

Application of the tyraliera counting method to the large-scale inventory of red deer *Cervus elaphus* in the northern part of Western Pomerania, Poland

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Abstract Game animal damage in the forests and fields of Central Europe, which dramatically increased at the turn of the 21st century, has undermined the reliability of the size of game population estimates. It is hypothesized that this problem can be attributed to errors in the assessment of animal density. This study conducted game inventories in a region characterized by a large ungulate population using a count method with drivers in line formation (direct counts in control plots). The size of the red deer population in the investigated area was estimated using generalized linear models assuming a negative binomial distribution based on the compound distribution (including the zero-inflated model). The mean red deer density in spring 2012 was 21.5 animals/km² of forest. The number of red deer determined during this study is often higher than hunters indicated in annual game management plans. For the rational management of populations, it is therefore necessary to verify those estimates periodically, e.g. every five years. The statistical analysis of data from tyraliera method counts may show the actual population size during spring. Thus, it can be the basis for adequately planning hunting bags. Adjusting the population density to the carrying environmental capacity should make it possible to reduce the pressure of red deer on forests and agricultural land.

Keywords: counting method, density, *Cervus elaphus*, game management, Poland.

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Introduction

The primary task for contemporary hunting is to maintain an optimal wildlife population size and to manage environmental conditions to limit potential conflict with, for example, farmers and foresters. At the turn of the 20th and 21st centuries, an upward trend was observed in red deer populations in many countries, such as Central Europe (Reimoser & Reimoser 2016) and France (Maillard et al. 2010). A direct consequence resulted in increased damage caused by the game species, reaching unacceptable levels by farmers and foresters (Reimoser & Reimoser 2010, Katona et al. 2011, Bleier et al. 2012). Such a situation was present mainly in the western parts of Poland (Kamieniarz & Panek 2008, Zalewski et al. 2018) where the main problem was browsing and trampling of crops and in forests, tree seedlings browsing and gnawing of young trees (Zalewski 2015, Zalewski et al. 2019). While there could be variation in densities (Tourani et al. 2023), humans are influencing most the species effectiveness (van Beeck Calkoen et al. 2023) and a rational game management policy requires information on the size and trends in animal populations. However, the data in game management plans is frequently far from the actual status, and conducting an animal inventory is problematic for science and hunting practices (Pucek et al. 1975, Lancia et al. 1994, Borkowski et al. 2011, Bobek et al. 2012). Those results are often significantly underestimated, especially in the case of big game populations (Csányi 1992, Pielowski et al. 1993, Bartel et al. 2003, Kamieniarz & Panek 2008, Reimoser & Reimoser 2010, Stubbe and Stubbe 2016, Zalewski et al. 2018).

One of the methods used to assess the population size of large herbivores is to conduct drive counts, which, initially, were only considered helpful to inventory roe deer (Pucek et al. 1975), rather than gregarious species (red deer, fallow deer, and wild

boars), since they are distributed in clusters within hunting areas (Fruziński 2002, Bobek et al. 2013). In contrast, Okarma & Tomek (2008) observed that red deer may be counted using the above-mentioned method since in early spring their distribution is of the cluster-random type. Computer simulations by Borkowski et al. (2011) showed that the accuracy of the method depends on the density of the deer, which should be a minimum of 5 animals per 1 km² of the forest.

During 2008-2011, an attempt was made to estimate the numbers of European elk, red deer, roe deer, and wild boars using drive counts in forest complexes in northeastern Poland. The results revealed that red deer populations had been underestimated by up to 300% from numbers concluded from occasional hunters' observations (Borowik et al. 2011). Counts by a line of drivers are typically conducted at the end of winter and beginning of spring (from mid-February until the first days of April) when the fields are not covered by crops in which animals could hide. Therefore, large ungulates remain in forested areas during the day and can be counted on randomly selected plots (Okarma & Tomek 2008).

The main problem with applying the drive count method to assess game populations is related to processing its results. An arithmetic mean has sometimes been used to calculate the expected value (the mean density in a GMR). However, the number of animals is a discontinuous variable; additionally, this distribution is skewed. For this reason, another distribution type should be used.

Earlier studies showed greater applicability of the Rayleigh distribution to estimate wildlife density rather than a normal distribution (Tomek & Bar 1997). The cluster character of distributions (Fruziński 2002, Bobek et al. 2013) also determines a certain number of zero observations. They have a considerable effect on the model assuming a non-continuous distribution, for example, the Poisson or the negative binomial distribution. To avoid an erroneous

estimation of the expected value, compound models are used (Lambert 1992, Brooks *et al.* 2017), in which the probability of a non-zero observation (using a binomial distribution) and the quantitative component, i.e. population size (using the Poisson distribution or the negative binomial distribution) are estimated separately. The application of inappropriate methods to estimate data not only results in the underestimation of expected values, but also in reduced trust in management which is based on incorrectly conducted analyses.

The aim of the study was to collect and analyze data on the actual red deer density in north-western Poland, in an area which, according to hunter's estimates, had one of the largest red deer populations in this country at that time. It was hypothesized that the number of animals in the area under investigation, constituting the basis for the development of hunting plans, had been underestimated. For the hypothesis verification it was crucial to determine which density estimation method was least burdened by formal errors.

