Reproductive characteristics of wild boar males (*Sus scrofa*) under different environmental conditions

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Abstract

The wild boar population has been on a permanent increase over the last decades, causing conflicts with the requirements of modern human society. Existing effort to stabilize wild boar numbers generally fails with one of the causes being the high reproductive potential of wild boar. The aim of this study was to assess the onset of sexual maturity in wild boar males with regard to age, physical frame and environmental conditions on the basis of testicle development and sperm production. This study assessed the dimensions of gonads and the occurrence of sperm in boars caught during common hunts. Environmental conditions were found as an important factor for growth and sexual maturity of wild boar males. The body weight was a more important factor for sperm production than the age of young wild boar males. The weight threshold for sperm production in the testes was 29 kg of live weight, which corresponds to 6 months of age on average. This study has proven that environmental conditions are a significant factor affecting the physical development of male wild boars, more specifically the growth rate of their body frames and the onset of sexual maturity. In a better quality environment boars grow faster and enter puberty at an earlier age. Poor food supply and/or high hunting pressure result in slower body and testicular growth, as well as the production of sperm at a later age (approx. 2–3 months later).

Testicles, gonads, mating season, sperm, feeding, body weight

The wild boar (*Sus scrofa*), is currently one of the most widely discussed large mammals of Europe and certain other areas of the world. The main reason for the interest in wild boar is the steady and rapid increase in their populations over the last decades (Massei et al. 2015) and the resulting conflicts with the requirements of modern human society. These conflicts are reflected e.g. in damage to agricultural crops (Herrero et al. 2006), negative effects on environmental diversity (Massei and Genov 2004), and the spread of parasites and diseases, e.g. the African swine fever (Sánchez-Vizcaíno et al. 2013) or hepatitis E virus (Carpentier et al. 2012).

Consequently, much attention is also paid to the factors contributing to the high reproduction rates of wild boar (Apollonio et al. 2010). Important factors include the disproportionate social structure of the population (there are considerably more female than male boars older than 2 years), easy access to a substantial amount of quality food throughout the year, favourable climate, and also a shift in the reproductive strategy of boars, which have begun to reproduce en masse in the first year of their lives (Oja et al. 2014).

The wild boar reproduction is seasonal and regulated by photoperiodicity (Keuling et al. 2018), but piglets can be born at virtually any time (Orłowska et al. 2013). Nevertheless, it can be stated that most females reproduce during the primary reproductive season from November to March (Mauget 1972). The social structure of wild boar populations over the course of the year is a dynamic system. Family groups formed by old sows, their adult

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daughters and young piglets of both sexes constitute its foundation. Adult males, which live by themselves, join the groups for reproduction seasons (Truvé and Lemel 2003). Young males leave their family packs when they are approximately one year old and form their own packs outside of the family groups. The mating system is commonly described as polygynous (Fernández-Llario et al. 1999), some authors, however, describe it as polygynandrous or promiscuous (Pérez-González et al. 2014) in view of evidence of multiple paternity within litters (Delgado-Acevedo et al. 2011).

Females begin reproducing when they are approximately 7 months old and weigh around 20 kg, with these parameters depending largely on the availability of food (e.g. Gethöffer et al. 2007). It is not clear to what extent these young and morphologically immature females are capable of mating with strong adult boars, and how reproductively mature similarly aged males are.

Table 1. Characteristics of environments (groups of sampling areas).

Environment	Level of year-round availability food	Altitude (m a.s.l.)	Forest stands	Availability of cereals on fields	Year-round hunting pressure	Details
GOOD	excellent	under 200	deciduous	high	low; only common hunts in winter	Year-round availability of quality food (e.g. acorns, beechnuts, maize, wheat, barley and supplementary feeding); typically lowland plain forests with intensive areas and flood wildlife care
MODERATE	medium	200-600	mixed	limited	medium	Average feeding hunting grounds (mixed forests, small agricultural fields)
POOR	poor	over 600	coniferous	no	high; individual and common hunts	Year-round unavailability of food (absence of fruitive trees, agricultural crops and supplementary feeding); esp. mountain areas with the absence of mast trees

Reproduction ability is determined by a number of factors influencing the animal in the provided environment; it is directly tied to its physical development. While females need to be sexually mature as well as be adequately physically developed and have sufficient fat reserves in order to take part in active reproduction, the reproductive ability of a young male is determined mainly by the development of his gonads and their capacity for producing viable sperm. In the last decades, young females have begun to reproduce en masse, it is therefore likely that environmental conditions have the same effect on males, which should be capable of fertilizing females of the same age (Murta et al. 2013).

