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Spatial Distribution of Red Foxes Vulpes vulpes in Winter¹

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The size of family territories of red foxes, Vulpes vulpes (Linnaeus, 1758) in central Poland was determined by snow-tracking. This size ranged from five to six-and-half km², and territories overlapped slightly (by about 12%). Each family tended to occupy the same territory during several successive winters. The mean length of a 24-hour route of foxes was 13.8 km, and the variability of this parameter during successive seasons was slight. The structured characteristics of the territory affected the composition of food consumed by foxes.

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1. INTRODUCTION

In previous works the composition of red fox diet (Goszczyński, 1986), the effect of foxes on small game (Goszczyński, 1985) and the intensity of territory penetration by these carnivores (Goszczyński, 1987) were studied. In the latter publication it was found that the intensity of penetration in different parts of a territory in winter was positively correlated with the distribution of hares, the presence of patches of wood in fields and the abundance of shelters, and negatively correlated with the density of buildings. The present work is a continuation of the studies on the ecology of foxes, and it was undertaken for a detailed study of the spatial distribution of fox families and its persistence in time.

2. STUDY AREA

The study was conducted in central Poland, near Rogów $(51^{\circ}48'N, 19^{\circ}53'E)$ on one of the hunting grounds of the Warsaw Agricultural University. The area covered more than 20 km² of forest and fields. The agriculture in this region was strikingly extensive in character, crop rotation was simple (in winter tilled fields and winter crops predominate), the fields were small, not exceeding one hectare,

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divided by dirt roads and balks. In autumn, the mean densities of small game per 100 hectares were as follows: European hare, Lepus europaeus (Pallas, 1778) — below 30 (Wasilewski, pers. commun.), partridge, Perdix perdix (Linnaeus, 1758) — 22 (Dudziński, 1989), and pheasant, Phasianus colchicus (Linnaeus, 1758) — 6-10 (Wasilewski, 1986). The densities of rodents, both field and forest species, were moderate. Although the density of field voles, Microtus arvalis (Pallas, 1779) rose to the level at 80 ind. per hectare (Goszczyński, 1985), this increase was much lower than in peak years of cyclic vole population occuring in western and northern Poland (see Truszkowski, 1982). Roe deer, Capreolus capreolus (Linnaeus, 1758) were very numerous, up to 50-60 per 100 hectares (Aulak & Goszczyński, 1986). Foxes do not hunt roe deer actively but they may devour carcasses of dead deer or residues after disembowelling.

3. METHODS

Snow-tracking was the basic method for determination of the size of red fox territories. During successive winters (1984/1985 - 1987/1988) foxes belonging to four families were tracked. Tracking began either at a fox burrow or at an arbitrary chosen place within the territory. In the first case, tracking was continued as long as this was possible, and the trail of each animal was drawn on

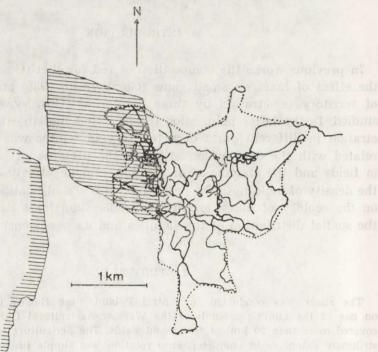


Fig. 1. Territory of one fox family: an example of outlining the territory on the basis of snow-tracking data (Family IV, season 1984/1985). Hatched area — the forests, continuous line — wandering of foxes from this family, dotted line — the borders of the territory.

a map of the study area. In the second case, foxes were tracked back to the place near or at the burrow, and the track was drawn again on a map. This method established to which family (social group) the trailed animal belonged. All registered wanderings of members of one family served for determination of the size of the family territory. Wanderings of animals which could not be classified unequivocally as belonging to a particular family and far wanderings of a patrolling nature were disregarded. Far wanderings, undertaken usually by males, were also observed telemetrically (Niewold, 1980; Maurel, 1983). They were not connected with territory protection or with everyday activity of the animals, and seemed to be only reconnaissance activities. Lines drawn between extreme points visited by foxes belonging to a given family, outlined the borders of the family territory (Fig. 1).

