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Less and less roe deer in the forest – population and habitat reasons

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ABSTRACT

In 2015-2019, basic ecological parameters were assessed in the roe deer *C. capreolus* population in the Zielonka Forest near Poznań (western Poland). The aim of the study was to determine the causes of the declining density of this species. The assessment of abundance with help by drivers moving in a line formation (direct counting in control plots) showed an average of 3.4 individuals per km^2 of the forest, and the dominance of females over males – an average of 2.6♀ per 1♂. The population was characterized by typical fertility – 1.8 *corpus luteum* per ovulating female, but very low productivity – 0.3 fawns per female in the autumn population. The determined average age in the adult females population was typical for this species – 4.0 years. The average eviscerated body mass was: males 15.6 kg, females 14.2 kg, and fawns 9.3 kg. Despite the lower density of roe deer in the Zielonka Forest than in the 1970s, their body mass not only did not increase but was about 10% smaller. It was found that the main reason for the low density of roe deer was the extremely low production in a population characterized by low body weight. Deterioration of food resources was identified as the reason for the decrease in body mass. Most likely, this happened as a result of the reduced presence of herbaceous vegetation (including under the canopy of deciduous trees or the invasive American bird cherry *P. serotina*) and the fact that most forest plantations were fenced with nets (often the only sunny areas in this forest). This has reduced the availability of food niches where roe deer – a species that feeds selectively – could find food rich in nutrients. The increase in the number of fallow deer *D. dama* in Zielonka Forest also had a negative impact, as they are competitors on the roe deer population.

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KEY WORDS

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Introduction

Roe deer *Capreolus capreolus* L. is the most numerous species of the deer family in Poland and in many European countries. It is characterized by high ecological plasticity, which is why it inhabits most forest environments. It also uses anthropogenic environments, including open agricultural land (Andersen *et al.*, 1998; Kamieniarz and Panek, 2008; Reimoser and Reimoser, 2016). The highest densities in Poland – 32-38 individuals per square kilometre – were found in small midfield forests (Wasilewski, 2001). They occurred less frequently – 10-25 roe deer per km^2, in large forest complexes (Fruziński *et al.*, 1983; Skorupski *et al.*, 2014). However, the lowest density – 2-14 individuals per km^2 – was characteristic of the roe deer population inhabiting open agricultural landscapes (Kamieniarz, 2013).

The number of roe deer in Poland has been increasing for many decades of the last century (Pielowski *et al.*, 1993). In the 1990s, such a trend was no longer observed in the reference populations determined in the national game management studies. At the same time, it was found that the numbers of roe deer determined using proven methods there were higher than those provided by hunters in official reports. In the last decade of the 20th century, the actual number of roe deer in small midfield forests and agricultural areas was on average 88% higher than that included in hunting reports (Kamieniarz and Panek, 2008). However, in the second decade of the 21st century, the verified numbers of this species in the forest complexes of Western Pomerania, were underestimated by only 12% (Skorupski *et al.*, 2014). This means that the increase in the number of roe deer shown in hunting reports at the turn of the 20th and 21st centuries actually reflected the process of making data on population size more realistic (Kamieniarz and Panek, 2008).

In some areas, however, roe deer densities were already declining in the late 1990s. One of the reasons for this could be a rapid increase in fox *Vulpes vulpes* L. density after rabies vaccinations and the pressure of these predators on fawns. A decrease in the proportion of juveniles in the population was observed near Kościan in western Poland, where roe deer inhabited the agricultural landscape (Kamieniarz and Bresiński, 2000). However, in the following years, it was found that the pressure of foxes on fawns occurred mainly during periods of low availability of voles (which are the main food for these predators). Therefore, the impact of foxes should not cause long-term changes in the number of roe deer (Panek and Kamieniarz, 2017).

In western Poland in the Zielonka Forest near Poznań, where in the half of 1970s there were in spring 19-21 roe deer per square kilometre (Fruziński *et al.*, 1983), in the last years of the 20th century the density ranged for 12 to 17 individuals per km^2 (Fruziński *et al.*, 2000). Consequently, hunting for females and fawns was completely stopped there. Despite this, the number continued to decrease and stabilized only at the level of 7-9 individuals per km^2 (Kamieniarz and Skubis, 2011).

In 2015-2019 it was decided to update the knowledge of basic ecological parameters of roe deer population from the Zielonka forest. It was investigated why the population of roe deer did not recover despite the restriction of shooting. It was assumed that reproduction in the local population has decreased.

