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Grzegorz KOPIJ¹,

SPATIAL AND TEMPORAL VARIATION IN POPULATION DENSITIES OF THE ROE DEER *Capreolus capreolus* AND THE RED DEER *Cervus elaphus* IN SW POLAND

SUMMARY

Being the most abundant cervid across most European countries, the roe deer and red deer have an increasing ecological and economic importance and are subjected to intensive management. Using the hunting bags data, spatial and temporal changes in population densities of both species during the years 1981–2020 in SW Poland (29 358 km², including 8411 km² forests) have been analyzed. In 1981–1990, 120 135, whereas in 1991–2000, 194 018 red deer were culled (61.5% increase). In 2001–2010 there were 195 563 individuals harvested (0.8% increase in relation to the previous decade). In 2011–2020, the harvest was 2.1-fold higher in relation to 1980–1990. Crude population densities of the roe deer was spatially very varied, ranging from 4.8 ind./1000 ha to 209.9 ind./1000 ha. The ecological density was much lower and much less spatially varied (4.0 ind./1000 ha to 14.4 ind./1000 ha). In 1981–1990, 28 698, whereas in 1991–2000, 45 255 red deer were culled (57.7% increase). In 2001–2010 there were 49 504 individuals harvested (9.4% increase in relation to the previous decade). In 2011–2020, the harvest was 3.2-fold higher in relation to 1980–1990. Crude population densities of the red deer ranged from 2.0 ind./1000 ha to 23.4 ind./1000 ha. The ecological density was less varied spatially (<0.1 ind./1000 ha to 13.7 ind./1000 ha), both deer species are overabundant, and require carefully planned management in some ecoregions in SW Poland.

Keywords: *Capreolus capreolus*, *Cervus elaphus*, deer population, wildlife management.

INTRODUCTION

Species of the deer family (Artiodactyla: *Cervidae*) are the most important large game in the Holarctic Region. In Central Europe, they are represented mainly by two species: the smallest European cervid the roe deer *Capreolus*

¹Grzegorz KOPIJ, (e-mail: gregorius.kopijus@gmail.com), Department of Vertebrate Ecology, Wrocław University of Environmental & Life Sciences, ul. Koźuchowska 5b, 51-631 Wrocław, POLAND.

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capreolus (15–35 kg) and the red deer *Cervus elaphus*, bigger than the previous one by an order of magnitude (150–255 kg). Two other indigenous species, the fallow deer *Dama dama*, and the elk *Alces alces* are of much lower ecological and economic importance. In the last few centuries, two other cervid species were introduced in Central Europe: the sika deer *Cervus nippon* from the Far East, and the axis deer *Cervus axis* from India. Both are of marginal importance (Macdonald & Barrett, 2001).

Being the most abundant cervid across most European countries, the roe deer and red deer have an increasing ecological and economic importance and are subjected to intensive management (Grabińska, 2007; Zalewski *et al.*, 2018; Valente *et al.*, 2020). Uncontrolled numbers of these species may cause considerable damage in forestry. The most severe damage is bark-stripping of trees. It may considerably lower the wood quality by the damage in the thickness at breast height and most valuable part of the tree trunk (Sporek *et al.*, 2022). Deer also reduce tree regeneration by browsing saplings (Renaud *et al.*, 2003). In the arable fields deer may forage on cultivated plants, especially often causing damage to the maize and root plants (Corgatelli *et al.*, 2019). Deer play a role in transmitting to livestock the food-and-mouth disease, bovine tuberculosis and other diseases (Gliński & Żmuda, 2021). They may also cause vehicle collisions (Gunson *et al.*, 2010). Information on the abundance and distribution of deer is therefore crucial for a mitigation of these conflicts (Burbaite & Csanyi 2010).

Although the roe deer and the red deer differ so much in body weight, they are essentially browsers in forests and overlap to certain extent their habitat and feeding niches (Gębczyńska, 1980; Latham *et al.*, 1999; Obidziński *et al.*, 2013). They may compete for food when this became limited. With increasing density of both species the potential for competition may become high and may have implications for managers and nature conservationists (Gaillard *et al.*, 2010). It is therefore advisable to conduct comparative population studies on these two species, especially in regard to their numbers.

The purpose of this study was to compare population densities of the roe deer and red deer in one of the Central European regions, characterized both by a high level of forestry and agriculture. The comparison is both spatial and temporal. It is conducted as to elucidate the main factors shaping the population densities, enabling in turn to formulate management strategies and actions.

MATERIAL AND METHODS

The study area comprises two provinces (actual 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 in the years 1975–1999): Opole, Wrocław, Legnica, Wałbrzych and Jelenia Góra (Fig. 1). Nowadays, the Opole hunting region is entirely located within Opole Province, 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, mountains) and administrative division (Fig. 1).

