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POPULATION DENSITY OF THE WILD BOAR (*SUS SCROFA*) IN SOUTH-WESTERN POLAND IN 1981–2020

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wild boar, population estimation, climate change, wildlife management, game animals, hunting bags

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Abstract

The study is based on the analysis of hunting bag data from the years 1981–2020. In 1980–1990, 38 016 wild boars, whereas in 1991–2000, 43 490 wild boars were culled (14.4% increase) in south-western Poland (29 358 km^2, forests comprise 28.6%). In 2001–2010, there were 69 052 individuals harvested (58.8% increase in relation to the previous decade). In 2011–2020, the harvest was 3-fold higher in relation to the previous decade and 5.6-fold higher in relation to 1980–1990. During the years 1981–1990, an estimated number of 51–100 wild boars were recorded only in five hunting districts, whereas there were 23 such districts in the next decade. After a population expansion in 2001–2010, there were 32 districts, each one with 101–200 wild boars. Ecological population densities (per forest area) of the wild boar was spatially greatly varied in south-western Poland, ranging from 9.1 ind./1000 ha in extensive woodlands of the Lower Silesian Forests to as much as 147.2 ind./1000 ha in the Wrocław Plain dominated by farmlands with forest fragments. The crude density was much lower and much less spatially varied than the ecological density; it was the lowest (7.4 ind./1000 ha) in the West Sudeten Mts. and the highest, 23.8 ind./1000 ha in the East Sudeten Mts. When only ecological density is calculated, a strongly distorted picture may emerge, where the highest density will always be in deforested areas with forest fragments, whereas it will be inevitably the lowest in the most afforested ones. The crude density will, therefore, reflect much better the actual population densities. In comparison with the line transect track index, the hunting bags analysis provide similar population density estimates, whereas in the comparison with the block count census, population densities based on the hunting bag analysis are underestimated. However, it should be emphasised that density estimates based on hunting bag analysis will always be lower than the real densities, as not all animals are harvested in a given population. The following ecological variables may shape wild boar population density in south-western Poland: food resources (maize, mast); temperature (winter and early spring); precipitation (snow and rainfalls); and diseases (especially African swine fever).

Cite as

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Щільність популяції свині дикої (*Sus scrofa*) у південно-західній Польщі протягом 1981–2020 років

Гжегож Копій

Резюме. Дослідження базується на аналізі мисливських здобувань за 1981–2020 роки. У 1980–1990 рр. 38016, а у 1991–2000 рр. — 43490 свиней диких (на 14,4% більше) було здобуто у південно-західній Польщі (29358 км^2, ліси складають 28,6%). У 2001–2010 рр. здобуто 69052 особини (на 58,8% більше порівняно з попереднім десятиліттям). У 2011–2020 роках здобування було у 3 рази вищим порівняно з попереднім десятиліттям і у 5,6 рази вищим порівняно з 1980–1990 роками. Протягом 1981–1990 рр. лише в п'яти мисливських районах було зареєстровано орієнтовну чисельність 51–100 свиней диких, тоді як у наступне десятиліття таких районів було 23. Після спалаху чисельності, що стався у 2001–2010 роках, таких стало 32 райони, у кожному по 101–200 свиней диких. Екологічні щільність популяції (на лісовкритих площах) свині дикої просторово сильно варіювала на південному заході Польщі, коливаючись від 9,1 особин/1000 га в лісових угіддях, прилеглих до Нижньосілезьких лісів, до 147,2 особин/1000 га на Вроцлавській низовині, де переважають сільськогосподарські угіддя з фрагментами лісу. Загальна щільність була набагато нижчою і просторово набагато менш мінливою, ніж екологічна щільність; вона була найнижчою (7,4 екз./1000 га) у Західних Судетах і найвищою (23,8 екз./1000 га) у Східних Судетах. Якщо розраховувати лише екологічну щільність, може виникнути сильно спотворена картина, де найвища щільність завжди буде у знелісених районах із фрагментами лісу, тоді як вона неминуче буде найнижчою в найбільш заліснених. Таким чином, загальна щільність набагато краще відображатиме фактичну щільність популяції. Якщо порівняти з показниками трансектного обліку, аналіз мисливських здобувань дає подібні результати оцінки щільності популяції, а у порівнянні з поголовним обліком за ділянками цей метод дає занижені результати. Однак варто наголосити на тому, що оцінки щільності популяції за даними мисливських здобувань завжди будуть нижчими за реальними показниками щільності, оскільки здобувають не всі особини даної популяції. На щільність популяції свині дикої у південно-західній Польщі можуть впливати такі екологічні фактори як кормовий ресурс (кукурудза, плоди лісових дерев), температура (взимку та ранньою весною), опади (сніг і дощ) та хвороби (зокрема африканська чума свиней).

Ключові слова: свиня дика, оцінка популяції, зміна клімату, управління дикими тваринами, мисливські тварини, мисливські здобування.

Introduction

The wild boar *Sus scrofa* is a cosmopolitan species found in all continents, except for Antarctica [Barrios-Garcia & Ballari 2012]. Although today it is widespread and common all over Europe, its population fluctuated strongly in the past. In the British Islands the wild boar had been extinct since the 13th century and reappeared in the wild again only at the end of the 20th century [Goulding *et al.* 2003]. In some other regions (e.g. Fennoscandia and Greece), it had been extinct for decades [Jędrzejewski et al. 1997; Tsachalides & Hadjistekrotis 2009] and now it is common again. This success may be related mainly to high reproductive potentials (r-reproductive strategy as in rodents and rabbits), high plasticity in food selection and foraging behaviour (the wild boar is an omnivore generalist); and lack of natural predators in most areas (mainly wolfs *Canis lupus*).