Materials and methods

Study area. The Zielonka Forest, located north-east of Poznań, has served as a research site for game management studies since 1965. At that time, the Game Management Centre 'Zielonka' was established there. Currently, it is part of the Hunting Experimental Institution at the Poznan University of Life Sciences. The study area covered an area of 135 km^2, including a large forest complex with small fragments of surrounding agricultural lands. As a result, the forest cover was 69%. Fresh mixed forest habitats predominated there (66%), with a significant admixture of fresh mixed coniferous forest (16%) and fresh forest (13%). Stands were mostly dominated by Scots pine *Pinus sylvestris* L. (75%), with a high admixture of oak forests *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. (16%). The stands were mainly medium-aged (53%) and mature (38%). The youngest stands occupied only 8% (PUL, 2018a, b).

The described forest complex has been intensively used by the public as a place of recreation for years. Additionally, at the end of the 20th century, this area started to be settled by people migrating there from Poznań. This caused a progressive urbanization and changes in the landscape structure (Szeląg, 2002). Residential development caused, among others, isolating large parts of the forest from agricultural areas that were previously feeding sites for forest animals.

Since the 1990s, forest plantations in the Zielonka Forest have been increasingly fenced (Fruziński *et al.*, 2000). This process was stimulated by changes in forest management that occurred along with the political and economic transformation in Poland. Large-scale clear-cutting in the forests was then abandoned in favour of small clear-cuttings called gap felling. Moreover, due to the high fertility of habitats, broadleaved species were promoted in newly established forest plantations (Jaszczak *et al.*, 2017).

In the study area there were roe deer, but also numerous populations of red deer *Cervus elaphus* L., wild boars *Sus scrofa* L. and especially fallow deer *Dama dama* L. The density of these species during the study period was 5, 7 and 16 individuals per 1 km^2, respectively. Fallow deer – unlike roe deer, whose population was in decline, dynamically increased their numbers. As a result, the size of hunting bag of both species changed over years (Fig. 1). The high density of fallow

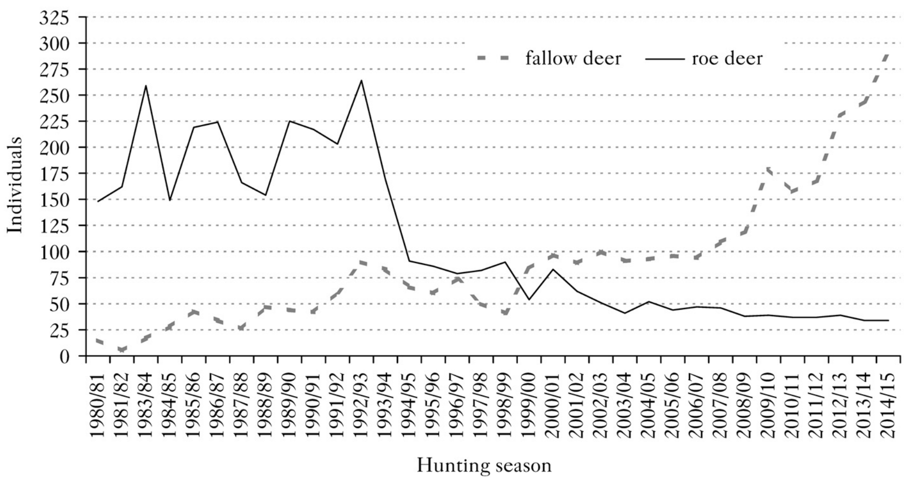

Fig. 1.

Shooting of fallow deer and roe deer in the hunting seasons 1980/1981-2014/2015 based on data from annual hunting plans for the research area deer meant that they were the common prey of wolves *Canis lupus* L., which began to appear regularly in the study area in 2016 (Department of Game Management and Forest Protection, unpubl. data).

ASSESSMENT OF POPULATION PARAMETERS. The density and sex structure were assessed every year. The animals were counted with help by drivers moving in a line formation (counting a line formation). This is a modification of the drive counts method, which is an accepted method for assessing the number of deer in forest areas (Flajšman *et al.*, 2018; Kamieniarz *et al.*, 2023). Counting events were conducted in March, after the end of the deer hunting season. They took place before the start of vegetation growth, to ensure unbiased detection of animals in the forest. Randomly designated control plots covered a total of 8.7 km^2 (16 plots with an average area of 0.54 km^2), which comprised 10% of forests in the study area. The counting teams consisted of approximately 15 observers standing at the periphery of the control plots and spaced at least 100 meters apart, and approximately 30 people forming a line formation who walked in rows, with intervals of 20-30 meters, through the controlled areas. Everyone only recorded animals passing from the left, recording the species and sex of the animal. In the case of roe deer living alone or in family groups, gender identification was not a problem because their tertiary sexual characteristics are clearly visible.

