

The Demographic Pattern of Wild Boars (*Sus scrofa*) Inhabiting Fragmented Forest in North-Eastern Poland

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Abstract

The high density of wild boar populations in the farmland-forest landscape on north-eastern Poland has resulted in crop damage and conflict with farmers. Any effective harvest plan has to consider the population demography. Therefore, the objective of the study was to estimate the age-sex structure and reproduction in the population of wild boars inhabiting an area of 1,310 km², where the share of fragmented forest amounted to 26.8 %. The study material consisted of 234 wild boars harvested during drive hunting between October and mid-January from 2012 to 2014. Among the animals harvested there were 63.3 % piglets, 15.8 % of yearlings and 20.9 % older individuals. The differences in carcass mass (CM) and in kidney fat index (KFI) between piglets and yearlings and between yearlings and adults were statistically significant, both of males and females. The sex ratio was male-biased in piglets (1:0.78) but in the cumulated group of yearlings and adult females predominated (1:1.53). In 117 studied females, the percentage share of pregnant individuals was 39.3 % and the mean size of litter was 5.2 ± 0.29 . All pregnant female piglets were aged 9-12 months and had significantly higher CM (37.6 ± 2.30 kg vs. 29.6 ± 1.82 kg) and KFI (1.67 ± 0.06 vs. 1.35 ± 0.05) than not pregnant ones. The farrowing took place in all months of the year except October. More than half of the piglets (57.4 %) were born in March, April and May. The harvest strategy to reduce the population density of wild boar in the study area is discussed.

Keywords: pregnancy, fat reserves, litter size, age structure, sex ratio, carcass mass

Introduction

Reducing the density of wild boar populations should be a priority for game management in Poland, as we face an uncontrolled increase in the number of wild boars, which began in the 1970s (Fruziński and Łabudzki 2002). Data obtained from the Central Statistical Office indicates that in the 2003-2013 period the wild boar hunting bag has increased from 122 thousand individuals to 242 thousand, i.e. by 98%. During this decade, countrywide compensation paid by hunters to farmers for damage caused by wild boars increased from 6.5 million to 18.4 million EUR (Budna et al. 2005, Grzybowska et al. 2014).

In north-eastern Poland, the farmland-forest mosaic landscape features one of the highest wild boar population densities in the whole country which, at the end of the hunting season, reaches up to 100 individuals/1,000 hectares of forest (Bobek et al. 2015a). It entails significant damage caused by wild boars to cultivated fields (Frąckowiak et al. 2013), creates the risk of classical

swine fever (CSF) outbreaks in wild boars as well as extending the area of occurrence of African swine fever (ASF), whose foci have been located about 200 km from our study area in Białystok region (Zakrzewski 2015, Truszczyński and Pejsak 2015).

At present, the main task of wild boar management in our study area is to reduce the population density because this factor explains 43% of the variability in damage caused by wild boar (Bobek et al. 2015a, 2016). Reaching this target will be attainable by knowing demographic variables data on age and sex structure of wild boars, the proportion of pregnant females, and the length of the farrowing period (Bieber and Ruff 2005, Servanty et al. 2011, Gamelon et al. 2012). Many studies, which were carried out in Europe, demonstrate that the demographic parameters of wild boar populations are greatly influenced by environmental factors operating through food resources and climate (Gethöffer et al. 2007, Servanty et al. 2009, Vetter et al. 2015, Frauendorf et al. 2016). Therefore, the objective of our study was to recognise the specific in re-

gion demographic variables in wild boars, which could be then be used to model an optimum structure for culling the population in the farmland-forest mosaic landscape in north-eastern Poland.

We have worked on the hypothesis that the results obtained in our study should be similar to the demographic pattern of wild boars living in the farmland-forest mosaic landscape of south-western Poland (Merta et al. 2011).

Study area

The study area is located in north-eastern Poland, its elevation ranges between 20-190 m a.s.l. and constitutes a mosaic of fragmented forest and farmland. The vegetation period lasts 190-210 days; snow cover persists for ca. 85 days while the annual mean temperature averages 7.5 °C. The average annual precipitation ranges from 630 to 660 mm (Starkel 1991). Wildlife management is performed in 21 hunting districts and is supervised by the local State Forest Service. The total wildlife management area constitutes 1,310 km² including 351 km² of forests.

The study area is characterized by a large number of fragmented forest complexes (436) administered by the Młynary Forest District and Zaporowo Forest District situated in Braniewo County, Warmian-Masurian Voivodeship. Deciduous and mixed deciduous forest cover 96.5 % of the forested area. The main forest-tree species are the following: oak (*Quercus* sp.), beech (*Fagus sylvatica*), birch (*Betula* sp.), and alder (*Alnus* sp.), which jointly account for 73.4 % of all tree stands (Bobek 2015).

In the agricultural landscape, large-sized farms predominate, chiefly those aiming at intensive cereal crop production, which cover 65 % of the entire cultivated area (Łączyński and Ziółkowska 2014). The samples were taken from 9 hunting districts, where 193 km² are forested area and 461 km² are farmland. The average number of wild boars harvested during two consecutive hunting seasons (2012/13, 2013/14) amounted to 1,301 specimens, i.e. 67.4 animals/1,000 ha of forest (Bobek et al. 2015b). The average area of crops damaged by wild boars in the period 2012-2014 amounts to 114.3 ha per year, and the value of the compensation paid to farmers in this period was 62.7 thousand EUR per year (Bobek 2015).