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). Data are not available for LSP 1990.

| 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 |

The total surface area of such defined study area is 29 358 km², which constitutes 9.4% of the Poland's surface area. The land is located almost entirely within the Odra drainage system. Forests occupy 8411 km², i.e. 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 mln 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 (towns and villages), rivers and water bodies, waste and industry areas in each hunting district.

The average annual air temperature in the lowlands in SW Poland is 10.6 °C, for Sudeten Mts 9.0 °C (the average for Poland is 9.9 °C). This average has increased from 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 Sudeten Mts. the average is doubled). 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 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 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 1988–1990 and 2006–2008 (Czarnecka, 2012).

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 roe deer and red deer harvested (hunting bags) and the number of these estimated (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).

Numbers of roe deer and red deer in particular hunting district were estimated in two ways: a) year-round observations, b) drive counts. In the entire period 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 numbers of deer 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, to maintain a visual contact. The observers on three sides were stationary, while those on the remaining side moved inside the compartment, penetrating the whole area of this compartment. All observers recorded all roe deer and red deer passing through the line of observers on their right side only, and the observers recorded all roe deer and red deer entering or leaving the

surveyed compartment (Zalewski *et al.*, 2018). Observations were analysed, summoned and assumed as estimations.

According to Polish Hunting Code, male roe deer can be hunted from 11 May to 30 September, females and young roe deer – from 1 October to 15 January. Male red deer can be harvested from 21 August to 28 February, females from 1 September to 15 January, young – from 1 September to 28 February (Dz. U. 2020.1683).

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.

Harvested numbers are expressed as the total number of roe deer or red deer shot in a given hunting district in a given hunting season. Each hunting season begins on 1st of April and ends on 31st of March of the next year. For each ecoregion (Fig. 1), six hunting districts were randomly selected to calculate mean population density. Population density is expressed as the mean number of roe deer or red deer 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 from 20 years (2001–2020).

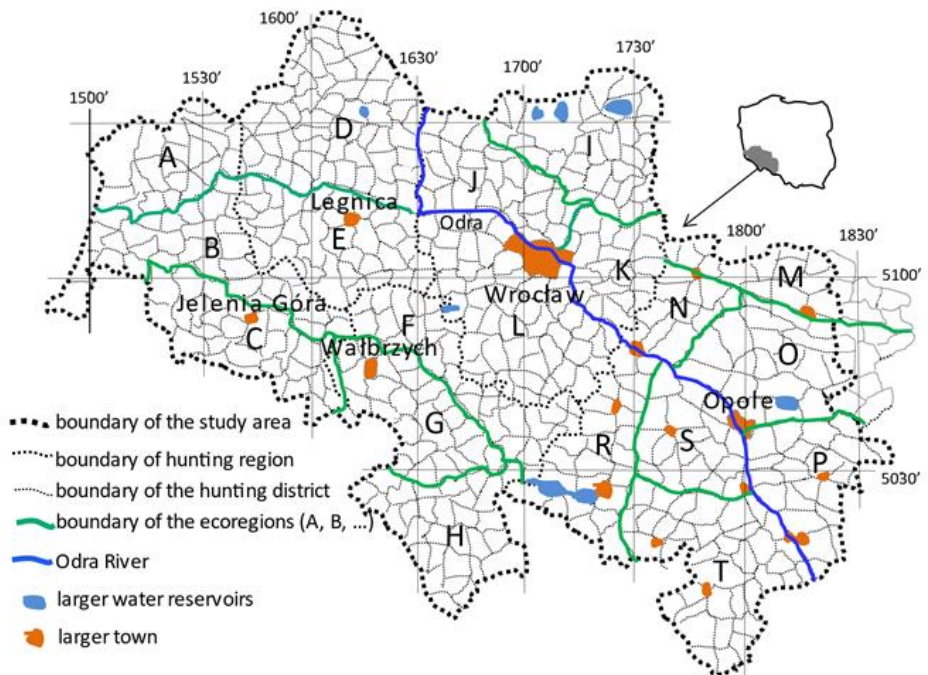


Figure 1. The study area, SW Poland, divided into hunting districts, 5 hunting regions and 19 ecoregions.