The fertility of roe deer was assessed based on the number of *corpus luteum* (CL) on the ovaries, which is a more accurate method than counting embryos in the uterus. This is because there is a possibility of failure of implantation of the fertilized blastocyst or early death of the embryo. The approximate number of fawns in this way could have been at most slightly underestimated due to the occurrence of monozygotic twins, but this is extremely rare in roe deer (Flajšman *et al.*, 2017). In the 2015/2016 and 2016/2017 hunting seasons, reproductive organs were collected from female roe deer shot between October 1 and mid-January. Organ dissection, including examination of the ovaries to detect *corpus luteum*, was performed in the laboratory.

In October and November 2015, only a few females (26%) showed signs of ovulation, while in December CLs were present in almost all of them (90%). Such a pattern of *corpora lutea* was observed that year in many roe deer in western Poland (Kamieniarz *et al.*, unpubl. data). This indicated the occurrence of a delayed late autumn oestrus (Pielowski, 1999; Hermes *et al.*, 2000). Therefore, individuals obtained in October and November 2015 were excluded from the fecundity assessment because they could have come into oestrus later if they had not been shot. In the following year we did not record the same phenomenon.

The productivity in population was determined on the basis of the number of reared fawns and the number of females present from the population in autumn (Fruziński and Łabudzki, 1982; Kamieniarz, 2013). Observations of roe deer were recorded at the turn of September and October, *i.e.* after the period of the highest mortality of young, which is high in the first weeks of life (Andersen *et al.*, 1998), but also increases at the turn of summer and autumn (Kamieniarz, 2013). At the same time, this term allowed for a clear distinction between juveniles and adults. Observations were recorded once in individual parts of the Zielonka Forest. The roe deer encountered were recorded, distinguishing adult males and females as well as juveniles. The shooting of females and juveniles was suspended until these observations were completed.

Roe deer mortality was characterized based on data on the size and structure of hunting bag. Information about other falls – despite the involvement of a large group of hunters and foresters in the data collection – was scarce. During the entire research period, males were shot (from May 11 to the end of September), while females and juveniles were harvested only in the 2015/2016 and 2016/2017 hunting seasons (from October 1 to mid-January). In each season, the mortality rate was calculated, which was the average number of roe deer shot per 1 square kilometre of forest. Additionally, the hunting intensity index was determined, which was the proportion of roe deer shooting in a given hunting season to the spring density at its beginning.

Body condition was described based on data on the eviscerated body mass of shot roe deer (in the case of males, additionally after cutting off the head with antlers), with an accuracy of 0.5 kg. The shooting of females and juveniles was evenly distributed during the hunting season (described above). The situation was similar in the case of males, except for the 2018/2019 hunting season. The small sample then came only from a short period at the turn of July and August. The body mass of roe deer is then higher than after winter, *i.e.* in May and June, therefore this data was excluded from the analysis of the males condition.

The age structure of the population was determined based on the patterns of teeth development in the jaws of hunted individuals. First, it was checked whether there were primary teeth characteristic for individuals in the first year of life. If these were missing, the mandible was dissected to determine the age of the individual based on histological examination according to the methodology described by Zalewski *et al.* (2009). The age of all roe deer was assessed for the body condition analysis. However, only data on females was used to assess the age structure of the population because the shooting of females was a random sample. Whereas, the shooting of adult males was subject to hunting selection regulations (Zalewski, 2022).

STATISTICAL METHODS. We analysed data using the R program (R Core Team, 2021). To estimate the density of roe deer at the level of individual control plots (continuous variable), we converted them into density per standardized unit of area (1 km^2) and discretized them. Density was determined using generalized linear models with fixed and random effects (Generalized Linear Mixed-effects Model; GLMM), assuming a Poisson distribution of the dependent variable. Then, we assessed whether the model is biased by zero-inflation through a formal zero-inflation test value inflation test (increasing the error in estimating the expected value) and whether there are problems with overdispersion using a formal dispersion test, both performed using the DHARMa package (Hartig, 2020). Finally we used a zero-inflated GLMM assuming a Poisson distribution, as we did not detect problems with overdispersion (Table 1).

A linear model with random and fixed effects (LMM) was used to describe the relationship between body mass and the age and/or sex of roe deer. The season in which the research material was obtained was considered a random effect. The models were developed using the lme4 package (Bates *et al.*, 2015). The proportion of variability explained by model was reported using the marginal and conditional coefficients of determination (R^2_m and R^2_c), expressing, respectively, what part of the variability is explained by fixed effects and fixed effects together with random effects (Nakagawa and Schielzeth, 2013).

Table 1.

