

Effect of rabies vaccination on population densities of *Vulpes vulpes* in south-western Poland (Carnivora: Canidae)

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Abstract. Despite intensive studies on the red fox (*Vulpes vulpes*), little is known about current spatial and temporal dynamics of red fox populations. This study analysed the spatial and temporal changes of red fox populations in the south-western part of Poland in relation to main factors shaping the changes, above all the rabies vaccination. After a long period of low population density depressed by rabies, a rapid increase took place in the last decade of the 20th century, as a consequence of vaccination applied on a wide scale throughout SW Poland. The populations reached the highest levels ever in the two first decades of the 21st century, they stabilized, and at the end of the second decade they began to decline. In 2001–2020, the crude population density ranged from 0.6 to 12 red foxes per 100 ha. It was highest in the regions with the lowest afforestation (6.7–12 ind./100 ha), whereas in the regions with the highest afforestation it was the lowest (0.6–0.8 ind./100 ha). The ecological consequences of these changes in the fox population densities are paralleled with changes in population densities of many prey species and fox's competitors.

Key words. Red fox, vaccination, monitoring, population dynamics, hunting bags, wildlife management.

INTRODUCTION

The red fox, *Vulpes vulpes* (Linnaeus, 1758), is a medium-sized carnivore, very versatile in food and habitat choice. Because of this high adaptability, it is a carnivore with the largest global distribution (LARIVIERE & PASITSCHNIAK-ARTS 1996). Typically it is an inhabitant of the ecotone zone (borderline of forest and open habitats), heterogenous and fragmented landscape in the temperate regions of its extensive range. However, in the last few decades it has adapted to many rural and urban habitats, such as gardens, parks, and even cemeteries (PANEK & BERESIŃSKI 2002). Small ground-dwelling mammals, lagomorphs and sciurids are the main components of its diet (SEQUEIRA 1980, LARIVIERE & PASITSCHNIAK-ARTS 1996, GOSZCZYŃSKI 1986, PANEK & BERESIŃSKI 2002, GOLDYN et al. 2003).

Despite intensive studies on the red fox, little is known about current spatial and temporal dynamics of red fox populations (undergoing expansion, stable, or in decline; DELCOURT et al. 2022). Fox density has an impact on wild species as well as on domestic animals, and even humans through the resurgence of diseases such as rabies, sarcoptic mange, canine distemper virus, echinococcosis, borreliosis, anaplasmosis, canine leishmaniasis, and tick-borne encephalitis (LARIVIERE & PASITSCHNIAK-ARTS 1996, CHAUTAN et al. 2014, DELCOURT et al. 2022).

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Table 1. Descriptive geographical data on the Opole (OP) and Lower Silesia Provinces (LSP) for 1990–2020 (based on the Statistical Yearbooks of the Opole Province 1990, 2000, 2010, 2020; Statistical Yearbooks of Lower Silesia Province 2000, 2010, 2020). No data available for LSP 1990.

parameter	1990	2000	LSP	2010	LSP	2020	LSP
	OP	OP		OP		OP	
overall surface area [km ²]	8535	9412	19947	9412	19947	9412	19947
inhabitants [million]	10.15	1.07	2.89	1.02	2.91	0.98	2.89
population density [inhab./km ²]	119	114	145	108	145	104	145
urbanisation [%]	52.1	52.6	68.2	52.4	69.4	53.1	70.5
forests [km ²]	2159	2466	5752	2609	6034	2619	6197
forests [%]	25.3	26.2	28.8	27.7	29.6	27.8	31.1
agricultural land [km ²]	5367	5747	11118	5519	9795	5164	11861
agricultural land [%]	62.9	61.1	55.7	58.6	49.1	54.9	59.5
arable land [km ²]	4388	4733	8732	4532	7753	4668	7384
arable land [%]	51.4	50.2	43.8	48.2	38.9	49.6	37.0
meadows and pastures [km ²]	?	801	2308	564	2036	431	1320
meadows and pastures [%]	?	8.5	11.6	6.0	10.2	4.6	6.6
waters [km ²]	187.6	189.1	?	191.6	177	203.0	184
waters [%]	2.2	2.0	?	2.1	0.9	2.2	0.9
protected areas [km ²]	1.9	636	2200	625.8	2178	624.8	2179
protected areas [%]	0.0	6.8	11.0	6.6	10.9	6.6	10.9
national parks	0.0	0.0	119.2	0.0	119.2	0.0	118.6
reserves	1.9	6.5	94.7	8.9	104.9	9.7	106.8
landscape parks	0.0	629.0	1986	616.9	1954	615.1	1954

The red fox also plays an important role in wildlife management as an efficient predator of livestock, small game and protected species.

