



Available online at:

<http://www.italian-journal-of-mammalogy.it/article/view/11324/pdf>

doi:10.4404/hystrix-26.2-11324

Research Article

Reproductive phenology and conception synchrony in a natural wild boar population

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Sus scrofa
reproduction
breeding synchrony
estrus
conception date
reproductive phenology

Article history:

Received: 25 May 2015

Accepted: 06 October 2015

Acknowledgements

We thank all those who contributed to the field and lab work, especially Nadia Cappai, Elisa Bertolotto, Emanuela Donaggio, and the collaborating teams of hunters. We are also grateful to C. Polli for linguistic revision. The research was financially supported by the Regional Administration of Tuscany, the Provincial Administration of Arezzo and the Italian Ministry of Education, University and Research (PRIN 2010–2011, 20108 TZKHC). AC had a PhD grant financed by the European Social Fund, Operational Programme 2007/2013 – Axis IV – Human Capital Investment.

Abstract

Reproductive synchrony among gregarious mammals has a strong adaptive value and may lead to cooperative behaviors aimed at maximizing offspring survival. Additionally, temporal clustering of estrus has important implications on individual mating tactics and ultimately affects the degree of polygamy in a population. Although several studies have examined the reproductive biology of wild boar (*Sus scrofa*), much remains to be understood about the patterns of timing and synchrony of reproduction in natural populations. We analyzed the spatiotemporal distribution of conception dates in an Italian wild boar population taking into account the effects of environmental and individual factors, in order to determine the main variables influencing the timing of reproduction and to detect the signs of a socially-driven reproductive synchrony. Specifically, for each litter belonging to 354 pregnant sows culled between 2006 and 2013 in a mountain area of Tuscany, we determined the conception date (CD) from an estimate of the mean fetal age and the culling date. We then investigated which factors drove the variation in CD, by implementing linear mixed models, Mantel tests and spatial autocorrelation analyses. The selected model showed significant effects of rainfall, temperatures, and previous and current productivity on CD, as well as a strong correlation of CDs among sows culled in close spatial and temporal proximity (i.e., in the same hunting ground and hunting season). Likewise, autocorrelation analyses and Mantel tests consistently indicated that custer sows had similar conception dates. Overall, our results confirm the effect of resource availability and climate on wild boar reproductive phenology, and suggest socially-driven reproductive patterns, in spite of a high turn-over in social groups due to hunting. Finally, possible advantages and evolutionary implications of reproductive synchrony in wild boar are discussed.

Introduction

Reproductive or breeding synchrony refers to the tendency of individuals to carry out some stages of the reproductive cycle (e.g., courtship, mating, birth) at the same time as other individuals of the population (Findlay and Cooke, 1982). Among gregarious mammals, breeding synchrony usually occurs by adjustment of the timing of estrus, but may also occur by gestation adjustment (Berger, 1992). Reproductive synchrony may have a strong adaptive value in that individuals capable of synchronizing their activities with neighboring conspecifics may have a number of selective advantages. For example, high density of newborns may lead to the satiation of predators (swamping), while decreasing the likelihood for a given newborn to be preyed upon (Plard et al., 2014). Moreover, breeding synchrony may account for an increased efficiency in food localization (Findlay and Cooke, 1982), a higher probability of detecting and repelling predators, and the possibility for the young to be communally nursed (e.g., adoptions, allosuckling etc.; Ims, 1990). Reproductive synchrony may have evolved as a mechanism to enforce monogamy in certain species. However, in systems in which males have the capability to monopolize spatially aggregated females, female reproductive synchrony can result in polygyny rather than monogamy (Ims, 1990).

On a population level, reproductive synchrony is especially common in seasonal environments, where individuals may select the same favorable time for reproduction in relation to climate and resource availability (Ims, 1990). Indeed, especially in these environments, repro-

ductive phenology of individuals is a key determinant of fitness, with the timing of reproduction affecting their reproductive output and future performance (e.g., lifetime reproductive success; English et al., 2012). In wild ungulate populations, inter-annual changes in resource availability (English et al., 2012), plant phenology (Post et al., 2003; Owen-Smith and Ogutu, 2013), and variations in rainfall (Moe et al., 2007; Ogutu et al., 2014; Plard et al., 2014) were shown to be associated with the timing and synchrony of births. Nevertheless, reproduction is often much more synchronous than expected if environmental seasonality alone were taken into consideration. Indeed, the temporal pattern of reproduction may also be shaped by many physiological, ecological and socio-biological processes (Ims, 1990). In fact, in several ungulate species, individual factors such as age, female condition and previous annual reproductive output were reported to affect spatiotemporal variation in ovulation and/or birth date (e.g., Garel et al., 2009; Plard et al., 2014). Moreover, exogenous factors such as hunting pressure and natural predation may play a role in determining spatiotemporal patterns in reproduction (e.g., Wissel and Brandl, 1988; Post et al., 2003). In some cases, the possibility that individuals have to adjust the timing of reproduction is constrained: in bighorn sheep (*Ovis canadensis*), for example, parturition date was reported to be partly heritable (Feder et al., 2008). However, the driving factor is often to be found in any biological interactions that may lead to tight clustering of reproductive events. This translates into reproductive synchrony on a social unit level. In several species of birds and mammals (including humans), social stimuli exchanged between neighboring females were found to induce reproductive synchrony (Ims, 1990; Mc Clintock, 1998). In particular, as for mammals, estrus synchrony can be achieved through

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the exchange of pheromones among females, or through the exposure to a male (Ims, 1990); indeed, the role of chemical signals was confirmed by experiments with hormone-like compounds (Thompson and Monfort, 1999; Jacob et al., 2004). Also spatial patterns of reproductive events can suggest that reproductive synchrony may be socially induced. For example, reproduction was shown to be more synchronized among neighboring individuals than among more distant ones in black-headed gull (*Larus ridibundus*) (Wissel and Brandl, 1988), wildebeest (*Connochaetes taurinus*) (Estes, 1976) and musk deer (*Moschus sifanicus*) (Meng et al., 2003). In red deer (*Cervus elaphus*), related females tend to group together, and this association was found to lead to synchronous estrus within kin groups (Iason and Guinness, 1985).

