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Authors: Bergqvist, Göran, Paulson, Sam, and Elmhagen, Bodil

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Effects of female body mass and climate on reproduction in northern wild boar

Göran Bergqvist, Sam Paulson and Bodil Elmhagen

G. Bergqvist (goran.bergqvist@jagareforbundet.se), Swedish Association for Hunting and Wildlife Management, Öster Malma, SE-611 91 Nyköping, Sweden, and: Southern Swedish Forest Research Centre, Swedish Univ. of Agricultural Sciences, PO Box 49, SE-230 53 Alnarp, Sweden. – S. Paulson, Nyköping, Sweden. – B. Elmhagen, Dept of Zoology, Stockholm Univ., Stockholm, Sweden.

Mammalian life history strategies depend on climate conditions. Hence, reproductive parameters may vary regionally, and knowledge on such patterns are important for sustainable management. Wild boar research has been biased towards south and central Europe. Here we investigate the effects of mother´s carcass mass, season and climate (summer temperature and precipitation as well as January temperature) on pregnancy rate and litter size in 601 free-ranging female wild boar from hemiboreal Sweden, close to the north border of wild boar distribution range in Europe. Pregnancy rate was on average 33.4 ± 1.94% (mean ± SE), whereas average litter size of pregnant females was 4.7 ± 0.12. Pregnancy rate was highest during the seasonal reproduction peak in winter and spring, and both pregnancy rate and litter size increased significantly with increasing female body mass. The probability of a female being pregnant exceeded 50% when carcass mass exceeded 58 kg, equivalent to a live mass of 113 kg, and litter size increased by one for each 16 kg increase in female carcass mass. We found no significant effects of temporal variations in climate, and suggest that such variations were not sufficiently large to affect wild boar reproduction. Alternatively, the reproductive strategy of wild boar may be adjusted to prevailing regional climate conditions. In that case, other life history traits, such as mortality, may be more sensitive to short-term climate fluctuations. Wild boar management needs to take temporal variations in reproduction, as well as in resource availability, into consideration when deciding on prudent management actions.

From an environmental standpoint, mammalian reproduction is ultimately determined by climate, weather and food availability (Bronson 1985). Mammalian life history strategies consequently depend on climate conditions, and variations in reproductive traits are generally linked to seasonality. For example, litter size increases in seasonally cold or dry environments in carnivores and many even-toed ungulates (Tökölyi et al. 2014). At the population and individual level, plasticity in life history traits can result in trait changes across environmental gradients, as well as in response to climate change (Nussey et al. 2007). Hence, to achieve sustainable and adaptive management, it is important to gain knowledge on regional reproductive parameters, as well as their propensity to vary over time.

One species where such needs are evident is the wild boar *Sus scrofa*. Wild boar is a suid, and because the life histories of suids differ from other ungulates in many respects, Tökölyi et al. (2014) did not include suids in their study of general patterns in ungulate reproduction in relation to climate conditions. Furthermore, in relation to body mass, wild boar has the highest reproductive potential of all European ungulates (Fonseca et al. 2011). It can breed all year around, although most litters are born in late winter and spring (Frauendorf et al. 2016, Malmsten et al. 2017). The average litter size increases with increasing female body mass (Rosell et al. 2012, Vetter et al. 2016), at least up to a threshold value, after which it levels off (Gamelon et al. 2013). In recent decades, the species has increased greatly in distribution and population density in many parts of Europe, including regions where it may reach its northern distribution limit (Liberg et al. 2010, Massei et al. 2015). This expansion may continue as current harvest levels generally fall short of the species reproductive output (Keuling et al. 2013). Although considered a valuable game by many, wild boar are also controversial since the species preference for agricultural crops can result in considerable damage to farmlands (Schley and Roper 2003, Cai et al. 2008, Schley et al. 2008).

