Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure

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Summary

1. Identifying which factors influence age and size at maturity is crucial for a better understanding of the evolution of life-history strategies. In particular, populations intensively harvested, hunted or fished by humans often respond by displaying earlier age and decreased size at first reproduction.

2. Among ungulates wild boar (*Sus scrofa scrofa* L.) exhibit uncommon life-history traits, such as high fertility and early reproduction, which might increase the demographic impact of varying age at first reproduction. We analysed variation in female reproductive output from a 22-year long study of an intensively hunted population. We assessed how the breeding probability and the onset of oestrus responded to changes of female body mass at different ages under varying conditions of climate and food availability.

3. Wild boar females had to reach a threshold body mass (27–33 kg) before breeding for the first time. This threshold mass was relatively low (33–41% of adult body mass) compared to that reported in most other ungulates (about 80%).

4. Proportions of females breeding peaked when rainfall and temperature were low in spring and high in summer. Climatic conditions might act through the nutritional condition of females. The onset of oestrus varied a lot in relation to resources available at both current and previous years. Between none and up to 90% of females were in oestrus in November depending on the year.

5. Past and current resources accounted for equivalent amount of observed variations in proportions of females breeding. Thus, wild boar rank at an intermediate position along the capital–income continuum rather than close to the capital end where similar-sized ungulates rank.

6. Juvenile females made a major contribution to the yearly reproductive output. Comparisons among wild boar populations facing contrasted hunting pressures indicate that a high demographic contribution of juveniles is a likely consequence of a high hunting pressure rather than a species-specific life-history pattern characterizing wild boar.

Key-words: capital–income continuum, life-history tactic, proportion of females breeding, *Sus scrofa*, ungulate

Introduction

Age and size at maturity are key life-history traits (Cole 1954; Schaffer 1974), that shape observed demographic tactics of vertebrate populations (Gaillard *et al.* 1989) through their influence on survival, reproduction and growth, as well as on offspring survival (Stearns 1992). In this context, factors influencing those life-history traits are expected to cause differences in individual fitness, and should thereby lead population abundance to fluctuate over time and evolutionary changes to occur (Lande 1982). More recently, an increasing number of studies have revealed that human activities impact the evolutionary changes observed in wildlife populations

(Palumbi 2001), and lead to influence markedly life-history traits, such as body mass and reproductive traits (e.g. de Roos, Boukal & Persson 2006; Proaktor, Coulson & Milner-Gulland 2007). This is especially the case in populations intensively exploited (i.e. fishery, hunting; see Milner, Nilsen & Andreassen 2007; Allendorf *et al.* 2008; Fenberg & Roy 2008; Darimont *et al.* 2009 for recent reviews). Hence, identifying the factors influencing age at first reproduction and reproductive output is crucial to understand the dynamics and evolution of populations under strong human influences.

In mammals, the age at maturity and to some extent the fecundity is condition dependent and females have to reach a threshold body mass above which they are able to breed (see Gaillard *et al.* 2000 for a review). Climatic conditions, habitat quality and population density generally drive variation in female performance, through their impact on food resources (Langvatn *et al.* 2004). According to differences in the origin of the energy allocated to reproduction, species have been ranked along a capital–income breeder continuum. At one end, capital breeders only used body reserves stored prior to the reproductive period, whereas at the other end income breeders only rely on the short-term acquisition of resources during the reproductive period (Drent & Daan 1980; Jönsson 1997). Most mammals use both body reserves and current resources to face with the energetic requirements of late gestation and early lactation, the most costly stages of reproduction in mammals (Oftedal 1985), but the relative proportion coming from body reserves varies a lot. In most large temperate ungulates, females mainly rely on reserves accumulated during the previous summer-fall to cover the relatively low energy expenditures they allocate to reproduction (Festa-Bianchet, Gaillard & Jorgenson 1998). With similar size (and thereby similar capacity of storing body reserves, e.g. Demment & Van Soest 1985) but higher reproductive effort, wild boar are expected to be more dependent on current resources than other ungulates and to rank closer to the income breeder end of the continuum.

We aimed to analyse variation in age at first reproduction in an intensively hunted wild boar (*Sus scrofa scrofa* L.) population, in which an individual has more than half a chance to be shot within a given hunting season (Toïgo *et al.* 2008). Wild boar in this population therefore had a short generation time. Variation in age at first reproduction is expected to be more influential on growth of a population with a short than with a long generation time (Gaillard *et al.* 2005). Moreover, among ungulates, wild boar are characterized by some peculiar life-history traits that might increase the demographic impact of variation in age at first reproduction. First of all, female wild boar can give birth for the first time at a younger age (1 year of age, Mauget 1982) than other similar-sized ungulates (2 or 3 years of age, Hayssen, Van Tienhoven & Van Tienhoven 1993). They also have a high fertility, with a mean litter size as high as five (e.g. Servanty *et al.* 2007), whereas most other similar-sized ungulates produce singletons (Hayssen *et al.* 1993). Finally, previous studies have shown that the onset of sexual maturity in wild boar females strongly depends on resource availability (e.g. Pépin & Mauget 1989),

and have highlighted the importance of acorn mast. Tree mast is a typical pulsed resource (e.g. Ostfeld & Keesing 2000), which fluctuates from year to year, and may then induce large variation in female reproduction and thereby in population growth rate [see Perrins 1979 in tits (*Parus* spp.), Hannon *et al.* 1987 in woodpecker (*Melanerpes formicivorus* Swainson 1827); Ostfeld, Jones & Wolff 1996 in the white-footed mice (*Peromyscus leucopus* Rafinesque 1818); Newton 1998 for a review in birds, Shimada & Saitoh 2006 for a recent review in rodents]. In this study, we aimed to identify the factors shaping yearly and age-specific variation in the timing of oestrus and in the proportion of females breeding at a given date. Our study encompassed a period of wide variation among years in temperatures, precipitations and tree-mast production. We tested the relative influence of phenotypic attributes (age and body mass) and environmental factors (winter resources, climatic factors known to influence plant phenology in spring and summer) on the proportions of females that were in oestrus at a given date (called proportion of females breeding thereafter). As we expected age-specific responses of reproductive traits to environmental variation (Gaillard, Festa-Bianchet & Yoccoz 1998), we measured the age-specific proportion of females breeding.