In the south-western part of Poland, population density of the red fox was never studied, although raw statistics on the red fox hunting bags are available from the Opole Hunting Region (KOPIJ 1996, KOPIJ et al. 2015). The aim of this study is to analyze spatial and temporal changes of red fox population in SW Poland in relation to main factors shaping the changes.

STUDY AREA

The study area comprises two provinces (current voivodships) in south-western Poland, i.e. Opole Province (województwo opolskie) and Lower Silesia Province (województwo dolnośląskie). These include the following hunting regions (former voivodships from the years 1975–1999): Opole, Wrocław, Legnica, Wałbrzych, and Jelenia Góra (Fig. 1). Nowadays, the Opole hunting region is entirely encompassed within the Opole Province, while the four other hunting regions are located within the Lower Silesia Province (Table 1). The Opole, Wrocław, and Legnica hunting regions are basically lowlands, while there are mountains in the southern parts of the Wałbrzych and Jelenia Góra hunting regions. In total, 19 ecoregions were distinguished in the study area, based on physiographical features, type and degree of afforestation (compartmental, fragmented), elevation (lowlands, hills, mountains), and administrative divisions (Fig. 1).

The total surface area of such defined study area is 29,358 km², which constitutes 9.4% of the Poland's area. The land is located almost entirely within the Odra drainage system. Forests occupy 8,411 km², i.e. 28.6% of the study area (Fig. 2). There are 42 districts, 240 communities (gminas), 127 towns, and 3,406 villages. The number of inhabitants was 3.87 million in 2020 (Table 1).

Each hunting region is covered with a net of hunting districts (Fig. 1). Although all hunting districts include both forested and arable grounds, the proportion between them is varied (Fig. 2). There are also meadows and pastures, human settlements, rivers and other water bodies, waste and industry areas in each of the hunting district.

The average annual air temperature in the lowlands of SW Poland is 10.6 °C, for the Sudeten Mts 9.0 °C (the average for whole Poland is 9.9 °C). This average has increased from 7.6 °C in 1981–1990 to 9.3 °C in 2020 (an increase of 0.29 °C per 10 years; IMGW 2021). The long-term (1901–2000) average precipitation for Wrocław is 583 mm per annum (in the Sudeten Mts. the average is doubled). The amount of rainfall may greatly vary from year to year (318–892 mm/year; DUBICKA et al. 2002). In the first half of the 20th century, in most decades (except for 1901–1910) the rainfall was above the long-term average, while in the second half of the 20th century, in most decades (except for 1971–1980) the rainfall was below the long-term average (583 mm; DUBICKA et al. 2002). In SW Poland, snow cover lasts for 30–40 days per year in lowlands, 40–50 days in uplands, and 70–80 days in mountains. During the years 1981–2020, the most snowy winters were in 2005–2006 and 2009–2010, whereas the least snowy winters were in two successive winters between 1988–1990 and 2006–2008 (CZARNECKA 2012, KOPIJ & PANEK 2016, KOPIJ 2022).