Materials and Methods

Study area

The research in question was conducted in the northern part of Western Pomerania in four game management regions (GMRs) according to Long-term Game Management Plan for Szczecin Regional Directorate of the State Forests 2007-2017. GMRs differed in size as each of them covered from one to four forest inspectorates (Fig. 1, Table 1). The study area covered 5185 km², of which 1722 km² were forests. The average forest cover was 33.2%, but it varied between the game management regions and was often divided into small fragments located on sites typical

of fertile and mesic broadleaved forests and mixed coniferous forests. Scots pine *Pinus sylvestris* L. was the dominant species on almost all the sites, either the forest-forming species or an admixture in the stands. GMR II (Międzyzdroje), was unique as its western and central part was located on islands in the Baltic Sea: Wolin, Uznam, and Karsibór. In Wolin, a fragment of the study area measuring 10 937 ha and with 43% forest cover was managed by the Wolin National Park.

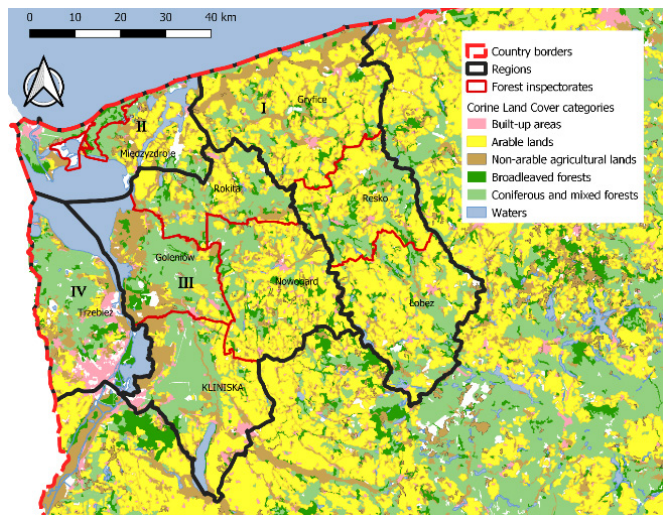


Figure 1 Game Management Regions and forest inspectorates in the northern part of Western Pomerania (Poland) included in the study area on the background of the Corine Land Cover map (<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>)

In the first three GMRs, the agricultural areas were characterized by a considerable share of fields with cereal and rape (Rocznik Statystyczny, 2015). However, in GMR IV (Trzebież), which has an exceptionally high forest cover (48%), agricultural areas were gradually being transformed into urbanized areas (Fig. 1). For many years, the study area was known for its high densities of red deer, roe deer, and wild boar populations, while in some locations it was inhabited by fallow deer and periodically visited by European elk (Pielowski *et al.* 1993, Kamieniarz & Panek 2008, Zalewski *et al.* 2018).

Table 1 Characteristics of investigated Game Management Regions (according to Long-term Game Management Plan for Szczecin Regional Directorate of the State Forests 2007-2017).

Game management region	Forest inspectorates	Area (ha)	Forest cover (%)
GMR I Resko	Gryfice	115 677	21.6
	Łobez	72 013	31.7
	Resko	44 840	40.5
	Total	232 530	28.4
GMR II Międzyzdroje	Międzyzdroje	35 537	33.3
GMR III Nowogard	Rokita	36 865	47.0
	Goleniów	37 627	46.8
	Nowogard	62 927	32.2
	Kliniska	69 005	34.0
	Total	206 424	40.0
GMR IV Trzebież	Trzebież	44 002	57.8
OVERALL		518 493	33.2

Data collection

The red deer inventory in the study area was organized by the research team of the Department of Hunting and Forest Protection, Poznań University of Life Sciences, together with foresters from the Regional Directorate of the State Forests (RDLP) in Szczecin at the end of February and beginning of March 2012. In this study, a modified drive count method was used, in which the animals were counted by drivers moving in line formation (tyraliera method). The tyraliera method counts may, but not necessarily, lead to the animals being flushed out from the monitored area. The assumed objective is attained by a large group of observers moving in line formation, maintaining visual contact with one another while at the same time being able to register not only the animals moving between the drivers but also those lying down, such as, for example, wild boars in a nest.

Control counts using this method consist of three stages:

i) The first stage comprises preliminary work, consisting of dividing the investigated forest complexes into areas of comparable size (50-100 ha) and close to rectangular shape, referred to as control plots. Only spots

challenging to traverse in the early spring are omitted, such as marshes or wetlands intersected by a network of wide ditches or canals. Additionally, areas covered by strict protection measures, such as species protection zones or wildlife reserves, were excluded from such drive counts. The decision not to include them eliminates areas with potentially high densities of game animal populations from the inventory. However, the rejection of potential outliers simultaneously stabilizes variance in the sample and provides more reliable estimations of the expected value. The study area is divided into drive plots by local administrators well-acquainted with the topography, including the network of access roads. Thanks to this, simultaneous arrival of observers may be planned at two or, preferably, four corners of the plot to be covered. As a result, the behaviors of the animals may be monitored before the lines of drivers meet.