Materials and Methods

The material for this study was collected during drive hunting that took place between October and mid-January, over two consecutive hunting seasons, in 2012/13 (N = 113) and 2013/14 (N = 121). The age of all bagged wild boars (N = 234) was determined on the basis of the degree of tooth eruption pattern, and the level of tooth wear in the lower jaw (Matschke 1967, Briedermann 2009). The animals were divided into three age classes:

(1) piglets - individuals under 12 months old, (2) yearlings - wild boars between 12 and 24 months old, and (3) adults - animals over 24 months old.

Carcass mass (CM), i.e. eviscerated body weight (without internal organs of harvested wild boars) was determined by weighing them on a portable dial scale within the accuracy of 0.1 kg. Fat reserves in wild boars were determined by calculating the kidney fat index (KFI). The right kidney with fat was dissected from each individual. Next, the amount of fat was standardized according to the criterion that the fat deposit adjacent to the kidney should not be larger than the surface of the kidney, calculated by the quotient of its length and width (Caughley and Sinclair 1994). The surplus fat was removed and then the kidney was weighed with fat and without it. The kidney fat index was the quotient of the kidney mass with fat and the kidney mass without fat (Riney 1955, Finger et al. 1981, Santos et al. 2013).

The pregnancy of female individuals was determined and in those that were pregnant the number of embryos/foetuses were counted. The pregnancy was defined in case of the presence of *corpora lutea* with a diameter greater than 5 mm and by the presence of embryos/foetuses (Gethöffer 2005). Data on the age of piglets was used to compile timing patterns for the farrowing period. The statistical calculations of the differences between carcass mass and the kidney fat index between sex and age classes were carried out by General Linear Models (GLM) with Statistica 10 software package. To calculate the differences between the age and sex structure of the wild boar population χ^2 estimator was used (Sokal and Rohlf 1995). Because there were no significant differences in population sex-age structure, carcass mass and kidney fat index between the two hunting seasons, we pooled data obtained from the distinguished age classes for further analyses.

Results

Age and sex structure. Out of 234 harvested wild boars 63.3 % (N=148) were piglets, 15.8 % (N=37) were yearlings and the adults made 20.9 % (N=49). Among piglets the sex ratio was male biased (1:0.78), but in the cumulated age classes of yearlings and adult females predominated (1:1.53). So, the percentage of males in compared groups of wild boars dropped from 56.1 % to 39.5 %. The differences between the proportions of males and females in the piglets, as well as in the cumulated group of yearlings and adults and between sex groups were significant ($\chi^2 = 5.96$, $p = 0.0147$, $df = 1$).

Carcass mass and kidney fat index. The carcass mass and kidney fat index increased with the age of wild boars (Table 1). The mean CM ranged from 27.1 ± 0.94 kg ($\bar{x} \pm SE$) in male piglets to 76.5 ± 1.53 kg in adult females. Male piglets and adult females showed the lowest

(1.36 ± 0.02) and the highest (2.03 ± 0.04) average value of KFI, respectively. In both sexes the differences in CM and KFI between piglets and yearlings and between yearlings and adults were statistically significant (Table 2). In the same age groups, males displayed lower carcass mass and lower kidney fat index than females but these differences were significant only in KFI between yearlings ($p = 0.03$).

Pregnancy and farrowing period. The proportion of pregnant females in the female segment increased with their age, and also depended on the carcass mass and fat

reserves. Out of 117 harvested females, 39.3% were pregnant and the mean number of embryos per pregnant female was up to 5.2 ± 0.29 ($\bar{x} \pm SE$). Among piglets, 16.9% of the females were pregnant, and all of them were aged 9–12 months. Using such age criteria, the proportion of pregnant piglets went up to 40.7% (Figure 2), and the number of embryos amounted to 4.1 ± 0.30 . Among piglets aged 9–12 months, the pregnant females had a significantly higher carcass mass (37.6 kg) and kidney fat index (1.67) than not pregnant ones (29.6 kg; 1.35, respectively) (Figure 2). 61.9% of female yearlings were pregnant and the mean number of embryos was up to 4.9 ± 0.26 . In this age class pregnant females were significantly heavier, than non-pregnant ones (70.5 kg vs. 55.3 kg), but KFI did not differ in the groups compared. The highest percentage of pregnant females (71.0%) was found among adult sows (Figure 2) and the mean number of embryos amounted to 6.6 ± 0.32 . In this age class there were no significant differences between CM and KFI between pregnant and non-pregnant females.

Except for October, farrowing occurred in all months of the year (Figure 3). More than half of 148 piglets were born in March (22.5%), April (17.8%), and May (17.1%). Other significant farrowing periods included February, when 12.4% of piglets were born, and June (10.9%).