This increase in numbers of the wild boar results in increasing damages to crop plants caused by this species. This human–wildlife conflict becomes especially severe in areas where fragmented forests border directly with agricultural lands of crop plant preferred by the wild boar as source of food (e.g. maize, potatoes, and rapeseed). There is therefore an urgent need to mitigate this conflict. Any control measures should be based on a sound knowledge of biology and ecology of this species. One of the most important aspect of ecology to be considered in this regard is population density.

In south-western Poland, Kopij [1996] has provided raw data on the population size and number of harvested wild boars during the years 1960–1990 in one of the five hunting regions in this province, but no analysis was attempted. The data from 1960–1980 refer either to the entire region or to a particular administrative district (powiat) within the Opole Province. The data after 1980 refer to particular hunting districts, but only to three selected hunting seasons: 1978–1979, 1983–1984, and 1988–1989. Fonesca *et al.* [2007] using the line intercept tracks method estimated population density

of the wild boar in a few areas in the Sudeten Mts. and in the Opole Province. Bobek *et al.* [2018] have estimated population densities of the wild boar in the 2017–2018 hunting season in various ecoregions in south-western Poland using the block count method. Kopij & Panek [2016] have analysed changes in population densities of the wild boar in a deforested region in the south-eastern part of Opole Province.

The purpose of this study is to estimate population size of the wild boar in all hunting districts in south-western Poland, separately for each of the four recent decades (1981–2020). This, in turn, will enable to calculate crude and ecological densities for particular ecoregions.

Material and Methods

This study is based on records from the years 1981–2020 kept by the Polish Hunting Association Research Station in Czempiń near Poznań. Records refer to the number of wild boards harvested (hunting bags) and the number of wild boars estimated (quotas) for each hunting district (hunting ground, management area) located in south-western Poland, that is, in five hunting regions [HR]: Opole, Wrocław, Wałbrzych, Legnica, and Jelenia Góra (Fig. 1).

Numbers of wild boars in particular hunting district were estimated in two ways: a) year-round observations; b) drive counts. In the entire period of 1980–2020, estimations were based on the same rules. At the beginning of spring of each year, members of a hunting club of a given hunting district and staff of forest districts located within this hunting district attempted to estimate the numbers of wild boars in their respective hunting district. This estimation was based on direct field observations conducted throughout the year in a given hunting district, as well as on the subjective opinions of experts. During drive counts forest compartments were selected for a survey. Such compartment cover about 10% of the surface area of a given hunting region. Each selected compartment was surrounded by observers, who were spaced one from another by a distance of 50–100 m, so that visual contact could be maintained. The observers on three sides were stationary, while those on the remaining side moved inside the compartment, 'combing' the whole area of this compartment. All observers recorded all wild boars passing through the line of observers on their right side only, and the observers recorded all wild boars entering or leaving the surveyed compartment [Pucek *et al.* 1975, Jędrzejewska *et al.* 1997]. Observations are analysed, generalised, and assumed as estimations.

According to the Polish Hunting Code, male and juvenile wild boars can be hunted throughout the year, while adult females from 31 September to 15 January (Dz. U. 2020.1683). So, this rule was applicable throughout the study period of 1980–2020. In the late 2010s, drastic measures were taken in Poland to control the African swine fewer (ASF) epidemic.

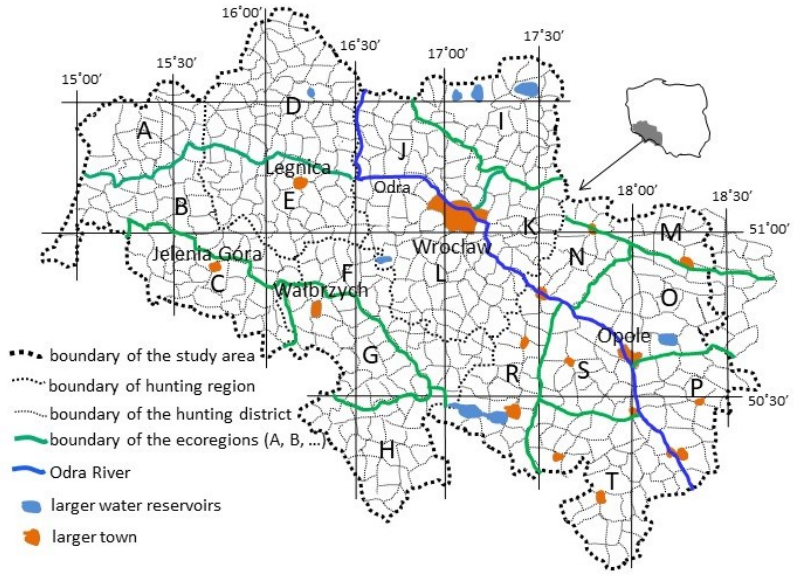


Fig. 1. The study area, south-western Poland, divided into hunting districts, 5 hunting regions and 19 ecoregions.

Рис. 1. Територія дослідження — південно-західна Польща, поділена на мисливські райони, 5 мисливських регіонів та 19 екорегіонів.

For each hunting district, the following parameters were calculated: the total surface area (including towns, villages, and 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.