Wild boar litter size increases with latitude (Bywater et al. 2010). Temperature and precipitation may also affect the proportion of breeding females (Servanty et al. 2009), with drier and warmer summers resulting in decreased reproduction (Cellina 2008). To our knowledge, no studies have

explicitly studied effects of winter climate on the reproductive output, but population density have been reported to correlate positively with winter temperature (Melis et al. 2006, Oja et al. 2014, Vetter et al. 2015). The species show a high level of plasticity and are able to explore increased or pulsed resources efficiently (Schley and Roper 2003). For instance, a high production of mast boosts wild boar reproduction (Gethöffer et al. 2007, Holland et al. 2009). Change in the use of agricultural crops, for instance an increased production of maize *Zea mays* may also result in increased wild boar reproduction (Gethöffer et al. 2007, Rosell et al. 2012).

Although many studies have been conducted on the reproductive output of wild boar (Cellina 2008, Frauendorf et al. 2016), there is a research bias towards southern and central Europe. For example, a review comprising 29 studies on wild boar litter size in Europe did not include any site in Fennoscandia or Russia, i.e. close to the northern distribution limit of the species (Bywater et al. 2010). In these northern regions, cold temperatures may impose stronger constraints on the life-history of wild boar, but such limitations may be relaxed in the future. In response to future climate change, wild boar could be expected to advance its distribution further north and increase in abundance, a pattern that has been observed in other southern species over the latest century (Elmhagen et al. 2015). Thus, knowledge on the reproductive output, and subsequent population development, are important for efficient management of northern wild boar.

In this study, we collected data on pregnancy rates and litter size in free-ranging wild boar in an area in southeast Sweden, within the region most exposed to summer droughts in the country, and close to the species northern distribution range in Europe. Based on the literature, we predicted that body mass of the female affects pregnancy rate and litter size positively, and that both variables may vary seasonally. Furthermore, we predicted that January temperature, summer temperature and/or summer precipitation may affect the same reproduction parameters negatively, given that January was sufficiently cold in one or more years during the study period, or that summers were sufficiently hot and/or dry.

Material and methods

The survey was conducted in the hemiboreal forest zone (Ahti et al. 1968), within the county of Södermanland, Sweden (approximate lat. 58°N, long. 17°E; Supplementary material Appendix 1). The county covers approximately 6280 km^2 composed of 52% productive forestland and 24% arable land with the remaining 24% comprising lakes, unproductive land and infrastructure such as roads, towns and cities (Statistics Sweden 2018). Oak *Quercus robur* constitutes 1.0% of the standing volume of trees (The Swedish Forest Agency 2012). The most common agricultural crops are ley, wheat, barley and oats (Jordbruksverket 2012). Supplementary feeding of game species is common all year around.

The area has a coastline towards the Baltic Sea, and the maritime influence can have a cooling effect in summer and a warming effect in winter. The southeast part of Sweden, where the study area is located, is the region most exposed to summer droughts in the country (Geological survey of Sweden 2017). During the study period, the annual mean summer (June, July, August) temperatures varied between 15.9 and 18.2°C, annual total summer precipitation between 179.8 and 280.2 mm, and annual mean January temperatures between –5.1 and 1.7°C (Supplementary material Appendix 2).

There are no official records of game population sizes in Sweden and population trends are primarily monitored using harvest statistics. The free-ranging wild boar population in the county under study is one of the densest in Sweden with an estimated annual harvest of 1.0 to more than 1.5 wild boar km^{-2} (Kindberg et al. 2008).

Wild boar are subject to the most generous hunting season of all ungulates in Sweden and, when open, allows hunting 24 h a day. The open season for adult wild boar is between 16 April and 15 February, but females followed by depending (normally striped) piglets are always protected. The hunting of piglets and yearlings is open all year round. A variety of hunting methods are allowed, the use of dogs, however, is restricted to the autumn and winter period (Swedish Association for Hunting and Wildlife Management 2015).