Despite many studies conducted in the past, much remains to be understood about the patterns of reproductive synchrony in several ungulates, including wild boar (*Sus scrofa*), a key species for wildlife management. Wild boar populations have been growing considerably over the past decades in both their native and introduced ranges (Massei et al., 2015), thus affecting both community structure and ecosystem function, but also impacting local economy, by causing extensive crop damages and vehicle collisions, and by transmitting diseases to livestock and wildlife (Schley et al., 2008; Apollonio et al., 2010; Barrios-Garcia and Ballari, 2012). Compared with other European ungulates, the wild boar is characterized by such peculiar life-history traits, as early onset of puberty (between 5 and 10 months of age; Fonseca et al., 2011), high fertility (with mean litter size ranging from 3.05 to 6.91 in different European populations; Bywater et al., 2010), and a relatively short gestation period (around 115–122 days; Henry, 1968; Vericad, 1983). Females have an estrus cycle of about 21–23 days, are receptive for 1–3 days (Henry, 1968), and generally produce one litter per year. Births have been reported from February to November, generally with a single peak in spring or late winter. However, a bimodal distribution was observed in some years (Markina et al., 2003; Maillard and Fournier, 2004), possibly due to resource availability and genetic introgression from the domestic pig. Habitat quality, climatic conditions, photoperiods, hunting pressure, amount of resources (particularly acorn and chestnut mast; Maillard and Fournier, 2004), and supplementary food were shown to affect many reproductive parameters in wild boar, including the timing and synchrony of births (e.g., Šprem et al., 2011). Servanty et al. (2009) demonstrated that the breeding probability and the onset of estrus in females respond to variations in female body mass at different ages under varying conditions of climate and resources availability. Furthermore, they showed that multiparous females can adjust the timing of their estrus, inducing a time delay in the reproduction, so that gestation may start in a different month every year.

However, little is known about sociobiological patterns of reproductive synchrony in wild boar. Their social organization is centered around philopatric adult females (Podgórski et al., 2014). Although the usual social unit is composed of a matrilineal group with one or more related adult females and one or more cohorts of offspring, deviations from this pattern were found (Iacolina, 2009). An outstanding contribution to the understanding of reproductive processes in wild boar was given by Meynhardt (1984), who made observations on mating habits and social behavior in several groups of free-living wild boar in Germany in the 1970s and 1980s. Meynhardt documented the existence of group-specific and highly repeatable (from year to year) dates of reproduction, and observed a very high within-group estrus synchrony, with the greatest intra-group difference in the date of estrus amounting to 8 days. Meynhardt also emphasized the key-role of the group leader sow: after her death, the group of females can experience a delay in reproduction and a loss of estrus synchrony. Furthermore, he observed no reproductive synchrony among different social units within a population, and no influence of mast production and group age structure on the timing of reproduction. Likewise, Dardaillon (1988) observed a good synchronization of births in wild boar groups in Camargue, and Delcroix et al. (1990) reported the occurrence of accurate within-group synchronization in reproductive processes in two groups of female wild boar kept in semi-natural conditions.

Nevertheless, given the number of factors which can affect ovulation time, as discussed above, and the possible variation of such factors in different ecological contexts, we expected population-specific deviations from the scenario described by Meynhardt (1984).

In the present study, we analyzed the spatiotemporal distribution of conception dates in an Italian wild boar population living in a less predictable environment in comparison to Central Europe, and exposed to a very high hunting pressure (with a substantial turnover in the social group composition, see Iacolina, 2009). In these conditions, within-group reproductive synchrony could be either reduced or not even observed.

We tested the occurrence of two alternative patterns of conception dates in the study population:

H0: Random distribution of conception dates (no reproductive synchrony is seen on a group level, and there is no influence of environmental factors);

H1: Conception dates respond to social and/or environmental factors, creating a spatial pattern in our study area.

The occurrence of similar conception dates on a local scale (patchy pattern) may indicate within-group estrus synchrony and/or the presence of local patterns in some environmental factors influencing the wild boar reproductive phenology. We accounted for the effects of environmental and individual factors, in order to detect the signs of reproductive synchrony with a possible sociobiological basis. According to the literature, we predict that higher age (Gethöffer et al., 2007), good body conditions (Servanty et al., 2009) and favorable environmental conditions (e.g., see Aumaitre et al., 1984 and Maillard and Fournier, 2004 for the effect of a greater food availability; see Plard et al., 2014 for the effect of rainfall) would anticipate the reproduction in the wild boar population.