Parameters of the roe deer density model along with expected values for the model estimating the number of non-zero observations and the model estimating the probability that a given observation will be non-zero

Model component (variable = intercept)	Factor	Standard error	Test statistic z	Pr(>|z|)	Expected value	95% confidence interval
Counting	1.600	0.197	8.123	<0.001	4.95	3.37-7.29
Probability of non-zero values	−0.357	0.346	−1.032	0.302	0.56	0.52-0.66

The significance of differences between years in the number of *corpora lutea* on the ovaries (a measure of fertility) and in the proportion of young to females (a measure of productivity) was determined using the *Chi*^{2} test.

Results

Density and sex ratio. During the study period the average density of roe deer in the Zielonka Forest was 3.4 individuals per square kilometre. Initially, the population trend was decreasing. The density was restored only in the spring of 2019, *i.e.* two years after the suspension of the shooting of females and fawns (Table 2).

The sex ratio was characterized by a predominance of females. It was most even in the spring of 2016, *i.e.* after the hunting season in which adult males and females were hunted with similar intensity (Table 3).

Reproduction and mortality. It was found that in 2015, 19 out of 21 females ovulated, and in 2016-2019 out of 20. The number of corpora lutea on ovaries did not differ between years (χ^2=2.8793, p=0.09), and the average for the two-year study was 1.8 CL per ovulating female and 1.6 CL for all females (from 2 years of age).

Data on the presence of juveniles in the fall showed that the survival rate of fawns was low. There were on average 0.3 fawns per female present in the autumn population. During the

Table 2.

Density and sex ratio in the roe deer population in the Zielonka Forest in 2015-2019 assessed with help from drivers moving in a line formation

Year	Density (ind./km^2) Mean ±SE	Sex ratio (♂:♀)
2015	4.8 ±0.6	1: 2.6
2016	3.7 ±0.5	1: 1.7
2017	2.5 ±0.3	1: 2.5
2018	2.2 ±0.3	1: 4.5
2019	3.8 ±0.5	1: 1.9

Table 3.

Hunting bag and body mass (eviscerated, kg) of roe deer of various ages in the Zielonka Forest in the hunting seasons 2015/16-2018/19

Season	Age (year of life)							
	juveniles		adults					
	5-8 months		second year		older		all	
	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$
Males								
2015/16	4	10.0	3	16.3	24	15.5	27	15.6
2016/17	3	10.3	2	16.5	20	15.6	22	15.7
2017/18	–	–	4	14.5	22	15.6	26	15.5
2018/19	–	–	N=7; data were excluded from analysis					
Total	7	10.1	9	15.6	66	15.6	75	15.6
Females								
2015/16	9	8.4	9	13.0	23	14.8	32	14.3
2016/17	4	9.8	5	14.0	14	14.0	19	14.0
Total	13	8.9	14	13.4	37	14.5	51	14.2

study period, the proportion of juveniles to females did not differ between years (χ^2=0.414, p=0.813) and ranged from 0.2 to 0.3.

Mortality was changing during the study period (Table 3). Initially, the shooting was carried out in all sex and age groups, but in 2017 and 2018 only adult males were hunted (only 7 bucks were shot in the latter year). As a result, 0.9 individuals were shot per 1 km^2 of hunting grounds in the 2015/2016 hunting season, and only 0.1 individuals/km^2 in the 2018/2019 season. This resulted in a reduction of population numbers by almost 20% in the 2015/2016 hunting season and only 3.5% in the 2018/2019 season.

Body mass. The average body mass of adult males was 15.6 kg and females – 14.2 kg. In the group of females, the average body mass in second years of life was 13.4 kg and was smaller than that of older, which weighed 14.5 kg. Male fawns weighed on average 10.1 kg and female fawns 8.9 kg (Table 3). The average body mass of juveniles of both sexes was 9.3 kg.

Body mass increased with age by an average of 0.66 kg, and males weighed on average 1.92 kg more than females. Both variables in the model, *i.e.* sex and age, had a significant effect (p<0.0001). There was no effect of a particular year on the average body mass of roe deer (standard deviation of the random effect <0.001), and the model explained 31.6% of the variability in body mass (Table 4, Fig. 2).

Age structure. The youngest individuals predominated among the hunted females (29%, Table 5). The significant share of the oldest individuals (≥5 years) in the first hunting season

Table 4.
Linear model of roe deer body mass as a function of age and sex

Variable	Factor	Standard error	Test statistic t	Pr(>|t|)
(Intercept)	10.7444	0.4734	22.694	<0.0001
Ratio = Males	1.9219	0.3877	4.958	<0.0001
Age	0.6624	0.1055	6.281	<0.0001