Harvested numbers are expressed as the total number of wild boards 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 this ecoregion. Population density is expressed as the mean number of wild boars 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 1000 ha. The mean value (long-term average) is based on data for 20 years (2001–2020). The ratio between the crude density and ecological density was calculated by dividing the ecological density by the crude density.

Study area

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

The total surface area of such defined study area is 29 358 km^2, which constitutes 9.4% of Poland's surface area. The land is located almost entirely within the Odra drainage system. Forests occupy 8411 km^2, that is, 28.6% of the study area (Fig. 2).

There are 42 districts, 240 counties (gminas), 127 towns and 3406 villages. The number of people living in this area was 3.87 million in 2020 (Table 1).

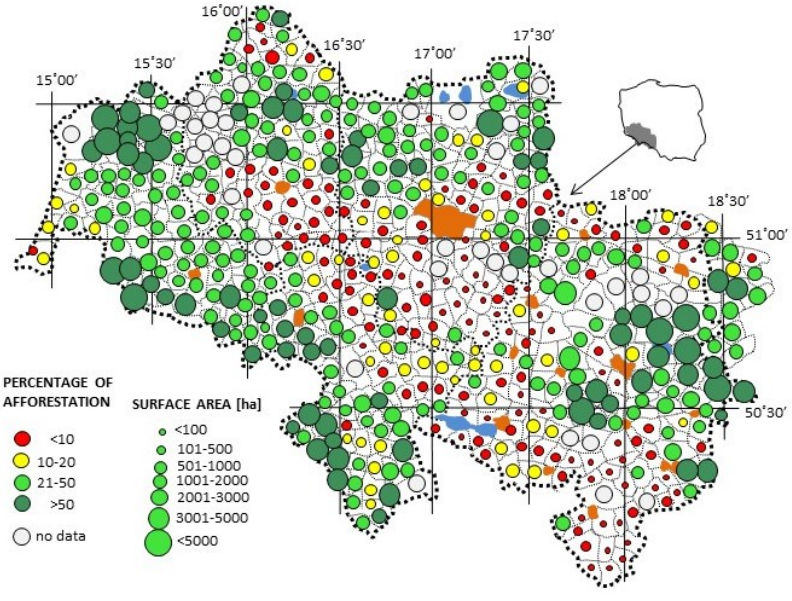


Fig. 2. Afforestation in particular hunting districts of south-western Poland in 2020.

Рис. 2. Залісення в окремих мисливських районах на південному заході Польщі у 2020 році.

Table 1. Land use and livestock in Opole Province (OP) and Lower Silesia Province (LSP) during the years of 1990–2020 (based on Statistical Yearbooks of Opole Province 1990, 2000, 2010, 2020; Statistical Yearbooks of Lower Silesia Province 2000, 2010, 2020)

Таблиця 1. Землекористування та тваринництво в Опольському воєводстві (OP) та Нижньосілезькому воєводстві (LSP) протягом 1990–2020 рр. (на основі статистичних щорічників Опольського воєводства за 1990, 2000, 2010, 2020 рр.; статистичних щорічників Нижньосілезького воєводства за 2000, 2010, 2020 рр.)

Parameter	1990		2000		2010		2020	
	OP	LSP	OP	LSP	OP	LSP	OP	LSP
Overall surface area [km^2]	8535		9412	19947	9412	19947	9412	19947
Number of people [mln]	10.15		1.07	2.89	1.02	2.91	0.98	2.89
Population density [people/1 km^2]	119		114	145	108	145	104	145
Urbanization [%]	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
Sown area [km^2]	2377		3454	5662	3222	5079	3350	5169
Wheat	1163		1651	2609	1479	2584	1519	2542
Rye	150		262	578	127	378	118	210
Barley	497		614	819	623	610	589	637
Oats	95		77	202	80	231	69	194
Triticale	220		166	184	258	331	332	466
Cereal mixtures	251		357	?	220	135	106	85
Maize	**43**		**325**	**461**	**422**	**492**	**614**	**985**
Potatoes	364		261	551	86	232	59	143
Sugar beet	315		238	311	145	191	159	203
Rape	52		450	680	876	1272	775	1271
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
Number of cattle [x10^2]	33.4		1445	1659	1226	1091	1020	1038
Cattle/100 ha of agricultural land	23.0		25.2	15.1	23.9	11.9	25.9	11.6
Number of pigs	600.1		6881	4662	6012	3007	3233	1576
Pigs/100 ha of agricultural land	131.0		119.9	42.5	117.2	32.7	82	17.5
Number of sheep	81.9		33.6	162	30.6	131	27.4	122
Sheep/100 ha of agricultural land	?		0.6	1.5	0.6	1.4	0.6	1.4
Number of horses	?		38.5	121	41.6	125	?	?
Horses/100 ha of agricultural land	?		0.9	1.1	0.8	1.1	0.9	?
Number of poultry	?		38450	47877	48839	59229	53814	70611
Poultry/100 ha of agricultural land	?		?		951.8	644.2	1164	786.3

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

The average annual air temperature is 10.6˚C in the lowlands of south-western Poland, and 9.0˚C for the Sudeten Mts. (the average for Poland is 9.9˚C). This average has increased form 7.6˚C in 1981–1990 to 9.3˚C in 2020 (0.29˚C per 10 years) (IMiGW PIB 2021). The long-term (1901–2000) average precipitation for Wrocław is 583 mm per annum (in the Sudeten Mts. the average is twice as much). The amount of rainfall may greatly vary from year to year (318–892 mm) [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 the years 1971–1980) the rainfall was below the long-term average (583 mm) [Dubicka *et al.* 2002]. In south-western 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 of 1981–2020, the most snowy winters were in 2005/2006 and 2006/2, whereas the least snowy winters were in two successive winters 1988–1990 and 2006–2008 [Czarnecka 2012].