Materials and methods

Data collection and reproductive tracts analysis

Data were gathered in an area of the Tuscan Apennines (Province of Arezzo, Central Italy), which extends over 134 km² and includes a protected area, the Oasi Alpe di Catenaiola (OAC, 28 km²). Elevation ranges from 330 to 1414 m a.s.l., with main peaks within the OAC. The study area is mainly covered with deciduous forests (67%), consisting of beech (*Fagus sylvatica*) at altitudes higher than 900 m, and Turkey oak (*Quercus cerris*) and chestnut (*Castanea sativa*) at lower altitudes. Conifer forests of black pine (*Pinus nigra*), silver fir (*Abies alba*) and Douglas-fir (*Pseudotsuga menziesii*) represent 7% of the area, while cultivated areas cover around 16%, and shrubs and pastures 7%. This area has a continental climate, with hot and dry summers, cold and rainy winters, high humidity rate and occasional snow from October to April above 100 m a.s.l.. Red fox (*Vulpes vulpes*) and wolf (*Canis lupus*) inhabit the study area, with the wild boar representing the most important prey for the latter (Bassi et al., 2012). Three hunting districts surround the OAC, subdivided into a total of 45 hunting grounds (Fig. 1) with a mean surface of 237 ± 145 ha, where the wild boar is regularly hunted from October to January by means of battues (i.e., dog drives), with 30–50 hunters and several hounds. Data from culled wild boar were gathered in 28 of these areas (with a minimum of 3 and a maximum of 41 observations in each area) during eight hunting seasons from 2006/2007 to 2013/2014.

The weight of each wild boar and the place and date of culling were recorded (when no precise location was available, the centroid of the hunting ground was used in the data analyses). All individuals were aged according to their tooth eruption and replacement pattern, as well as their tooth consumption (Briedermann, 1986), and assigned to one of the following age classes: juvenile (< 12 months), yearling (12–24 months), and adult (> 24 months).

The reproductive tracts (uteri and ovaries) of 2313 females were collected and examined in the laboratory. The uteri were dissected for examination and the fetuses in each uterus of pregnant females were counted, weighed, and sexed (when possible). The fetal age (FA, in day) was then estimated by using the Huggett and Widdas (1951) formula, which had already been applied to the wild boar by Vericad (1983). Vericad

measured the gestation length in a sample of captive sows and the birth weight of piglets, and used fetuses of known age to validate the equation:

$$FA = \frac{(\sqrt[3]{mW} + 2.3377)}{0.097}$$

with mW being the mean weight of fetuses in a litter. For each female with at least one weighed fetus, an estimate of the conception date (CD) was determined by using the date of culling and the mean estimated age of the litter obtained with the Vericad method. CD was then converted into a numeric variable, by setting, for each year, March 01 (year x)=0, and February 28 (year $x+1$)=364. Differences across years in the mean and distribution of CD were tested by Kruskal Wallis test in R.

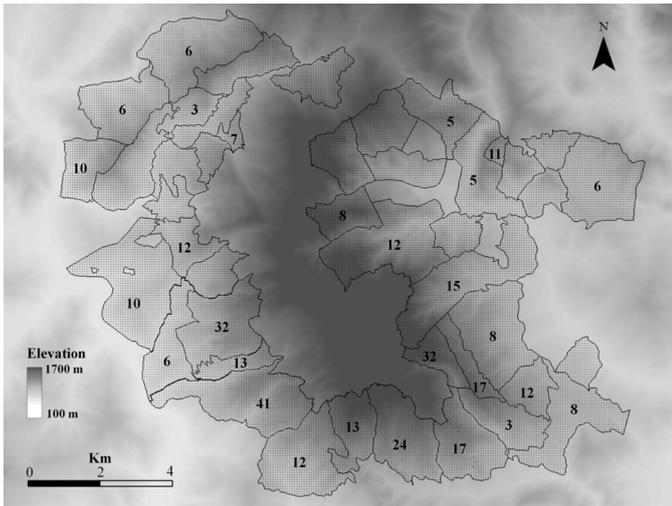


Figure 1 – Map showing the 45 hunting grounds (dotted) in the Italian Apennine study area and the distribution of the 354 culled sows used for the analyses. The protected area (Oasi Alpe di Catenaiia), with higher elevations, is located among the hunting grounds.

Linear mixed models

CD was used as response variable in linear mixed models fitted by using R version 2.15.3 (R Core Team, 2013), with the following environmental and individual factors as fixed effects:

- (i-ii) individual factors (i.e., varying on an individual level): (i) BODY MASS, the weight of each individual; (ii) AGE, the age class of each individual (either subadult or adult). We removed juveniles from the dataset, since only two juvenile females with measurable fetuses were collected;

- (iii-iv) variables measured on a hunting ground scale, representing environmental heterogeneity within the study area: (iii) HABITAT, a categorical variable with two levels, summarizing the environmental features of each hunting ground. It was obtained by calculating the relative abundance of eight habitat types (i.e., deciduous, conifer and mixed forests, shrubs, sparse vegetation, crops, meadows/pastures and urban areas) in each hunting ground using ArcGIS 10.1 (ESRI Inc., Redlands, CA, USA). A Hierarchical Cluster Analysis was then performed in R, and its consistency was ascertained by using the CIVALid package (Brock et al., 2008), comparing the results of different clustering methods (hierarchical, divisive hierarchical, k-means, and model-based clustering) and groupings (2-6 groups of areas), by using the internal validation measures. A Principal Component Analysis was then performed in R on the same data, to help interpret the clustering obtained (i.e., which habitat types drove the clustering); (iv) BCT COVER, the sum of the relative abundances of beech, chestnut and Turkey oak, calculated for each hunting ground;