The plots on which the drive counts are to be conducted are selected randomly to ensure the sample's representative character. The control plots' code numbers are selected randomly from the set of plots designated in a given forest inspectorate. It is recommended that up to 10% of the total area in each analyzed forest complex is monitored. The drawing of lots should be performed only once thus the number of control plots drawn should be 10% greater than that required in a given area. This reserve is needed since adjacent plots are occasionally drawn. In such a case, this would result in the possibility that animals moving between these plots would be counted twice; for this reason, the adjacent control plot is excluded, and another is selected from the list. Thanks to this approach, drive plots were separated from each other by about 500 meters.

ii) The second stage consists of counting animals residing on the randomly selected control plots. The monitored plots are lined with stationary observers (posters) on three sides, who stand at 100-150 m apart so that they can notice all medium-sized and large

mammals leaving the drive plot. The fourth side (one of the shorter sides) is occupied by mobile observers (drivers) very closely spaced – at 20-30 m from one another. Their role is to traverse the monitored area in line formation, push the animals out of the driven plot, and count the animals that move between them to the previously penetrated part of the area or those that remain in the lairs. In turn, the observers on three sides of the drive plot count the animals coming between them from the monitored plot before the line of drivers reaches them. Animals leaving between the individual pairs of posters or drivers are recorded; therefore, to avoid double counting, the number of animals is entered on the observation record card by only one person, i.e. the one who has the animal(s) on a specified side (for example on the left side).

The total number of drivers and posters in the team counting animals to be a minimum of 50 individuals (hunters, foresters, and life scientists). Those moving at the extreme ends of the line formation need to maintain visual contact with the stationary observers standing at the longer sides of the drive plot to check the entire established area.

After the drivers reach the main line formation, they are told to assemble again and take positions identical to those assumed before the drive count on a given control plot. The animals recorded on the observation cards are reported, and potential discrepancies are explained, such as the number of animals in large groups (it is worth using video and photo cameras to record images of such numerous groups). Any animals that entered the control plots during the drive count, then left the area, and were recorded by observers from another party are excluded from the total number of animals given in the drive plot.

All the stakeholders participated in the tyraliera method count, i.e., local foresters, hunters leasing their hunting districts in the area, and representatives of the research team. Because of the extensive study area and the need to conduct the drive counts quickly, the

inventory covered 5% of the forests in a given spatial forest inspectorates. The control plots were in forest complexes and mid-field forests, with a minimum size of the drive plot of 50 ha in the area. The drive counts in individual forest inspectorates were organized in a short time (day after day). The counts were always conducted by only one drive count team, which covered 5-6 control plots within a day. The drive counts were performed on 109 control plots randomly selected with a total area of 88,4 km² (Table 2).

Table 2 Characteristics of control plots in GMRs and forest inspectorates in the northern part of Western Pomerania (Poland). Drive plots are calculated as a sum of area for each forest compartment within a control plot, provided by forest management plans.

GMR	Forest inspectorates	Control plots	
		N	Area (km ²)
I	Resko	11	10.42
	Łobez	11	9.76
	Gryfice	11	9.44
II	Międzyzdroje and Wolin National Park	11	8.51
	Nowogard	11	11.29
III	Rokita	12	11.08
	Kliniska	15	8.97
	Goleniów	13	7.22
IV	Trzebież	14	1.173
	OVERALL	109	8.842

The second data source concerning the number of red deer was provided by annual game management plans (AGMP) prepared for the 2012-2013 season for individual hunting districts in the study area. The Szczecin Regional Directorate of the State Forests (RDLP Szczecin) provided the documents. The data in AGMP included estimates of the spring number of red deer in 2012, mostly based on year-round observations of hunters and foresters, while inventory methods prepared for large animals were rarely used. The data were analysed using R software (R Core Team

2019). Before the analyses, red deer densities (a continuous variable) were recalculated and converted into the number of individuals per 1 km². Red deer density was estimated using three spatial scales: forest district, sub-region (wildlife management unit - WMU), and whole region (the Regional Directorate of the State Forests), to show how model uncertainty varies among the spatial scales. In each case, model development was started based on generalised linear models (GLMs), assuming the Poisson distribution of the dependent variable.

Further, it was verified whether a given model met the assumptions based on zero inflation tests and the models' overdispersion. In the case of zero-inflation, the model was converted into zero-inflated GLMs. In contrast, in the case of significant overdispersion, the Poisson distribution was replaced with the negative binomial distribution, which does not assume a priori a lack of overdispersion. Overdispersion (a more significant variability of data than expected in the model) is a problem in models with the Poisson distribution. Zero-inflated models are hurdle models, which estimate two parts of the distribution count (assuming the Poisson or negative binomial distribution) and probability of presence (assuming the binomial distribution). Therefore, such models are less prone to providing many empty observations and make it possible to parametrise the proportion of empty plots in the data. Afterward, the residuals were tested *versus* the fitted values, as well as quantile-quantile plots, while formal tests for hypotheses on a lack of outliers and residual uniformity were conducted using the DHARMA package (Hartig 2020).

