Acta Theriologica 37 (4): 329 – 338, 1992.
PL ISSN 0001 – 7051

STUDIES ON THE EUROPEAN HARE. 46

Predation of foxes on a hare population in central Poland

Jacek GOSZCZYŃSKI and Michał WASILEWSKI

Goszczyński J. and Wasilewski M. 1992. Predation of foxes on a hare population in central Poland. Acta theriol. 37: 329 – 338.

The relationship between foxes *Vulpes vulpes* (Linnaeus, 1758) and hares *Lepus europaeus* (Pallas, 1778) was investigated in central Poland. The consumption of hares by foxes was the highest (up to 50% of biomass eaten) during the spring seasons. The negative correlation between small mammal and hare consumption by foxes was recorded throughout the study. Lack of small mammals in spring as well as low temperatures and deep snow cover in winter intensified the fox hunting on hares. The reduction of hares by foxes was about 16% during spring to autumn and 8% in winter. Predators were responsible for 50% of the total mortality of adult hares. By snow-tracking of foxes it was established that the mean distance between successful hunts on hares was 263 km of fox trail. Foxes captured on average one hare every 19 days. About 7% hare hunts by foxes were successful.

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

Key words: *Lepus europaeus,* population dynamics, *Vulpes vulpes,* predation, hunting success

Introduction

The fox *Vulpes vulpes* (Linnaeus, 1758) in central Europe widely exploit hares *Lepus europaeus* (Pallas, 1778) as food. In some seasons, e.g. in spring, the consumption of hares by these predators may rise up to 50% of biomass eaten (Goszczyński 1986).

For several years foxes and hares were studied separately in the same area in central Poland (Goszczyński 1989a, b, Wasilewski 1991). In this study, we attempted to analyze the relationship between the two species. Specifically, we aimed at estimating the reduction of hare population due to fox predation and at analysing the factors that modify the impact of the predator on its prey.

Study area

The study was carried out in the vicinity of Rogów (51°48'N, 10°53'E), central Poland. The study area (89.2 km^2) was a mosaic of fields, meadows, orchards, forests, and human settlements. The forests covered approximately 17% of the whole area. On the remaining area, small crop fields predominated. In some parts of the study area (13.5 km^2) either fox or hare did not occur. These areas included small towns and villages, fenced parcels, etc. They were omitted from density calculations. More detailed information regarding study area and densities of foxes and hares is given by Goszczyński (1989a) and Wasilewski (1991). Fox and hare populations has been exploited by hunters during the study period according to hunting rules typical for the whole country (Wasilewski 1986).

Methods

Estimation of hare density

The hare population was studied in 1985 – 1989. Density assessments of hares were carried out in open field area twice a year in spring (March) and autumn (November), by the transect census method (Pielowski 1969). The total transect length was about 56 km. It was assumed that the density in forested areas was similar to that estimated for open areas. This assumption was made on the basis of numbers of hares observed during regular battue assessments of roe deer, caried out twice a year in the woods of our study area (W. Aulak, pers. comm.). These numbers were comparable to those observed in the open fields. Mean spring and autumn densities were estimated at 24.5 and 29.0 hares per 1 km^2, respectively (Wasilewski 1991). On the basis of numbers of the breeding females (11.8 indiv. per 1 km^2, according to Wasilewski 1991) and numbers of young produced by a female (7.4, Raczyński 1964, Pielowski 1976a) the number of young born each year was calculated. It was 87.3 young per 1 km^2 per year (Wasilewski 1991). Lens dry mass of hares shot in the beginning of winter was used for age determination. The percentage of young in the population was calculated. Until the beginning of winter 19.1 adults and 9.9 young survived on average per 1 km^2 (Wasilewski 1991). The above data were used for estimating abundance of prey available to foxes.

Dynamics of fox population

The mating season of foxes occurred in the first half of February. Mean day of conception was estimated for the 6th of February. The gestation lasted about 53 days. It was assumed that young were born on 1 April. The mean number of dens with young foxes per year was 10 and mean number of adult individuals in the whole study area on 1 April was 25.1 (Goszczyński 1989a). The litter size was estimated to be 5.5 pups per an occupied den. From each litter on average 3.8 fox cubs survived till 1 June. Until the beginning of winter (1 November) 29 young and 23 adults predators (totally 52) survived. Out of these, 48% individuals survived till next spring (1 April; Goszczyński 1989a). On the basis of these data we have computed, by interpolation, the numbers of foxes present in the study area at the beginning of each month.