Table 1. Carcass mass (kg) and kidney fat index of wild boar harvested in north-eastern Poland during autumn-winter periods of 2012/2013 and 2013/2014 hunting seasons. Mean (\bar{x}), standard error (SE) and sample size (N) are given

Age and sex		Carcass mass $\bar{x} \pm SE$	Kidney Fat Index $\bar{x} \pm SE$	N
Piglets	Males	27.1 ± 0.94	1.36 ± 0.02	83
	Females	29.0 ± 1.06	1.41 ± 0.03	65
Yearlings	Males	59.2 ± 2.13	1.64 ± 0.05	16
	Females	64.7 ± 1.86	1.85 ± 0.04	21
Adults	Males	75.2 ± 2.01	1.87 ± 0.05	18
	Females	76.5 ± 1.53	2.03 ± 0.04	31

Table 2. Differences between carcass mass and kidney fat index evaluated for different age and sex classes of wild boar harvested in north-eastern Poland during autumn-winter periods of 2012/2013 and 2013/2014 hunting seasons. (* 0.05 > p > 0.01; ** 0.01 > p > 0.001; *** 0.001 > 0.0001; NS is the lack of significant differences)

Age class		Carcass mass	Kidney Fat Index
Piglets: males - females		NS	NS
yearlings: males - females		NS	*
adults: males - females		NS	NS
piglets - yearlings		***	***
Males	yearlings - adults	***	*
	piglets - adults	***	***
piglets - yearlings		***	***
Females	yearlings - adults	***	*
	piglets - adults	***	***

Discussion

The comparison of demographic pattern of wild boar populations inhabiting the farmland-forest landscape of north-eastern (NE) and south-western (SW) parts of Poland indicates that our research hypothesis has been con-

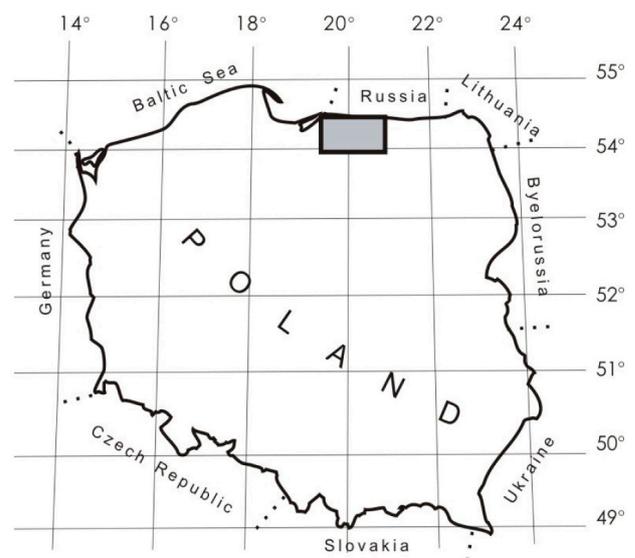


Figure 1. Mlynary Forest District and Zaporowo Forest District: the location of study area

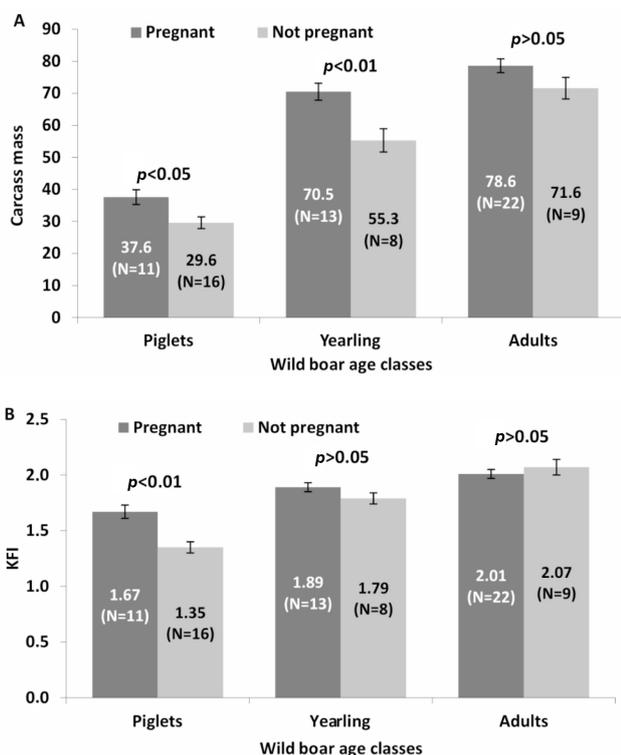


Figure 2. Carcass mass (kg) (A) and kidney fat index (B) of pregnant and non-pregnant females of wild boar harvested in north-eastern Poland during autumn-winter period in 2012/2013 and 2013/2014 hunting seasons. Group of piglets concerns animals of 9-12 months old. The significance level (*p*), mean (*x*) standard error (*SE*) and sample size (*N*) are given