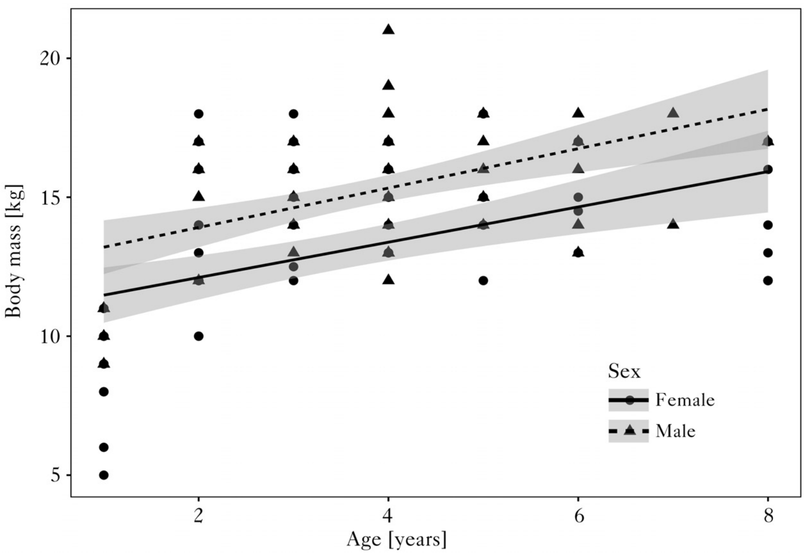

Fig. 2.
The relationship between body mass and age of male and female roe deer in the Zielonka Forest

Table 5.
Age structure of adult female roe deer shot in the Zielonka Forest in the hunting seasons 2015/16-2016/17

Season	N	Age (year of life)						Average age
		2	3	4	5	6	≥7	
2015/16	33	10	4	6	5	3	5	4.1
2016/17	19	5	3	5	2	2	2	3.9
Total	52	15	7	11	7	5	7	4.0

could stem from the fact that before these studies, females had not been shot in the Zielonka Forest for many years. The average age of hunted females was 4 years and the age structure did not differ between the analysed hunting seasons (χ^2=0.869; p=0.97).

Discussion

According to data from the national hunting reports – the number of roe deer in Poland had an increasing trend in the second half of the 20th century. However, at the beginning of the 21st century it began to stabilize (Kamieniarz and Panek, 2008). Meanwhile, in the Zielonka Forest, a decrease in the number of roe deer was observed already in the 1990s (Fruziński *et al.*, 2000), and in the following decade the density stabilized at the level of 7-9 individuals/km^2 (Kamieniarz and Skubis, 2011). It was considered as low compared to many other forest areas in western Poland. At that time, in the mid-field forest in the south of Greater Poland, there were from 30 to 52 roe deer/km^2 (Nawrot, 2010), and in large forest complexes in the northern part of Western Pomerania in 2012, an average of 21 individuals/km^2 (Jakubowski, 2017).

Mortality is the parameter that most often causes population decline. In areas without large predators (which applied to the Zielonka Forest until 2016), hunting could have been a significant cause of population losses. Especially since information on other falls – despite the involvement of a large number of hunters and foresters in data collection – was scarce (mainly roadkill's). Therefore, when the decline in numbers was noticed, the shooting of females and fawns was stopped there. However, the number of roe deer did not increase and only stabilized at a low level for several years (Kamieniarz and Skubis, 2011). Afterwards it decreased again and in the years 2015-2019 the density oscillated between 2 and 5 individuals/km^2. These oscillations were synchronized with a small shooting of females and fawns for research purposes in the 2015/2016-2016/2017 hunting seasons. Therefore, giving up hunting is a solution that benefits the conservation of the species, but in the Zielonka Forest it has not solved the problem of low density.

Reproduction also determines dynamics of the population. The high fertility of roe deer allows for the number restitution of this species. Majority of roe deer have twins and less often single or triple pregnancies (Andersen *et al.*, 1998; Flajšman *et al.*, 2017). In the Zielonka Forest in the 1970s, the fertility rate was 1.8 embryos per pregnant female (Fruziński and Łabudzki, 1982). A similar one was registered there in 1999-2000 (Fruziński *et al.*, 2000). Also in 2015 and 2016, the fertility of roe deer, described by the number of *corpora lutea* on the ovaries, was similar – 1.8 CL per female that showed oestrus. This is also the average value of this parameter in Europe (Flajšman *et al.*, 2018).