- (v-x) variables measured on an annual basis, referred to the whole study area, representing annual variations in climate, population density and resource availability: (v-vi) SEED PROD and PREV.SEED PROD, representing the annual seed production of beech, chestnut and

Turkey oak in the study area in the current and the previous year, respectively. The data for seed production were available from three permanent plots of beech, chestnut and Turkey oak in the Alpe di Catenaiia study area, each 1 ha in size (data available from Consiglio per la Ricerca e la sperimentazione in Agricoltura, Forestry Research Centre - CRA-SEL - Arezzo; Tab. 1 in Cutini et al. 2013 lists the main stand characteristics of each plot). Estimates of the annual seed production were obtained by using the litterfall method, whose procedures, sampling strategy, reliability and accuracy are described by Chianucci and Cutini (2013); (vii): CULLED, for each year, the total number of boars culled in the three hunting districts, recorded and reported to the Fish and Wildlife Service of the Province of Arezzo, which checked and validated data. Assuming a constant effort over years, we considered hunting bag records as a proxy of wild boar population density (see Davis et al., 2012; Cutini et al., 2013 for further details on the relationship between annual census and hunting bag data); (viii-x): T.MAX, T.MIN, and RAINFALL, for each year, the average maximum temperature ($^{\circ}\text{C}$) during the hottest month, the average minimum temperature during the coldest month ($^{\circ}\text{C}$), and the total annual rainfall (mm), respectively. Values were obtained by averaging the data on temperatures and precipitations from four weather stations located in the study area (Ufficio Territoriale per la Biodiversità, Pieve S. Stefano, Province of Arezzo, official data).

Additionally, the variable HGROUND/YEAR was included as a random effect in all the models, representing groups of sows culled in the same hunting ground during a given hunting season, in order to evaluate specifically the correlation in conception dates among close animals. The hunting grounds were designed according to the landscape morphology, and their surfaces were relatively small and comparable to the size of the annual home range of a wild boar female group in the study area (Apollonio et al., 2007). Moreover, family groups are only weakly spatially affected by hunting disturbance (Keuling et al., 2008), and, therefore, two females culled in the same hunting ground within a tight time window are far more likely to belong to the same social group than two animals randomly selected from the database. Thus, we considered HGROUND/YEAR a rough proxy of social group. Hence, as in the case of other ecological studies focusing on heterogeneity, the random effect HGROUND/YEAR represented an actual variable of interest (see Bolker et al., 2009). Individuals with missing values in one or more variables were removed from the database, in order to have the same number of observations in all the models considered. All the quantitative variables were centered at their mean value. Four biologically meaningful interactions were also included in our full model (T.MAX \times RAINFALL; BODY MASS \times AGE; SEED PROD \times BCT COVER; PREV.SEED PROD \times BCT COVER).

We tested the inclusion of the random term HGROUND/YEAR in the model by performing a likelihood ratio test between two nested models via the anova command in R: we compared two full models (i.e., where the fixed component contained all explanatory variables and as many interactions as possible), with and without the random term, both fitted with restricted maximum likelihood estimation (REML), as suggested by Zuur et al. (2009). We found the optimal fixed component of the model by using the backwards selection approach illustrated in detail in Zuur et al. (2009). We started from the full model fitted by using maximum likelihood by dropping one variable at a time. We performed likelihood ratio tests between the full model and each nested model obtained in this way, each time removing the less significant variable (highest p -value) until all the variables were significant at the 5% level. The final model obtained was then refitted by using the REML estimation and validated by checking the assumptions of normality, homoscedasticity and independence, by inspecting the standardized residuals plots as described in Zuur et al. (2009). Then, we calculated the intraclass correlation coefficient ICC (which provides the measure of the correlation among the observations from the same year and the same area) as $d^2/(d^2 + \sigma^2)$, where d is the standard deviation of the random intercept, and σ is the residual standard deviation (Zuur et al., 2009). To quantify the goodness of fit of each model, we estimated R^2 following Magee (1990): $R^2 = 1 - \exp(-2/n(\log LM - \log L0))$, where n is

the number of observations, $\log LM$ is the standard log-likelihood of the model (which includes fixed and random effects) and $\log L0$ is the standard log-likelihood of the null model (containing intercept and random effects only). In presence of a patchy spatial pattern in conception dates, not exclusively due to environmental heterogeneity and at least partially caused by social interactions, we predicted the inclusion of the random term in the final model, and a high ICC (i.e., a large amount of variance explained by HGROUND/YEAR). On the contrary, in presence of a spatial pattern solely due to environmental heterogeneity in the study area, we predicted the inclusion of the variables iii and/or iv in the model, and a low effect of the random term HGROUND/YEAR. Neither the random term nor environmental factors are expected to be included in the selected model, if the distribution of conception dates were completely random in our study area (H0).

Mantel tests and spatial autocorrelation analysis

In addition, in order to reveal possible spatial patterns in reproduction, two dissimilarity matrices between individuals were constructed for each hunting season: a matrix of distance in conception date (REPR matrix), and a matrix of geographic distance (GEO). Then, the matrix correlation between REPR and GEO was calculated by the Mantel statistic r , as implemented in the R package Vegan (Oksanen et al., 2010), by using 999 permutations to test for significance. We expected non-significant Mantel tests in the presence of no spatial pattern, and significant tests in the presence of a patchy spatial pattern in conception dates on account of similar conception dates among neighboring individuals.