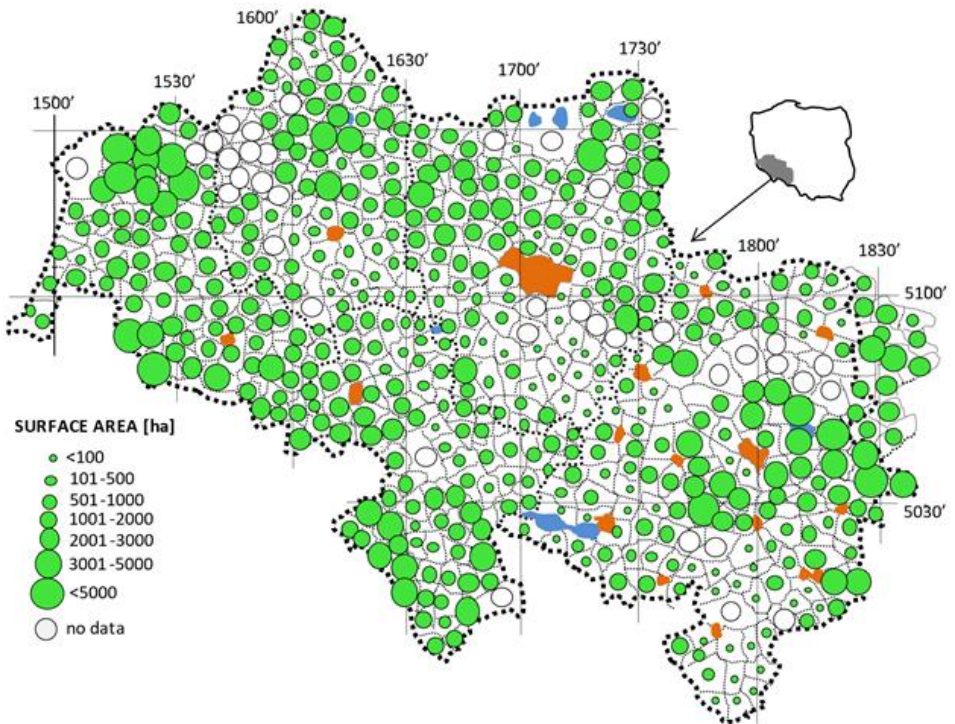


Figure 2. Afforestation in particular hunting district in SW Poland in 2020.

RESULTS

Roe deer

During the years 1981–1990, more than 300 roe deer were recorded only in two hunting districts in Opole HR. In 1991–2000, there were six hunting districts in SW Poland (all in Opole HR), each with more than 300 individuals. In all other hunting regions there were only five such hunting districts. In the next decade (2001–2010) there were 43 hunting district (including 19 in Opole HR), each one with more than 300 roe deer. During the years 2011–2020, more than 300 individuals were recorded in each of 35 hunting districts in Opole HR, and 25 hunting districts in the remaining four hunting regions (Fig. 3).

In 1981–1990, more than 800 roe deer were culled in each of 20 hunting districts in SW Poland, including 16 districts in Opole HR. Similar harvest took place in the next two decades (1991-2010). However, in 2011-2020, more than 800 individuals were harvested in the each of 35 districts in Opole HR, and 21 districts in the remaining hunting regions (Fig. 3).

In 1981–1990, 120 135, whereas in 1991–2000, 194 018 red deer were culled (61.5% increase). In 2001–2010 there were 195 563 individuals harvested (0.8% increase in relation to the previous decade). In 2011–2020, the harvest was 2.1-fold higher in relation to 1980–1990.