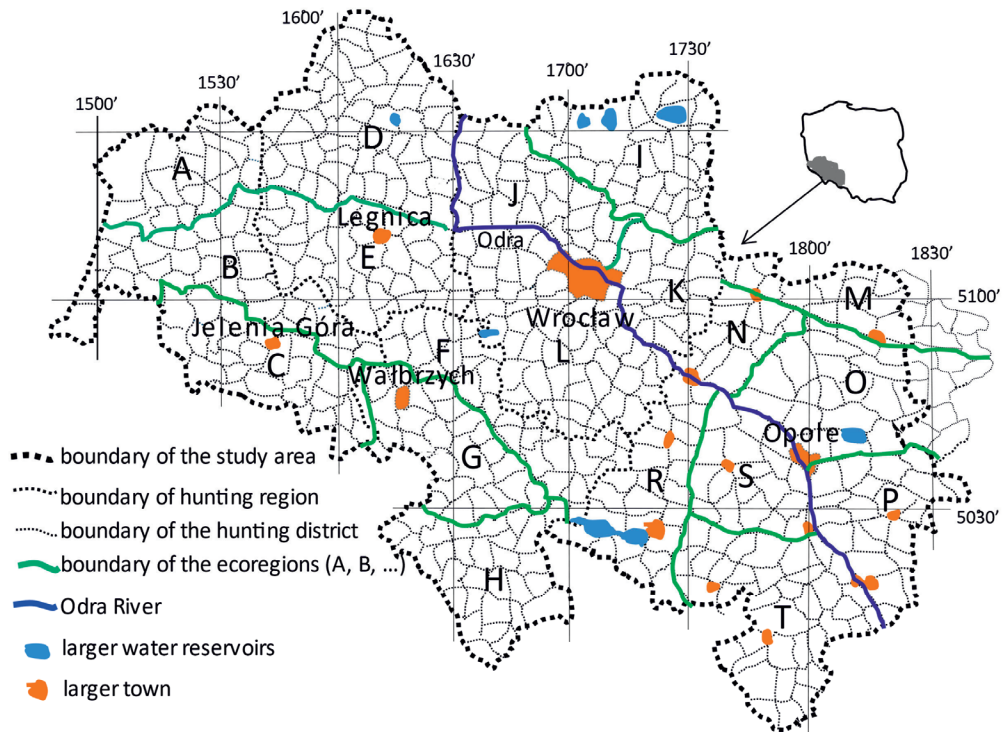


Fig. 1. The study area of south-western Poland divided into hunting districts, five hunting regions and 19 ecoregions.

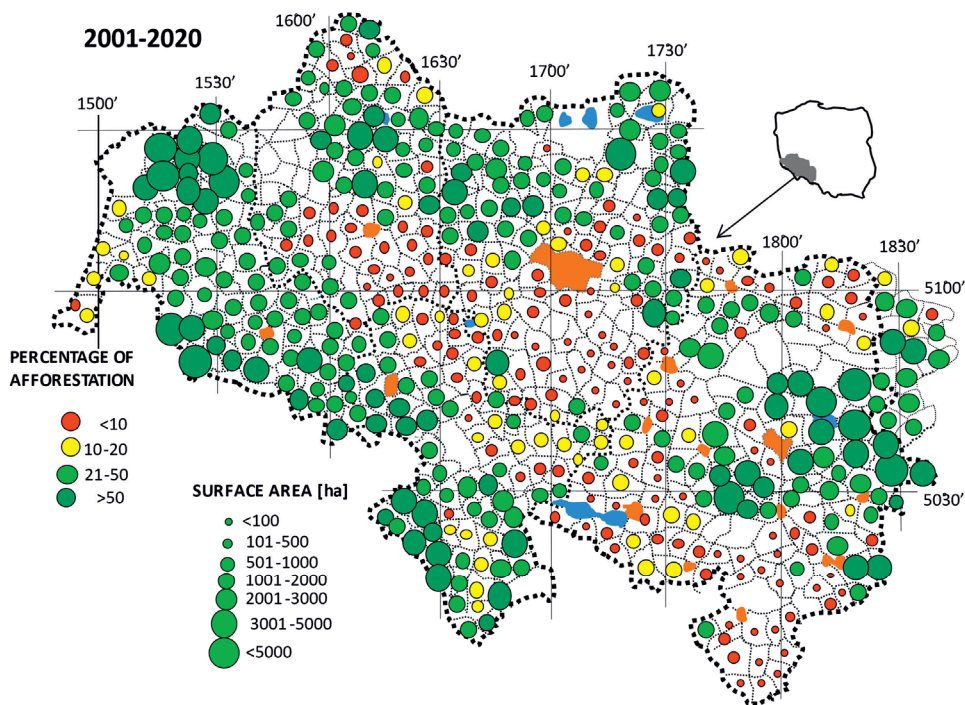


Fig. 2. The afforestation level in particular hunting districts of south-western Poland in 2020.

MATERIAL AND METHODS

This study is based on records from the years 1981–2020 kept by the Polish Hunting Association Research Station in Czempin near Poznań. Records refer to the number of red foxes harvested (hunting bags) and the estimated number of individuals (quotas) for each hunting district (hunting ground, management area) located in SW Poland, i.e. in five hunting regions (HR): Opole, Wrocław, Wałbrzych, Legnica, and Jelenia Góra (Fig. 1).