In models for the sub-regional and regional scales, generalised mixed-effect linear models (GLMMs) were based on analogous assumptions, with the forest district and subregion as random intercepts, to account for the spatial dependence of the observations within the respective administrative division units. The glmmTMB package was used

to build GLMs and GLMMs (Brooks et al. 2017). The estimates were presented by giving the name of the final model, the result of the overdispersion test, i.e. the ratio of observed to simulated dispersion parameters (the ratio of deviance to the number of degrees of freedom), and the test p-value to ensure that the final models were not affected by overdispersion. The expected values and 95% confidence intervals (CI) for both model elements, i.e., the count and probability of non-zero observations, were presented. This showed which component was more variable in each particular case. Differences between the estimated annual hunting plans and the estimates based on GLMs/GLMMs at all spatial scales were assessed using the linear mixed-effects model, assuming the estimation method as a fixed effect and the sampling unit as a random effect. Thus, the mean pairwise difference between the densities obtained by both methods was determined. Here, two coefficients of determination were calculated: marginal coefficients of determination (R^2_m) expressed the variance explained only by fixed effects, while conditional coefficients of determination (R^2_c) expressed the variance explained by both random and fixed effects. These coefficients were calculated using the MuMIn:r-squaredGLMM function (Bartoń 2020).

Results

The densities of red deer populations per observation unit (drive plot) ranged from 0 to 203 animals/km² of forest, with a mean of 21.5 animals/km² of forest (SE=3.4) (Fig. 2). In each administrative unit exceeded 5 red deer/km² of forest investigated. For 30.3% we accounted zero observations within individual forest districts ranging from 15.4% (Goleniów) to 46.7% (Kliniska). Analysis of the red deer densities showed that regardless of the sampling unit size, the data were burdened with zero inflation and overdispersion. Only in the case of the density model for the entire

study area was overdispersion statistically significant (although the numerical value of the overdispersion parameter was relatively low, and the high p-value resulted from the sample size). For this reason, in all the cases, a decision was finally made to apply the GLM/GLMM model, assuming zero inflation and a negative binomial distribution (Table 3).

The estimated range of red deer densities in the forest inspectorates ranged from 10 to 34.3 individuals/ km² forest, with a mean of 22.8 (SE=2.8). At the regional level (i.e.

GMRs), red deer density ranged from 18.7 to 26.8 individuals/ km² forest, with a mean of 21.1 (SE=1.7). The results were characterized by a considerable range of uncertainty both in terms of the count estimate and the presence of empty drive plots. Uncertainty of the lower limit for 95% CI ranged from 13.5 to 77.6% of the expected value, with a mean of 52.0% (SE=4.5%). In turn, the uncertainty of the upper limit was from 128.8 to 739.0% of the expected value (although this was an extreme case – sub-region II, while the next

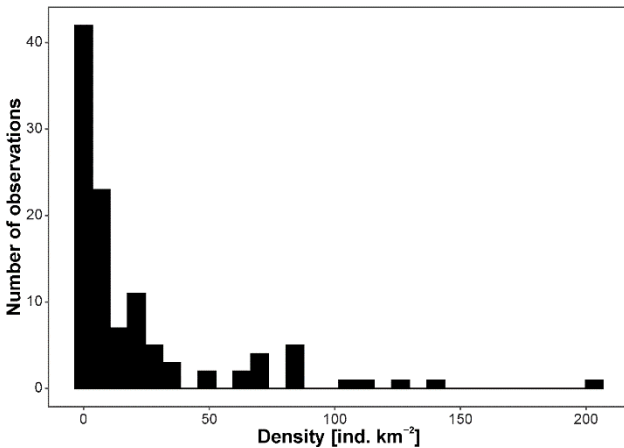


Figure 3 Histogram of red deer density frequencies in control plots in the northern part of Western Pomerania (Poland) recorded during drive counts conducted in line formation in spring 2012. Bars indicate frequency of particular quantiles of red deer density.

maximum value was 246.4%), with a mean without outliers of 187.3% (SE=11.0%).

A comparison of the values obtained in the study with the AGMP data showed that regardless of the spatial unit analyzed, the densities in the annual game management plans were 18.38 ± 1.98 red deer/km² lower than those found because of the drive counts conducted in line formation (Table 4, Fig. 3). The standard deviation of the random effect for the spatial unit amounted to 1.1 individuals/ km² forest, i.e. almost 18-fold lower than the difference in densities. In

Table 3 Models of red deer density in forest inspectorates, game management regions, and the whole study area, with their parameters and estimates density.

Forest inspectorates	GMR	n	Final model	Odpar	p	Cest	Cest 95%CI	Best	Best CI	Dest	Eff SD
Resko	I	11	ziNB	1.3238	0.424	3.23	15.23-68.49	0.27	0.09-0.59	23.6	-
Łobez	I	11	ziNB	1.0640	0.720	1.38	8.09-23.48	0.27	0.09-0.59	10.0	-
Gryfice	I	11	ziNB	1.2510	0.568	3.02	12.24-74.33	0.25	0.07-0.60	22.5	-
Rokita	III	11	ziNB	1.1762	0.480	4.11	24.26-69.64	0.17	0.04-0.48	34.3	-
Nowogard	III	12	ziNB	1.2816	0.368	1.88	9.23-38.2	0.27	0.09-0.59	13.8	-
Kliniska	III	15	ziNB	1.2263	0.584	4.72	19.23-115.72	0.46	0.23-0.71	25.6	-
Goleniów	III	13	ziNB	0.9437	0.960	3.80	19.74-73.23	0.15	0.03-0.46	32.4	-
-	I	33	ziNB	1.2643	0.336	2.55	16.24-39.96	0.50	0.50-1.00	18.7	0.1
Międzyzdroje + Woliński NP	II	11	ziNB	1.2071	0.472	0.63	0.86-46.8	0.75	0.58-0.98	19.8	0.3
-	III	51	ziNB	1.0865	0.608	3.67	25.70-52.47	0.50	0.50-1.00	26.8	0.1
Trzebież	IV	14	ziNB	1.1093	0.688	2.93	15.27-56.36	0.36	0.15-0.62	18.9	-
-	all	109	ziNB	1.1165	0.024	3.10	23.75-39.42	0.50	0.5-1.00	21.5	0.1