The aim of this study was to assess the onset of puberty and sexual maturity in wild boar males with regard to body size, age, and environmental conditions on the basis of testicle development and sperm production. We hypothesized that: 1) young boar males living in high-quality environment grow faster and reach their sexual maturity earlier, and 2) the sexual maturity of wild boar males depends more on their body size than their age.

Materials and Methods

The sexual maturity of males was assessed by analysing the reproductive organs of animals harvested during collective hunts from November 2014 to January 2015. Samples were collected from 21 unfenced areas that were distributed unevenly across the Czech Republic. Sampling areas were divided into three groups according to the quality and management of the environment during the whole year (Table 1, Fig. 1).

Males were weighed before (live weight) and after evisceration, their age was determined from tooth eruption and wear (Briedermann 1965; Matschke 1967; Boitani and Mattei 1992), and body length was measured to the

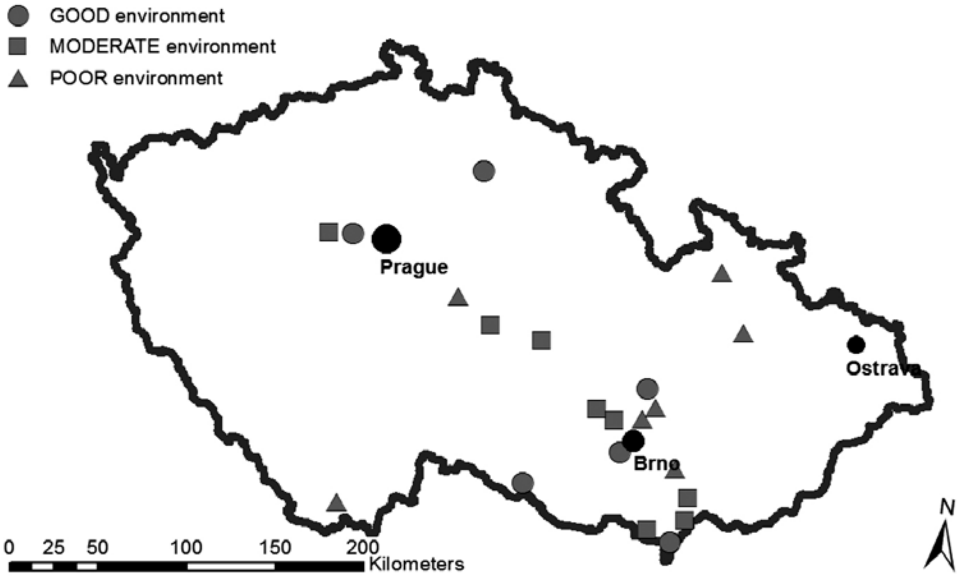

Fig. 1. Localization of sampling areas in the Czech Republic according to the quality of environmental groups

nearest millimetres (distance of snout-tail). In order to minimize errors, all determining and measuring was performed by the same person. After that, the testes with their epididymides were removed and frozen until the time of the analysis. The excisional incisions were made by transecting the ejaculatory duct, the vas deferens, 10 cm from the epididymis.

After defrosting at room temperature (20 °C), both testes with epididymides were stripped of excess tissue and the length and width of the each testis and its epididymis was determined to the nearest 0.01 mm (selected parameters from Věžník et al. 2004) and the weight of each testis with and without the epididymis was determined to the nearest 0.01 g. Testicular volume was calculated using the following formula (Bekaert et al. 2012): Volume = length × width^2 × (π/6). The gonadosomatic index (GSI) was calculated using the following formula (Barber and Blake 1991):

GSI = testis weight / body weight × 100.

The testes were cut in 3 places – the head, body, and tail of each epididymis – and the imprinting preparations were placed on microscope slides. Subsequently, the presence or absence of sperm was determined under a microscope at a ×300 magnification.

All biological material was handled in accordance with the relevant veterinary and health directives and was disposed of adequately.

All analyses were performed in the R software (R Development Core Team 2008):

1. Modelling individual relationships between body parameters and environment quality: Individual relationships were modelled using generalized linear models and log-linear regression. Multiple comparisons were carried out using a likelihood-ratio test.