Results

During the years of 1981–1990, more than 800 wild boars were harvested in only one hunting district near Olesno. More than 600 were culled in two hunting districts in Opole HR and one hunting district in Wrocław HR (in Barycz Valley). In 29 other hunting districts, 201–400 wild boars were harvested in each district (Fig. 3). In the next decade (1991–2000), there were four hunting districts in Opole HR, each with more than 800 wild boars culled. In all other hunting regions there were only single districts with such high number of wild boars.

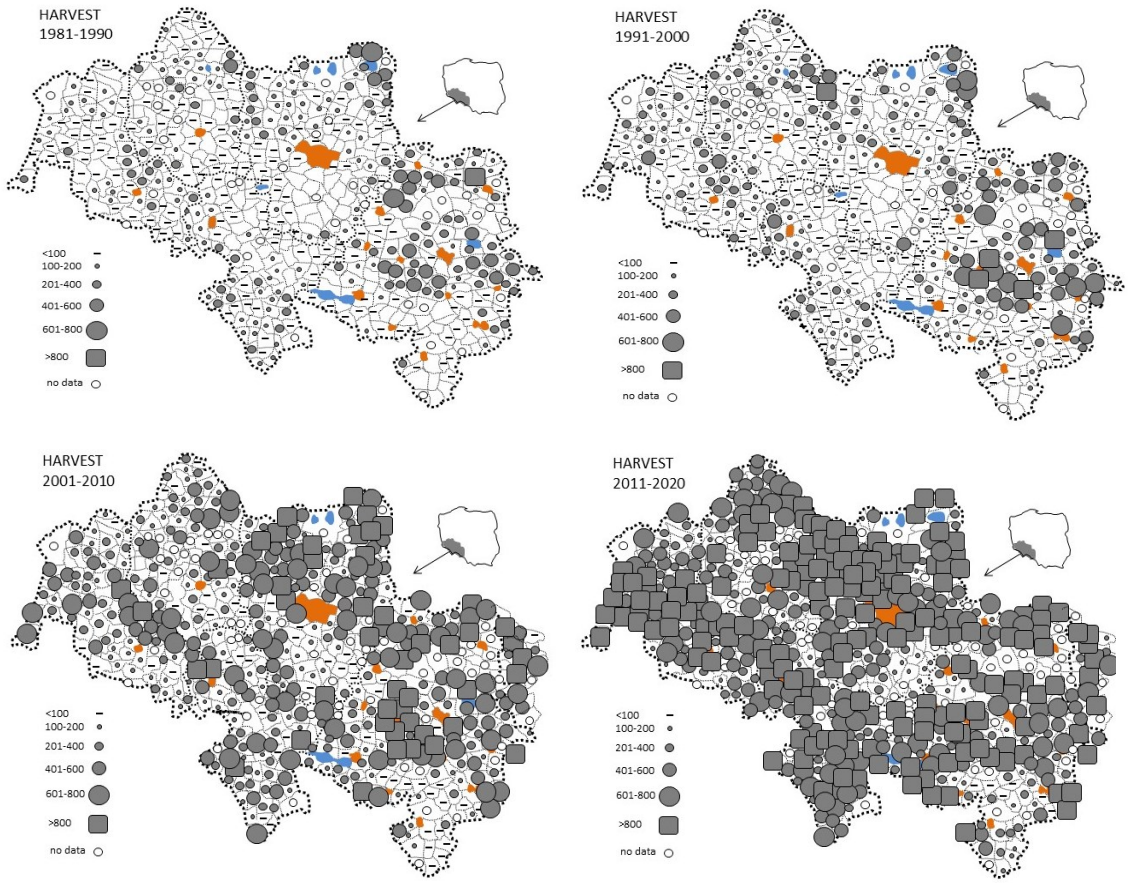


Fig. 3 (*a–d*). Total number of wild boars harvested in particular hunting districts of south-western Poland during the years of 1981–2020.

Рис. 3 (*a–d*). Загальна кількість свиней диких, здобутих у певному мисливському районі на південному заході Польщі протягом 1981–2020 років.

An expansion took place in the first decade of 21st century. There were 22 hunting districts in Opole HR with more than 800 wild boars harvested (including 11 districts in the Niemodlin Forests), 17 hunting districts in Wrocław HR (all in the northern part), and only seven in three remaining hunting regions. During the years of 2011–2020, more than 800 wild boars were culled in about 50 hunting districts in Opole HR, and about 50 hunting districts in the remaining four hunting regions (see: Fig. 3). In 1980–1990, 38 016 wild boars, whereas in 1991–2000 43 490 wild boars were culled (14.4% increase). In 2001–2010, there were 69 052 individuals harvested (58.8% increase compared to the previous decade). In 2011–2020, the harvest was 3-fold higher in relation to the previous decade and 5.6-fold higher in relation to 1980–1990.

In most hunting districts in south-western Poland, less than 20 wild boards in each districts were recorded in 1981–2000 (Fig. 4). There were 13 such districts in 2001–2010, an only four in 2011–2020 (see: Fig. 3). During the years of 1981–1990, an estimated number of 51–100 wild boars were recorded only in five hunting districts in Opole HR. In the next decade, there were 17 such districts in Opole HR, 4 in Wrocław HR, and only 2 in the other three hunting regions. After an expansion in 2001–2010, there were 32 districts, each one with 101–200 wild boars (15 in Opole HR, 14 in Wrocław HR, and 3 in other hunting regions); only in one hunting district more than 200 wild boars were recorded. However, there were eight districts with such high number of wild boars in 2011–2020. In that period, 101–200 wild boars were recorded in each of the 78 hunting districts (including 20 in Opole HR, and 30 in Wrocław HR).