Note: Odpar: overdispersion parameter; Cest: count estimate; Best: binomial estimate; Dest: estimated density [ind. 1000 ha⁻¹]; Eff SD: random effect; ziNB – zero-inflated negative binomial distribution.

this model, the fixed effect (method) explained 78.1% variation ($R^2_c=0.781$), while the location (the random effect) explained 1.1% ($R^2_m=0.792$).

(Fruziński 2002), has, with time, become common practice and is typically the only source of data used when preparing game management plans (Okarma & Tomek 2008).

Nevertheless, annual panel observations are not a suitable method for taking game inventory, since they lack a methodological background that would define their systematic manner and guarantee the repeatability of results (Okarma & Tomek 2008, Bobek et al. 2013, Kamieniarz & Skorupski 2016). Based on multiannual data from the Silesia region (Poland) at the end of the 20th century, Nasiadka (1998), showed that if the number of red deer indicated in the AGMPs is true - then

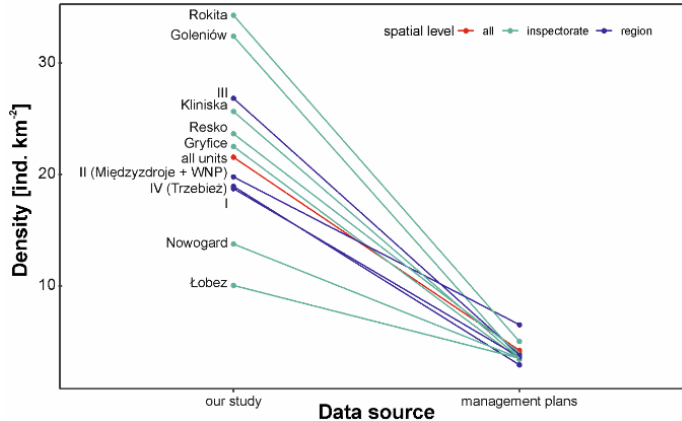


Figure 4 Differences between red deer densities calculated in this study and available in annual game management plans, assessed at three levels of spatial aggregation: all area, GMRs, and forest inspectorates. Lines join points representing the same unit, therefore slope of each line represents the magnitude of difference.

Table 4 Parameters of linear mixed-effects model assessing differences between two methods of red deer density estimations.

Variable	Est	SE	df	t	Pr(> t)
(Intercept)	22.33	1.44	21.95	15.56	<0.0001
source='AGMP'	-18.38	1.98	11	-9.29	<0.0001
Eff. SD	Sunit	1.1	Res	4.85	-

Eff: Random effects; Est: Estimate Sunit: Sampling unit; Residuals

Discussion

At the turn of the 20th and 21st centuries, numerous sources indicated discrepancies between the size of the population of game animals living in open hunting grounds and the data on the same populations provided in the hunting documentation. Underestimation of the numbers of big game, including red deer, resulted from rarely conducted wildlife counts and the common practice of obtaining annual panel data from hunter-reported observations (Kamieniarz & Panek 2008, Okarma & Tomek 2008, Reimoser & Reimoser 2010). This method recommended only as an auxiliary method in Polish literature concerning hunting

despite the annual arrival of yearlings - the size of the hunting bag there will make the local population disappear in few years. Csányi (1992) stated that in Hungary the number of red deer in hunting documentation was underestimated by 40-60%. In contrast, the estimate prepared in the twenty years later for the numbers of red deer in 47 forest districts in different regions of Poland indicated that the actual density of red deer may have been twice as high as that given in the official hunters reporting data (Bobek et al. 2013). Borowik et al. (2011) showed that the underestimation of the red deer numbers in north-eastern Poland reached 300%. Only occasionally, e.g. in Bulgaria (Popova et al. 2018), methodical counts provide results comparable to the official hunting documentation data. But in this country, the red deer population has been in decline since the 1980s (Zlatanova et al. 2019). The above review shows that the size of the differences between the estimates of the number of red deer in hunting plans, and those obtained through methodical counts increases

with increasing densities.

The mean red deer density in northern part of Western Pomerania (Poland) determined by the drive count method with drivers in line formation was 21.5 animals/km² of the forest and each administrative unit exceeded 5 red deer/km². However, the obtained results are based on a solid methodological approach, with less errors that might be found when using drive counts to inventory large cervids (Borkowski *et al.* 2011). An analysis of the accuracy of the methodological assumptions for the models showed that data on the red deer population size were burdened by zero inflation and overdispersion, preventing the application of the Poisson distribution. For this reason, using generalized linear models is recommended when conducting similar studies, assuming the negative binomial distribution, including the zero-inflated negative binomial GLM.