Furthermore, we calculated the autocorrelation in conception dates through space (over multiple distance classes) by performing a spatial autocorrelation analysis with GENALEX 6.41 (Peakall and Smouse, 2006) using the REPR and GEO matrices. Eight distance classes were considered, each being 1500 m wide, except for the first smaller one (500 m) meant to include only individuals culled closely to each other (and therefore more likely to belong to the same social unit), and the last wider one (5500 m) meant to include a sufficient number of observations (Tab. 3). A total of 999 permutations and 999 bootstraps were run so as to generate 95% confidence intervals around the null hypothesis (no autocorrelation) and around the estimated value (r), respectively. This analysis allowed to evaluate whether and how much the data correlation varied with distance. In the presence of a patchy pattern in conception dates, we expected strong autocorrelation mainly in the first distance class.

Results

Of the 2313 females examined, 742 (32.08%) were pregnant. Of these, 382 had at least one fetus weighed. The conception dates estimated had different mean, median and distribution among years, with some years showing a clear bimodal shape (Fig. 2). Mean and distribution of conception dates differed among years (K-W test: $\chi^2=117.39$, $df=7$, $p<0.001$), with means ranging between October 10 and November 19.

Of the aforementioned 382 females, 354 (194 adults and 160 subadults) were included in our models, having no missing data in any of the variables considered. The results of the analysis performed with CValid indicated that $K=2$ was the optimal number of clusters to summarize the environmental features of the hunting grounds, and the PCA allowed us to identify deciduous forests as the habitat type that drove the clustering. The likelihood ratio test between the full model with and without the random term was highly significant (CD, L-ratio 33.07, $p<0.001$). Therefore, the inclusion of HGROUND/YEAR in our models was strongly supported, thus indicating correlation in conception dates on a local scale. The final model selected (MS) included T.MAX, T.MIN, RAINFALL, SEED PROD, PREV. SEED PROD, and the interaction T.MAX×RAINFALL as fixed factors, thus confirming a significant environmental and climatic influence (on an annual basis) on wild boar conception dates, as it could have been hypothesized considering the noticeable fluctuations of CD among years (Fig. 2). This model was refitted with REML and found to meet the assumptions of normality, homoscedasticity and independence. The hypothesis of ran-

dom distribution of CD in our study area (H0), corresponding to the intercept-only model, was then rejected.

The summary of MS is reported in Tab. 1. The variance for the random intercept was 13.04 and the residual variance was 15.92, thus giving a relatively high intraclass correlation (ICC=0.402). In other words, 40.2% of CD variance was observed among groups, each composed by animals culled in the same hunting season and in the same hunting ground. The fixed part of the model accounted for 15.3% of variance ($R^2=0.153$). The slopes of all the predictors significantly differ from 0 at the 1% level, except for the slope of T.MIN, which was significant on the 5% level (Tab. 1). With all the other predictors at baseline (i.e., average values of rainfall, past and current productivity, temperatures), the estimated conception date was October 17 (corresponding to the intercept 230).

Table 1 – Summary of Linear Mixed Model MS, explaining the variability of conception dates estimated with the Vericad method in an Italian Apennine wild boar population. Proportion of explained variance (R^2), number of parameters, Intraclass Correlation Coefficient (ICC), residual standard deviation (RSD), standard deviation of the random intercept (RISD), parameter estimates with corresponding standard errors (SE) and t-test are reported.

n	Parameters	R^2		
354	9	0.153		
Fixed effects				
	Value	SE	t-value	p
(Intercept)	229.927	3.246	70.825	0.000
T.MAX	25.485	4.896	5.205	0.000
T.MIN	3.343	1.419	2.355	0.020
RAINFALL	-4.960	1.012	-4.903	0.000
SEED PROD	-72.596	12.912	-5.623	0.000
PREV.SEED PROD	59.463	10.109	5.882	0.000
RAINFALL×T.MAX	0.171	0.035	4.928	0.000
Random effects				
HGROUND/YEAR				
RSD	15.917			
RISD	13.041			
ICC	0.402			

The conception date was earlier in years with high productivity ($\beta=-72.60\pm 12.91$), and later with high values of both productivity in the previous year ($\beta=59.46\pm 10.11$) and high temperatures, (T.MAX and T.MIN, $\beta=25.49\pm 4.90$ and 3.34 ± 1.42 , respectively), with T.MAX seemingly having a greater effect than T.MIN. Conception dates were also anticipated in rainy years (RAINFALL, $\beta=-4.96\pm 1.01$), though

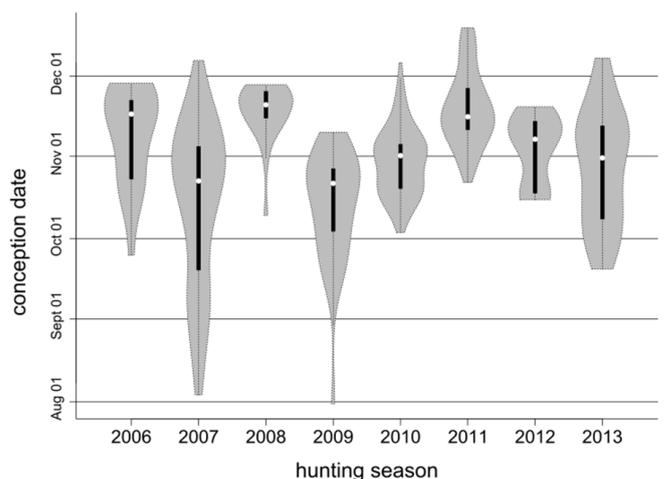


Figure 2 – Conception dates in a sample of 382 litters belonging to wild boar females culled during eight hunting seasons in an Italian Apennine population. The violin plots show median (white point), quartiles and distribution of conception dates estimated with the Vericad method, for each year.

this effect was reduced in case of hot summers ($T_{MAX} \times RAINFALL$, $\beta=0.17 \pm 0.03$).