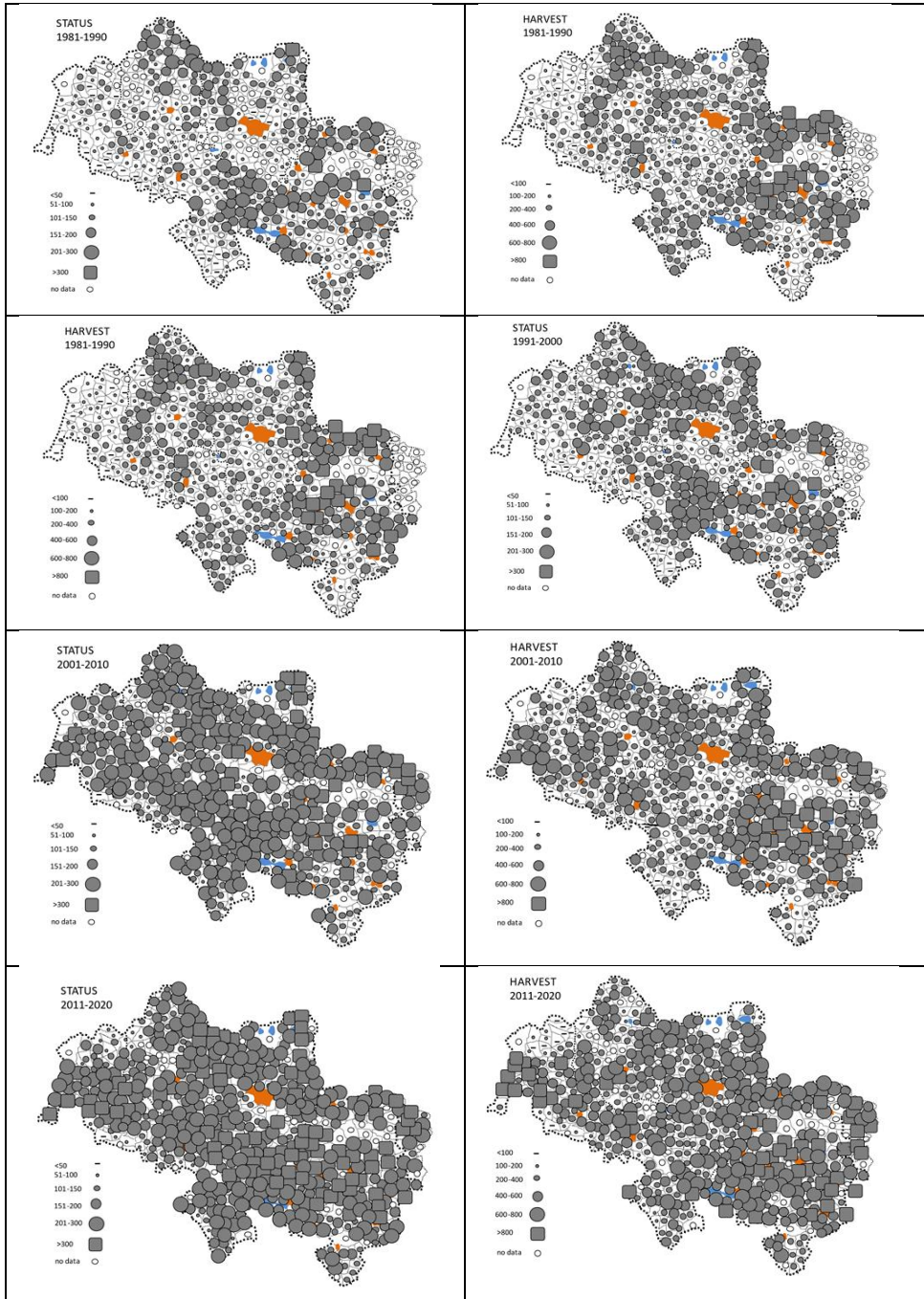


Figure 3. Estimated mean number (maps in left column) and the number of harvested (maps in right column) roe deer in particular hunting district in SW Poland during the years 1981–2020.