2. Model of the relationship between GSI and body weight: Various models were compared in performance terms by means of nested Monte Carlo cross-validation with 10,000 iterations. Tested models included various penalized polynomial regressions (LASSO, Ridge and Elastic Net Regularization) and 21 different sigmoid functions implemented in the drc package (Ritz et al. 2015) – these were included on the basis of visual assessment of the data. Mean cross-validated error served as a criterion for the final model selection.

3. Complex models: The variable selection problem was addressed by the elastic net algorithm implemented in the glmnet package (Friedman et al. 2010), where the regularization parameter lambda was determined through cross-validation. Hyperparameters optimization and model selection was performed via nested Monte Carlo cross-validation with 10,000 iterations. The final model was selected based on the mean cross-validated error. In the case of modelling the continuous response variable – the testicle weight – the forecast accuracy was expressed by the mean absolute percentage error (MAPE). In the case of logistic regression – modelling the probability of sperm presence – the criterion for model selection was the misclassification rate.

Results

Altogether, the reproductive organs of 145 males from 21 areas divided into three environments were analysed (Table 1, Fig. 1). As mostly piglets in the first year of their life (81%) were analysed, the age structure of the males was unbalanced, but the number of equally old individuals (in the key age of 6–11 months) was balanced across the environmental quality. Adult males accounted for 11% and half of these were males aged 2–3 years. There were only 7 fully adult males older than 3 years (Table 2). The body weight ranged from 11 to 60 kg in piglets, from 62 to 102 kg in young adults, and from 84 to 145 kg in adults. In all dead boars, this parameter seemed to be closely correlated with age (r = 0.86; $P < 0.001$), with the biggest correlation apparent in piglets (r = 0.67; $P < 0.001$). The proportion of internal organ weight to the weight of a live boar ranged from 1/4 in piglets to 1/6 in adults (r = -0.49; $P < 0.001$), which is related to the development of musculature and skeleton during the process of morphological and physiological maturation. Table 3 shows an overview of the measured physical parameters.

Table 2. Numbers and basic characteristics of wild boar males.

Class of age	Age (months)	Anim (n)	Mean body weight (kg)	Proportion of viscera (% body weight)	GSI (%)	Individuals with sperm (%)
Piglets	1–12	118	37.3 ± 10.1	25.5 ± 5.2	0.09 ± 0.08	66.9
Yearlings	13–24	11	79.0 ± 13.1	20.8 ± 3.0	0.36 ± 0.07	100.0
Adults	24<	16	105.8 ± 16.8	17.2 ± 3.9	0.39 ± 0.07	100.0

Anim – animals; GSI – gonadosomatic index

Table 3. Mean body weight and length of wild boar males.

Age (months)	(n)	Body weight (kg)	Body length (mm)
2	1	11.0	720.0
3	1	14.0	790.0
5	6	25.7 ± 4.3	925.3 ± 38.9
6	33	32.5 ± 7.3	990.6 ± 72.3
7	18	33.8 ± 8.9	997.1 ± 133.1
8	21	38.3 ± 5.1	1086.7 ± 72.2
9	21	43.5 ± 8.2	1124.7 ± 65.2
10	12	48.1 ± 8.6	1128.4 ± 81.9
11	3	51.5 ± 5.6	1175.0 ± 25.5
12	2	55.0 ± 0.8	1176.7 ± 70.4
13–24	11	79.0 ± 13.7	1372.0 ± 84.9
24<	16	105.8 ± 17.3	1428.4 ± 121.5

Body length depended the most on body weight and less on age. There was a strong relationship between body length and body weight: r = 0.88; $P < 0.001$ (all cases) and r = 0.81; $P < 0.001$ (piglets). A significant relationship was also found between body length and age: r = 0.75; $P < 0.001$ (all cases) and r = 0.67; $P < 0.001$ (piglets).

Basic characteristics of reproductive organs

The total volume of gonads (both testes) ranged from 41.4 mm^3 in piglets to 598.7 mm^3 in adult males. The highest value was measured in a male aged 6 years; the volume of testes was 903.6 mm^3 with the weight of one testicle a little over 250 g (0.5 kg including epididymis). The determined parameters of the gonads are detailed in Table 4.