In the winter of each year the members of a hunting club of a given hunting district and staff of forest districts located within this hunting district attempt to estimate numbers of foxes in their respective hunting district. Numbers of red foxes in particular hunting district were estimated by snow tracking and den counts. In the entire period 1980–2020, estimations were based on the same rules (ZALEWSKI et al. 2018).

Den counting is the most efficient and most frequently used method (ZALEWSKI et al. 2018). Dens are searched for throughout the year, but mostly in autumn and winter, and plotted on a map. Searching in snowy winter is especially efficient, as it is easy to determine (footprints) whether the den is currently inhabited by the fox and not by the badgers or racoon dogs, which are inactive in this period. Each den is revisited in early spring to record whether it is occupied or not; and again in late spring in order to determine whether it is occupied by breeding animals (the presence of young animals, their excrements left around the den entrance, presence of prey remnants and playing grounds). Each den occupied in early spring is an equivalent of 2–2.5 individuals; dens with young animals are used to calculate a density of breeding groups.

Harvested numbers are expressed as the total number of red foxes shot in a given hunting district in a given hunting season. Each hunting season begins on 1 April and ends on 31 March of the next year. For each ecoregion (Fig. 1), six hunting districts were randomly selected to calculate mean population density in the ecoregion. Population density is expressed as the mean number of red foxes harvested per one hunting season and per total surface of a hunting district (crude density) or per the surface of afforested area within the hunting district (ecological density). The densities are expressed as the number of individuals harvested per 100 ha. The mean value (long-term average) is based on data from 20 years (2001–2020). The ratio between the crude density and ecological density was calculated by dividing the ecological density by the crude density.

According to the Polish Hunting Code, male and juvenile red foxes can be hunted throughout the year, while adult females from 31 September to 15 January only (Dz. U. 2020.1683). So, this rule was applicable throughout the study period 1980–2020.

For each hunting district the following parameters were calculated: the total surface area (including towns, villages, roads), the percentage of arable ground coverage and the percentage of forest coverage. These calculations were made by the Polish Hunting Associations and were continually updated if any changes in the land use structure took place.

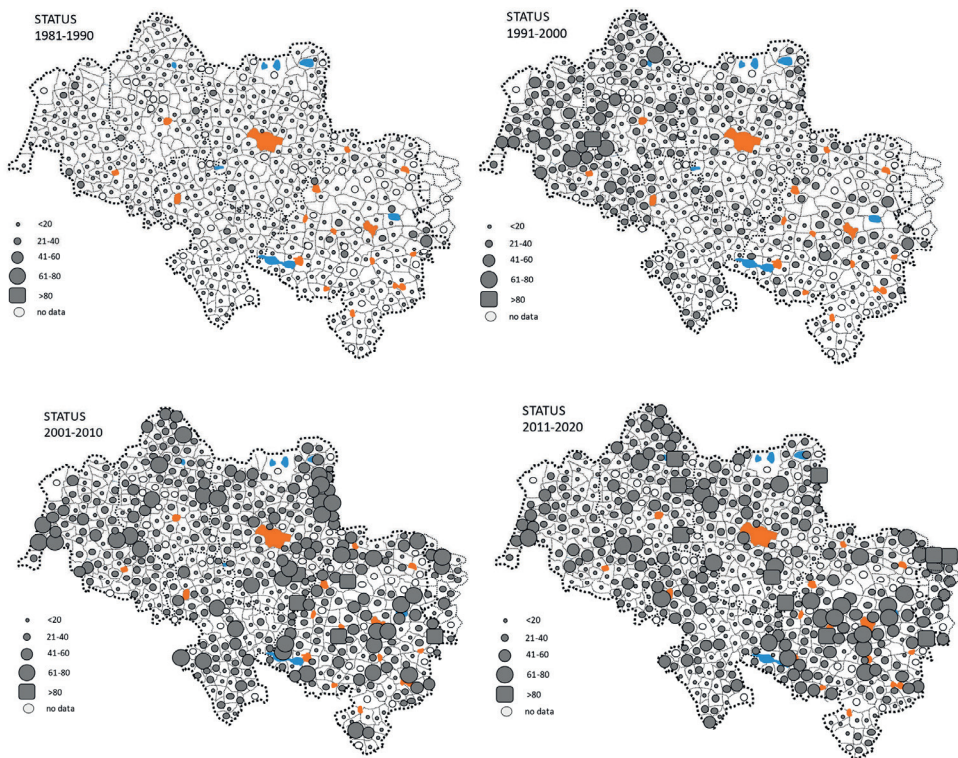


Fig. 3. Estimated mean number of foxes in particular hunting districts of south-western Poland before (1981–1990), at the beginning (1991–2000), during (2001–2010) and after (2001–2020) the rabies vaccination campaign.