For establishing whether this method of territory estimation was adequately accurate coloured baits were also used. Within each territory additional food was placed, mixed with coloured plastic markers shredded very finely (Ryszkowski et al., 1971). The faeces of foxes were collected and checked for the presence of plastic markers. When they were found, their location was marked on the map. The sites of bait placement and those of faeces with bait were connected with straight lines. It was then established whether these lines lay within the territories determined by snow-tracking or not.

Food used as bait consisted of fish (an attractive food although unknown to foxes in this area), roe-deer and hare meat, as well as carcasses of other animals found in the study area. Baits were exposed in small quantities, in order not to affect the normal activity and diet composition of foxes. It was estimated that this additional food consumed by foxes accounted for about $6^{0}/_{0}$ of their total consumption.

Data from snow traking were used to calculate the distance covered by the foxes during 24 hours. This distance represents penetration of the animals and the availability of food in the area. Tracking the foxes for 24-hours (from the fox burrow or from the resting place to the burrow) to establish the distance of their daily wandering was unfeasible for the following reasons:

(1) The high density of foxes and other animals (roe-deer and hares) in the area, resulting in a high density of different tracks, caused that the track of a particular animal was often lost.

(2) Differing weather conditions in forest and in open areas often made it impossible to have well preserved tracks in both habitats at the same time; e.g. during windy days the tracks could be seen well in the forest, but invisible on the fields; and during thawing weather the tracks could still be read in open areas, but were completely obliterated in forests.

For this reason a calculation method was developed to reconstruct the distance of the 24-hour wandering of an average fox from data on smaller parts of the total distance covered. The average length of wandering was calculated with the following formula:

(Daily movement distance) DMD Sum of tracks in the forests (km) Sum of burrows and shelters used

Sum of outgoings into the fields

Sum of burrows and shelters used

Sum of tracks in the fields (km) Sum of entries into forests

The first part of this formula determines the length of wandering in the forest, the second part contains the number of loops in the fields, and the third part is the length of an average loop (wandering) in the fields. In this method, contrary to the method of territory size determination, tracking a particular animal was not necessary, since it uses randomly selected segments of wanderings of various animals.

For determining to what degree the structure of the territory (proportion of forests and fields within the territory) affected the diet composition, the faeces of foxes were collected. The locations of faeces were marked on the map of the territory. All scat samples found within the territory of a given family (those found in the overlapping parts of the territories and those with plastic markers were disregarded) were used for establishing diet composition. The analysis was carried out according to Lockie (1959) and Goszczyński (1974). Conversion factors described by these authors were used for determination of the biomass of the consumed food items. The diet composition was established on the basis of 839 scat samples.

4. RESULTS

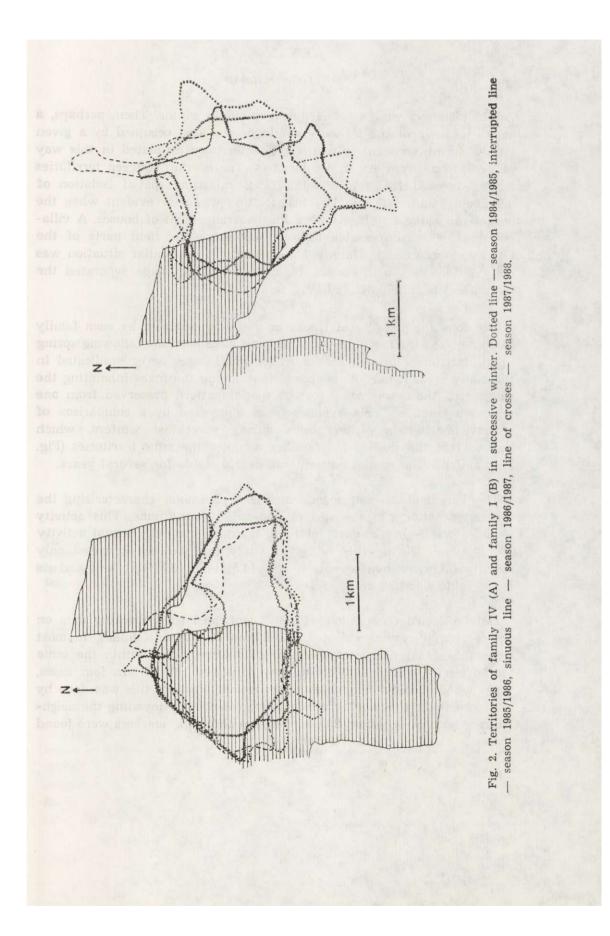
4.1. The size of Family Territories and its Variability