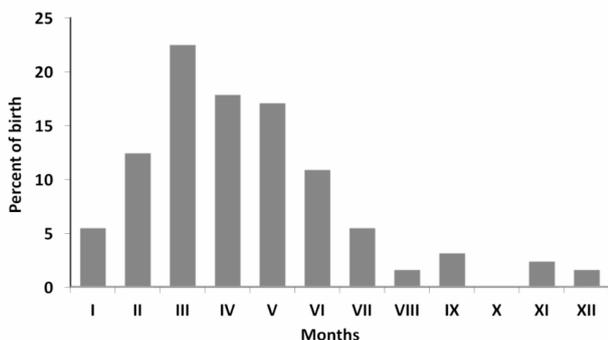


Figure 3. Farrowing period based upon 148 piglets harvested in north-eastern Poland during autumn-winter periods of 2012/2013 and 2013/2014 hunting seasons

firmed only in part. The length of farrowing period (10 months), percent of piglets born in February and March (61.4 %) and mean litter size (5.3 per pregnant female) based on 191 animals harvested in SE area during the 2008/09 hunting season (Merta et al. 2011) are in line with our results. Differences regarding the pregnancy among females, proportion of piglets in the population,

and the carcass mass are shown. In our study area the percentage of pregnant females and the proportion of piglets in wild boar population was higher (39.3 % vs. 28.4 % and 63.3 % vs. 53.4 %, respectively) as compared with data reported previously by other authors (Merta et al. 2011, 2015, Bobek et al. Unpubl. data). Also, the mean carcass mass of particular age classes in wild boars living in the NE region was higher: piglets (27.9 kg vs. 24.3 kg), yearlings (62.3 kg vs. 46.9 kg), and adults (76.0 kg vs. 69.4 kg) (Merta et al. 2011). However, our results on the wild boar demography are based upon two-year data only. In case of heavy mast year, both pregnancy rate and carcass mass can be higher than those presented in our paper (Groot Briunderink et al. 1994, Maillard and Fournier 2004, Servanty et al. 2009, Frauendorf et al. 2016). The obtained differences could reflect the effects of the lower quality of food in the SW environment (Merta et al. 2014), as well as more severe climate in the NE study area, which is situated 750 km north-east of the SW region. Our results confirm previous indications for the applicability of Bergmann’s rule to the wild boar as animals of this species in colder regions are indeed heavier (Vetter et al. 2015). The climate in north-eastern Poland is much more severe than climate in the south-western part of the country. In north-eastern Poland, the mean number of days with snow cover is 85 days and the length of growing season is equal on average to 200 days. In the southwestern part of the country, snow cover persists for 60 days and the length of growing season amounts to 230 days (Woś 1999, Starkel 1991).

In Europe, previous studies on wild boar reproduction indicate that there are three types of farrowing patterns:

1. Farrowing has one evident peak in March, April, and May, and the birth rate in other months is not significant (Fernández-Llario and Carranza 2000, Maillard and Fournier 2004, Łabudzki et al. 2009, Merta et al. 2011). Such a farrowing pattern is characteristic of habitats, where wild boars have limited access to high-quality food.

2. Piglets are born almost throughout the whole year, and farrowing has two peaks. The first one comes in March-April, and the second one in June-August (Moretti 1995, Gethöfferet al. 2007). The habitat includes rich deciduous forest and farmlands.

3. Farrowing continues almost all year round but there is one evident peak. In severe mountain climates, the farrowing peak falls in May (Boitani et al. 1995, Durio et al. 1995) or April (Santos et al. 2006, Ježek et al. 2011). Wherever the climate is milder, the farrowing peak takes place earlier and occurs in March and April (Fonseca et al. 2001, Maillard and Fournier 2004, Gethöfferet al. 2007, Cellina 2008, Łabudzki et al. 2009, Merta et al., 2011, Orłowska et al. 2013). These habitats mainly include farmland and mixed forest.

The 3rd pattern of farrowing period was confirmed in this paper. In our study area, the population of wild boar

has seasonal access to high quality food, which is indicated by the 114.3 ha of agricultural crops damaged every year by wild boars (Bobek et al. 2015c). The rich deciduous forest habitat also provides major amounts of high-protein biomass in the form of earthworms (Plisko 1965), underground organs of ground vegetation (Tumidajowicz 1971), soil insects (Scheu et al. 2003) and rodents (Bobek 1973). Additionally, during each hunting season hunters provide supplemental feeding in an amount 5.4 metric tonnes/1,000 ha of forest of concentrated fodder, principally cereals (Bobek 2015). It means that the population of wild boar has access to high quality forage both during the growing season and winter.

During drive hunting, the culling of wild boars on the study area is made in a random way, therefore the sex and age structure of harvested animals reflects primarily the structure of free-roaming population of wild boars (Merta et al. 2015). Therefore, results obtained in the present paper may serve as an example of the demographic pattern of wild boar under conditions, where high quality food is easily available. In wild boar populations and domestic pigs, the sex ratio of fetuses is determined by litter size. Small litters, under 6 fetuses, are heavily male skewed (Górecki 2003, Servanty et al. 2007). This is the case in our study area, where the mean litter size was 5.2 ± 0.29 and is determined by small litter sizes in female piglets and yearlings. It probably contributed to the male-skewed sex ratio in piglets. The rapid decrease in the proportion of males in groups of yearlings and adults may be the result of high mobility associated with the high dispersion of males from natal areas during the growing season (Andrzejewski and Jezierski 1978, Truve and Lemel 2003, Keuling et al. 2010, Nasiadka 2013). At this time, the males are more likely to be culled by hunters, who hunt wild boars individually (Boitani et al. 1995, Fruziński and Łabudzki 2002).