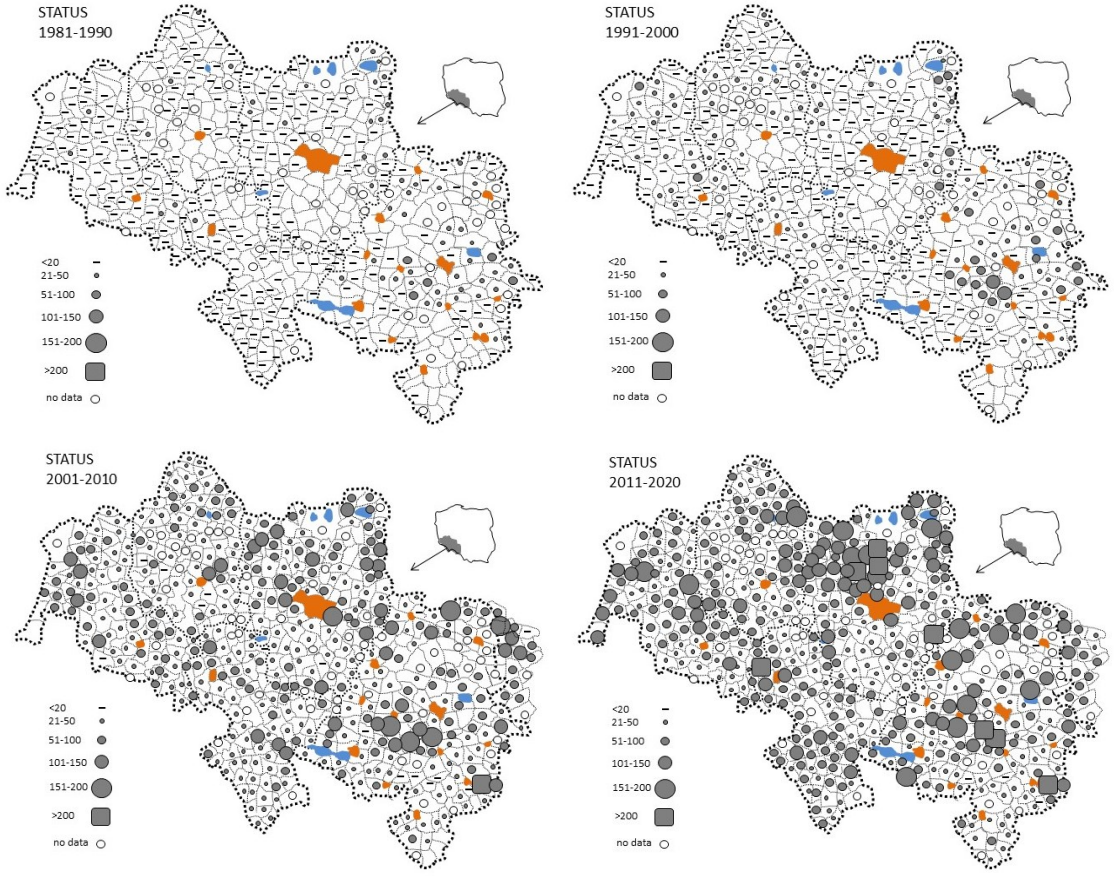


Fig. 4 (*a–d*). Estimated mean number of wild boars in particular hunting districts of south-western Poland during the years of 1981–2020.

Рис. 4 (*a–d*). Розрахункова середня кількість свиней диких в окремих мисливських районах на південному заході Польщі протягом 1981–2020 років.

Table 2. Population densities (individuals per 1000 ha) of the wild boar (average for 2001–2020). Symbols in the first column (A, B, C…) refer to those in Fig. 1. Ecological density refers to the number of harvested wild boars/1000 ha of forest, whereas the crude density refers to the number harvested wild boar/1000 ha of the total surface area

Таблиця 2. Щільність популяції (особин на 1000 га) свині дикої (середня за 2001–2020 рр.). Символи в першому стовпці (A, B, C…) відповідають аналогічним на рис. 1. Екологічна щільність — кількість здобутих свиней/1000 га лісу, тоді як загальна щільність — кількості здобутих свиней/1000 га загальної площі