Roe deer populations are characterized by high productivity due to their high fertility. However, litter size depends on latitude and body mass (Flajšman *et al.*, 2018). The fertility in a predator-free area in Norway was as high as 2.0-2.4 fawns per female (Andersen and Linnell, 2000), hence with the 18% summer mortality (Andersen and Linnell, 1998), an average of 1.75

fawns/♀ survived until autumn. The productivity is always inversely proportional to the density. In France it ranged from 0.9-1.3 juv./♀ (Vincent *et al.*, 1995), and when the density was very high, as in Italy (53.8 ±4.8 roe deer/km^2), it was at the level of 0.75 ±0.4 juveniles per female (Focardi *et al.*, 2002). Roe deer populations in Poland, despite low densities, were characterized by a low productivity. At the beginning of the 21st century, in field roe deer in western Poland it was 0.3-0.7 juv./♀ (Kamieniarz, 2013), in forest roe deer in this part of Poland it was on average 0.5 juv./♀ (Zych, 2020) and 0.6 juv./♀ in the eastern part of this country (Flis, 2005). In the Zielonka Forest, productivity was 0.6 juv/♀ in the 1970s (Fruziński and Łabudzki, 1982), but in the 1990s decreased to only 0.3 juv./♀ (Fruziński *et al.*, 2000). It was also that small in 2015-2019.

Losses during pregnancy in roe deer are considered to be small (Danilkin, 1996; Flajšman *et al.*, 2017). In contrast, they are large after birth, especially in the first month of life (Andersen and Linnell, 1998).The survival of the offspring depends on the quality of postnatal care, and this in turn depends on the condition of the mother, which is influenced by food resources (Andersen *et al.*, 2000). As a result, the fawn mortality is higher in areas with limited food supply (Pettorelli *et al.*, 2003). At the same time, female roe deer are income breeders (Andersen *et al.*, 2000). They provide higher maternal allocation towards daughters. In areas with limited food resources, male fawns are therefore in poorer condition – both in terms of body weight and body size (Toïgo *et al.*, 2006). Under unfavourable environmental conditions, they have a lower chance of survival than female fawns. During hunting in the Zielonka Forest, twice as many female fawns were shot as male fawns. In addition, females had an advantage over males during spring counts throughout the study period. This was also the case after the 2015/2016-2016/2017 hunting seasons, when young and adult roe deer of both sexes were hunted. The low growth rate of fawns in the Zielonka Forest was most likely caused by the high mortality of offspring, especially male individuals. This is the first indication that the food resources for roe deer in the study area were limited.

The population of adult females from the Zielonka Forest was characterized by an average age 4 years, which is typical for this species in western Poland (Kamieniarz, 2013). The body mass of roe deer changed evenly with the age of the animals, and during the study period it did not differ between years. However, adult females, *i.e.* those potentially raising offspring (≥3 years old), had a significantly lower average body mass than in the past – 14.5 kg compared to 16.5 kg in the 1970s. The body mass of middle-aged and older males changed similarly – 15.6 kg *vs.* 17.1 kg (Fruziński *et al.*, 1982). There was also a decrease in the average mass of fawns – 9.3 kg *vs.* 10.1 kg in 1986-93 (Łabudzki and Szczegóła, 1996). Meanwhile, in another experimental area – in the agricultural landscape near Kościan (70 km south of the Zielonka Forest), adult females weighed 18.6 kg (Kamieniarz, 2013) *vs.* 16.6 kg in the 1970s (Fruziński *et al.*, 1982). At the same time, the productivity there was 0.7 fawns per female (Kamieniarz, 2013), so it was twice as high as in the Zielonka Forest. As a result, after limiting the hunting of females and fawns, the population from the Kościan area (initial density of 3 individuals/km^2) doubled after a few years (Kamieniarz, 2006).

One of the factors influencing the condition and mortality of roe deer are diseases, including parasitic ones (Štěrba and Zámek, 1985; Pielowski, 1999). However, no falls due to disease were observed during the study period. The increase in parasite invasion was also not the direct cause of the decline in body condition, as parallel studies showed a decrease in the intensity and prevalence of parasite infestation in the Zielonka Forest (Kamieniarz *et al.*, 2020) compared to parasites found there in the 1980s (Klejnotowski, 1992).

The decline in the body mass – that accompanied the decrease in the density of roe deer in the Zielonka Forest – most likely have resulted from changes in food resources (Pielowski, 1999). Melis *et al.* (2009) found that – in the absence of large carnivores – food availability was the major factor shaping population density of roe deer in Europe. Roe deer abundance increased with the overall productivity of vegetation cover and with lower forest cover (sparser forest cover means that a higher proportion of overall plant productivity is allocated to ground vegetation and thus is available to roe deer). Meanwhile, the studied area description indicates that at the turn of the 20th and 21st centuries, in Poland (including the Zielonka Forest) there were changes in the forest spatial structure. Large-scale clear-cutting in the forests was abandoned in favour of small clear-cuttings called gap felling. Moreover, broadleaved species were promoted in newly established forest plantations due to the fertility of habitats (Jaszczak *et al.*, 2017). The frequent occurrence of broadleaved species resulted in their browsing by deer. Therefore, forest plantations have been increasingly fenced since the 1990s (Fruziński *et al.*, 2000). Currently, most forest plantations in the Zielonka Forest are fenced, as only a few pine plantations were protected against deer with repellents. Mesh fences mostly protected small plantations that resulted from small clear-cuttings known as gap felling, whose area did not exceed 0.5 ha. In the spring of 2024, fenced forest plantations in the Zielonka Forest covered 577.8 ha, and the fences were 353.3 km long (SILP database of the Łopuchówko Forest District, unpubl. data; Database of the Forest Experimental Station in Murowana Goślina, unpubl. data). As a consequence of these changes, there was decrease in the availability of sunny, open areas where animals could find valuable food in the form of various herbaceous plants, mainly representing forest edge (*Artemisietea*), clearing site (*Epilobietea*) and meadow (*Molinio-Arrhenetheretea*) communities. This type of food is required by roe deer, which is characterised by a relatively small stomach in the ruminant group. Therefore they selectively chooses plants or their parts with a great concentration of nutrients and low fibres (Hofmann *et al.*, 1988; Obidziński *et al.*, 2013; Adhikari *et al.*, 2016).