The differences between carcass mass and kidney fat index in particular sex and age classes can be interpreted in the light of the different strategies adopted by males and females in order to reach reproductive success. The body mass and kidney fat index in males and females within the piglet class did not differ significantly (Tables 1, 2). However, the pregnancy of females in this age class depended on reaching the minimal critical body mass, which in our study area was equal to 30 kg (carcass mass). However, this is much higher than minimal carcass mass of pregnant piglets which ranged from 20.0 to 24.1 kg in Italy (Pedone et al. 1991), France (Maguet and Pepin 1991), Germany (Gethoffer et al. 2007), Luxemburg (Cellina 2008), Portugal (Fonseca et al. 2011) and Croatia (Šprem et al. 2015). Data from the latter four countries were recalculated from live weight (Haber 1969).

In the second year of life, the increase in body mass in both sexes is similar, as females increase their mass

by 35.7 kg (123 %), and males by 32.1 kg (118 %). Nevertheless, because of significantly lower levels of fat reserves in male yearlings (Tables 1, 2), it can be supposed that the body mass increases in females in their second year of life constituted markedly higher levels of fat than those in males in the same age class. This phenomenon was very likely associated with the prospective male – male competition among males older than 2 years during the rut, which among polygynous ungulates is usually won by heavier individuals (Geist 1971, Clutton-Brock et al. 1982, Van Ballenberghe and Miquelle 1996). Thus, it seems that in the second year of life, males increased their body mass mainly by adding muscle tissue and developing their skeletons, while accumulating fat tissue to a lesser extent. As producing proteins from their metabolic processes is more expensive than producing fat (Pullar and Webster 1977, Robbins 1983, Oftedal 1985), it is the reason why males do not achieve significantly higher body masses than females.

According to many publications, the differences between the body mass of males and females begin to reveal as late as among the older yearlings (Gallo Orsi et al. 1995, Moretti 1995a, Pedone et al. 1995, Spitz et al. 1998, Markina et al. 2004). Males older than two years were reported to have significantly greater body masses than females. No such relationship was found in our study. Nevertheless, it is very probable that towards the end of summer the adult males in our study area could have reached higher body masses than the adult females, as a result of major increases of body mass during the vegetation season, most of these increases being fat reserves. However, the study material for this paper consisted of males culled either in the rutting season or immediately after its end, where animals had used up their fat and protein reserves accumulated in the summer and therefore their carcass mass did not differ significantly from the carcass mass of females. The above hypothesis can be true because in the populations of other polygynous ungulates, the loss of body mass during the rutting by males can reach up to 30 % (Geist 1971, Bobek et al. 1989, Dzieciółowski and Pielowski 1993, Franzmann and Schwartz 1997).

Conclusions

1. The results obtained in our study area confirm pattern No. 3 of the farrowing period, which is characteristic for wild boar living in the environment with major access to high quality food. Piglets are born almost throughout the whole year, but there is one evident peak.

2. The management of the wild boar population living in our study area should lead to the limitation of the number of reproducing female piglets. It can be obtained by high participation of piglets in hunting bag. The participation of these groups in reproduction is not recom-

mended because their offspring, which are born in late spring and early summer, are characterized by low carcass mass and low fat reserves, which are not likely to be restored before the winter. The reduced number of females with young will also diminish the level of damage caused to farmland by the species.

3. It is recommended to develop a mathematical model of population dynamics, especially the model including sex-age structure of boar in north-eastern Poland. Performing simulations of various scenarios should allow to select an appropriate option of hunting bag, which – when applied in practice – would produce a decline of population size of wild boar and reduction of the number of female piglets taking part in reproduction. Collective hunts are very effective, but unfortunately selective harvest during collective hunts is not accepted by hunting clubs. The data obtained during our study could be used to simulate population dynamics and allowing to recommend options to manage wild boar in north-eastern Poland.