The results of Mantel tests (Tab. 2) indicated a weak though significant correlation between the dissimilarity matrices of conception date (REPR) and geographic location (GEO) in six out of eight years. Significant r ranged between 0.095 and 0.221. Hypothesizing intra-group reproductive synchrony, we did not expect very high r values, since even though close animals are assumed to have similar conception dates, distant groups do not necessarily have different CD (indeed, the group effect is assumed to be random and normally distributed around 0). Only in 2006 and 2012 no significant correlation was found, but these were also the years with the lowest number of observations.

Table 2 – Correlation between geographic distance and distance in conception dates in female wild boar of the Italian Apennine study population. For each year, number of individuals (n), Mantel's correlation (r) and its p -value are reported. Significant tests are shown in bold.

YEAR	n	r	p
2006	25	0.075	0.142
2007	79	0.113	0.008
2008	29	0.197	0.033
2009	41	0.212	0.015
2010	65	0.221	0.002
2011	58	0.120	0.012
2012	22	0.056	0.150
2013	63	0.095	0.020

Moreover, significant spatial autocorrelation of conception dates occurred in the first distance class (0–500 m, Tab. 3) in seven out of eight years (highly significant in six cases), with relatively high r (significant r between 0.089 and 0.524, with mean across all years equal to 0.271). This indicated that the timing of reproduction was similar in sows sampled in the same area and in the same year (rejection of H_0), possibly suggesting within-group synchronization, in agreement with the model results. Significant autocorrelation was also found in four out of eight years in the second and third distance classes, but generally with lower r .

Discussion

Conception dates had high within-year variance (with a maximum in 2007, Fig. 2), possibly due to the high ecological plasticity of the species and to the favorable climatic and environmental conditions in the study area which enable different groups/individuals to adopt different strategies (e.g., to delay the reproduction). The bimodal distribution of births in some years and their peak in late winter-spring previously reported for other regions (Markina et al., 2003; Maillard and Fournier, 2004) match what we observed in our study population. However, it should be remarked that the conception dates we obtained did not give us a comprehensive picture of the wild boar reproductive phenology through the year, because the sampling was only carried out between October and January, and the gestation period lasts around 120 days in *S. scrofa*.

Mean and distribution of CD varied significantly across years. This result was somewhat unexpected, given that conception dates in wild boar social units were reported to be highly repeatable from year to year (Meynhardt, 1984). The strong hunting pressure in the study area and the resulting high turnover in social units may represent one of the possible explanations for our findings. We may speculate that a significant number of leader sows (whose role in determining the group-specific date of reproduction is crucial, Meynhardt, 1984) was culled each year in the study area.

Actually, as highlighted by our model, the main causes of CD variation among years are to be found in inter-annual variation in productivity, rainfall, and temperatures. High seed production and rainfall can create favorable conditions for the wild boar. Our model predicted that, in these conditions, sows tended to anticipate the conception date, possibly to ensure that their offspring could take full advantage of resource

abundance and grow fastly prior to the onset of the harsh season. Conversely, warmer years (i.e., with higher maximum temperatures during the hottest month, or higher minimum temperatures during the coldest month) may correspond to unfavorable conditions (e.g., drought) and turned out to be associated with a delay in the timing of reproduction. Our model is consistent with Aumaitre et al. (1984), who reported that in exceptionally good years the wild boar birth peak can occur up to two months earlier than usual. Moreover, Servanty et al. (2009) highlighted the effect of resource availability on the wild boar reproductive phenology. Our results are also consistent with Plard et al. (2014), who showed that rainfall is often associated with anticipated parturition date in other ungulate species, and Ogotu et al. (2014), who reported that dry conditions may lead to delayed births in African ungulates. However, our findings are inconsistent with Fernández-Llario and Mateos-Quesada (2005), who showed that dry summers and autumns are associated with an early period of conception in a Spanish wild boar population, and with Meynhardt (1984), who suggested no influence of mast production on the timing of reproduction. Since the sensitivity to certain environmental conditions can have a genetic basis, different population histories leading to different genetic make-up of populations may therefore imply local differences in behavioral or physiological responses to similar environmental stimuli. Our model also showed that high values of productivity in the previous year delayed the mean conception date. This can be related to an increase in the time required for the recovery of body condition, following a great maternal investment in the previous year (see Servanty et al., 2009). Previous works (e.g., Feder et al., 2008; Servanty et al., 2009) provided evidence for the effects of body condition and age on parturition date in wild boar and other ungulates. Interestingly, neither individual variables (AGE and BODY MASS) nor habitat differences in our study area (BCT COVER and HABITAT) were found to explain a significant amount of variance in conception dates.