The material analysed in the present paper is part of a larger study, conducted during February 2003 until June 2009, where local hunters voluntarily supplied data on hunting methods. For all animals, we recorded date of kill and carcass mass (i.e. without head, skin, lower legs, blood and viscera). In order to determine pregnancy rate and litter size, the uterus was cut open and checked for occurrence of fetuses visible to the naked eye in 610 female wild boar. Females harvested during all months of the year were included in the study, but sampling was biased towards autumn and winter, when dogs are used and the main harvest is conducted (Supplementary material Appendix 3). In addition, only yearlings were harvested during late February until mid-April, due to hunting regulations. For a total of 117 wild boar (55 male and 62 female), both live mass and carcass mass was recorded. Carcass mass was thus estimated at 51.4 ± 0.45% (mean ± SE) of live mass (Supplementary material Appendix 4).

Female wild boar need to reach a threshold of 27–33 kg live mass before breeding for the first time (Servanty et al. 2009), equivalent to a carcass mass of approximately 15 kg. We therefore limited our analysis to females with a carcass mass of 15 kg or more (n = 601). Based on harvest date, all females were grouped into seasons: winter (December, January, February), spring (March April, May), summer (June, July, August) and autumn (September, October, November). The use of season, rather than month, was to ensure a sufficient number of observations in each group.

In our analysis, we tested effects of female body mass and season, as well as temporal variations in mean January temperature (sensu Melis et al. 2006, Oja et al. 2014), mean summer temperature and total summer precipitation (sensu Cellina 2008), on wild boar pregnancy rate and litter size. Following the approach of Grosbois et al. (2008), we used generalized linear models (GLM) and analysis of deviance to determine which predictor variables that potentially could affect the response variable, with the effect of year taken into account, and consequently which covariates that should

Table 1. Analysis of deviance tables for the proportion of females with visible fetuses (n = 601) and average number of fetuses per pregnant female (n = 204). Covariates with R^2Dev-values of 0.20 or more included in the models.

Model	Deviance	Change in deviance	df	Pr(>χ)
Proportion of females with visible fetuses				
NULL	770.07		600	
Female carcass mass	748.64	21.435	599	<0.0001
Season	692.18	56.462	596	<0.0001
Summer temperature	691.16	1.018	595	0.3129
January temperature	690.52	0.633	594	0.4262
Average number of visible fetuses per pregnant female				
NULL	130.40		203	
Female carcass mass	106.98	23.412	202	<0.0001
Season	103.54	3.446	199	0.3278

be included in the final models. We first calculated R^2dev-values, i.e. the fraction of the temporal variation accounted for by each covariate, with year taken into account:

$$R^2\text{dev} = \left(\text{dev}\left(\text{mod.const}\right) - \text{dev}\left(\text{mod.cov}\right)\right) \Big/ \left(\text{dev}\left(\text{mod.const}\right) - \text{dev}\left(\text{mod.year}\right)\right)$$

where dev(mod.const) = residual deviance of a GLM with only intercept, dev(mod.year) = residual deviance of a GLM with only year (as factor) and dev(mod.cov) = residual deviance of a GLM with only the covariate in question (female carcass mass, season, mean January temperature, mean summer temperature or total summer precipitation). Covariates with R^2dev-values of at least 0.20 were included in the final models.

Factors affecting pregnancy rate, i.e. the occurrence of visible fetuses, were analysed using logistic regression (GLM with binomial family and logit link), and McFadden pseudo R^2 was calculated in order to test for goodness of fit. Factors affecting litter size, i.e. the number of visible fetuses in females where fetuses were found, were analysed using Poisson regression (GLM with Poisson family) and a deviance goodness of fit test was performed. All analyses were performed using R ver. 3.3 with the package popbio for creating probability functions from the logistic regression and the package pscl for calculating the McFadden pseudo R^2 (<www.r-project.org>).

Results

Out of the 601 females checked for pregnancy, 204 contained visible fetuses. The proportion of pregnant females varied between 25.7% and 42.7% per year (Supplementary material Appendix 5), and was on average 34.6 ± 2.18% (mean ± SE). Mean carcass mass of the 601 females was 33.3 ± 0.49 kg (median 30 kg, range 15–80 kg), equivalent to a live mass of approximately 65 kg. We recorded pregnant females in all months except August and September.