The size of territories calculated by winter snow-tracking varied from 313 to 638 hectares. The territories of various families overlapped slightly (Table 1). The territory of each family was composed of forest and field parts. The seasonal variability of the forest parts of the territories was somewhat lower than that of the field parts (the coefficient of variability was 10% and 16.9% respectively), but the difference was statistically not significant (0.1>p>0.05). It is possible, however, that despite intensive snow-tracking, the whole territory occupied by a given family could not be accurately outlined since not all wanderings of all

Tab	ne	T.

Size of the territories of red fox families (in ha). Percentage overlap between territories is given in brackets.

Contraction		Total distance			
Season	I	II	III	IV	of snow tracking (km)
1984/85 1985/86 1986/87 1987/88	440 (14.0 362 (0.8 351 (3.2 401 (4.2	$\begin{array}{c} 446 (0.0) \\ 521 (0.9) \end{array}$	406 (12.7) 324 (2.5) 392 (0.2) 379 (1.9)	$\begin{array}{c} 423 \ (15.1) \\ 313 \ (1.7) \\ 327 \ (2.3) \\ 326 \ (7.2) \end{array}$	290.3 168.7 151.0 83.0
Mean size	388	537	375	347	
Total territory size during 4 seasons	500 (14.8	646 (4.6)	499 (13.0)	512 (17.3)	



family members were tracked during a single winter. Then, perhaps, a better measure of the territory would be the area occupied by a given family during consecutive winters. The territory estimated in this way ranged in size from 499 to 646 hectares. The overlap between territories never exceeded 18% (mean value 12%), indicating spatial isolation of neighbour families (Table 1). This isolation was very evident when the border ran along a village with a linear arrangement of houses. A village provided an impassable barrier, separating the field parts of the territories occupied by family I and family II. A similar situation was observed in the north-eastern region where the village separated the territories of families III and IV.

The constant presence of tracks in the areas occupied by each family in winter, and the fact that young animals were born the following spring in all territories proved that a whole family was never eradicated in the study area. It may be supposed that among the foxes inhabiting the study area there was some sort of spatial pattern preserved from one winter to another. This hypohesis was supported by a comparison of spatial distribution of territories during successive winters, which showed that the studied fox families occupied the same territories (Fig. 2, A and B). The spatial pattern was nearly stable for several years.

The length of 24-hour wanderings is a parameter characterizing the locomotor activity of the species under local conditions. This activity includes wandering in quest of food, territory marking, sexual activity and playing. During this four-year study this parameter varied only slightly (in successive seasons it was 14.5, 14.0, 13.5, 13.1 km) and its mean value was 13.8 km.

Data collected from coloured baits, confirmed snow-tracking data on the territorial system and spatial isolation of various families. In most cases (61 of 65) plastic markers in scats were found within the same territories in which coloured baits were placed (Fig. 3). In four cases, foxes wandered into neighbouring territories. Perhaps this was done by young nomadic foxes or by resident foxes incidently invading the neighbouring territories. About 23% of faeces with plastic markers were found

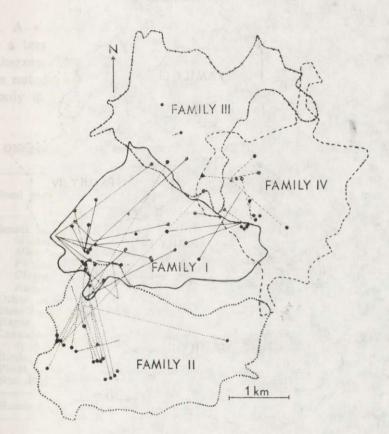


Fig. 3. Distribution of the territories of the observed families and wandering of foxes determined by coloured baits. Heavy lines are the boundaries of family territories determined by snow-tracking in 1984/1985—1987/1988, all kinds of the thin lines show the wandering of foxes, dots show the sites where faeces with plastic markers were found.

either at the site of bait placement or in close proximity (Fig. 3). This indicates that the animals returned often to the places where they had previously found food.