RESULTS AND DISCUSSION

During the years 1981–1990, more than 20 red foxes were reported only from 23 hunting districts in SW Poland, including 10 districts in the Opole hunting region (HR). In the next decade, 20 and more red foxes were reported from most hunting districts in the Jelenia Góra and Legnica HR. In the Wałbrzych, Wrocław and Opole HR, the increase was much less pronounced (Fig. 3).

In 2001–2010, more than 20 red foxes were reported from most hunting districts in all hunting regions. There were 44 hunting districts, each with more than 60 red foxes (Fig. 3). In the following decade, the numbers of red foxes in most hunting districts remained similar to the years 2001–2010. In the Opole HR, more than 60 red foxes were reported from 19 hunting districts, whereas there were 15 such districts in the remaining hunting regions in SW Poland (Fig. 3).

During the years 2001–2010, 200 and more red foxes (i.e. 20 per year per district) were harvested from most hunting districts. A similar situation of harvesting remained in the next decade. The harvesting was also evenly distributed over all hunting regions (Fig. 4).

The crude population density ranged from 0.6 to 12 red foxes per 100 ha. It was the highest in ecoregions with the lowest afforestation, i.e. the Głubczyce Plateau (12 ind./100 ha), Nysa region (8.5 ind./100 ha) and the Wrocław Plain (6.7 ind./100 ha), whereas in the regions with the highest afforestation it was the lowest (Lower Silesian Forests – 0.6 ind./100 ha, Stobrawa Forests – 0.8 ind./100 ha). A reverse situation was recorded while calculating ecological density (Table 2).

Population density of the red fox can be assessed by a wide range of methods. Each one has advantages and disadvantages, particularly in terms of their applicability to different habitats, time expenditure and financial costs. These methods can be divided in two groups: direct (counting animals) and indirect (counting scats, footprints, dens etc.).

The indirect methods include: footprint counts on snow along a transect, faecal count along a transect, breeding den counts in selected area, acoustic surveys, visitation rates to food stations, shed hairs and faecal material containing DNA used to derive a genetic profile of individual animals. Indirect methods are relatively cheap, and can be applied in various habitats, but their main limitation is that their relationship with absolute animal density requires validation

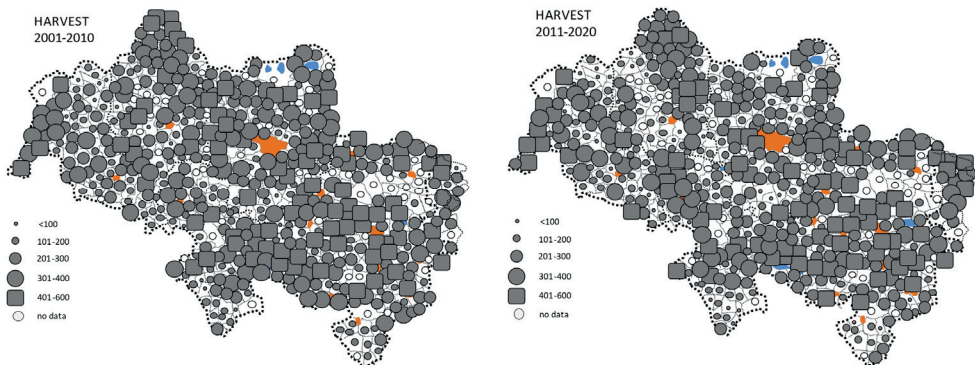


Fig. 4. Total numbers of foxes harvested in particular hunting districts of south-western Poland during (2001–2010) and after (2011–2020) the rabies vaccination campaign.