Food composition of foxes

The diet of foxes was studied by analysis of scat contents. Each scat was thoroughly washed and particular components were distigushed (hairs, bones and teeth, feathers, parts of fruits, fragments of insects, etc.). In that way the main food items (small mammals, hares, cervids, birds, fruits, insects, etc.) were distinguished. Dry weight of remains belonging of each category was multiplied by correction factors characterizing the intensity of food digestion (Lockie 1959, Goszczyński 1974, 1986). Among small mammals and birds further division to particular species or genus was made on the basis of skeleton fragments or hair structure (Goszczyński 1974, 1986). By summing up the biomass of all items, the total biomass of consumed food was estimated for each season. The data were presented in form of percentage of weight which characterised the share of particular food item in total biomass consumed. All together 1,914 scats were analysed during the period 1978 – 1991. Part of these data was published (Goszczyński 1989b) but also new data are included in this paper.

Food requirement of foxes and utilization of killed hares

It was assumed that food requirements of an adult fox is 470 g per day (Ryszkowski *et al.* 1973). The food requirement of vixen during gestation (6 February – 31 March) increases approximatelly by one fourth (Szuman *et al.* 1955). During lactation (April) females double their food consumption (Sargeant 1978). The food consumption by young during the period of growth (1 May – 1 November) was assumed after Ryszkowski *et al.* (1973) to be 447 g per day per animal. During the remaining period (winter), food requirement of young was assumed to be the same as that of adult foxes.

During scat analysis, the remains of hares (teeth, paws, bone fragments) were collected. They were compared with equivalent parts of hares with known body mass. This allowed us to distinguish 3 size groups of hares consumed by foxes from 1 April to 1 November: large (body weight approxim. 4 kg), medium (approxim. 2 kg), and small (about 500 g). Hares belonging to the first category were considered adult, to the second – subadult, and belonging to the third as young. These categories occurred in the scats in the following proportions: 2 : 4 : 12. An attempt was made to assess how predators utilized bodies of hares belonging to different size groups of prey. During winter tracking the places where foxes captured hares, and food caches were inspected for remnants of prey. The inspections of hare remains at fox burrows were also performed. On the basis of these lustrations it was stated that bodies of adult hares weighing aproximatelly 4 kg were consumed in 80%. Predators rejected, as a rule, hind feet, parts of skull, fur and gut tract. Medium-sized hares were eaten in 90%, and small ones almost totally (95%). Taking this into account, a total biomass of hares consumed by foxes was divided into the three size categories of hares which formed: adults – 33.2%, subadult – 37.3% and young – 29.5%. These data were used for computing the number of hares eaten by predators. For this computation hares belonging to the second and third category (subadult and young) were pooled.

Estimation of the hare consumption by foxes

For determining the number of hares eaten by foxes we used the following parameters: (1) dynamics of the fox numbers, (2) weight percentage of hares in the predator diet, (3) food requirements of predator during given period, (4) the mean body mass of prey and the utilisation of prey body by predator. To compute the number of hares eaten by foxes during one month (NH) we used the following formula:

$$NH = [((N_{t1} + N_{t2}) / 2) \times t \times w\% \times DFC] / (HBM \times u\%),$$

where: N_{t1}, N_{t2} – number of foxes at the beginning and end of a given month, t – number in days per month (28...31), w% – per cent of weight of the hares in fox diet, DFC – daily food consumption by fox (g/24 hrs per animal), HBM – mean hare body mass (g), u% – per cent of utilization of hare body by foxes.

For the summer, the monthly biomass of hares eaten by foxes (the numerator of above formula) was distributed into hare size groups and then divided by HBM and u%. During the winter period (1 November – 28 February) all hares were treated as one size group (large hares). The number of hares eaten by foxes in a particular period: winter or summer was compared to the number of hares presents at the begining of these periods in the study area and to the total number of hares lost during the season. In this way the reduction of hares and the share of foxes in their total mortality were determined.

Direct estimations of the impact of foxes on hares

During snow-tracking of foxes in the period 1979 – 1991 interactions between the predators and hares were recorded. On a 788.3 km of fox trail 3 successful attacks on hares were observed. The success of hunting was judged by presence of blood, fur fragments, remains of body, and accumulation of fox tracks near the capture place. Another 42 attemps of hunting on hares were recorded as indicated by signs of fox exploing hare beds, marked changes in trail direction, and chases after hares. Also 16 cases of visits near remains of earlier captured hares were observed.