4.2. Structure of the Territory and its Effect on Diet Composition of Foxes

The territories occupied by various families were adjoining and they were very similar with respect to tree species composition, age of tree--stands, and the type of crops cultivated on the fields. In the territories occupied by families II and IV patches of wood in the fields were present, including alders along brooks (family II) and blackthorn-belts (family IV). The only factor markedly differentiating these territories was

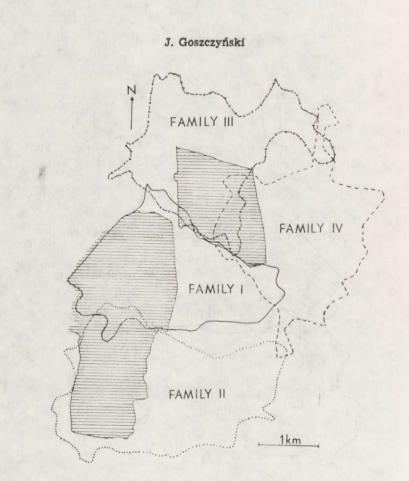


Fig. 4. Differences in the proportion of forest area included into fox territories (forest area is hatched).

the ratio of forest to ifeld areas included in a territory (Fig. 4). The area covered by forest was smallest in the territory of family IV (18%), intermediate in the territories of families II and III (36.5% and 29.3%, respectively) and greatest in the territory of family I (53.6%). An analysis of diet composition of various families showed that the most important components of diet were hares, small rodents, birds and carcasses of roe-deer, boars and dogs (Table 2). A positive correlation (significant at the level $\alpha = 0.05$) was found between the proportion of forest areas in the territory and the proportion of carrion in the diet. A similar correlation was found between the proportion of field areas and the proportion of small rodents in the fox diet. It may be assumed that rodents such as mice of genus *Apodemus* and bank voles were caught by foxes in forests. whereas field voles were caught in open areas. The proportion of forests in the

territory. A similar correlation was noted between the proportion of fields in a territory and the consumption of field voles (Fig. 5, A and B). Furthermore, in the food of family IV the highest proportion of fruit was noted, with predominance of sloes — produced by blackthorn present only in this territory.

Table 2 Composition of food of four red fox families (weight percentage

Righ.

-	Family				
Food composition	I	II	III	IV	
Small rodents (total)	22.68	27.48	29.15	33.87	
Microtus arvalis	10.21	15.86	22.80	28.46	
Microtus oeconomus	1.05	0.67	0.75	1.40	
Pitymys subterraneus	0.46	2.68	1.12	0.17	
Clethrionomys glareolus	9.31	6.26	3.36	1.92	
Apodemus sp.	1.65	2.01	1.12	1.92	
Other rodents	0.22	2.70	1.44		
Insectivores	0.87	0.89		1.25	
Hares	34.60	28.11	35.33	25.17	
Carcasses					
(roe deer, wild boar, dog)	20.05	16.83	13.71	11.14	
Birds	18.74	21.83	17.96	23.07	
Plant food (mainly fruit)	0.59	0.78	0.75	2.62	
Non-determined components	2.25	1.47	1.66	2.88	
Number of scats analysed	249	201	139	250	

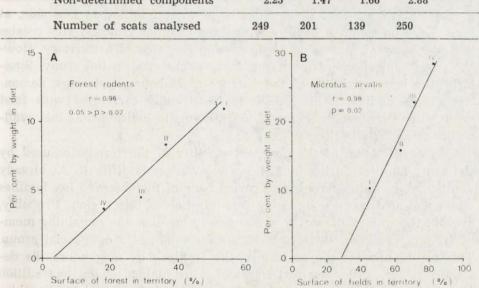


Fig. 5. The relationship between the proportion of forest area in a territory and the weight percentage of forest rodents (A) and between the proportion of field area in a territory and the weight percentage of field voles (B) in the fox food (Roman numerals designate the families).