Table 2. Population densities (individuals per 100 ha) of the red fox in the period after the rabies vaccination campaign (average for 2001–2020). Letters (#) in the first column refer to those in Fig. 1. Ecological density refers to the number of harvested foxes/100 ha of forest, whereas the crude density refers to the number of harvested foxes/100 ha of the total area.

#	region	hunting districts	area [ha]		% forests	density		
			whole	forests		crude	ecol.	
Jelenia Góra Hunting Region								
A	Lower Silesian Forests	5, 7, 12, 15, 16, 20	33,211	27,782	83.7	0.59	0.50	
B	Silesian-Lusatian Lowland	31, 33, 39, 40, 43, 52	25,500	6,438	25.2	3.03	0.76	
C	West Sudeten Mts.	54, 55, 66, 71, 78, 80	28,332	20,249	71.5	0.63	0.45	
Legnica Hunting Region								
D	Northern (lowland) part	1, 2, 17, 18, 33, 35	22,795	8,467	37.1	2.33	0.86	
E	Southern (hills) part	62, 67, 69, 71, 72, 78	29,400	3,754	12.8	5.35	0.68	
Wałbrzych Hunting Region								
F	Sudeten Upland	6, 7, 21, 31, 38, 39	26,700	3,730	14.0	3.91	0.55	
G	Middle Sudeten Mts.	10, 18, 23, 25, 28, 30	26,715	10,576	39.6	1.79	0.71	
H	East Sudeten Mts.	54, 67, 69, 70, 72, 82	16,191	9,491	58.6	1.26	0.74	
Wrocław Hunting Region								
I	Barycz Valley and Trzebnica Hills	2, 7, 8, 13, 15, 16	30,127	10,091	33.5	1.42	0.47	
J	Głogów-Milicz Depression	10, 30, 32, 45, 47, 59	27,803	9,090	32.7	1.43	0.47	
K	Oleśnica Plain	71, 85, 86, 95, 96, 107	27,283	9,154	33.6	2.24	0.75	
L	Wrocław Plain	67, 79, 90, 100, 113, 116	28,938	1,884	6.5	6.74	0.44	
Opole Hunting Region								
M	Northern part of the Opole Prov.	3, 7, 12, 14, 15, 16	32,497	4,375	13.5	5.15	0.69	
N	Brzeg Land	17, 19, 20, 21, 50, 51	33,704	11,738	34.8	2.15	0.75	
O	Stobrawa Forests	28, 33, 34, 35, 36, 39	38,926	32,444	83.3	0.75	0.62	
P	East-central part of the Opole Prov.	82, 83, 91, 123, 126, 129	41,259	20,721	50.2	1.11	0.56	
R	Nysa Land	74, 76, 78, 114, 120, 122	34,320	2,258	6.6	8.54	0.56	
S	Niemodlin Forests	47, 59, 64, 67, 96, 101	41,259	20,721	50.2	1.30	0.67	
T	Głubczyce Plateau	105, 109, 132, 133, 138, 146	34,320	2,258	6.6	11.95	0.51	

(TREWHELLA et al. 1988, SADLIER et al. 2004, WEBBON et al. 2004, VINE et al. 2009, KEULING et al. 2011, CORTAZAR-CHINARRO et al. 2019, PALENCIA et al. 2021, DELCOURT et al. 2022).

The following direct methods can be used to assess fox population density: driven counts, spotlight counts, capture-mark-recapture/resight, radio-tracking, counts of road traffic or poisoning casualties, sighting and questionnaire surveys, hunting bag statistics (SADLIER et al. 2004, WEBBON et al. 2004, VINE et al. 2009, KEULING et al. 2011, CORTAZAR-CHINARRO et al. 2019, PALENCIA et al. 2021, DELCOURT et al. 2022). Hunting bag statistics is the most frequently applied method. It is especially applicable to monitor changes in numbers over large areas. The main limitation of this method is that the results are directly affected by the hunting effort.