As predicted, pregnancy rate varied with female body mass and season, but in contrast to the hypothesis climate effects were not significant. Specifically, of the covariates under consideration, female carcass mass (R^2dev = 2.66), season (R^2dev = 6.61), summer temperature (R^2dev = 0.32) and January temperature (R^2dev = 0.51), but not summer precipitation (R^2dev = 0.08), were included in the final model for predicting pregnancy rate. According to a logistic regression, female carcass mass and season had a significant influence on pregnancy rate (Table 1, 2). The model correctly predicted 88.4% of the non-pregnant females but only 28.9% of the pregnant females. The probability of a female being pregnant exceeded 50% when carcass mass exceeded 58 kg, equivalent to a live mass of 113 kg, and the probability of being pregnant was significantly higher in winter and spring compared with summer and autumn, according to a Tukey post hoc test (Fig. 1). These results should be interpreted with some caution since the model showed signs of

Table 2. Estimates, standard errors and significance for models including covariates with R^2dev-values of 0.20 or more on the proportion of females with visible fetuses (n = 601) and average number of fetuses per pregnant female (n = 204).

Model	Estimate	Std. error	Z-value	Pr(>z)
Proportion of females with visible fetuses				
Intercept	–5.011	1.809	–2.770	0.0056
Female carcass mass	0.039	0.008	4.776	<0.0001
Season: spring	1.979	0.378	5.238	<0.0001
Season: summer	0.755	0.434	1.737	0.0823
Season: winter	1.896	0.353	5.373	<0.0001
Summer temperature	0.085	0.104	0.819	0.4130
January temperature	–0.031	0.039	–0.796	0.4262
Average number of visible fetuses per pregnant female				
Intercept	1.114	0.186	5.969	<0.0001
Female carcass mass	0.011	0.003	3.915	<0.0001
Season: spring	–0.034	0.156	–0.218	0.828
Season: summer	–0.054	0.186	–0.292	0.771
Season: winter	0.095	0.142	0.670	0.503

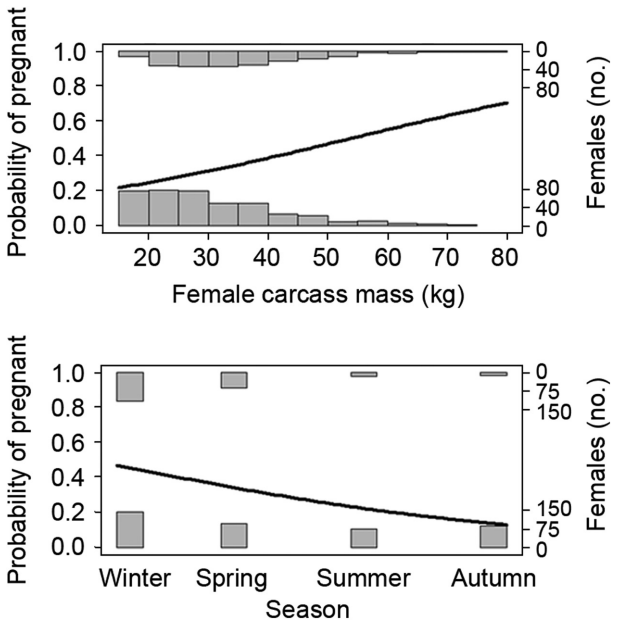

Figure 1. The probability of a female being pregnant (black line) depending on female carcass mass (upper graph) or season (lower graph). Probability values are shown on the left-hand y-axis. The grey, vertical bars show the number of females in each mass class or season in the sample, with pregnant females in the upper part of each graph and non-pregnant females in the lower part of each graph. The right-hand side y-axis show the number of females in each bar.