Close correlations were discovered between testicular weight and body weight (r = 0.94; $P < 0.001$) and also the mean testicle length and body length (r = 0.88; $P < 0.001$). Differences between the left and right testicle in volume, weight, and dimensions were not observed ($P < 0.001$). The measured physical parameters and dimensions of the testes correlated at the values of r = 0.7–0.8 ($P < 0.001$). On average, the ratio of gonad weight to body weight (GSI) was 0.14 ± 0.13% (Fig. 2). The relationship between GSI and body weight was best explained by the following Weibull model:

Table 4. Mean testicular parameters of wild boar males.

Age (months)	Anim (n)	Anim with (%)	Testicle length (mm)	Testicle width (mm)	Testicle weight (g)	Epididymis weight (g)	Testicle volume (cm^3)
2–5	8	0.0	29.5 ± 4.2	16.3 ± 2.1	5.1 ± 1.8	2.7 ± 0.7	4.2 ± 1.5
6	33	42.4	32.3 ± 4.6	19.6 ± 3.2	8.3 ± 7.0	4.1 ± 1.7	6.9 ± 3.5
7	18	41.2	34.5 ± 10.4	21.0 ± 6.2	9.7 ± 8.4	5.7 ± 6.7	10.2 ± 13.1
8	21	95.2	38.4 ± 9.7	23.5 ± 6.4	14.5 ± 10.9	5.6 ± 3.8	13.4 ± 11.2
9	21	95.5	52.4 ± 14.4	33.4 ± 9.1	34.2 ± 22.2	14.0 ± 9.6	37.1 ± 26.9
10–11	15	100.0	57.0 ± 17.1	36.1 ± 12.3	44.4 ± 28.9	16.3 ± 11.5	49.9 ± 40.0
12–16	4	100.0	73.5 ± 17.2	48.9 ± 15.1	89.5 ± 61.4	33.0 ± 18.2	108.7 ± 75.2
17–24	9	100.0	92.0 ± 13.0	61.1 ± 8.5	141.6 ± 38.7	68.8 ± 28.8	187.2 ± 71.4
25≤	16	100.0	109.3 ± 9.2	71.8 ± 6.8	208.6 ± 52.3	122.7 ± 42.0	299.4 ± 82.0

Anim – animals

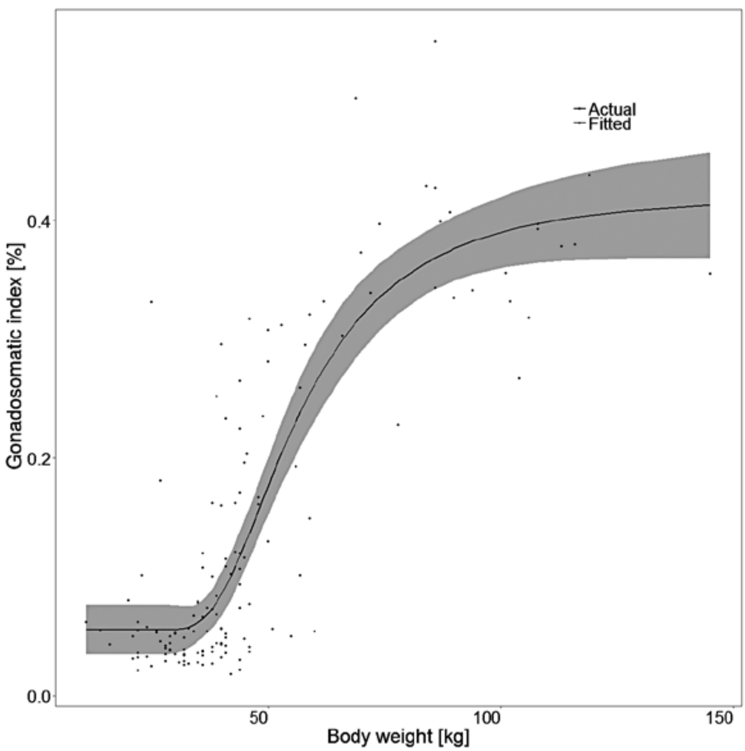

Fig. 2. Relationship between body weight and gonadosomatic index in wild boar ($r^2 = 0.66$; $P < 0.001$)

GSI (body_weight) = 0.056c + (0.421d – 0.056c)exp(–exp(3.637b(log(x) + log(51.442e))))

The formula implies that the fastest growth of GSI occurs for the body weight of 51.44 kg, which corresponds to approximately 11 months of age.