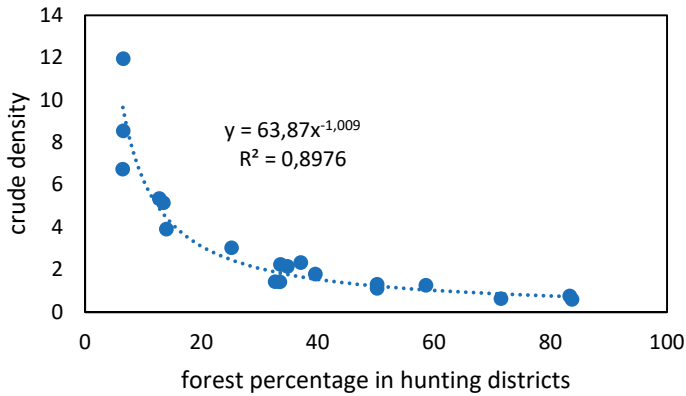


Fig. 5. Comparison of the percentage of forests in hunting districts and the crude density of foxes.

However, if this effort is standardized over a certain area and time then the limitation is not so important. Hunting may also induce too much mortality, thus influencing the population dynamics. However, it has been proved that in most cases, this removal has little to no impact on the population dynamics on a large scale, because local mortality is soon compensated through immigration. There may be only a local (area of less than 10 km²) impact in a particular hunting district (HEYDON & REYNOLDS 2000, BAKER & HARRIS 2006).

In this study, population densities were assessed using the hunting bag statistics. It should be emphasized that the population densities calculated in this way represent always the minimum values, as hunters never eliminate all red foxes in a given hunting district. According to KOŠKA et al. (2013), red fox density should be 0.1–0.3 ind./100 ha. In all ecoregions in SW Poland,

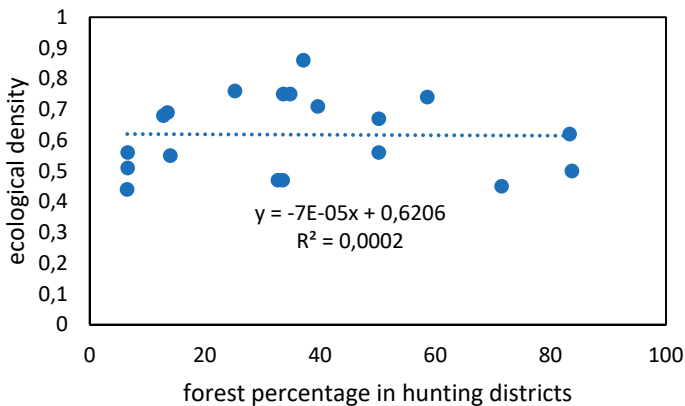


Fig. 6. Comparison of the percentage of forests in hunting districts and the ecological density of foxes.

Table 3. Population density (individuals per 100 ha) of the red fox in Poland. Years of the rabies vaccination campaign are bold-typed

locality	period	ind./100 ha	reference
Suwałki Landscape Park, NE Poland	1995–1996	0.3	GOSZCZYŃSKI 1999
Białowieża Forest, NE Poland	1985–1989	0.2	JĘDRZEJEWSKA & JĘDRZEJEWSKI 1993
	2000–2006	0.4	JĘDRZEJEWSKA & JĘDRZEJEWSKI 1993
	2011–2016	0.7	GRYZ & KRAUZE-GRYZ 2017
central-eastern Poland	1998–1999	0.3	BOMBIK et al. 2014
	2002–2003	0.5	BOMBIK et al. 2014
	2006–2007	0.8	BOMBIK et al. 2014
Rogów countryside, Central Poland	1979–1987	0.7	GOSZCZYŃSKI 1989
	2011–2012	0.9	KOŚKA et al. 2013
Czempiń countryside, W Poland	1997–2000	1.3	PANEK & BERESIŃSKI 2002
Poznań surroundings, W Poland	1999–2000	1.9	GOSZCZYŃSKI et al. 2008
SW Poland	2001–2020	0.6–12.0	this study

the density was higher than 0.6 ind./100 ha, and in some regions, it was higher by an order of magnitude (Table 2). It is also much higher than in other regions of Poland (Table 3), and higher than in many of the European countries (STUBBE 1980, WEBBON et al. 2004, HEYDEON et al. 2020, DELCOURT et al. 2022). It should be therefore assumed that most ecoregions in SW Poland are overpopulated by the red fox.