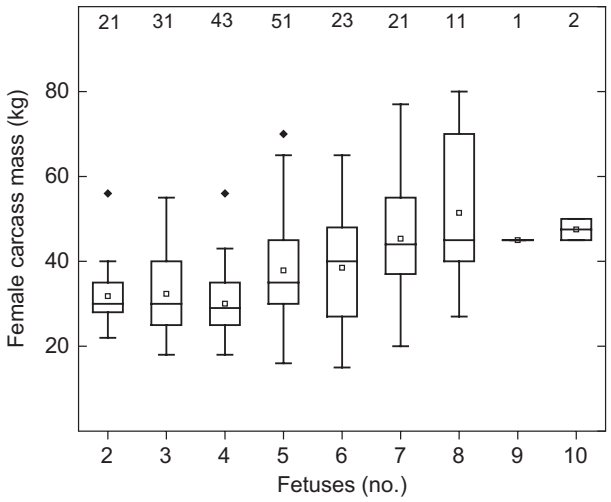

Figure. 2. Female carcass mass per litter size, with mean (small square within box), median (line within box), 25% and 75% interquartile range (box), observations up to 1.5 times the interquartile range (whiskers) and outliers (black squares outside whiskers). The number of samples per litter size is shown in the upper part of the graph.

over-dispersion (McFadden pseudo $R^2 = 0.103$). Given the data at hand, it was not possible to obtain a better fit.

In total, we recorded 964 fetuses, rendering an average of 4.7 ± 0.12 fetuses per pregnant female. During the study period, yearly mean litter size varied between 4.4 and 5.0 (Supplementary material Appendix 6). Ranging from two up to ten, the majority of females (61%) had between three and five fetuses (Fig. 2). Mean carcass mass of the 204 females with visible fetuses was 36.4 ± 0.86 kg (median 35 kg, range 15–80 kg), equivalent to a live mass of approximately 71 kg and, on average, the number of fetuses increased by one for every 16 kg increase in carcass mass of the mother (Supplementary material Appendix 7).

As predicted, litter size varied with female body mass. However, in contrast to our hypothesis, there was no significant effect of season or climate. Specifically, female carcass mass (R^2dev = 12.19) and season (R^2dev = 6.24), but not summer temperature (R^2dev = 0.00), January temperature (R^2dev = 0.00) or summer precipitation (R^2dev = 0.18) were included in the final model of litter size. However, only female carcass mass showed a significant influence on litter size (Table 1, 2). The model was highly significant and well fitted to the data (goodness of fit, $p > 0.05$).

Discussion

In this survey, comprising 601 free-ranging female wild boar harvested in an area in hemiboreal Sweden, we recorded a significant and positive effect of female body mass on both pregnancy rate (average 34.6%) and litter size (average 4.7), thereby largely confirming our first prediction. In contrast to the prediction, only pregnancy rate varied with season.

Wild boar is a short day breeder, and show a marked seasonality in reproduction (Malmsten and Dalin 2016). Our results confirm this pattern, with significantly higher pregnancy rates in winter and spring compared to summer and autumn. It should be noted that our sampling is biased towards autumn and winter when most wild boar are harvested (Supplementary material Appendix 3) and, furthermore, that only yearlings and piglets were harvested during late February to Mid-April, due to hunting restrictions.

Reports regarding pregnancy rates are highly variable in the literature and may depend on the size distribution of females included in different studies or the definitions of pregnancy used. For instance, Malmsten and Dalin (2016) reported that 16.6% of investigated females had attained puberty when based on presence of corpus luteum or previous signs of pregnancy in uterus, but 85.7% when based on presence of corpora luteum or ovarian follicles 4 mm or larger. Cellina (2008) reported that 18.1% of the sows in Luxembourg were gestating, whereas Fernández-Llario and Mateos-Quesada (1998) found that 31% of sows on the Iberian Penninsula were gestating or lactating. Other studies show considerably higher pregnancy rates, e.g. 43–100% in Germany (Gethöffer et al. 2007) and 52% in Spain (Rosell et al. 2012).

Increasing litter size with increasing female body mass has been reported by, for example, Nahlik and Sandor (2003), Rosell et al. (2012) and Malmsten et al. (2017). In Swedish hunting regulations, females followed by depending piglets are always protected. This may lead to an underestimation of the proportion of the largest females in the sample and, thus, an underestimation of actual mean litter size in the population (Spplementary material Appendix 8). On the other hand, we counted fetuses rather than piglets, something that may lead to an overestimation of the actual

reproductive output due to prenatal mortality, such as abortion or mummification of fetuses (Roić et al. 2005), or perinatal mortality (Fonseca et al. 2011). In a Swedish survey, embryonic or fetal mortality was found in 9% of the females (Malmsten et al. 2016).