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References

- Andrzejewski, R. and Jezierski, W. 1978. Management of wild boar population and its effects on commercial land. *Acta Theriologica* 23: 19-30.
- Bieber, C. and Ruf, T. 2005. Population dynamics in wild boar *Sus scrofa*: Ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology* 42(6): 1203-1213.
- Bobek, B. 1973. Net production of small rodents in a deciduous forest. *Acta Theriologica* 18: 403-434.
- Bobek B., Perzanowski K. and Weiner, J. 1989. Energy expenditure for reproduction of male red deer. *Journal of Mammalogy* 71: 230-232.
- Bobek B., Frąckowiak, W., Furtek, J., Kopeć, K., Wojciuch-Płoskonka, M., Ziobrowski, M. and Ziolkowska, E. 2015a. Dynamika liczebności i pozyskania dzikich kopytnych w Polsce [Population dynamics and harvest rates of wild ungulates in Poland]. In: S. Gorczyca (Ed.), *Łowiectwo w Polsce w XXI wieku - realia i oczekiwania*. SITLiD Gdańsk, T. II, p.51-70 (in Polish with English summary).
- Bobek, B., Albiński A., Bobek, J., Matusik, P. and Mańko, W. 2015b. Dynamika liczebności i pozyskania dzików: metody inwentaryzacji i roczny przyrost zrealizowany populacji [Population dynamic and harvest rate of wild boar: census methods and annual net increase of population size]. In: B. Bobek and A. Czyż (Eds.) *Gospodarka łowiecka populacją dzika w mozaice polno-leśnej nadleśnictw położonych w północno-zachodniej części Regionalnej Dyrekcji Lasów Państwowych w Olsztynie*, p. 9-13 (in Polish).
- Bobek, B., Furtek, J., Bobek, J., Merta, D. and Wojciuch-Płoskonka, M. 2016. Crop damage in time in a space-resolving conflicts between farmers and wild boar (*Sus scrofa*) in northeastern Poland. *Crop Protection* (in print).
- Bobek, J. 2015. Charakterystyka szkód wyrządzanych przez dziki w uprawach rolnych na terenie północno-zachodniej części województwa warmińsko-mazurskiego. [Characteristics of damages caused by wild boars to agricultural crops in the north-western part of Warmian-Masurian Voivodeship]. Ph. D. Diss., Pedagogical University of Cracow, 36 pp. (in Polish).
- Bobek, J., Furtek, J., Frąckowiak, W. and Wojciuch-Płoskonka, M. 2015c. Charakterystyka szkód wyrządzonych przez dziki w uprawach rolnych [Characteristics of damages caused by wild boars to agricultural crops]. In: B. Bobek and A. Czyż (Eds.) *Gospodarka łowiecka populacją dzika w mozaice polno-leśnej nadleśnictw położonych w północno-zachodniej części Regionalnej Dyrekcji Lasów Państwowych w Olsztynie*, p. 21-22 (in Polish).
- Boitani L., Tarapanese, P. and Mattei, L. 1995. Demographic pattern of a wild boar *Sus scrofa* L. population in Tuscany, Italy. *IBEX Journal of Mountain Ecology* 3: 197-201.
- Briedermann, L. 2009. Schwarzwild. Kosmos Verlag, Stuttgart, Germany, 598 pp.
- Budna, E., Grzybowska, L. and Żytecka-Karolak, M. 2005. Forestry. Central Statistical Office. Warsaw, Poland, 261 pp.
- Caughley, G. and Sinclair, A. R. E. 1994. Wildlife ecology and management. Blackwell Science. Cambridge, Massachusetts, USA, 334 pp.
- Cellina, S. 2008. Effects of supplemental feeding on the body condition and reproductive state of wild boar *Sus scrofa* in Luxembourg. Ph.D. Thesis. University of Sussex, UK, 141 pp.
- Clutton-Brock, T. H., Guinness, F. E. and Albon, S. D. 1982. Red deer: behavior and ecology of the two sexes. University of Chicago Press, Chicago, 400 pp.
- Durio, P., Gallo Orsi, U., Macchi, E. and Pedone, A. 1995. Structure and monthly birth distribution of a wild boar population living in mountainous environment. *Ibex, Journal of Mountain Ecology* 3: 202-203.
- Dzięciołowski, R. and Pielowski, Z. 1993. Łoś [Moose]. Wydawnictwo Anton-5, Sp. z o.o. Warszawa, 208 pp. (in Polish).
- Fernández-Llario, P. and Carranza, J. 2000. Reproductive performance of the wild boar in a Mediterranean ecosystem under drought conditions. *Ethology, Ecology and Evolution* 12: 335-343.
- Finger, S. E., Brisbin, J. L., Smith, M. H. and Urbston, D. F. 1981. Kidney fat as a predictor of body condition in white-tailed deer. *Journal of Wildlife Management* 45: 964-968.
- Fonseca, C., Sousa, J., Vingada, J., Cancela, J. and Soares, A. M. V. M. 2001. Monthly birth distribution of the wild boar (*Sus scrofa* L.) in central Portugal. *Galemys* 13: 199-204.
- Fonseca, C., Alves da Silva, A., Alves, J., Vingada, J. and Soares, A. M. V. M. 2011. Reproductive performance of wild boar females in Portugal. *European Journal of Wildlife Research* 57: 363-371.
- Frąckowiak, W., Gorczyca, S., Merta, D. and Wojciuch-Płoskonka, M. 2013. Factors affecting the level of damage by wild boar in farmlands in north-eastern Poland. *Pest Management Science* 69: 362-366.
- Frauendorf, M., Gethöffer, F., Siebert, U. and Keuling, O. 2016. The influence of environmental and physiological factors on the litter size of wild boar (*Sus scrofa*) in an agriculture dominated area in Germany. *Science of the Total Environment* 541: 877-882.