The red deer density determined in north-western Poland confirmed that it is the region with the highest population of this species. In simultaneous studies in several other regions (Bobek *et al.* 2013), the maximum density was 12.8 red deer/km² - in one forest complex in south-western part of Poland. It should be stressed that local densities in the Western Pomerania reached 32.4-34.3 individuals/km², i.e. were close to the extreme of 42.6 red deer/km², which was recorded in the heather moorlands of Scotland (Pérez Barbería *et al.* 2013).

A comparison of the results provided by drive counts using line formation with the data available from hunting documentation showed, on average, a 5-fold underestimation of red deer densities in north-western Poland. Since the scale of the underestimation of red deer densities increased at the turn of the 20th and 21st centuries, it is high time more realistic data was obtained constituting the basis for the hunting management of wildlife populations. Game management must be based on scientific foundations, which should reduce the environmental impact of large herbivores

and ensure the transparency of utilizing natural resources for the general public. Because of the considerable differences between assessments of population size provided by research projects and those given by hunters in the second decade of the 21st century, counts have started to be conducted in successive regions of Poland using the drivers in line formation or by remote sensing (Okarma 2015, Zalewski 2015). Results obtained in the 2015-2016 inventories confirmed an underestimation of the red deer population in Poland ranging from 200% to over 400% (M. Skorupski, unpublished data). Moreover, counting with the tyraliera is a method that allows the participation of not only direct stakeholders, i.e., hunters and foresters, but also representatives of NGOs often contesting game management methods in Poland (Tomek *et al.* 2015, Chylarecki 2016).

High wildlife densities result in increasing wildlife damage in forests and fields (Reimoser and Reimoser 2010, Bleier *et al.* 2012, Zalewski 2015). Thus, it is obvious that north-western Poland, with its high red deer densities, has suffered from exceptionally high damage in forested areas (Jakubowski 2018). Moreover, cervids together with wild boars have damaged many crop fields (Stosik 2013). Given the above, the question arises whether providing more realistic data on red deer populations should automatically cause the reduction of population. In the opinion of Beszterda & Przybylski (2011), the decision should be based on the condition and prospective sustainability of the environment (forest and agricultural crops) rather than on an error in the estimation of the population size. Moreover, Bleier *et al.* (2012) stressed that the density of wildlife populations is not the only factor determining the volume of damage on arable land and crops. The problem of the carrying environmental capacity being exceeded and the resulting damage caused by game animals, as early as the mid-1970s, brought to the carrying capacity being established for cervids in forest hunting districts (Bobek *et al.* 1979).

In 1990. years, the maximum density for Polish forests determined on 5 red deer/km². A new assessment of environmental capacity should be conducted, considering the biomass of the forest vegetation cover. In this manner, the admissible levels of cervid densities in forests may be more realistic (Wajdzik et al. 2015). The described method of large-area inventory of cervids makes this task real by enabling verification of their density in forests with different food abundance.

However, a problem may arise due to the limited data on the biomass of forest vegetation cover in various types of forests (Woziwoda et al. 2014, Czapiewska et al. 2019). Therefore, it is worth collecting such data because combining knowledge about the environment with data on animal populations makes it possible to improve the management of natural resources for the benefit of humans and nature. For example, very high densities of red deer and fallow deer limit the possibility of roe deer occurrence (Borkowski et al. 2021, Szymański 2022).

Author Contributions

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Conflicts of Interest

The authors declare no conflict of interest. The financial supporters had no role in the design of the study, in the collection, analyses, or interpretation of data, in the writing of the manuscript, or in the decision to publish the results

References

- Act on Hunting Law, 1995. Act of 13 October 1995 Hunting Law (unified text in the Journal of Laws Dziennik Ustaw of 1995 no. 147, item 713 with later amendments).
- Bartel M., Becker J., Hoffmann D., Zahn C., Strauss E., Nösel H., Greiser G., 2003. Wildtier-Informationssystem der Länder Deutschlands. Deutscher Jagdschutz-Verband e.V., Bonn.
- Bartoń K., 2017. MuMIn: Multi-Model Inference. URL: <https://cran.r-project.org/package=MuMIn>
- Beszerda P., Przybylski A., 2011. Rejony hodowlane – koncepcja i praktyka po 10 latach [Wildlife management units – the concept and reality after 10 years of practice]. Annals of Warsaw University of Life Sciences-SGGW Animal Science. 50: 11-18.
- Bleier N., Lehoczki R., Újváry D., Szemethy L., Csányi S., 2012. Relationships between wild ungulate density and crop damage in Hungary. Acta Theriol. 57: 351-359.
- Bobek B., Dzięciołowski R., Fruziński B., Tomek A., 1979. W sprawie nowych norm pojemności łowisk [On new standards for the carrying capacity of hunting areas]. Łowiec Polski 5: 5-6.
- Bobek B., Albiński A., Albrycht M., Bobek J., Frąckowiak W., Furtek J., Kopeć K., Maślanka J., Merta D., Orłowska L., Standio A., Trętowska K., Ulejczyk S., Wojciuch – Płoskonka M., Ziobrowski M., 2013. Ocena dynamiki liczebności i zagęszczenia populacji dzikich kopytnych przy użyciu różnych metod w czterech regionach Polski [Assessment of population dynamics and density of wild ungulates using different methods in four regions of Poland]. Studia i materiały CEPL w Rogowie, 15, 36(3): 88-101.
- Borkowski J., Banul R., Jurkiewicz-Azab J., Hołdyński C., Świączkowska J., Nasiadko M., Załuski D., 2021. There is only one winner: The negative impact of red deer density on roe deer numbers and distribution in the