The effect of environmental quality on physical development and reproductive organs

Due to insufficient data for adult boars, environmental influence was only evaluated in piglets. Environmental quality significantly affected the growth of piglets in the first year of their lives and the development of their reproductive organs. The GSI, body weight and body length (Fig. 3) of males living in POOR environment were significantly lower compared with males living in GOOD and MODERATE environments ($P < 0.001$). There was also a significant difference in body weight between boars living in GOOD and MODERATE environments ($P < 0.001$).

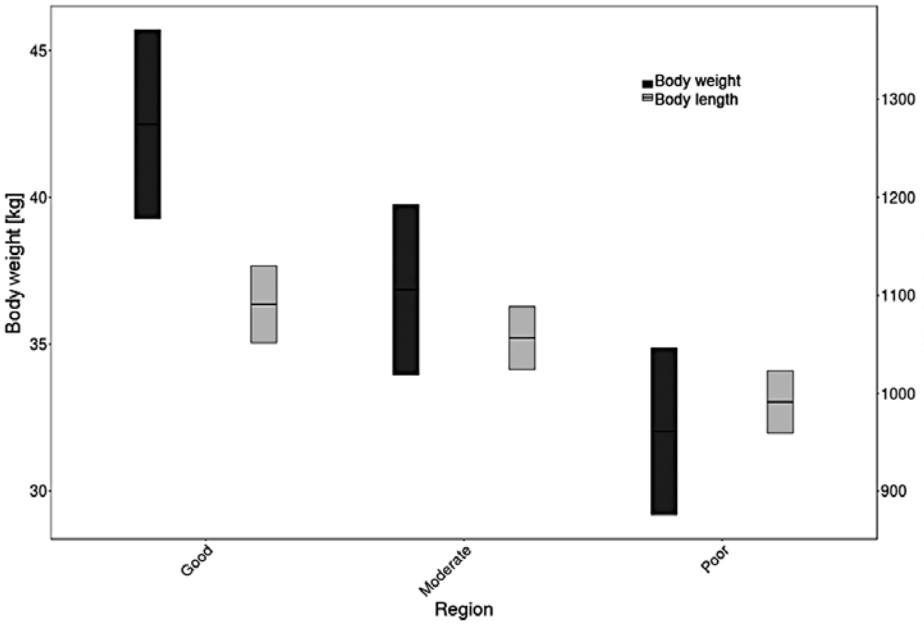

Fig. 3. Body weight and length of piglets 5–11 months old depending on the quality of the environment

The environment significantly affected the GSI values of piglets (Fig. 4). In GOOD environments, despite higher body weight, testes were relatively bigger than in other environments (GSI in GOOD environment: 0.13%; MODERATE environment: 0.10%, and POOR environment: 0.05%). The differences in GSI between locations were caused by testicular weight ($r = 0.93$; $P < 0.001$) to a higher extent than by body weight ($r = 0.81$; $P < 0.001$). Boars living in high quality conditions grow and sexually mature faster, so their testes were significantly more developed. The most notable connection between the acquired data about testes and body parameters was observed between body weight and testicular length ($r = 0.67$; $P < 0.001$).

Sperm was not observed in piglets younger than 5 months. In piglets aged 6–7 months, sperm was observed in 63% of piglets living in GOOD and MODERATE environments, but only in 17% of piglets from a POOR environment. Every piglet aged 8 months and living in GOOD or MODERATE conditions had sperm in its testes, while piglets from POOR conditions had sperm only in 83% of cases (100% from 9 months on). Every piglet weighing 29 kg and more already had sperm in its testes. This corresponds to 23 g in gonad