#	Region	Hunting districts	Surface area [ha]		%	Density	
			general	forests	forests	ecol.	crude
A	Lower Silesian Forests	5, 7, 12, 15, 16, 20	33211	27782	83.7	9.1	7.6
B	Silesian–Lusatian Lowland	31, 33, 39, 40, 43, 52	25500	6438	25.2	90.9	22.9
C	West Sudeten Mts.	54, 55, 66, 71, 78, 80	28332	20249	71.5	10.3	7.4
D	Northern (lowland) part of Legnica Hunting Region	1, 2, 17, 18, 33, 35	22795	8467	37.1	29.4	10.9
E	Southern (hills) part of Legnica Hunting Region	62, 67, 69, 71, 72, 78	29400	3754	12.8	107.1	13.7
F	Sudeten Upland	6, 7, 21, 31, 38, 39	26700	3730	14.0	69.3	9.7
G	Middle Sudeten Mts.	10, 18, 23, 25, 28, 30	26715	10576	39.6	35.2	13.9
H	East Sudeten Mts.	54, 67, 69, 70, 72, 82	16191	9491	58.6	40.7	23.8
I	Barycz Valley and Trzebnica Hills	2, 7, 8, 13, 15, 16	30127	10091	33.5	53.4	17.9
J	Głogów–Milicz Depression	10, 30, 32, 45, 47, 59	27803	9090	32.7	65.5	21.4
K	Oleśnica Plain	71, 85, 86, 95, 96, 107	27283	9154	33.6	58.1	19.5
L	Wrocław Plain	67, 79, 90, 100, 113, 116	28938	1884	6.5	147.2	9.6
M	Northern part of the Opole Province	3, 7, 12, 14, 15, 16	32497	4375	13.5	90.1	12.1
N	Brzeg Land	17, 19, 20, 21, 50, 51	33704	11738	34.8	52.3	18.2
O	Stobrawa Forests	28, 33, 34, 35, 36, 39	38926	32444	83.3	16.3	13.6
P	East-central part of the Opole Province	82, 83, 91, 123, 126, 129	41259	20721	50.2	22.5	11.3
R	Nysa Land	74, 76, 78, 114, 120, 122	34320	2258	6.6	129.4	8.5
S	Niemodlin Forests	47, 59, 64, 67, 96, 101	41259	20721	50.2	22.5	11.3
T	Głubczyce Plateau	105, 109, 132, 133, 138, 146	34320	2258	6.6	129.4	8.5

Ecological population densities of the wild boar was spatially very varied, ranging from 9.1 ind./1000 ha in extensive woodlands of the Lower Silesian Forests to as much as 147.2 ind./1000 ha in the Wrocław Plain dominated by farmlands with forest fragments (Table 2). The crude density was much lower and much less spatially varied; it was the lowest (7.4 ind./1000 ha) in the West Sudeten Mts., and the highest (23.8 ind./1000 ha) in the East Sudeten Mts. (see: Table 2).

Discussion

Estimating the number of wild boars directly in the field is a difficult, expensive, and time-consuming task [Jędrzejewski *et al.* 1997; Bobek *et al.* 2018]. Indirect counts, although less precise, are much less laborious. There are few methods to estimate wild board population indirectly: 1) hunting bag statistics [Keuling *et al.* 2018]; 2) counting tracks, faeces, or farrowing nests [Acevedo *et al.* 2007; Pihal *et al.* 2014]; 3) winter route census [e.g. Fonesca *et al.* 2007]; 4) drive census [Jędrzejewski *et al.* 1994]; 5) capture-mark-recapture [Andrzejewski & Jezierski 1978]; 6) DNA-genotyping [Ebert *et al.* 2012]. Each method is based on certain assumptions and produces errors and biases. It should be emphasised, however, that in the whole set of data, the range of local errors is likely to be low compared with the large-scale range of observed variation in population density (0.1–100 ind./1000 ha).

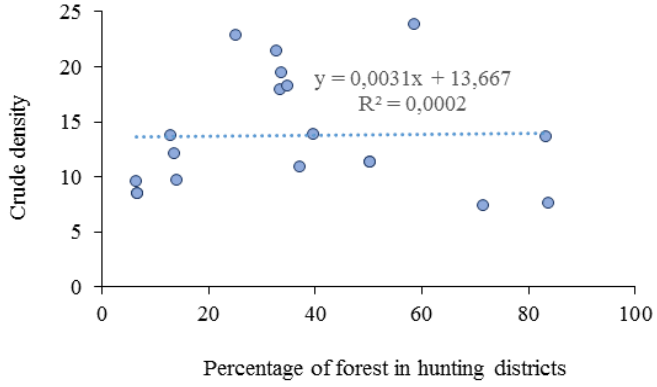
Hunting bags analysis is of crucial importance to monitor population dynamics and to develop proper wildlife policies [Fanelli *et al.* 2021], as it is relatively simple, and time-saving. Despite this, it is considered a good measure for population density estimation [Geisser & Reyer 2005; Santilli & Varuzza 2003]. The method assumes a close correlation between the number of harvested animals and the actual population density. Similarly to other methods, hunting bags analysis have limitations and biases. The completeness of data on the number of culled wild boars is difficult to assess here [Acevedo *et al.* 2007; Engeman *et al.* 2014]. In some hunting districts the number of wild boars harvested may be linked to hunting quotas, but in others there is no such a link. Poaching and illegal hunting is not accounted for the official statistics and it is unknown what proportion of wild boars is removed in this way. There are two sources of bias in this estimation: year-to-year changes (population dynamics), and different intensity of human hunting. Also hunting may induce compensatory population responses, such as birth given earlier than normally, or more first-year females giving birth than normally.

The wild boar is a highly adaptable generalist omnivore [Bywater *et al.* 2010]. It is an exception among ungulates, as it has high litter size, which correlates with the latitude: it increases by c. 0.15 piglets per one degree of the latitude [Tack 2018]. In temperate forests of Central Europe, the mean litter size oscillates between 5 and 7. As a result, wild boar population density is also highly variable both temporarily and spatially. In Poland alone, densities differed by an order of magnitude within the same hunting season [Fonesca *et al.* 2007; Popczyk 2016; Zalewski *et al.* 2018; this study]. While the numbers were the highest in the Szczecin (25.8 ind./1000 ha), Legnica (20.8), Koszalin (19.5), Wrocław (19.4), and Wałbrzych (19.3) hunting regions, these were the lowest (1.8–2.8 ind./1000 ha) in central and eastern Poland (PZŁ 2022). In Opole HR (south-western Poland), merely 2000 wild boars were harvested in the 1980–1981 hunting season, whereas over 12 000 were culled in the 2018–2019 hunting season (this study).