- Słowiński National Park and its vicinity. *Ecol. Evol.*, 11: 6889–6899. <https://doi.org/10.1002/ece3.7538>
- Borkowski J., Palmer S. C. F., Borowski Z., 2011. Drive counts as a method of estimating ungulate density in forest: mission impossible? *Acta Theriol.* 56 (3): 239–253.
- Borowik T., Wawrzyniak P., Jędrzejewska B., 2011. Doświadczenia z inwentaryzacji ssaków kopytnych metodą pędzeń próbnych w północno-wschodniej Polsce [Experiences from inventories of ungulates by drive counts in north-eastern Poland]. Materials from seminar “Monitoring of game population size and sustainable hunting”. Instytut Biologii Ssaków PAN Białowieża.
- Brooks M.E., Kristensen K., Benthem K. J., van Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Mächler M., Bolker B. M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9: 378.
- Chylarecki P., 2016. Trudności i ograniczenia w analizie danych uzyskanych metodą pędzeń próbnych na przykładzie inwentaryzacji łosia w RDLP Lublin [Problems and limitations in analysis of data collected from drive counts based on inventory of European elk in the Lublin Regional Directorate of the State Forests]. I Wszechnica Łowiecka. Instytut Badawczy Leśnictwa. Sękocin Stary. www.ibles.pl.
- Csányi S., 1992. Red deer population dynamics in Hungary. Management statistics versus modeling. In: Brown R. D. (ed.) *The Biology of Deer*, Springer Verlag Nowy York: 37-42.
- Czapiewska N., Dyderski M. K., Jagodziński A. M., 2019. Seasonal Dynamics of Floodplain Forest Understory – Impacts of Degradation, Light Availability and Temperature on Biomass and Species Composition. *Forests*, 10(1): 22. <https://doi.org/10.3390/f10010022>
- Fruziński B., 2002. Gospodarka łowiecka [Game management]. Wydawnictwo Łowiec Polski, Warszawa: 88s.
- Jakubowski M., 2018. Gospodarowanie populacjami jeleniowatych w wybranych rejonach hodowlanych RDLP Szczecin [Management of deer populations in selected wildlife management units of the Szczecin Regional Directorate of the State Forests], Uniwersytet Przyrodniczy w Poznaniu, manuscript PhD dissertation.
- Kamieniarz R., Panek M., 2008. Game animals in Poland at the turn of the 20th and 21st century. *Stacja Badawcza – OHZ PZŁ w Czempiniu*: 132s.
- Kamieniarz R., Skorupski M., 2016. Dyskusji o liczeniu zwierzyny ciąg dalszy [Continuation of a discussion on wildlife counts]. *Brać Łowiecka*, 2: 32-35.
- Katona K., Szemethy L., Csányi S., 2011. Forest management practices and forest sensitivity to game damage in Hungary. *Hungarian Agricultural Research*, 1: 12-16.
- Lambert D., 1992. “Zero-inflated Poisson Regression, With an Application to Defects in Manufacturing.” *Technometrics*, 34: 1–14. <https://doi.org/10.2307/1269547>
- Lancia, R. A., J. D. Nichols, K. H. Pollock., 1994: Estimating the numbers of animals in wildlife populations In: T. A. Bookhout (ed.). *Research and management techniques for wildlife and habitats*, the Wildlife Society, Maryland, 5: 215-253.
- Nasiadka P., 1998. The accuracy of year-long direct observation by hunters for estimating red deer (*Cervus elaphus* L.). Zomborszky (ed.). *Advances in deer biology. Proceedings of the 4th International Deer Biology Congress*. Kaposvar: 25-28.
- Okarma H., Tomek A., 2008. *Łowiectwo [Hunting]*. Wydawnictwo Edukacyjno-Naukowe H₂O. Kraków: 503 s.
- Okarma H. (2015): Wykorzystanie teledetekcji do ustalania liczebności zwierzyny grubej w wybranych kompleksach leśnych. Raport Dyrekcji Generalnej Lasów Państwowych [Application of remote sensing to determine population size of large game in selected forest complexes. Report of the Directorate General of the State Forests]. Report from project no. ER-2717-1/14. www.lasy.gov.pl
- Pérez-Barbería F. J., Hooper R. J., Gordon I. J., 2013. Long-term density-dependent changes in habitat selection in red deer (*Cervus elaphus*). *Oecologia*, 173: 837-847. <https://doi.org/10.1007/s00442-013-2686-8>
- Pielowski Z., Kamieniarz R., Panek M., 1993. Report about game animals in Poland. Państwowa Inspekcja Ochrony Środowiska, Warszawa: 128s.
- Popova E., Stepanov I., Ahmed A., Genov P., Todev I., 2018. Red deer (*Cervus elaphus* L.) population density in a hunting area in the central Balkan Mountains (Bulgaria) revealed by camera traps. In: *Proc. of 11th Seminar of Ecology – 26-27.04.2018*, Sofia: 14–21.
- Pucek Z., Bobek B., Łabudzki L., Miłkowski L., Morow K., Tomek A., 1975. Estimates of density and numbers of ungulates. *Pol. Ecol. Stud.*, 2: 121-136.
- Reimoser F., Reimoser S., 2010. Ungulates und their management in Austria. In: Apollonio M., Andersen R., Putman R. (eds.) *European ungulates and their management in the 21st century*. Cambridge University Press: 338-356.
- Reimoser F., Reimoser S., 2016. Long-term trends of hunting bags and wildlife population in Central Europe. *Beiträge zur Jagd- und Wildforschung*, 41: 45-58.
- Rhodes J. R., 2015. Mixture Models for Overdispersed Data. In: G. A. Fox, S. Negrete-Yankelevich, and V. J. Sosa, (eds.), *Ecological Statistics*. Oxford University Press, Oxford: 378 and 381.
- Rocznik statystyczny województwa zachodniopomorskiego, 2015. *Rolnictwo 2015 [Statistical Year Book of the Zachodnio-pomorskie province 2015. Agriculture 2015]*. Urząd Statystyczny w Szczecinie: 290-295.
- Stosik T., 2013. Zależność między występowaniem dzika (*Sus scrofa*) a rozmiarem szkód łowieckich w uprawach i płodach rolnych w północnej części RDLP w Szczecinie [The dependence between occurrence of wild boar (*Sus scrofa*) and the volume of wildlife damage in plant