The information on the frequency of successful hunting on hares (expressed as a distance between consecutive successful hunts), the mean daily movement of foxes and fox dynamics allowed for another estimation of numbers of hares captured by foxes. These data were used to check the accuracy of results obtained from the calculations of prey consumption.

Results

Importance of hares in fox diet

The foxes in the study area used mainly three types of food items: small mammals (mainly rodents), hares and birds (Fig. 1). These three food components made up together 81% of consumed biomass. Consumption of hares was highest

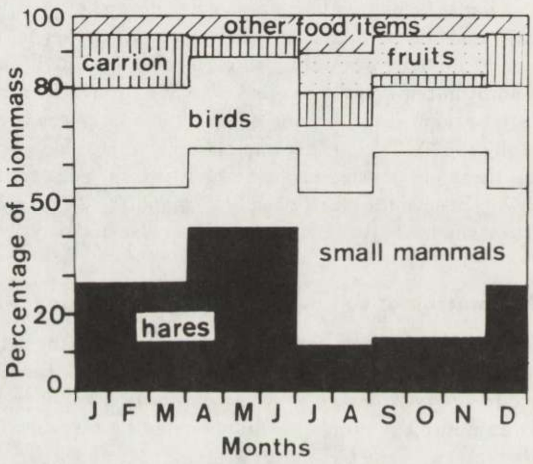

Fig. 1. Diet of foxes (percentage of weight).

in spring (43% by weight), lower in winter (28%), and lowest in summer – autumn (12 – 15%). The proportions of hares in the fox diet varied in a narrow range between winters (C.V. = 34.1%) and springs (C.V. = 37.2%). The variation was much greater in summer and autumn (C.V. = 114.9% and C.V. = 61.6%, respectively).

In data pooled for whole year, the negative correlation between the consumption of the hares and small mammals was found ($r = -0.70$, $p < 0.001$, Fig. 2). The correlations between consumption of hares and birds, and between hares and carrion were not significant ($r = 0.12$, $p > 0.1$; $r = -0.07$, $p > 0.1$, respectively).

Factors modyfing the consumption of hares

Although for combined data for all the year the negative correlation between consumption of small mammals and hares was found, for winter season alone no correlation existed neither between those two food types ($r = -0.24$, $p > 0.1$) nor between hares and birds ($r = -0.48$, $p > 0.05$) in the fox diet. This caused us to examine the effect of meteorological factors on fox hunting. Two parameters which could have an impact on hare condition and effectiveness of fox hunting were chosen. The first was mean daily temperature (1), the second was mean daily snow depth (2). By multiple regression method it was stated that none of these factors, assuming the stability of another, correlated with the consumption of hares by foxes (3) ($r_{13.2} = -0.36, p > 0.1; r_{23.1} = 0.27, p > 0.1$). However, the combined effect of both factors explained 47% of the observed variability in hare consumption by foxes (R = 0.47, p = 0.03).

During spring seasons there was a significant negative correlation between the consumption of small mammals and hares ($r = -0.78$, $p < 0.01$, Fig. 3).

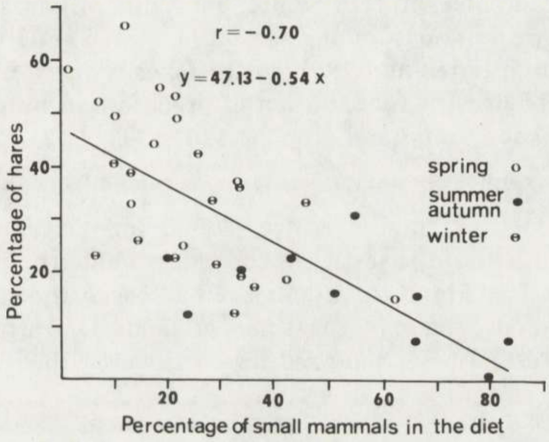

Fig. 2. Correlation between consumption of small rodents and hares by foxes (combined data for all the years expressed as percentage of weight).

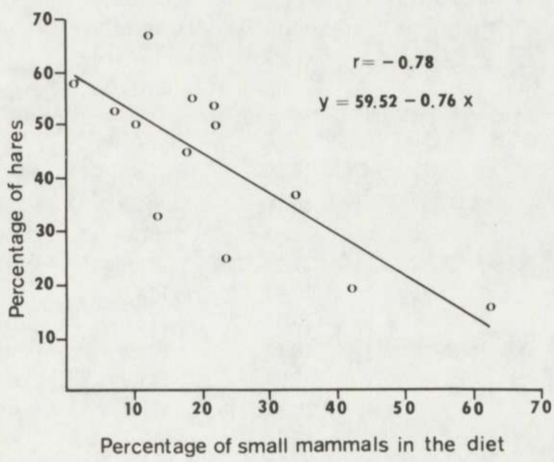

Fig. 3. Correlation between consumption of small mammals and hares during spring seasons (percentage of weight).