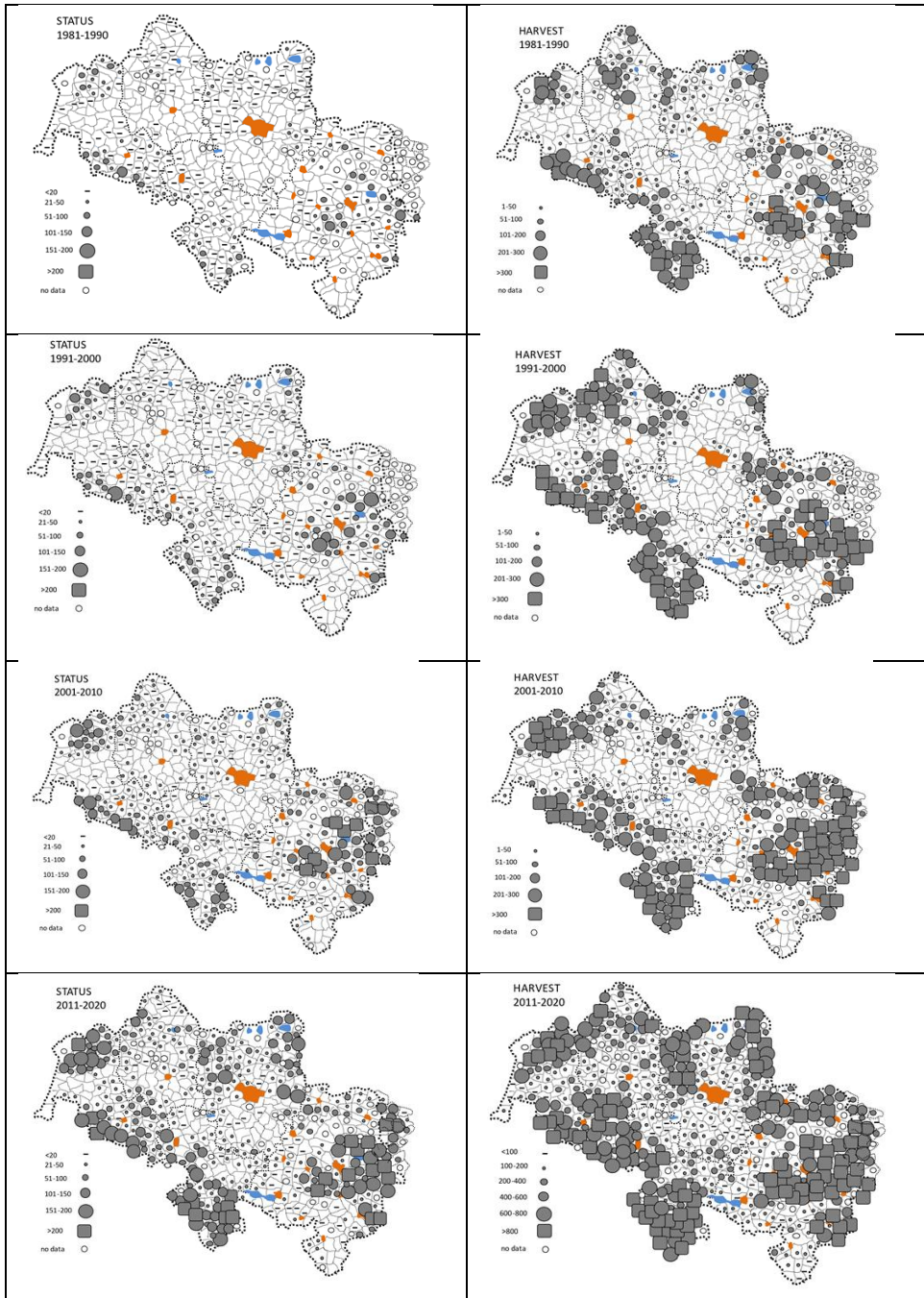


Figure 4. Estimated mean number (maps in left column) and the number of harvested (maps in right column) red deer in particular hunting district in SW Poland during the years 1981–2020.

Table 2. Population densities (individuals per 1000 ha) of the roe deer and red deer (average from 2001–2020). Symbols in the first column (A, B, C...) refer to these in Fig. 1. The ecological density refers to the number of harvested deer/1000 ha of forest, whereas the crude density refers to the number harvested deer/1000 ha of the total surface area.

| # | Region | Hunting districts | Surface area [ha] | | % | Roe deer density | | Red deer density | |
|---|---|------------------------------|-------------------|---------|------|------------------|-------|------------------|-------|
| | | | general | forests | | forests | ecol. | crude | ecol. |
| | Jelenia Góra Hunting Region | | | | | | | | |
| A | Lower Silesian Forests | 5, 7, 12, 15, 16, 20 | 33211 | 27782 | 83.7 | 4.8 | 4.0 | 7.5 | 6.2 |
| B | Silesian-Lusatian Lowland | 31, 33, 39, 40, 43, 52 | 25500 | 6438 | 25.2 | 47.0 | 11.9 | 2.0 | 0.5 |
| C | West Sudeten Mts. | 54, 55, 66, 71, 78, 80 | 28332 | 20249 | 71.5 | 7.5 | 5.4 | 11.9 | 8.5 |
| | Legnica Hunting Region | | | | | | | | |
| D | Northern (lowland) part | 1, 2, 17, 18, 33, 35 | 22795 | 8467 | 37.1 | 25.9 | 9.6 | 4.5 | 1.7 |
| E | Southern (hills) part | 62, 67, 69, 71, 72, 78 | 29400 | 3754 | 12.8 | 76.7 | 9.8 | 4.5 | 0.6 |
| | Wałbrzych Hunting Region | | | | | | | | |
| F | Sudeten Upland | 6, 7, 21, 31, 38, 39 | 26700 | 3730 | 14.0 | 61.3 | 8.6 | 2.3 | 0.0 |
| G | Middle Sudeten Mts. | 10, 18, 23, 25, 28, 30 | 26715 | 10576 | 39.6 | 19.8 | 7.8 | 14.1 | 5.6 |
| H | East Sudeten Mts. | 54, 67, 69, 70, 72, 82 | 16191 | 9491 | 58.6 | 19.4 | 11.4 | 23.4 | 13.7 |
| | Wrocław Hunting Region | | | | | | | | |
| I | Barycz Valley and Trzebnica Hills | 2, 7, 8, 13, 15, 16 | 30127 | 10091 | 33.5 | 25.0 | 8.4 | 8.9 | 3.0 |
| J | Głogów-Milicz Depression | 10, 30, 32, 45, 47, 59 | 27803 | 9090 | 32.7 | 29.9 | 9.8 | 5.0 | 1.7 |
| K | Oleśnica Plain | 71, 85, 86, 95, 96, 107 | 27283 | 9154 | 33.6 | 42.9 | 14.4 | 11.4 | 3.8 |
| L | Wrocław Plain | 67, 79, 90, 100, 113, 116 | 28938 | 1884 | 6.5 | 131.8 | 8.6 | 12.7 | 0.8 |
| | Opole Hunting Region | | | | | | | | |
| M | Northern part of the Opole Province | 3, 7, 12, 14, 15, 16 | 32497 | 4375 | 13.5 | 82.3 | 11.1 | 18.1 | 2.4 |
| N | Brzeg Land | 17, 19, 20, 21, 50, 51 | 33704 | 11738 | 34.8 | 38.5 | 13.4 | 12.5 | 4.3 |
| O | Stobrawa Forests | 28, 33, 34, 35, 36, 39 | 38926 | 32444 | 83.3 | 13.3 | 11.1 | 12.5 | 10.4 |
| P | East-central part of the Opole Province | 82, 83, 91, 123, 126, 129 | 41259 | 20721 | 50.2 | 17.8 | 8.9 | 20.3 | 10.2 |
| R | Nysa Land | 74, 76, 78, 114, 120, 122 | 34320 | 2258 | 6.6 | 118.4 | 7.8 | 4.8 | 0.3 |
| S | Niemodlin Forests | 47, 59, 64, 67, 96, 101 | 41259 | 20721 | 50.2 | 27.3 | 14.0 | 18.3 | 9.4 |
| T | Głubczyce Plateau | 105, 109, 132, 133, 138, 146 | 34320 | 2258 | 6.6 | 209.9 | 8.9 | 5.0 | 8.9 |