Overall, our results indicated the occurrence of a patchy spatial pattern in the wild boar reproductive phenology across the study area, a case falling in our hypothesis H1. On a local scale, closer sows showed similar conception dates. Indeed, for six out of eight years, the Mantel tests revealed weak to moderate (significant) spatial autocorrelation for the conception dates estimated. This spatial relationship was not statistically significant in the two years with the lowest n, possibly due to the sampling of a low proportion of females belonging to the same social group. The patchy pattern was confirmed by the results of the spatial autocorrelation analysis: females sampled at 0–500 m from each other had correlated conception dates (Tab. 3).

Accordingly, the linear mixed model results highlighted the primary importance of HGROUND/YEAR in explaining the conception date variance. Considering that the effect of individual and environmental factors was accounted for in our analysis, the high correlation (40%) in conception dates among sows culled in the same year and in the same area may indicate intra-social group reproductive synchrony, as observed by Meynhardt (1984) in Germany, and suggested by Mauget (1980) and Briedermann (1986). These findings are also consistent with the study of Delcroix et al. (1990), who observed estrus synchrony in wild boar in captivity.

Spatial patterns of reproductive synchrony have been shown for many mammal species and argued to be a consequence of socio-sexual interactions. For instance, Mc Clintock (1971) pointed out the role of pheromones in inducing estrus synchrony in humans. The stimuli involved seemed to have mainly an olfactory nature, often originating from the male. For example, Whitten (1956) observed that the presence of a male caused a synchronization of estrus in mice (*Mus musculus*), and this was also demonstrated in sheep (*Ovis aries*) and goats (*Capra hircus*) (Underwood et al., 1944; Shelton, 1960). On the contrary, the synchronization appeared to be caused by interactions between females in red and musk deer (Iason and Guinness, 1985; Meng et al., 2003), as well as in captive wild boar (Delcroix et al., 1990). Similarly, in American bison (*Bison bison*), unmated females were observed to use olfactory cues to explore the status of other females prior to their own estrus, but not afterwards (Berger, 1992).

Table 3 – Results of spatial autocorrelation analysis of conception dates of wild boar litters in the Italian Apennine study population. The number of pairs, autocorrelation coefficient *r* and its significance for each year and distance class (the end point, in km, is shown in the first row) are reported. Highly significant values (*p*<0.01) are shown in bold.

		0.5	2	3.5	5	6.5	8	9.5	15
2006	n	26	28	53	33	28	46	19	67
	<i>r</i>	0.524	0.270	-0.053	-0.106	0.140	0.022	0.147	-0.319
	<i>p</i>	0.001	0.007	0.785	0.872	0.082	0.389	0.106	0.999
2007	n	125	299	392	404	592	577	382	310
	<i>r</i>	0.291	0.013	0.053	-0.021	0.038	-0.040	-0.115	0.036
	<i>p</i>	0.001	0.316	0.041	0.795	0.025	0.960	1.000	0.094
2008	n	54	16	31	129	25	47	54	50
	<i>r</i>	0.384	0.300	0.003	-0.306	0.162	0.091	0.169	-0.179
	<i>p</i>	0.001	0.005	0.525	1.000	0.027	0.058	0.006	0.987
2009	n	39	123	130	115	203	100	76	75
	<i>r</i>	0.048	-0.009	0.124	-0.050	-0.027	-0.053	0.019	-0.029
	<i>p</i>	0.258	0.577	0.008	0.882	0.827	0.862	0.362	0.731
2010	n	131	165	402	328	363	339	203	149
	<i>r</i>	0.089	-0.017	0.072	-0.047	0.007	-0.016	-0.018	-0.060
	<i>p</i>	0.042	0.708	0.005	0.952	0.377	0.761	0.721	0.946
2011	n	86	109	154	195	362	211	259	277
	<i>r</i>	0.209	0.145	0.139	-0.023	-0.091	-0.013	0.007	-0.041
	<i>p</i>	0.006	0.013	0.002	0.777	0.998	0.665	0.406	0.932
2012	n	29	21	25	28	41	19	24	44
	<i>r</i>	0.457	-0.127	-0.297	0.194	-0.434	0.418	-0.428	0.305
	<i>p</i>	0.007	0.843	0.982	0.038	1.000	0.004	0.995	0.001
2013	n	137	205	256	156	364	239	159	437
	<i>r</i>	0.169	0.080	0.037	-0.033	0.009	-0.007	0.093	-0.140
	<i>p</i>	0.005	0.032	0.100	0.817	0.402	0.616	0.017	1.000

Reproductive synchrony in wild boar on the social group level is highly adaptive, in that it offers a number of possible advantages:

(i) piglets can be communally nursed. Both adoptions and allosuckling (i.e., suckling from a female other than the mother) are known to be extremely common in wild boar (Delcroix et al., 1985; Meynhardt, 1987). Allosuckling was observed in other ungulates (e.g., fallow deer *Dama dama*, Ekvall, 1998; red deer, Landete-Castillejos et al., 2000; reindeer *Rangifer tarandus*, Engelhardt et al., 2014), and found to be a means for pups to broaden their passive access to antibodies after birth (Garnier et al., 2013), but is rarely adopted as a group strategy. This is not the case of wild boar, among which allosuckling is widespread and lactation (occurring approximately at hourly intervals) can be synchronized within a group (Massei and Genov, 2000). This behavior can foster a better development of the piglets through an optimal feeding and may significantly increase their survival. This is especially advantageous in Southern Europe, where summer is the limiting season and summer drought can cause substantial losses among piglets (Fernández-Llario and Mateos-Quesada, 2005).