5. DISCUSSION

Since within a social group (family) of foxes the male has a dominant position and includes the home ranges of females into his territory, the territories of families are equivalent to those of males. The estimation of the size of the territories have been the subject of many studies in which the size was found to differ widely (from several tenths of hectares to about ten square kilometres: Niewold, 1980; Boitani, Barrasso & Grimod, 1984; Voigt & Macdonald, 1985; Artois, 1985 and others). The size of the territories of 5 to 6.5 km², found in this study, falls approximately in the middle of the values reported in the literature. The variability in the size of territory, found by different authors has been explained as a result of differences in the local food available, the proportion between food-providing and shelter-providing areas within a local habitat, or different hunting pressure (Ables, 1969; Maurel, 1983; Kolb, 1984 and others).

Unquestionably, the Rogów region is not aboundant in small rodents, however, there is much small game (hares and birds) and carcasses available in winter. This fact probably, caused the low variability of the size of territories used by various fox families in successive winters. The specific features of the studied area *e.g.* distribution of forests within a cropland meant that the territories of most families on one side, at least, have no common borders with those of other families. This creates the possibility of increasing or decreasing the area of a territory. However, this "pulsation" of territories was not observed in this study. Similarly, the low variability of the distance of 24-hour wanderings, demonstrated by studies in the USSR, to be strongly correlated with food availability (Heptner & Naumov, 1967), seems to indicate that this availability was stable in the studied area.

An interpretation of the observed stability of the territories used by the same families during four successive winters is difficult. As already mentioned, in the analysed time period none of the observed fox families was eradicated despite intensive fox hunting in this region. Probably, even in the case of the death of one family member the remaining member(s) protected the territory until the formation of a new social group. This would prevent the capture of the territory by neighbours. To determine whether the territorial system is maintained owing to tradition (survival of at least one territory owner) and existing social relationships with neighbours, or is determined by the habitat structure (*e.g.* the distribution of forests and general availability of food in the area), the experiment could be done only by completely destroying the present system and observing its reconstruction.

The composition of diet was affected by the ratio of forest to field areas in the given territory. This can be explained by the opportunistic feeding strategies of foxes, well established in the literature, but for the first time demonstrated on a microhabitat scale in the present study. Although in the studied region forests were used mainly as shelter-providing areas, they were exploited by foxes also as hunting grounds. This was particulary evident in the case of family I, completly surrounded by territories of neighbours. The members of this family frequently used food provided by the forest.

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ROZMIESZCZENIE PRZESTRZENNE LISÓW VULPES VULPES W SEZONIE ZIMOWYM

Streszczenie

W ciągu czterech sezonów zimowych (od 1984/1985 do 1987/1988) w okolicach Rogowa w środkowej Polsce badano rozmieszczenie i wielkość terytoriów zajmowanych przez rodziny lisa *Vulpes vulpes* (Linnaeus, 1758). Powierzchnię rewiru oceniano na podstawie tropień zimowych (Ryc. 1) a dokładność tej metody sprawdzano stosując barwne przynęty wykładane w obrębie terytoriów.

Wielkość terytoriów zawierała się w granicach od 313 do 638 ha (Tabela 1). Stwierdzono, że poszczególne rodziny zajmowały w kolejnych sezonach praktycznie te same tereny (Ryc. 2). Ponieważ w trakcie jednego sezonu nie ujawnia się całości terytorium zajmowanego przez rodzinę, lepszą miarą wielkości rewiru jest powierzchnia terenu wykorzystywanego przez lisy w ciągu kilku sezonów. Tak oceniona wielkość terytorium wynosiła średnio ok. 540 ha (od 499 do 648 ha). Terytoria tylko w nieznacznym stopniu (średnio ok. 12%) nachodziły na siebie. Karmienie lisów pokarmem z barwnymi przynętami wykazało również izolację poszczególnych rodzin a rejestrowane wędrówki lisów mieściły się w obrębie terytoriów wyznaczonych na podstawie tropień zimowych (Ryc. 3). Długość dobowej wędrówki lisów oceniono na 13,8 km.

Stwierdzono, że choć analizowane terytoria były fizjograficznie mało zróżnicowane to jednak powierzchniowy udział lasów w każdym z nich był inny (Ryc. 4). Wykazano, że rodziny zajmujące rewiry o dużym powierzchniowym udziale lasów częściej korzystają z pokarmu zdobywanego w terenach zadrzewionych (Tabela 2 i Ryc. 5).