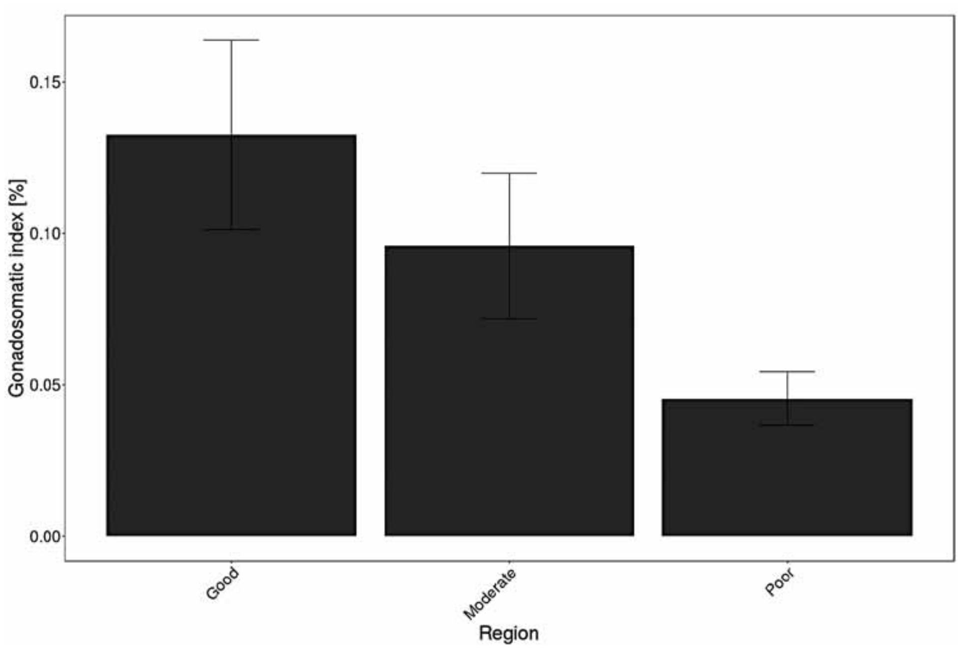

Fig. 4. Gonadosomatic index of piglets 5–11 months old depending on the quality of the environment

weight (GSI = 0.08%); sperm was individually observed starting at 8 g (the mean weight of one testicle was 4 g, Table 4).

The final selected model of probability of sperm occurrence with the highest accuracy (92%) had the following formula:

Sperm_presence (body_weight, testicle_length, testicle_weight) = 0.164 body_weight + 0.013 testicle_length + 0.041 testicle_weight – 18.406

In addition, it can be concluded that the presence of sperm is more dependent on body weight than on age (Fig. 5).

Discussion

This study complements findings from the field of wild boar reproductive biology. While females have been studied extensively, there are few studies focusing on males. From an ecological point of view, its reproductive strategy is somewhere between r- and K-selection; the boar is able to reach high population density in a very short period of time (Frauendorf et al. 2016). This is determined by the litter size, positively influenced by high precipitation and temperatures in the summer, as well as higher oak mast yield, and also, indirectly, by the climate, which affects the weight of the mother through nutrition.

The weight of the mother and the entire population is also supported by agricultural policy oriented towards extensive production of energy crops (maize, rapeseed or grain) (Cahill et al. 2003; Herrero et al. 2006) and supplementary feeding from hunters (Oja et al. 2015). This way, the boar never feels nutritionally deprived, not even out of growing seasons (Oja et al. 2014). Unless it is burdened with major health problems or other types of stress, the increase in average weight and body frame size can continue undisturbed, depending on environmental conditions (especially energy-rich food sources). It differs