- cultures and crops in the northern part of the Szczecin Regional Directorate of the State Forests]. Uniwersytet Przyrodniczy w Poznaniu, MSc thesis manuscript: 68s.
- Stubbe M., Stubbe A., 2016. Dynamik von Wildtierbeständen. Beiträge zur Jagd- und Wildforschung, 41: 19-28.
- Szymański M. 2022. Populacyjne przyczyny zmniejszenia liczebności sarny europejskiej w Puszczy Zielonka [Population reasons for the decrease in the number of roe deer in the Zielonka Forest]. Uniwersytet Przyrodniczy w Poznaniu, manuscript PhD dissertation: 84s.
- Tomek A., Bar A., 1997. Distributions of densities of cervids in large forest tracts investigated by sample drives. J. Wildl. Res. 2(3): 210-218.
- Tomek A., Dziedzic R., Balik B., Bar O., 2015. Liczebność i zagęszczenie łosia na obszarze Regionalnej Dyrekcji Lasów Państwowych w Lublinie [Population size and density of the European elk in the Lublin Regional Directorate of the State Forests]. Manuscript submitted at the Lublin Regional Directorate of the State Forests: 1-16.
- Tourani M., Franke F., Heurich M., Henrich M., Peterka T., Ebert C., ... & Peters W., 2023. Spatial variation in red deer density in a transboundary forest ecosystem. Scientific Reports, 13(1), 4561. <https://doi.org/10.1038/s41598-023-31283-7>
- Wajdzik M., Tomek A., Kubacki T., Nasiadka P., Szyjka K., 2015. Pojemność gospodarcza łowisk leśnych na przykładzie Nadleśnictwa Kluczbork [Carrying capacity of forest hunting areas based on the Kluczbork Forest District]. Sylwan, 159 (11): 958-968.
- Woziwodza B., Parzych A., Kopeć D., 2014. Species diversity, biomass accumulation and carbon sequestration in the understorey of post-agricultural Scots pine forests. *Silva Fennica*, 48(4): #1119. <https://doi.org/10.14214/sf.1119>
- Zalewski J., 2015. Rola łowiectwa w zrównoważonej gospodarce leśnej. Łowiectwo w zrównoważonej gospodarce leśnej [The role of hunting in sustainable forest management. Hunting in sustainable forest management]. Winter Forest School at the Forest Research Institute. Sękocin Stary. 7th Session: 24-32.
- Zalewski D., Okarma H., Panek M., 2018. Monitoring liczebności i jakości populacji dzikich zwierząt [Monitoring of wildlife population size and quality]. Uniwersytet Warmińsko-Mazurski w Olsztynie. Agencja Fotograficzno-Wydawnicza „MAZURY”, Olsztyn: 118s.
- Zalewski D., Markuszewski B., Wójcik M., 2019. Szkody w gospodarce wyrządzane przez dzikie zwierzęta. [Damage to the economy caused by wild animals]. Wyd. Uniwersytetu Warmińsko-Mazurskiego, Olsztyn: 96s.
- Zlatanova D., Popova E., Ahmed A., Stepanov I., Andreev R., Genov P., 2019. Red deer on the move: home range size and mobility in Bulgaria. *Ecologica Montenegrina*, 23: 47-59.
- van Beeck Calkoen S.T., Kuijper D.P., Apollonio M., Blondel L., Dormann C.F., Storch I., & Heurich M., 2023. Numerical top-down effects on red deer (*Cervus elaphus*) are mainly shaped by humans rather than large carnivores across Europe. *Journal of Applied Ecology*, 60, 12: 2625-2635. <https://doi.org/10.1111/1365-2664.14526>