- Franzmann, A. W. and Schwartz, C. C. 1997. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, DC., USA, 733 pp.
- Fruziński, B. and Labudzi, L. 2002. Management of wild boar in Poland. *Zeitschrift für Jagdwiss* 48: 201-207.
- Gallo Orsi, U., Macchi, E., Perrone, A., and Durio, P. 1995. Biometric data and growth rates of wild boar population living in the Italian Alps. *Ibex Journal of Mountain Ecology* 3: 60-63.
- Gamelon, M., Gaillard, J.-M., Servanty, S., Gimenez, O., Toigo, C., Baubet, E., Klein, F. and Lebreton, J.-D. 2012. Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar. *Journal of Applied Ecology* 49(4): 833-841.
- Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, 383 pp.
- Gethöffer, F. 2005. Reproduktionsparameter und Saisonalität der Fortpflanzung des Wildschweins (*Sus scrofa*) in drei Untersuchungsgebieten Deutschlands [Reproduction parameters and seasonality of reproduction of wild boar (*Sus scrofa*) in three study areas in Germany.]. Zur Erlangung des Grades einer Doktorin der Veterinärmedizin. Institut für Wildtierforschung, Hannover, 143 pp. (in German).
- Gethöffer, F., Sodeikat, G. and Pohlmeier, K. 2007. Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. *European Journal of Wildlife Research* 53: 287-297.
- Górecki, M. T. 2003. Sex ratio in litters of domestic pigs (*Sus scrofa domestica* Linnaeus 1758). *Biological Letters* 40: 111-118.
- Groot Briunderink, G. W. T. A., Hazebroek, E. and Van Der Voot, H. 1994. Diet and condition of wild boar, *Sus scrofa scrofa*, without supplementary feeding. *Journal of Zoology* 233 (4): 631-648.
- Grzybowska, L., Pac, T. and Raczowska, J. 2014. Forestry. Central Statistical Office. Warsaw, Poland, 324 pp.
- Haber, A. 1969. Dzik. Monografia przyrodniczo-łowicka [Wild Boar. Monograph on its biology and harvest]. PWRiL, Warsaw, Poland, 231 pp. (in Polish).
- Ježek, M., Štípek, K., Kušta, T., Červený, J. and Vicha, J. 2011. Reproductive and morphologic characteristics of wild boar (*Sus scrofa*) in the Czech Republic. *Journal of Forest Science* 57: 285-292.
- Keuling, O., Lauterbach, K., Stier, N. and Roth, M. 2010. Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. *European Journal of Wildlife Research* 56: 159-167.
- Labudzi, L., Górecki, G., Skubis, J. and Wlazelko, M. 2009. Wild boar seasonal farrowing pattern analysis based on the harvest data of the piglets and yearlings shot in the Zielonka Game Investigation Centre in 2005-2008. *Acta Scientiarum Polonorum Silvarum Colendarum Ratio et Industria Lignaria* 8: 59-66.
- Łączkowski, A. and Ziolkowska, E. 2014. Statistical Yearbook of Agriculture. Central Statistical Office. Warsaw, Poland, 445 pp.
- Maguet, R. and Pepin, D. 1991. Energy intake, growth and timing of puberty in the European wild boar *Sus scrofa* L. *18th IUGB Congress*, Krakow, Swiat Press: 205-209.
- Maillard, D. and Fournier, L. 2004. Timing and synchrony of births in the wild boar (*Sus scrofa* Linnaeus, 1758) in a Mediterranean habitat: the effect of food availability. *Galemys* 16: 67-74.
- Markina, F. A., Sáez-Royuela, C. and De Garnica, R. 2004. Physical development of wild boar in the Cantabric Mountains, Alava, Northern Spain. *Galemys* 16: 25-34.
- Matschke, G. H. 1967. Aging European Wild Hogs by Dentition. *Journal of Wildlife Management* 31: 109-113.
- Merta, D., Albrycht, M., Frąckowiak, W., Furtek, J. and Marmok, T. 2011. Reproductive performance, birth date and body condition of wild boar (*Sus scrofa*) inhabiting forest and forest-farmland environment in southwestern Poland. *Abstracts of 8th European Vertebrate Pest Management Conference*, Berlin: 233-234.
- Merta, D., Mocala, P., Pomykacz, M., and Frąckowiak, W. 2014. Autumn-winter diet and fat reserves of wild boars (*Sus scrofa*) inhabiting forest and forest-farmland environment in southwestern Poland. *Folia Zoologica* 63(2): 95-102.
- Merta, D., Bobek, B., Albrycht, M. and Furtek, J. 2015. The age structure and sex ratio in wild boar (*Sus scrofa*) populations as determined by observations of free-roaming populations and by harvests of collective hunts in southern Poland. *European Journal of Wildlife Research* 61:167-170.
- Moretti, M. 1995. Birth distribution, structure and dynamics of a hunted mountain population of wild boar (*Sus scrofa* L.), Ticino, Switzerland. *IBEX Journal of Mountain Ecology* 3: 192-196.
- Moretti, M. 1995a. Biometric data and growth rates of a mountain population of wild boar (*Sus scrofa* L.) Ticino, Switzerland. *IBEX Journal of Mountain Ecology* 3: 56-59.
- Nasiadka, P. 2013. Dispersion and movement pattern of wild boar (*Sus scrofa* L.) in agro-forestry landscape under strong pressure from urbanization in central Poland. *Sylwan* 152(12): 937-945 (in Polish with English summary).
- Oftedal, O.T. 1985. Pregnancy and lactation. In: Bioenergetics of wild herbivores R.J. Hudson and R.G. White (Eds.), CRC Press, p. 215-238.
- Orłowska, L., Rembacz, W. and Florek, C. 2013. Carcass weight, condition and reproduction of wild boar harvested in north-western Poland. *Pest Management science* 69(3): 367-370.
- Pedone, P., Mattioli, L., Mattioli, S., Siemoni, N., Lovari, C., and Mazzarone, V. 1991. Body growth and fertility in wild boars of Tuscany, Central Italy. *XX congress of the international union of game biologists*, Gödöllő, Hungary, P. 604-609.
- Pedone, P., Mattioli, S. and Mattioli, I. 1995. Body size and growth patterns in wild boars of Tuscany, central Italy. *Ibex Journal of Mountain Ecology* 3: 66-68.
- Plisko, J. D. 1965. Materiały do rozmieszczenia geograficznego i ekologii dżdżownic w Polsce (*Oligochaeta, Lumbricidae*). [Geographical distribution and ecology of *Lumbricidae* in Poland]. *Fragmenta Faunistica* 12: 57-108 (in Polish).
- Pullar, J. D. and Webster, A. J. F. 1977. Energy cost of fat and protein deposition in rat. *British Journal of Nature* 37:355-367.
- Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elephas*), with special reference to New Zealand. *New Zealand Journal of Science and Technology* 36: 429-463.
- Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press New York, 337 pp.
- Santos, P., Fernández-Llario, P., Fonseca, C., Monzón, A., Bento P., Soares A. M. V. M., Mateos-Quesada, P. and Petrucci-Fonseca, F. 2006. Habitat and reproductive phenology of wild boar *Sus scrofa* in the western Iberian Peninsula. *European Journal of Wildlife Research* 52:207-212.
- Santos, J. P. V., Fernández-de-Mera, I. G., Acevedo, P., Boadella, M., Fierro, Y., Vicente, J. and Gortázar, Ch. 2013. Optimizing the sampling effort to evaluate body condition in ungulates: a case study on red deer. *Ecological Indicators* 30: 65-71.
- Scheu, S., Albers, D., Alpei, J., Buryn, R., Klages, U., Migge, S., Platner, C. and Salamon, J.-A. 2003. The soil fauna community in pure and mixed stands of beech and spruce of different age: Trophic structure and structuring forces. *Oikos* 101: 225-238.
- Servanty, S., Gaillard, J. M., Allainé, D., Brandt, S. and Baubet, É. 2007. Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. *Behavioral Ecology* 18 (2): 428-432.