Crude population densities of the roe deer was spatially very varied, ranging from 4.8 ind./1000 ha in contiguous woodlands of the Lower Silesian Forests to as much as 209.9 ind./1000 ha in the Głubczyce Plateau dominated by farmlands with forests fragments (Table 2). The ecological density was much lower and much less spatially varied; it was the lowest (4.0 ind./1000 ha) in Lower Silesian Forests, and the highest in the Oleśnica Plain (14.4 ind./1000 ha), Niemodlin Land (14.0) and Brzeg Land (13.4) (Table 2). The biggest difference between the crude and ecological densities was in Nysa Land, Głubczyce Plateau and Wrocław Plain; the least in Sudety Mts., Stobrawa Forests and Lower Silesian Forests.

Red deer

There was no hunting district in SW Poland with more than 200 red deer in 1981–2000. In 2001–2010, there were already eight districts with such number; all but one were in Opole HR (Niemodlin and Stobrawa Forests). During the years 2011–2020, four areas emerged in SW Poland with high population density (most hunting districts with more than 100 red deer): Niemodlin Forests, Stobrawa Forests, Lower Silesian Forests and Sudeten Mts. (Fig. 4).

In 1981–1990, more than 300 red deer were shot in each of 12 hunting districts in Opole HR, and 9 in the remaining hunting regions in SW Poland (Fig. 4). There were already 49 such districts in 1991–2000; 23 in Opole HR, 17 in Sudeten Mts., and 9 in Lower Silesian Forests. In the next decade, markedly more deer were culled only in Opole HR. However, in 2011–2020, in most hunting

districts harvesting almost doubled, especially in the northern part of the Lower Silesian Forests, Lower Silesian Voivodship and in Sudeten Mts. (Fig. 4).

Crude population densities of the red deer ranged from 2.0 ind./1000 ha in Silesian-Lusatian Lowland to 23.4 ind./1000 ha in East Sudety Mts. (Table 2). The ecological density was less varied spatially; it was the lowest in Sudety Upland (<0.1 ind./1000 ha), Nysa Land (0.3) and Silesian-Lusatian Lowland (0.5); the highest in the East Sudety Mts. (13.7 ind./1000 ha) (Table 2). The biggest difference between the crude and ecological densities was in Wrocław HR; the least in Sudety Mts., Stobrawa Forests and Lower Silesian Forests.

In 1981–1990, 28 698, whereas in 1991–2000, 45 255 red deer were culled (57.7% increase). In 2001–2010 there were 49 504 individuals harvested (9.4% increase in relation to the previous decade). In 2011–2020, the harvest was 3.2-fold higher in relation to 1980–1990.

DISCUSSION

Precision and accuracy of population estimations

Several methods has been developed to estimate deer population density, such as hunting bag analysis, distance sampling, capture-mark-recapture, drive counts, pellet groups counts (Gaillard *et al.*, 1993; Alberto *et al.*, 2009; Borkowski *et al.*, 2011; Bobek *et al.*, 2013; Morimando *et al.*, 2016; Orłowska and Rembacz 2016; Zalewski *et al.*, 2018; Marcon *et al.*, 2019). All these methods are well known to be inaccurate and unprecise. These drawbacks are especially acute under forest condition when population densities are low. Even decreasing the interval of abundance estimates counterintuitively cannot compensate for this inaccuracy (Hagen *et al.*, 2014). In addition, some of these methods are very time-consuming and monetary expensive, and as such are inefficient in sampling large areas on a yearly basis. Low precision and low accuracy lead to incorrect and incomplete information on population density and these in turn lead to uncertainty regarding decision-making processes in wildlife management.