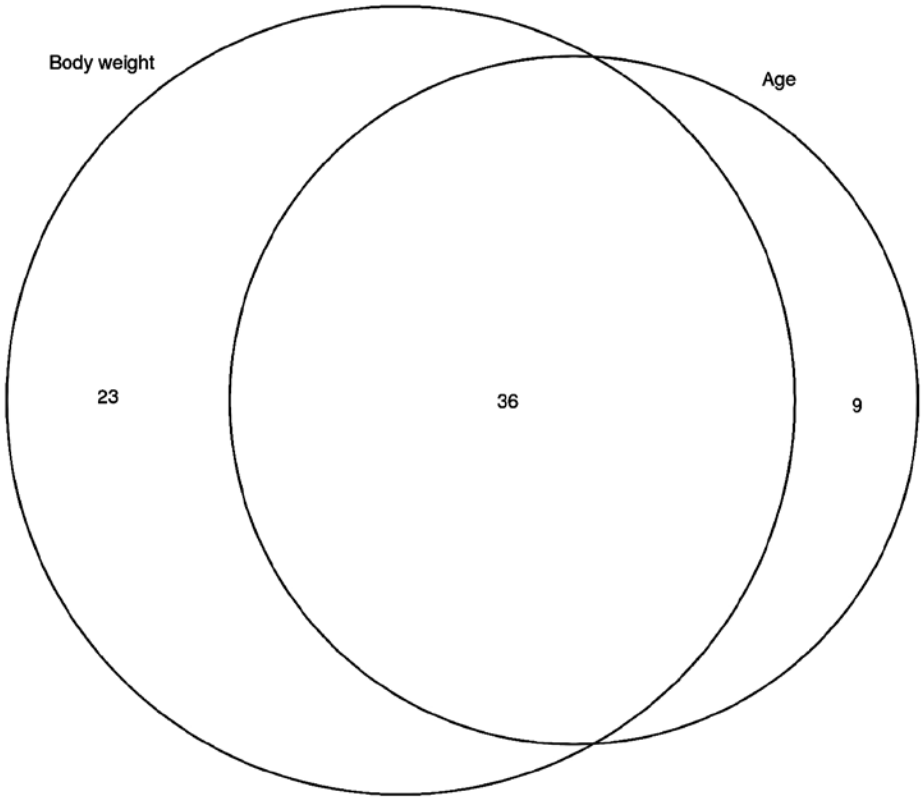

Fig. 5. Percentage of variability in sperm presence explained by body weight, age and both

in males and females. Pedone et al. (1991) and Gallo Orsi et al. (1995) discussed the weight differentiation between sexes under 12 months of age, when males invest all their energy into growth, while females must also invest it in reproduction, causing them to grow slower. Ježek et al. (2011) also state that the effect of location as a factor affecting morphometric parameters is very important in boars in their first year of life. This factor also proved to be important in the present study focused on males. In a high-quality environment where boars were not stressed by hunts over the course of the year and had enough rest, shelter and nutrition, they reached larger body sizes and higher weights sooner than boars in an environment with fewer resources (especially with limited availability of energy-rich nutrition) and generally more stressful environments.

An important role is also played by wild boar diseases, which may affect the growth and overall form of piglets in particular. As a result of their organisms coping with infection, they may fall behind in growth (Patra et al. 2013). García-González et al. (2013), for example, found a 41.01% prevalence of metastrongylosis in boars caught in Southwestern Spain. However, evaluating the state of their health was not the aim of this study. In general, Pedone et al. (1995) indicate that a boar acquires 50% of its adult weight within the first 12 months and 70% of its adult weight within the first 22 months. These findings are also confirmed by the results of this study.

The mean weights of the three main age groups of this study showed similar values to the ones found by Sprem et al. (2011), although they were higher than values found by Herrero and Fernandez de Luco (2003) and Delgado et al. (2008). Using body parameters, it is possible to compare body lengths of the examined boars according to research by Ježek et al. (2011), who evaluated boars caught in several different areas of the Czech Republic using similar age groups, and found values very close to the values observed in our study. They were also very close to the values observed in other parts of Europe such as Germany (Gethöffer et al. 2007) and Switzerland (Hebeisen 2007).

The sampling areas (hunting grounds) for this study were selected in order to match the pre-defined types of environment considering the wider surroundings. Areas with ambiguous environmental characteristics were excluded from the study in advance, according to the study by Truvé and Lemel (2003). They found that young males begin to disperse at the age from 10 to 16 months within a maximal distance of 16.6 km from their natal sites. As the average size of the home range is about 800 ha (Keuling et al. 2018), hunting grounds with a minimum area of 1000 ha had been selected in order to make sure that the hunted wild boars were present in the areas also during the growing season. This confirmed the assumption that wild boars were born, lived and were hunted in the same type of environment. This study assessed the dimensions of gonads and the occurrence of sperm in boars killed during common hunts. These usually take place during a time referred to as the main reproductive period of the wild boar (November–January). An effect of the shortening light phase of the day on physiological changes stimulating the reproductive function of the testes was proven not only in females, but also in males (Smital 2009). Most studies were aimed at domestic pigs kept on farms, but Kozdrowski and Dubiel (2004) state that the ejaculates of domestic pigs and wild boars are not significantly different. Pig ejaculate tested in autumn and in early winter showed a higher concentration of sperm and their total volume, as well as a higher proportion of motile sperm (Mauget and Boissin 1987; Marchev et al. 2003; Kozdrowski and Dubiel 2004; Sancho et al. 2004; Smital 2009). Schopper et al. (1984) showed the highest steroid hormone production values in autumn and early winter. Mauget and Boissin (1987) point out that testicular weight and volume, as well as testosterone concentrations in the blood, are at their highest in winter. Chinchilla-Vargas et al. (2018), on the other hand, point out changes in reproductive characteristics in domestic pigs caused by climatic phenomena and phases of the moon.