Consumption of hares by foxes and the role of predation in hare mortality

The biomass of hares captured by foxes changed in various months from 94 kg to 406 kg (Table 1). These values resulted from fox food requirement and the numbers of predators. This biomass has been divided according to the hare body size (small, medium, and large ones). The prey from two first groups were treated as young individuals, the large prey as adults. By comparing the annual number of hares present in the study area with the number of hares captured by foxes it was estimated that foxes eliminated 18% of prey individuals (Table 2). In winter (1 November – 28 February) the overall consumption of hares by foxes was as high as 180 individuals or 8% of hares present in the population at the beginning of winter. The share of foxes in total winter mortality of hares amounted to 53% (Table 2). During spring and summer season (1 March – 31 October) the foxes eliminated 1158 young hares and 184 adults. Foxes reduced up to 17% of young and to 10% of adult hares. A contribution of predators in hare mortality during this season was 20% for young and 45% for adults (Table 2).

Impact of foxes on hares during winter as revealed from snow tracking

During fox tracking (total trail distance – 788,3 km) 45 attempts of hunting on hares were recorded. Only 3 cases were succesful. Thus, the hunting success of foxes was approxim. 7% of hunting attempts. In 14 cases, the attempts of hunting were performed in woods, and in 30 cases in open fields. One attempt was recorded on the edge of a forest. Among captured hares, 2 were killed in forests and one

Table 1. Numbers and biomass of hares consumed by foxes in the Rogów study area (89.2 km^2) in central Poland. [1] – estimated on the first day of each month, [2] – the extra food consumption of pregnant vixen was included, [3] – the extra food consumption of lactating females was included.

Month	Mean number of foxes on the whole study area[1]		Percentage of hares in fox diet (% of biomass)	Biomass of hares consumed by foxes (kg)	The number of hares eliminated by foxes	
	Total	Young			Total	Young
April	80.1	55.0	42.90	211.4[3]	197.0	175.1
May	71.4	46.4	42.90	405.9	378.3	336.2
June	66.2	38.0	42.90	361.3	336.8	299.3
July	60.5	36.2	11.53	97.0	90.4	80.3
August	58.4	34.4	11.53	93.6	87.2	77.5
September	56.3	32.6	15.11	114.5	106.7	94.8
October	54.3	30.8	15.11	114.0	106.2	94.4
November	52.2	29.0	15.11	105.5	33.0	
December	46.8		28.24	181.2	56.6	
January	41.3		28.24	158.4	49.5	
February	35.7		28.24	130.7[2]	40.8	
March	30.7		28.24	125.1[2]	39.1	
April (next year)	80.1	55.0				

in the open field. It may indicate that foxes were more succesfull when hunting in the forest (14%) than in the fields (3%). Due to low number of recorded huntings it was not possible to verify statistically the above hypothesis (d = 1.34, $p > 0.1$, test for comparison between two percentages). Observations made during fox tracking indicated also that predators often visited the remains of hares captured previously or found dead. In 16 cases, it was established that hare carcasses were visited by foxes several times. Such revisited remains of hares were observed on 11 ocassions in woods, and on 5 ocassions in open fields. This additionally supports the suggestion that hunting by foxes is more succesful in forested area.

Data from snow tracking indicated that for capturing one hare a fox had to travel on average 262.8 km. Since a fox daily covered on average a distance of 13.8 km (Goszczyński 1989a), one hare was captured every 19 days. Numbers of foxes present in the whole study area decreased between 1 November and 1 March from 52.2 to 30.7 individuals. Taking this into consideration, as well as daily distance covered by one fox and length of time for which the estimation was made (120 days), it was calculated that foxes in the study area during winter covered the distance of 68,641 km. Assuming that the distance between two successful

Table 2. The impact of foxes on hare population in a 89.2 km^2 study area in central Poland.

