadzonych w okolicach Rogowa (województwo skierniewickie) oceniono zagęszczenie lisów i ich śmiertelność w tym okresie. Zagęszczenie zmieniało się w niewielkim stopniu z roku na rok i przeciętnie wynosiło ok. 0.45 osobników/km². Redukcję lisów w okresie od listopada do kwietnia oceniono na 52%. Jest ona głównie efektem odstrzału. Wahania liczebności tego drapieżnika są, jak się wydaje, związane z różną przeżywalnością młodych do sezonu polowań. Stwierdzono, że w latach obfitujących w drobne ssaki (przede wszystkim gryzonie) udział młodych lisów wśród zwierząt odstrzelonych był istotnie wyższy niż w latach niedoboru tego pokarmu. Znaleziono także istotną zależność między dostępnością drobnych ssaków a liczbą szczeniąt w miocie (Ryc. 3). W trakcie badań liczba nor z młodymi zmieniała się nieznacznie co prawdopodobnie wiąże się ze stabilnością układu terytorialnego.

Analizy przeżywalności wykazały, że przeszło 75% szczeniąt nie przeżywa pierwszego roku (Tabela 6). Przewidywaną długość życia w momencie urodzin (E_0) oceniono na 0.84 lat w przypadku samców i 0.91 lat w przypadku samic. Przeżywalność dorosłych lisów wynosi 48—49% w skali rocznej (Tabela 5). Najstarsze osobniki osiągają wiek 4,75 lat (samce) i 6,75 lat (samice). Wśród osobników dorosłych w populacji przeważają samice (54.5%). Intensywne pozyskanie będące głównym czynnikiem śmiertelności wpływa na strukturę płciową populacji i długość życia lisów.