Thus, there is a correspondence between the reproductive periods of females and sperm production in males, with the female reproductive activity being strongly seasonal. The ovarian cycles of females can be interrupted due to food shortages in winter, but also due to, e.g. high summer temperatures (Thibault et al. 1966; Peltoniemi et al. 1999; Tummaruk et al. 2000). It is a time when follicles do not mature in the ovaries of the wild sow and fertilizable eggs are not released. According to the study conducted by Schopper et al. (1984), the libidos of domestic pigs were disrupted from mid-July to mid-September; they refused to jump on the figurine used to collect sperm for the artificial insemination of domestic sows. Kozdrowski and Dubiel (2004) discovered an absence of copulation as early as in May. The maximum productivity of the testes coincides with the main reproductive period of the females (Smital 2009).

As mentioned above, many authors considered the weight of young females to be a more important factor influencing the onset of sexual maturity in piglets than the actual physiological age of the animal. Through analyses of the occurrence of sperm in testes of young adult males, this has also been confirmed in this study. Changes in dimensions of the testes occurring as a part of their physiological development are caused by cytological and structural changes to the testes within the relevant age groups (Ogwu et al. 2009). This suggests a close relationship between testicle sizes for each age group and the spermatogenic and endocrinal activity in the testes. In the first few months, they initially exhibit slow growth as a result of the cell proliferation period (Thomas and Raja 1980). As puberty approaches, the growth accelerates due to the expansion of lumen and thickening of the walls of seminiferous tubules. After reaching their sexual maturity, the growth slightly slows down due to an increase in the volume of connective tissue (Schinckel et al. 1983; Assis Neto et al. 2003; Murta et al. 2013). This accelerated growth in puberty and the post-pubertal period is related to an increase in the volume of Sertoli cells and the mitotic division of reproductive cells in seminiferous tubules, which leads to the formation of primary spermatocyte out of spermatogonia. Environment quality has been proven to cause an earlier onset of sexual maturity in piglets. This is due to the piglets achieving threshold weight faster in quality environments, which is also related to the weight (and volume) of their gonads (Ogwu et al. 2009).

The ratio of body and testicular weight was initially more or less constant; this was followed by rapid growth starting at month 8 and peaking during month 10, which could be caused by impending puberty, as described by Murta et al. (2013) and Ferreira et al. (2004). After that, the growth gradually slowed and reached constant values again. The gonadosomatic index growth is represented by a sigmoid curve. The acquired GSI values corresponded to the findings of similar studies of boars of comparable ages and in comparable seasons. Almeida et al. (2006) state that GSI fluctuates during the rutting season (November/January). In males of the Brazilian population of *Sus scrofa scrofa* aged around 10 months, these authors found a GSI of 0.3% (which corresponds to the present mean value acquired from young adults). The high correlations found between gonad parameters and the weight/age of the males in this study have already been described in both domestic pigs (Thomas and Raja 1980; França and Cardoso 1998; França et al. 2005) and wild boars (Sprem et al. 2011). Domestic pigs exhibit higher GSI values compared to wild boars. Almeida et al. (2006) think this is caused by the selective reproductive process on farms, which leads to an increase of the effectiveness of Sertoli cells, or an increase in total testicular weight.

The weight threshold for sperm occurrence in the testes was 29 kg of live weight, which corresponds to 6 months of age. This observation does not match the findings of Mauget and Boissin (1987), who observed the presence of spermatozoa in the epididymides of boars from midwestern France, starting at 10 months of age, with a mean testicular weight of 53 g. However, our observation does correspond to the weight threshold for sperm occurrence (30–35 kg) observed by Mauget and Boissin (1987). The correlation coefficient between testicular and body weights was very high in comparison to other studies (Mauget and Boissin 1987: r = 0.67; Schinckel et al. 1983: r = 0.51–0.70; Murta et al. 2013: r = 0.90).

This study has proven that environmental conditions are a significant factor affecting the physical development of male wild boars, more specifically the growth rate of their body frames and the onset of sexual maturity. In an environment with sufficient food, rest, and shelter, boars grow faster and enter puberty at an earlier age. In environments with hunters and fewer resources, the boars are exposed to long-term stress, which leads to slower body and testicular growth, as well as the production of sperm at a later age (approx. 2–3 months later).

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