Analysed parameters	Total	Adult	Young
Number of hares in spring (1 April)	1855	1855	
The number of newborn between 1 March – 30 October	6610	–	6610
Total summer mortality of hares (1 March – 30 October)	6269	412	5857
Summer mortality caused by foxes:			
n individuals killed	1342	184	1158
percentage of total mortality	20%	45%	20%
The reduction of hare population by foxes (1 March – 30 October)	16%	10%	17%
The autumn numbers of hares (1 November)	2195	1442	753
Total winter mortality of hares (1 November – 28 February)	340		
Winter mortality caused by foxes:			
n individuals killed	180		
percentage of total mortality	53%		
The reduction of hare population by foxes during winter	8%		
Total number of hares present in the study area in one year period	8464		
Total annual mortality of hare	6610		
Annual mortality caused by foxes:			
n individuals killed	1522		
percentage of total mortality	23%		
Annual reduction of hare numbers by foxes	18%		

huntings was 262.8 km, it was estimated that predators captured 261 hares during the winter season. This value is by 45% higher than the number of hares eaten by foxes estimated on the basis of food requirements of foxes, the share of hares in their diet, and the number of foxes in the area.

Discussion

The results of this study indicate that consumption of hares by foxes depends on small mammal (especially rodent) abundance. Although in central Poland cyclic outbreaks of common vole *Microtus arvalis* were not observed, even small seasonal and annual variations in rodent densities seem to affect hare consumption by foxes. This is most clearly seen in spring when the density of rodents is lowest in the year.

In winter, the consumption of hares depends mainly on weather. Low temperatures and compact snow may affect the physical condition of hares and facilitate fox hunting. In the study area a positive correlation was observed between the number of hare tracks and intensity of area searching by foxes (Goszczyński 1987). Such correlation was never found in western Poland where common vole occurred periodically in very high densities. In that area a strong relationship was observed between local densities of rodents in particular habitat patches and the intensity of area searching by foxes (Goszczyński 1977).

Only a few papers report on fox hunting intensity on hares in winter. Korytin (1968) in his study in Kirov District (east Europe, lowland, approx. 750 km E of Moscow) noted only 1 case of successful hunting on mountain hare during fox tracking on the 260 km of fox trail. This value is close to the value estimated in our paper. Also his estimates of the share of hares in fox diet (approx. 30%) are comparable to those recorded by us in central Poland. Palm (1970) in Sweden on 41 km of fox trail noted 3 attempts of capturing hares which is 0.07 attempts per 1 km of the fox trail. This value is also close to the hunting intensity by foxes observed in our study (approx. 0.06 attempts per 1 km of fox trail).

The hunting success of foxes on hares is not very high. It was estimated at about 7% of hunting attempts. In their huntings for rodents foxes are more effective. Hunting success may be as high as 16 – 22% (Goszczyński 1990) or it even sometimes exceeds 50% (Palm 1970). In most cases, the foxes hunted for hares by stealthy approach to the resting animals or by out-sprinting them in relatively short chase. Results of this study suggest that predators have better chance for successful capturing hares in woods than in open fields. In the former habitat they can come closer to the prey; it is also possible that a hare looses its speed advantage, when forced to run away among trees. It is also important that in woods foxes may hunt for hares also during daytime when the prey sleep in shelters. Tracking and observations of foxes in forests and in open fields revealed, that in woods foxes were quite often seen during daytime, whereas they avoided open fields. Probably such behaviour resulted from heavy hunting exploitation of foxes in this area during hunting season.

The numbers of hares captured by foxes during winter, estimated by two methods on the basis of data from snow tracking and by indirect method based on diet, density, and daily food requirement by foxes were similar: 261 individuals, 180 individuals, respectively. A higher value obtained from snow tracking may be explaind by the fact that the tracking was usually made in periods of low temperature and fresh, deep snow cover, which are the conditions that facilitate fox hunting. The lack of snow cover and frost may automatically decrease the effectiveness of fox hunting. So the assumption that chances of hare capturing are the same during the whole winter, probably overestimated the predator impact.

In spring the consumption of hare by foxes was the highest throughout a whole year. It coincides with seasonally low vole densities. Also in the areas of western Poland, where voles were usually more abundant and foxes depended more on rodents for food, it was observed that in the years of vole depression foxes compensated for the lack of rodents by increased hare consumption (Goszczyński 1977). Also Soviš (1967) and Kožena (1988) in Czecho-Slovakia indicated the importance of hare in fox diet in spring. The presence of young hares in spring more vulnerable to the fox predation may also rise the consumption of this species by foxes.