There is a widespread misconception regarding estimation of population density of the wild board. Usually, the density is expressed as the number of individuals per 1000 ha of forest. In hunting districts with forest surface area larger than 66% of the total surface, such density may well reflect the actual population density. However, if this ecological density refers to hunting districts with low contribution of forests (farmlands with forest fragments), the actual density may, in fact, be much lower. In hunting districts where open space predominate in the landscape (especially those with forests accounting for less than 30%), habitats (especially foraging habitats) outside the forest are equally important as these in forests. In some hunting districts with less than 10% of forests (e.g. in Głubczyce Plateau in Opole HR), habitats outside forests may even play a more important role than these in forests. If only ecological density (number of individuals per 1000 ha of forest) is calculated, a strongly distorted picture may emerge, where the highest density will always be in deforested areas, and it will be inevitably the lowest in the most afforested ones (Fig. 5). The crude density will reflect much better the actual population densities (Fig. 6). It is therefore a more accurate approach to calculate density, especially in cases when a comparative analysis of population densities is attempted over larger and diverse ecoregions/ecosystems, as it is in the present study.

Compared to the line transect track index, the hunting bags analysis provide similar population density estimates, whereas in the comparison with the block count census, population densities based on the hunting bag analysis are underestimated (Table 3). However, it should be emphasised that density estimations based on hunting bag analysis will always be lower than the real densities, as not all animals are harvested in a given population.

The following ecological variables may shape wild boar population density in south-western Poland: food resources (maize, mast); temperature (winter and early spring); and precipitation (snow and rainfalls). In other words, both density-independent mortality (caused for example by harsh winter) and density-dependent mortality (reflecting competition for food resources) may play a role in this regard. Among density-independent factors, weather conditions have multidirectional effects, operating through differential mortality either directly (winter and spring temperature, duration and depth of snow cover) or indirectly (influencing amount of food resources). It should be stressed, however, that in a particular year the population density can be better explained by food and temperature conditions in the current year than by those conditions in the previous year.



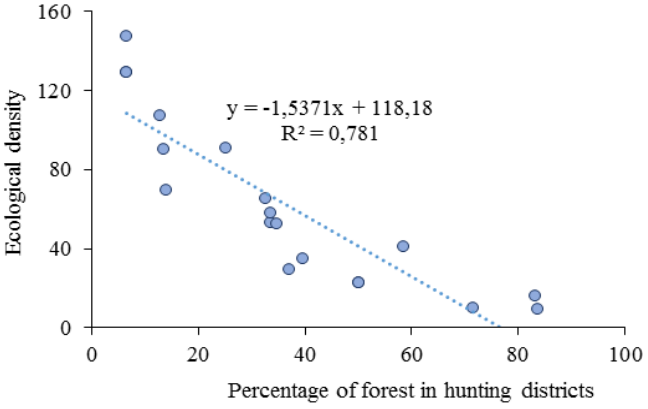


Fig. 5. The relationship between percentage of forest in hunting districts and the crude density (*a*) and ecological density (*b*).

Рис. 5. Зв'язок між відсотком лісів у мисливських районах та загальною щільністю (*a*) та екологічною щільністю (*b*).

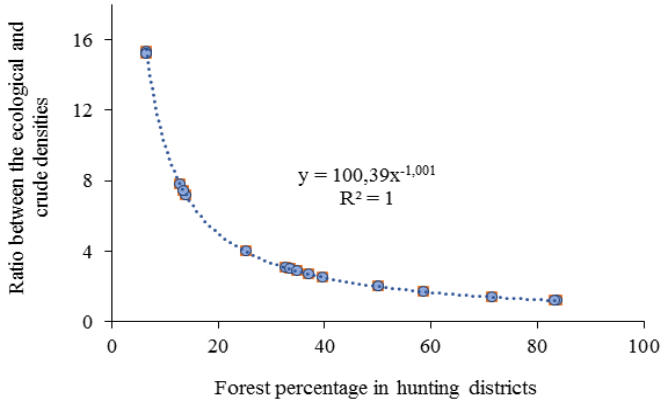


Fig. 6. The relationship between the forest percentage in hunting districts and the ratio between crude and ecological densities in south-western Poland during the years of 2001–2020.

Рис. 6. Зв'язок між відсотком лісів у мисливських районах та співвідношенням між загальною та екологічною щільністю на південному заході Польщі протягом 2001–2020 років.

At a local scale, snow cover and low winter temperatures are often the main factors influencing the year-to-year variations in wild boar population density [Caboń 1958; Okarma *et al.* 1995; Melis *et al.* 2006]. Deep snow cover and frozen soil may cause high mortality among wild boars, as it makes foraging difficult. In Poland, the average number of days with snow cover between 1971–2015 declined by 30–40% [Limanówka *et al.* 2012]. This could contribute to the increase in the number of wild boars. The population increase is correlated with higher than average winter and spring temperatures (reduced juvenile mortality). The low winter temperature causes mortality mainly among the young from the previous year, while low spring temperature affects mainly piglets born in the current spring [Geisser & Reyer 2005]. In the Białowieża Forests, the wild boar population increased over 100 years from 10 ind./1000 ha when annual temperature averaged 6˚C to 30 ind./1000 ha when the annual temperature averaged at 8˚C [Jędrzejewski *et al.* 1997].