An alternative feeding site is the overexposed old-growth forest in fresh mixed coniferous habitats, where light reaches the forest floor more often and enables the development of herbaceous vegetation (Barabasz, 1994). However, fresh forest habitats dominated in the Zielonka Forest. The development of the undergrowth is limited there by lower light transmission through the more compact crowns of broadleaved species (Jagodziński *et al.*, 2019; Landuyt *et al.*, 2020). The share of broadleaved species in the forest stands of the Zielonka Forest increased from 9.8% to 18.2% in the years 1963-2014 (Jaszczak *et al.*, 2017). In turn, the development of ground cover in coniferous habitats was limited by the common occurrence of American bird cherry *Prunus serotina* Ehrh. in the understory layer (Rutkowski *et al.*, 2002). Between 1994 and 2004 alone, the area of occurrence of this invasive species in the Zielonka Experimental Forest District increased by 32%. As a result, American bird cherry was the main understory species on 71% of the local forest stands (Grajewski *et al.*, 2010).

The consequence of changes in the forest environment, and probably also climate change, were floristic and phytosociological changes in the Zielonka Forest (Konatowska and Rutkowski, 2021). In the 1950s and 1960s, 332 species of vascular plants, mainly herbaceous plants, were found on control plots in experimental forests (Nowaczyk, 1964). By the beginning of the 21st century, as many as 144 species had already disappeared from these sites, and at the same time only 26 new ones had appeared (Konatowska and Rutkowski, 2021). Changes in forest structure, especially the disappearance of open forest ecosystems, have been recognized today as the cause of the decline in species diversity among herbaceous plants, but also among vertebrates and invertebrates in vast areas of the eastern United States (Hanberry *et al.*, 2020). The transformed species and spatial structure of the Zielonka Forest may therefore limit the availability of ecological niches for roe deer within this large forest complex.

Finding food rich in nutrients and at the same time easily digestible may be especially difficult when there are competing species, especially fallow deer. The overlap between the food niches of fallow deer and roe deer is high and reaches 52%. Competition may increase especially during periods of food shortage, including autumn and winter, as well as in areas with large numbers of fallow deer (Obidziński *et al.*, 2013). Meanwhile, in the Zielonka Forest, where the number and hunting bag of roe deer decreased, there was a parallel increase in the number and shooting of fallow deer (Fig. 1). It is therefore worth to analyse the spatial distribution of fallow deer and roe deer living in this forest complex, as numerous studies indicate antagonisms between these species. In Sweden, it was observed that roe deer avoid the presence of fallow deer when choosing feeding grounds (Kjellander *et al.*, 2006; Cederholm, 2012). In turn, Italian research indicated the possibility of fallow deer driving roe deer away from natural feeding grounds (Ferretti *et al.*, 2008). Focardi *et al.* (2006) even stated that a high density of fallow deer resulted in smaller body mass and a decline in the number of the local roe deer subspecies *Capreolus capreolus italicus* Festa. Interspecies competition could influence changes in the area utilization by roe deer, hence reduction of the number of fallow deer was indicated as one of the ways to protect this relict subspecies. In Poland, the fallow deer was considered an alien species, therefore the further population growth of this species will be limited (Głowaciński *et al.*, 2011; Ustawa, 2021). However, in areas where fallow deer densities are already high, a reduction in population size should be considered. In the Zielonka Forest, where the roe deer situation is poor, hunting for this species was abandoned and at the same time fallow deer shooting was intensified.

Conclusions

The reduction in the density of roe deer in the Zielonka Forest was accompanied by a decrease in the body mass of adults and young, and, as a consequence, the produce of fawns in the population was low.