The reduction of hares by foxes estimated in this paper (approx. 18%) was higher than that computed by Pielowski (1976b) (1 – 4%). In Pielowski's study in western Poland, however, the density of hares was higher and the density of foxes lower than in our study area. Schantz (1980) and Erlinge *et al.* (1984) in Sweden evaluated the reduction of young hares by foxes to approx. 12 – 14% of annual production. Their results are close to our estimate (17.5%). In a small part of the investigated area where the density of foxes was higher than elsewhere their predation more strongly affected hare survival (Goszczyński 1985).

The share of foxes in hare mortality was rather high in winter when it exceeded 50% of the total hare mortality. The rest of mortality was mainly due to hunting. In summer, about 20% of the total mortality was caused by foxes. The adult mortality due to fox predation amounted to 45% of total mortality in this age group whereas in the case of young hares the foxes were responsible for only 20% of their losses. Thus, in summer the predation by foxes can be regarded as an important mortality factor only for adult hares.

References

Erlinge S., Frylestam B., Göransson G., Högsted G., Liberg O., Loman J., Nilsson I. N., Schantz T. von and Sylven M. 1984. Predation on brown hare and ring-necked pheasant populations in southern Sweden. Holarctic Ecology 7: 300 – 304.

Goszczyński J. 1974. Studies on the food of foxes. Acta theriol. 19: 1 – 18.

Goszczyński J. 1977. Connections between predatory birds and mammals and their prey. Acta theriol. 22: 399 – 430.

Goszczyński J. 1985. The effect of structural differentiation of ecological landscape on the predator-prey interaction. Rozprawy Naukowe i Monografie SGGW-AR, 46: 1 – 80. [In Polish with English summary]

Goszczyński J. 1986. Diet of foxes and martens in central Poland. Acta theriol. 31: 491 – 506.

Goszczyński J. 1987. Habitat use by red foxes. Abstract of XVIIIth Congress of Game Biologist. Suppl. Jagiellonian University, 2: 2. Poland 1987.

Goszczyński J. 1989a. Population dynamics of the red fox in central Poland. Acta theriol. 34: 141 – 154.

Goszczyński J. 1989b. Spatial distribution of red foxes *Vulpes vulpes* in winter. Acta theriol. 34: 361 – 372.

Goszczyński J. 1990. Scent marking by red foxes in central Poland during the winter season. Acta theriol. 35: 7 – 16.

Korytin S. A. 1968. Zimnaja ekologia lisicy v Kirovskoi oblasti. Biull. MOIP, Biol. 73: 33 – 44.

Kožena I. 1988. Diet of the red fox (*Vulpes vulpes*) in agrocenoses in southern Moravia. Acta Sc. Nat. Brno 22: 1 – 24.

Lockie J. D. 1959. The estimation of the food of foxes. J. Wildlife Manage. 23: 224 – 227.

Palm P. D. 1970. Rödrarens naringsekologi. Zool. Revy 32: 43 – 46.

Pielowski Z. 1969. Belt assessment as a reliable method of determining the numbers of hares. Acta theriol. 14: 133 – 140.

Pielowski Z. 1976a. Number of young born and dynamics of the European hare population. [In: Ecology and management of European hare populations. Z. Pielowski and Z. Pucek, eds.]. PWRiL, Warszawa: 75 – 78.

Pielowski Z. 1976b. The role of foxes in the reduction of the European hare populations. [In: Ecology and management of European hare populations. Z. Pielowski and Z. Pucek, eds.]. PWRiL, Warszawa: 135 – 148.

Raczyński J. 1964. Studies on the European hare. V. Reproduction. Acta theriol. 9: 305 – 352.

Ryszkowski L., Goszczyński J. and Truszkowski J. 1973. Trophic relationships of the common vole in cultivated fields. Acta theriol. 18: 125 – 165.

Sargeant A. B. 1978. Red fox prey demands and implication to prairie ducks production. J. Wildlife Manage. 42: 520 – 527.

Schantz von T. 1980. Prey consumption of a red fox population in southern Sweden. Biogeographica 18: 53 – 64.

Soviš B. 1967. Prispevok k potravnej ekologii a populacnej dynamike liski obycajnej so zretelom na jej hospodarski vyznam. Acta zootech. 15: 161 – 171.

Szuman J., Woliński Z. and Kulikowski J. 1955. Zwierzęta futerkowe. PWRiL, Warszawa: 1– 425 .

Wasilewski M. 1986. Sytuacja zajęcy w łowiskach środkowej Polski. Łow. pol. 11/12: 20 – 21.

Wasilewski M. 1991. Population dynamics of the European hare *Lepus europaeus* Pallas, 1778 in central Poland. Acta theriol. 36: 267 – 274.

Received 10 July 1992, accepted 30 September 1992.