We recorded no significant effects of climate (summer temperature, summer precipitation, January temperature) on pregnancy rate or litter size, hence our second prediction was not confirmed. One may expect such climate effects, for instance, following a dry and hot summer, as this may decrease wild boar reproduction (Cellina 2008, Servanty et al. 2009). During the study period, summer temperatures were very close to the 30-year normal value in the area (15.7°C), and summer precipitation was considerably higher than the 30-year normal value of 170.8 mm (Swedish Meteorological and Hydrological Institute 2013). Even though our study area is located within the part of Sweden most exposed to summer droughts it is not regarded as arid, and we suggest that the summer climate during the study period was never sufficiently hot and/or dry in order to affect wild boar reproduction.

Bywater et al. (2010) reported a strong positive correlation between average litter size and latitude in European wild boar, with litter size increasing by 0.15 per degree of latitude within the range 37–53°N. Accordingly, large litters are reported from, for example, Germany (mean 6.6; Frauendorf et al. 2016). The somewhat lower litter sizes recorded in Sweden may be an effect of a harsh winter climate at northern latitudes, since the population density of wild boar declines by three orders of magnitude within the latitude span 37–60°N (Melis et al. 2006). Although wild boar originally is a native species in Sweden, it was eradicated due to extensive hunting and assimilation into domestic pig populations (Jonsson 1986), likely in the first part of the 18th century. The present population originates from wild boar escaped from enclosures, and their genetic origin is largely unknown. Therefore, we do not know if wild boar in Sweden are optimally adapted to northern conditions. However, we could not confirm any effects of mean January temperature on reproduction, indicating that winters were not sufficiently harsh during the study period, and suggest that climate and/or resource conditions may act indirectly, via maternal body mass, on the litter size variation in wild boar (Frauendorf et al. 2016).

Based on 204 females with a carcass mass of 15–80 kg, equivalent to a live mass of approximately 30–155 kg, we recorded an average of 4.7 fetuses per female. Other studies in Sweden, counting both embryos and fetuses, reports litter sizes of 4.8 (13 females, 21–65 kg dressed mass; Malmsten and Dalin 2016) and 5.4 (101 females, >30 kg live mass; Malmsten et al. 2017). We suggest that differences in mean litter size reported in studies conducted under similar conditions (e.g. in adjacent areas and during the same years) are mainly a reflection of the mass distributions of the females included.

To conclude, we found a positive and significant effect of female carcass mass on both pregnancy rate and litter size in female wild boar harvested in an area close to the northern border of wild boars distribution range in Europe. Pregnancy rate showed a marked seasonality, which is expected for a short day breeder, whereas we recorded no significant effects of temporal variations in climate on pregnancy rate or litter size. We suggest that summers were never sufficiently hot and/or dry, or January never sufficiently cold, in order to affect wild boar reproduction. It is also possible that the reproductive strategy of wild boar is relatively fixed within populations, meaning that e.g. litter size is adjusted to the mean climate conditions that the population experience. If so, other life history traits such as mortality may be more sensitive to short-term fluctuations in climate.

Implications for management

As shown in this and other studies, the sex- and size-distribution of wild boar are important determinants of the reproductive output. Therefore, there is a need to monitor temporal variations in the composition of wild boar populations, together with data on available resources, in order to decide on prudent management actions. Information on additional life history parameters such as mortality, in relation to resource availability and climate conditions, are also needed. In Sweden, methods for systematic hunter observations of wild boar are presently being developed and may, if successful, generate valuable data for wild boar management in the future.

We suggest that further studies are conducted regarding the effects of sex- and age-distribution on population development in northern free-ranging wild boar populations, as well as the potential for different hunting strategies in order to manipulate population development and regulate population growth.

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Supplementary material (available online as Appendix wlb-00421 at <www.wildlifebiology.org/appendix/wlb-00421>). Appendix 1–8.