The decrease in body mass of roe deer was the result of limited food resources in the Zielonka Forest. Most likely, this happened as a result of the reduced presence of herbaceous vegetation (including under the canopy of deciduous trees or the invasive American bird cherry), the fact that most forest plantations were fenced with nets (often the only sunny areas in this forest) as well as the competition from a very large population of fallow deer.

Authors' contributions

R.K. – concept and organization of research, counts and roe deer observations, final editing of the manuscript; M.Sz. – source roe deer and samples for laboratory tests, counts and roe deer observations, preparing a draft manuscript, discussion of the manuscript; M.D. – statistical analyses, discussion of the manuscript; G.G., M.S., J.S. – counts and roe deer observations, discussion of the manuscript; B.J., M.W.-W. – laboratory analyses of reproductive organs; discussion of the manuscript; D.Z. – age assessment of roe deer by histological method, discussion of the manuscript.

Conflicts of interest

The authors declare no conflicts of interest.

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STRESZCZENIE

Coraz mniej saren w lesie – przyczyny populacyjne i środowiskowe

Liczebność saren *C. capreolus* w Polsce w drugiej połowie XX w. wykazywała tendencję wzrostową, po czym w XXI w. ustabilizowała się. Odmienna sytuacja miała miejsce w Puszczy Zielonka koło Poznania, gdzie populacja tego gatunku zmniejszała zagęszczenie od końca lat 90. XX w. Równolegle na tym terenie rozpoczął się wzrost liczebności danieli *D. dama*. Konsekwencją było ograniczanie odstrzału saren, a zwiększanie pozyskania łowieckiego danieli (ryc. 1). Celem badań prowadzonych od wiosny 2015 r. do wiosny 2019 r. było wskazanie populacyjnych przyczyn niskiego zagęszczenia saren w tym kompleksie leśnym.

Oceny liczebności saren prowadzone w latach 2015-2019 metodą liczeń tyralierą i estymowane za pomocą modelu GLMM zakładającego rozkład Poissona z korektą inflacji wartości zerowych (tab. 1) wykazały niskie zagęszczenie – średnio 3,4 osobn./100 ha lasu – oraz przewagę samic nad samcami (tab. 2). Populacja odznaczała się typową płodnością – 1,8 ciałka żółtego na owulująca samicę – ale bardzo niskim przyrostem młodych jesienią: 0,3 koźlaka na kozę. Pozyskanie łowieckie było niewielkie (tab. 3) i służyło uzyskaniu danych o masie ciała, płodności i strukturze wieku w tej populacji. Masa ciała różniła się w zależności od płci i wieku (ryc. 2; tab. 3 i 4) i wynosiła średnio: rogacze 15,6 kg, kozy 14,2 kg, a koźlęta 9,3 kg. Średnia wieku wśród dorosłych samic wynosiła 4 lata (tab. 5) i była typowa dla tego gatunku w zachodniej Polsce.

Badania wykazały, że zmniejszaniu zagęszczenia saren w Puszczy Zielonka towarzyszył spadek masy ciała osobników dorosłych i koźląt. Masa tuszy była o około 10% mniejsza w porównaniu z latami 70. XX w., mimo że wówczas zagęszczenie saren było większe. Ponadto w tym samym okresie przyrost młodych oceniany jesienią zmniejszył się z 0,7 do 0,3 koźlaka na samicę. Tymczasem w monitorowanej w analogicznym okresie populacji saren w okolicach Czempinia (70 km na południe od Puszczy Zielonka) masa ciała zwiększyła się o około 10%, a przyrost młodych zmienił się nieznacznie: z 0,8 do 0,7 koźlaka na samicę w okresie jesieni. Spadek masy ciała saren w Puszczy Zielonka wynikał najprawdopodobniej z ograniczenia dostępu do pokarmu bogatego w składniki pokarmowe i o małej zawartości błonnika, a więc zwłaszcza do roślinności zielnej. Taki pokarm jest niezbędny dla saren, które, choć są przeżuwaczami, mają mały żołądek i selektywnie pobierają pożywienie.

Przyczynami ograniczenia zasobów pokarmowych dla saren w Puszczy Zielonka mogło być:

- zmniejszenie obecności i dostępności nasłonecznionych powierzchni otwartych, w związku z odchodzeniem od rozległych rębni zupełnych na rzecz niewielkich rębni gniazdowych, a następnie grodzeniem upraw leśnych płotami z siatki;
- ubożenie runa leśnego w konsekwencji zmniejszającej się transmisji światła słonecznego w drzewostanach na siedliskach lasowych, gdzie coraz liczniej występował dąb i inne gatunki liściaste, a także na siedliskach borowych, gdzie nastąpiła inwazja czeremchy amerykańskiej;
- wzrost liczebności danieli – zwierząt obcych w krajowej faunie, które są konkurentami wobec saren.