- Servanty, S., Gaillard, J.-M., Toïgo C., Serge B. and Baubet, É.** 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *Journal of Animal Ecology* 78: 1278-1290.
- Servanty S., Gaillard, J.-M., Ronchi, F., Focardi, S., Baubet, É. and Gimenez, O.** 2011. Influence of harvesting pressure on demographic tactics: implications for wildlife management. *Journal of Applied Ecology* 48: 835-843.
- Sokal, R. R. and Rohlf, F. J.** 1995. Biometry – the principles and practice of statistics in biological research. W.H. Freeman and Company, New York, USA, 887 pp.
- Spitz, F., Valet, G. and Brisbin Jr., J. L.** 1998. Variation in body mass of wild boars from southern France. *Journal of Mammalogy* 79:251-259.
- Šprem, N., Piria, M., S. Prdun, S., Novosel, H. and Treer, T.** 2015. Variation of Wild Boar Reproductive Performance in Different Habitat Types: Implications for Management. *Russian Journal of Ecology* 46 (6): 579–585.
- Starkel, L.** 1991. Geografia Polski. Środowisko przyrodnicze [The Geography of Poland. The natural environment]. Wydawnictwo Naukowe PWN, 582 pp. (in Polish).
- Truszczyński, M. and Pejsak, Z.** 2015. Importance of wild boar in the spread of African Swine Fever, particularly in relation to Europe. *Medycyna Weterynaryjna* 71 (2): 71-74 (in Polish with English summary).
- Truvé, J. and Lemel, J.** 2003. Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. *Wildlife Biology* 9 (Suppl. 1): 51-57.
- Tumidajowicz, D.** 1971. Phenology of increase of underground organs of the herb layer plants in the deciduous Tilio-Carpinetum association of the Niepołomice Forest. *Bulletin Academy Polish Sciences* 19(12): 795-799.
- Woś, A.** 1999. Klimat Polski [The Climate of Poland]. Wydawnictwo Naukowe PWN. Warsaw. Poland, 302 pp. (in Polish)
- Van Ballenberghe, V. and Miquelle, D.** 1996. Rutting behavior of moose in central Alaska. *Alces* 32:109-130.
- Vetter, S. G., Ruf, T., Bieber, C. and Arnold, W.** 2015. What is a mild winter? Regional differences in within-species responses to climate change. *PLoS ONE* 10(7): e0132178. doi:10.1371/journal.pone.0132178.
- Zakrzewski, T.** 2015. Ocena stanu sanitarnego dzików na terenie powiatu Braniewo [Evaluation of the health status of wild boar population in Braniewo County]. In: B. Bobek and A. Czyż (Eds.) Gospodarka łowiecka populacją dziką w mozaice polno-leśnej nadleśnictw położonych w północno-zachodniej części Regionalnej Dyrekcji Lasów Państwowych w Olsztynie, p. 8 (in Polish).

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