(ii) Synchronous births enhance the mobility potential of a given social unit by reducing the time span during which the group movements are constrained by the presence of small piglets. Indeed, it was shown that the female daily home range in the weeks immediately prior and following the birth is drastically reduced in wild boar (from 40-80 ha to 1-3 ha according to Janeau and Spitz, 1984). A similar reduction in female home range was observed in many ungulates (*Odocoileus virginianus* Schwede et al., 1993; *Dama dama* Ciuti et al., 2006; *Capra ibex* Grignolio et al., 2007; *Capreolus capreolus* Bongi et al., 2008) where it is often related to a hider strategy.

(iii) synchronized births may contribute to a collective and consequently more efficient defense of the young against such predators as the wolf and the red fox, that are common in the study area and in most of the European range of wild boar; furthermore, a stronger dilution effect reduces the individual probability of piglets to be killed by a predator. Both communal defense and dilution effect are well-known anti-predatory strategies adopted by ungulates (Jarman, 1974). Piglets are quite vulnerable to predation if not properly assisted by sows; in the study area, they frequently occur in the diet of both wolves and foxes (Bassi et al., 2012). Conversely, a group of sows is able to successfully

cope with predators, thus reducing predation upon piglets. In this regard, even such effective predators as the wolf were seen to be chased by wild boar groups (pers. obs.). Predator harassment can be an effective anti-predator strategy (Mukherjee and Heithaus, 2013), and was observed in some ungulate species (Jarman, 1974; Berger, 1979; Carbyn and Trotter, 1987; Berger and Cunningham, 1995; Prins, 1996). Indeed, adult wild boar weighting more than twice their predator and having sharp canine teeth are very likely to exploit this option.

Moreover, reproductive synchrony may also have evolved to favor polygamy (Ims, 1990) and this can, in turn, influence genetic variation and quality of newborns. Prior to the rutting period (falling mainly in late autumn and early winter), adult male wild boars get restless and increase their marking behavior and fights with other males. In the rutting period, photoperiodism and possibly other environmental factors trigger the seasonal increase in the endocrine activity of testes (Šprem et al., 2011). Males travel long distances in search of a group of sows, fighting against potential rivals and persistently chasing the sows (Dardaillon, 1988; Massei and Genov, 2000). Once joined a female group, a male is able to maintain a monopoly over the aggregated females (though this does not seem to be the rule for all populations, see Poteaux et al., 2009), until the arrival of a stronger male, or until he has mated with all the females (Massei and Genov, 2000). In the presence of high estrus synchrony within a social group, the probability of the latter occurrence increases. Furthermore, since the time spent with a single group is reduced, a male can maximize the number of groups visited, thus increasing the number of matings. As a consequence, high reproductive synchrony can increase the fitness of dominant males and promote the dissemination of their genes across a wider area. Actually, after mating with all the synchronized females, a boar may spend additional time with the group, trying to prevent other males from gaining access to still receptive females (post-copulatory mate guarding), as argued by Delgado et al. (2008), or it may decide to leave and approach another female group. In the latter case, other (subordinate) males may have the opportunity to mate with groups of still receptive unguarded females. In this scenario, multiple mating by females (i.e., polyandry) may be promoted, inducing a post-copulatory competition among mating boars, in which the fertilization success of a given male depends on the relative amount/quality of semen it can ejaculate (i.e.,

sperm competition; Aguilera-Reyes et al., 2006). By this way, high estrus synchrony would promote sperm competition and possible multiple paternity within litters. Multiple paternity was observed by Delgado et al. (2008) and Poteaux et al. (2009) in Portuguese and French wild boar, respectively, and had been previously documented in feral pig populations in Australia (Spencer et al., 2005). Preliminary data revealed its occurrence also in our study area (Iacolina, 2009). Interestingly, Aguilera-Reyes et al. (2006) showed that, in domestic pigs, the sow can influence the possibilities of success of the ejaculations from different males, slanting the paternity towards the male with the higher genetic variability (strategy known as “cryptic choice”). Both single paternity by a dominant male and multiple paternity may have genetic advantages for females, by leading to a possible inheritance of “good genes” by the litter in the former case and increasing the genetic diversity among sibs in the latter. In highly unpredictable environments, the second strategy may be adaptive, as it improves the chance to have a successful progeny.

Finally, the possible effect of kinship on estrus synchrony in sows remains unknown. In red deer, female relatives associate together, and this association leads to synchronous estrus within kin groups which is not due to kinship per se (Iason and Guinness, 1985). Conversely, kinship may influence reproductive patterns in bighorn sheep, in which the parturition date was shown to be partly heritable (Feder et al. (2008)). If the timing and synchrony of reproduction have, at least partially, a genetic basis, even the introgression from the domestic pig into the wild boar gene pool may lead to altered reproductive patterns. Wild boar can crossbreed with domestic pigs both in natural conditions (where open-air pig farming is still practiced) and in captivity (see Canu et al., 2014). In fact, genetic introgression from domestic pigs into wild boar populations was detected by various authors (e.g., Koutsogiannouli et al., 2010; Scandura et al., 2011; Frantz et al., 2013; Goedbloed et al., 2013) and was suggested to have important ecological consequences, by altering such traits as behavior and reproductive performances (Goedbloed et al., 2013). Further genetic studies together with reproductive data are recommended to investigate the possible heritability of such life history traits as timing and synchrony of reproduction in wild boar, also considering their impact on the species’ demography and its management. ☞

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Associate Editor: L.A. Wauters