Table 3. Wild boar population densities (individuals/1000 ha of forest) in various ecoregions of south-western Poland estimated by different methods during the years of 2001–2020

Таблиця 3. Щільність популяції свині дикої (особини/1000 га лісу) у різних екорегіонах на південному заході Польщі, оцінена різними методами протягом 2001–2020 років

Name of ecoregion	Line intercept track index	Block count census	Hunting bags analysis
Years	2001–2004	2017	2001–2020
Sudeten Mts.			
Karkonosze Mts./ West Sudeten Mts.	9.4	28.4	10.3
Sowie Mts./ Middle Sudeten Mts.	26.7	72.4	35.2
Kłodzko Valley/ East Sudeten Mts.	–	46.5	40.7
Forest fragments			
Sudeten Foothills	–	96.0	69.3
Trzebnica Hills	–	85.5	53.4
Barycz Valley	–	8.5	
Śląska Lowland	–	89.5	90.9; 147.2
Odra Valley/Głogów-Milicz Depression	–	83.3	65.5
Lowland forests			
Lower Silesian Forests	–	25.5	9.1
Niemodlin Forests	30.5	–	22.5
Stobrawa Forests	18.3	–	16.3
Source	Foneca *et al.* 2007	Bobek *et al.* 2018	This study

Under Central European conditions, acorns, and to a lesser extend also beech nuts, constitute the main diet of the wild boar in forests. Peaks of their abundance occur at 3–9 years intervals [Pucek *et al.* 1975; Jędrzejewska *et al.* 1997; Bisi *et al.* 2018]. The mast years are caused by weather conditions and are synchronised all over temperate forests of Europe. High rainfall in the spring of the current year affect positively acorn biomass production, while summer rainfall of the previous year has an opposite effect [Bisi *et al.* 2018]. In good mast years, 90% of females may reach reproductive status in their first year. Young females reach a minimal body weight for the first reproduction (30–40 kg) in their second year, but under favourable feeding conditions the increase in body weight is accelerated and females first mate at the age of 8–10 months.

Crop plants may constitute up to 81% of wild boar summer diet [Fruziński 1992]. Maize is often its main component. It is a highly energetic food. When collected in the field in late autumn, the grain is often contaminated with zearalenon (mycotoxine), a highly oestrogenic substance causing changes in the oestous cycle and increasing fertility [Zawadzki *et al.* 2011]. It has been shown that in south-western Poland the ever increasing surface area of the maize is the major factor causing the population increase of the wild boar [Kopij & Panek 2016]. In 1990, there were about 400 000 ha of maize in Poland, while c. 1 200 000 ha in 2014 [Popczyk 2016]. It is suggested therefore that maize may affect population density in most other regions in Poland.

The wild boar population may also increase due to improved habitat, caused by land abandonment, reduced livestock and action taken by hunting organization to maintain wild boar population [Ebert *et al*. 2012; Storie & Bell 2016]. Hunting districts, where forest cover exceeds 40%, had the highest wild boar density. The wild boar prefers deciduous forests over coniferous ones, as mast, tubers and soil invertebrates are more abundant in deciduous than in coniferous forests [Borowik *et al.* 2013]. The proportion of deciduous forests has gradually increased in Poland from 13% in 1945 to 24% in 2019 [IBL 2020].

Also supplementary feeding (mostly with maize) has likely contributed to the widely observed increase in wild boar numbers. The number of the livestock in south-western Poland has been in decline since 1990 (Table 1), and this may, in turn, contribute to the wild boar population increase.

The main factors shaping wild boar population density appear to be regionally different. In the boreal zone, the most important factors are mean winter temperature, and the depth and duration of

the snow cover [Fadeev 1973]. In north-eastern Poland, climate appears to be notably more important than predation [Jędrzejewski *et al.* 1997; Jędrzejewsja & Jędrzejewski 2005]. In south-western Poland, with winters milder than in north-eastern Poland, acorn and maize abundance is more important than climate [Kopij & Panek 2016], which boost reproductive success by younger age at first reproduction, larger litter size and earlier onset of oestrus within a season [Geisser & Reyer 2005]. Under Mediterranean conditions, the most important appears to be the rainfall influencing vegetation productivity (especially acorn and chestnut mast production). Llario-Fernandez & Mateos-Quesada [2003] showed that both the percentage of pregnant females and litter size of second year females were higher in rainy years than in dry ones. Dry summers and autumns determined an early rut period and a high concentration of births. Although the rainfall had no effect on foetal sex ratio, in dry years the heaviest piglets in litters were mostly males. In south-western Poland, reforestation and climate change are the main factors influencing the long-term and wide-scale increase. The increase of the surface area of the maize, sunflower, and rapeseed cultivations may have the largest effect on a local scale.

Few factors play a role in controlling wild boar populations: law (game rules), environment (environmental capacity and extent of damage to crops), and socio-economy (compensations for these damages). The main regulatory mechanisms for the growing wild boar population include hunting, especially important in Central Europe, where natural predators are rare; a ban on artificial feeding; and fertility control through immune-contraceptives [Ebert *et al.* 2012]. Fertility control should be applied in areas where hunting is unfeasible (e.g. in urbanised parklands). Under good environmental conditions (mast years) reducing the number of juvenile individuals will have the largest effect, while under poor environmental conditions, reducing the proportion of adult females may lead to the most effective population control.

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