The hunting bags analysis is somehow different, as it is relatively simple, and time-saving method, and as such it can be applied over large areas. It assumes a close correlation between the number of harvested animals and the actual population density. Like other methods, it has limitations and biases. First of all, the completeness of data on the number of culled animals is difficult to assess. In some hunting districts the number of deer 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 deer 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. Despite this, it is considered a good measure for population density estimation (Santilli and Varuzza, 2003). The hunting bags analysis is especially suitable for large spatial scale comparisons (country level) and for long-time

series (at least a decade) (Imperio *et al.*, 2010; Bonenfant and Gaillard, 2015). In the presented study, the time of these series is 40 years.

Population densities and overabundance

Being widespread all over Europe, both roe deer and red deer are ecologically flexible species, occupying various habitats and foraging a wide range on various plant materials, such as trees, shrubs, heaths, brambles *Robus spp.*, grasses, sedges, rushes, forbs, herbs, ferns, lichens, etc. (Gębczyńska 1980; Cornelis *et al.*, 1999; Latham *et al.*, 1999; Gebert *et al.*, 2001; Barančková *et al.*, 2010; Krojerova-Prokeš *et al.*, 2010; Obidziński, 2013). As a result of this flexibility, population densities of these species are temporarily and spatially variable in SW Poland (Table 2, Fig. 3, 4), as well as in other regions of Poland (Grabińska, 2008; Zalewski *et al.*, 2018; PZŁ, 2022). In 2017, the roe deer density (individuals / 1000 ha) was the highest in western Poland, i.e. in Leszno (52.3), Wrocław (52.2), Gorzów (51.6), Szczecin (50.6) and Opole HR (50.6) (Zalewski *et al.*, 2018); while in north-eastern Poland it was the lowest (13.8 in Łomża, 15.0 in Białystok, and 16.6 in Ostrołęka HR). A similar situation was recorded for the red deer in 2017; population densities were the highest in the south-western and north-western Poland, i.e. in Wałbrzych (73.8), Wrocław (66.6), Szczecin (77.4) and Gdańsk H.R. (62.1); the lowest (1.3) in central Poland (Zalewski *et al.*, 2018). In well-preserved Białowieża Forests, in 1957–1987 population densities ranged in red deer from 15 to 78 ind./1000 ha; in roe deer from 2 to 7 ind./1000 ha (Jędrzejewska *et al.*, 1997). Under high predation pressure and hunting, deer population density may be as low as 10–20 roe deer per 1000 ha of forest. On the other hand, in temperate forests with no large predator and no hunting, densities can be higher than 400 roe deer per 1000 ha of forest (Bonenfant and Gaillard, 2015).

Deer population density is shaped by density-independent mortality (caused for example by harsh winter) and density-dependent mortality (reflecting competition for food resources). During the years 1981–2020, the percentage of afforested areas in SW Poland markedly increased (IBL 2020; Table 1). It has been shown that afforestation positively affect deer population densities (Borowik *et al.*, 2013; Jędrzejewska *et al.*, 1997). Over the last 40 years winters became milder, with higher average temperatures, and with shorter period with snow cover (see ‘Study area’ section). Food resources are especially important factor controlling the population. Most studies on diet composition of deer show small proportion of cultivated plants, because these studies were conducted on individuals originated from forests (Gębczyńska 1980; Gebert *et al.*, 2001; Verheyden *et al.*, 2006; Barančková *et al.*, 2010; Krojerova-Prokeš *et al.*, 2010; Obidziński 2013). Cornelis *et al.* (1999) summarized data on diet composition of the roe deer in various habitats. They have shown that in agro-ecosystems with small forest fragments, the diet is dominated (69%) by cultivated plants, whereas in forests – by woody plants (68% in deciduous, 65% in coniferous, and 63% in mixed forests). The red deer diet is dominated by woody browse, *Vaccinium/Calluna*, grasses and sedges (Latham *et al.*, 1999; Krojerova-Prokeš *et*