In the case of the red fox, the crude density is usually calculated. It is expressed as the number of individuals per 100 ha of the total surface area. In hunting districts where open space predominates in the landscape (especially those with forests accounting for less than 30%), habitats (especially foraging habitats) outside the forest are equally important to the red fox as those in

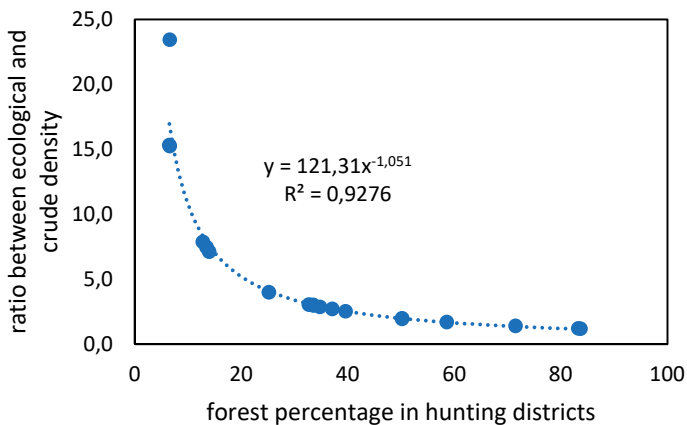


Fig. 7. Relationship between the percentage of forests in hunting districts and the ratio between crude and ecological densities in south-western Poland in 2001–2020.

forests. In hunting districts with less than 10% of forests (e.g. the Głubczyce Plateau in the Opole HR), habitats outside forests play an even more important role than those in forests. As a result, the crude density is negatively correlated with the degree of afforestation in a given ecoregion in SW Poland (Fig. 5), but there is an absolute lack of such correlation for the ecological density (number of individuals per 100 ha of forest; Fig. 6). The ratio between the crude and ecological density is therefore very high (>5) for landscapes with forest fragments (afforestation lower than 20%), and falls below 3 when the afforestation is higher than 30% (Fig. 7).

The major finding of the presented study is that in 1981–2000 the red fox population in SW Poland rapidly expanded eastwards, stabilized in 2001–2010, and in 2011–2020 slightly expanded westwards. As rabies is regarded as the main factor limiting fox numbers (TRYJANOWSKI et al. 2002, BOMBIK et al. 2014), it is not surprising to find that the pattern of red fox population growth in SW Poland coincides with a campaign against rabies. In Poland, the vaccination of red foxes against the rabies started in 1993 in the areas bordering Germany, and in the following years it was gradually introduced eastwards, so that by the year 2002 the whole territory of Poland was under this programme (BOMBIK et al. 2014). A similar population growth was recorded in the remaining parts of the country. While in 1976, the average population density of the red fox in Poland was 0.3 ind./100 ha (PIELOWSKI 1976); in 1989 it was 0.6 ind./100 ha (GOSZCZYŃSKI 1995), while in 2012 it was 0.8 ind./100 ha (KOŚKA et al. 2013). Two-three-fold increase over these years was also evidenced in the Białowieża Primeval Forest and in the Rogów region (a farmland with forest fragments; Table 3). Besides vaccination, few other factors could contribute to this expansion: decline in targeted hunting effort, climate change, adaptation to urban habitats, and higher use of the abundant human-generated garbage (PANEK & BRESIŃSKI 2002, TRYJANOWSKI et al. 2002, GOSZCZYŃSKI et al. 2008).

After the expansion, the red fox population stabilized in most hunting districts in SW Poland (Figs. 2 and 3). There are, however, some indices of a slight population decline in certain regions, e.g. in the southern part of the Opole HR or in the Lower Silesian Forests. This decline could be caused by resource depletion in some hunting districts or by an emergence and transmission of a new disease, the sarcoptic mange. This disease is already widespread in western Europe. It is epizootic and may cause population decline, mainly through reduced growth rate and fertility (DELCOURT et al. 2022).

To be concluded, after a long period of low population density depressed by the rabies, a rapid increase took place in the last decade of the 20th century, as a consequence of vaccination applied on a wide scale throughout SW Poland, other regions of the country, and in other European countries. The population reached the highest level ever in the two first decades of the 21st century, it stabilized, and at the end of the second decade it begun to decline. The ecological consequences of these changes in fox population densities are paralleled with changes in population densities of many prey species (e.g. *Perdix perdix*, *Lepus europaeus*, *Oryctolagus cuniculus*, *Capreolus capreolus*) and fox's competitors (*Meles meles*, *Nyctereutes procyonoides*, *Mustela vison*, *Mustela putorius*, *Martes* spp., free-ranging dogs).

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