al., 2010). Gebert *et al.* (2001) summarized 13 diet studies from Europe, showing everywhere only small proportion of cultivated plants in the red deer diet. However, in a mosaic of forests and farmlands in SW Poland red deer are known to forage intensively on maize in late summer and early autumn (G. Kopij, own observ.). Maize cultivations may, therefore, affect population density of red deer, while rape and oat cultivations – the roe deer. The marked increase of areas with these cultivated plants which took place in SW Poland in the last few decades (Table 1) could contribute to the parallel increase in the number of both roe deer and red deer in this region. A strong positive correlation between the increase of maize cultivation area and numbers of the wild boar has been shown in Opole HR (Kopij 1996, 2022; Kopij *et al.*, 2015; Kopij & Panek 2016). Such a correlation in the case of both deer species requires, however, further investigation. In addition, supplementary feeding in winter has been also intensified in the last few decades in SW Poland. This might also contribute to the increase of deer population densities. In the last two decades of the 20th century, the population size (and hunting bag) of roe and red deer increased in most European countries (Melis *et al.*, 2009; Appollonio *et al.*, 2010; Carpio *et al.*, 2020; Balciauskas, 2022; PZŁ, 2022). During 1984-2003, red deer numbers in Europe increased from 1.1 million to 1.7 million and hunting bag from 275 thousand to 429 thousand individuals (Burbaite and Csányi, 2010). This increase causes human-wildlife conflicts, such as damage to agricultural crops, and forest plantations, disease transmission and an increase in collisions with vehicles. Permissible densities of the roe deer in temperate forests were calculated as follow: deciduous forests: 40–60 ind./1000 ha of the habitat; mixed forests: 20–40 ind./1000 ha; pine forests: 10–20 ind./1000 ha. Permissible densities of the red deer in deciduous forests: 10–20 ind./1000 ha of the habitat; mixed forests: 10–15 ind./1000 ha; pine forests: 4–8 ind./1000 ha (Balciauskas, 2022). It appears, therefore, that in some ecoregions in SW Poland and elsewhere in this country (Grabińska, 2007; Zalewski *et al.*, 2018) both deer species may be overabundant.

Management recommendations

Defining overabundance level is important, in order to determine management strategies and actions. Overabundance (overpopulation) of the roe deer or red deer in a given locality occurs when its population status affects human life or livelihood; affects the fitness of the overabundant species; reduces the density of other species with an economic or aesthetic value; or causes disfunctions in agriculture and forestry (damage to agricultural crops and trees in forests, disease transmission to domestic animals, vehicle collisions, etc.). Effective management of deer is important because of its economic (meat and hunting), recreational (hunting, wildlife photography) and ecological value (biodiversity). Few factors play a role in controlling deer populations: law (game rules), environment (environmental capacity and extent of damage to crops) and socio-economy (compensations for these damages). Management options (e.g. supplementary feeding, fencing, re-locations, fertility control, predation by large carnivores, culling) depend on the context (situation) of overpopulation. The

main context include: forests, farmlands, urbanized environment, and protected areas. In addition, these contexts should cover three perspectives: biological (traits of individuals and populations, such as body weight, productivity, antler size); ecological (impact on ecosystems); and socio-economical (wildlife–human conflicts) (Verheyden *et al.*, 2006; Apollonio *et al.*, 2010, Valente *et al.*, 2020).

In the past, the main factors affecting deer abundance were predation by large carnivores (wolf, lynx, brown bear), winter temperatures and the presence of forest cover. At present, the main factors influencing the abundance are hunting, winter foods and wildlife-forest management measures (Balčiauskas, 2022). In deer management important is not only accurate estimation of population density, but also estimation of survival and reproductive patterns. The proportion of deer females seen with a calf at heel at the end of the birth season can be used as a proxy of birth rate. On the other hand, the decrease in female to young ratio over time and the ratio between the yearlings: females in year $t + 1$ and calves: females in year t can be used to obtain juvenile survival rates (Benfant *et al.*, 2005). In Norway the proportion of male calves of the red deer shot each autumn declined markedly as population density increased. Female red deer thus reared fewer sons as nutritional stress increased with increasing population density and with increasing severity of climate (Longvatn and Loison, 1999; Mysterund *et al.*, 2000).

CONCLUSIONS

At the beginning of the twenty-first century, in many ecoregions in SW Poland roe deer and red deer become overabundant. Probable reasons for their rapid increase in numbers include an enlargement of afforested areas, climate change (mild winters, with higher average temperatures, and with shorter period with snow cover); an enlargement of cultivated plants such as the maize and rape (alternative food resource of both species) and supplementary feeding in winter. The choice of such management options as selective culling (e.g. higher proportion of younger than older animals, or more females than males), relocation, supplementary feeding or field fencing should be based on population density, population situation (e.g. protected versus unprotected areas, farmland vs. woodland; urbanized vs. unurbanized areas), and management perspectives, such as mitigation of human-wildlife problem, or improvement of deer body condition.

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