We tested the following three hypotheses: (H1) based on the relatively early age at first reproduction of wild boar and on the short generation time of this intensively hunted population, we expected that the threshold body mass to breed for the first time should be less than 80% of the asymptotic adult mass, the value generally observed in ungulates (Gaillard *et al.* 2000), (H2) for a given age class, we expected higher proportions of breeding in heavy than in light females. The proportions of females breeding should also increase throughout the hunting season because an increasing proportion of females enter in oestrus throughout the winter (Mauget 1982), and (H3) we expected increased availability of resources to influence positively proportions of females breeding. Moreover, as current reproduction is costly in terms of energy, and may involve costs in terms of future reproduction and body mass, we expected the availability of resources both in the current and previous year to be related to the proportions of females breeding a given year. Wild boar should thus have a more intermediate position on the capital–income breeder continuum than similar-sized ungulates that are closer to the capital end.

Materials and methods

STUDY AREA AND HUNTING PROCEDURE

The study was conducted in the 11 000 ha Châteauvillain-Arc en Barrois forest (Haute-Marne), in the north-eastern part of France (48°02′ N; 4°55′ E). In this area, the climate is intermediate between continental and oceanic. During the last 20 years, the mean annual rainfall was 890 mm and the mean monthly temperature has ranged from 2 °C in January to 18·5 °C in August (Météo France). This forest is mainly composed of oak (*Quercus petraea* Liebl. 1784, 41%) and beech (*Fagus sylvatica* L., 30%). The forest clump is administratively divided into two parts: (i) the 8500 ha core, which is managed
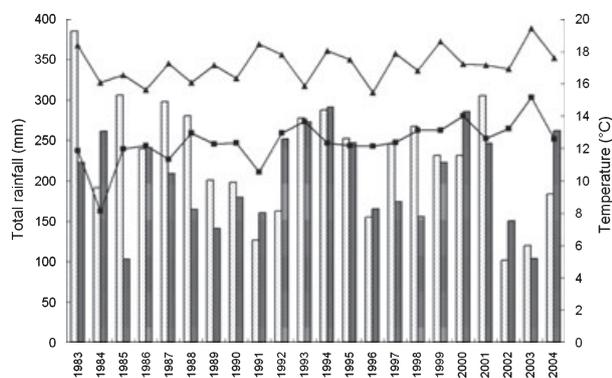
Fig. 1. Climatic conditions during spring and summer since 1983. Spring rainfall (punctuated bars), summer rainfall (shaded bars), spring temperature (squares) and summer temperature (triangles) are displayed.

by The Office National des Forêts (ONF; National Forestry Department), and is divided by forest trails into plots of about 15 ha and (ii) the 2500 ha periphery, which only includes private or communal areas. The study area is surrounded by a cultivated plain and bordered by a highway at the north-east, limiting exchanges with other wild boar populations.

Three ungulate species are present in the forest (i.e. wild boar, red deer *Cervus elaphus* L. and roe deer *Capreolus capreolus* L.). The wild boar has no natural predator when adults but is intensively hunted every year since 1976. Depending on the year, the hunting season begins between mid-October and the first week-end of November in the forest part managed by the ONF. The hunting season ended late January until 2000, but, thereafter ended 1 month later. Intense drives are organized each week-end within the hunting season in the forest part managed by the ONF. Hunters are posted around a hunted area (a patch of 250–500 ha) and are waiting for wild boars startled by beaters and flushing dogs. The number of hunted wild boar consistently increased between 1986 and 1996 (from 165 to 1261), and remained high since then (see Fig. 1 in Toïgo *et al.* 2008).

During 3 weeks in June and July, supplementary feeding (in most cases, maize *Zea mays* L.) is used as a dissuasive tool in the forest part managed by ONF to reduce wild boar damage to agricultural crops (Vassant 1997). The amount of food supplied varies between 0·06 and 0·12 kg per ha per feeding day. Similarly, maize is provided every second or third day from October to April (only in years with no mast production) to prevent damage to the surrounding fields and/or meadows.

DATA COLLECTION

In the part of the forest managed by the ONF, the mass, the ovaries and the reproductive tract of each hunted female were collected from 1983 to 2005. As hunting drives performed during a given year cover the whole forest, the reproductive tracts we analysed accurately reflect female reproduction at the population level. Dressed body mass (± 1 kg) was measured after the animal had been eviscerated (i.e. without the digestive system, heart, lungs, liver, reproductive tract and blood). Dressed body mass corresponds to about 80% of total live body mass (Gaillard, Brandt & Jullien 1993) and was then used as a measure of the maternal body condition.

In a seasonal breeder like wild boar the reproductive status can be assessed by examining the reproductive tracts and the ovaries (e.g.

Abaigar 1992). Rut generally begins in mid-December, but can occur earlier in acorn-mast years (e.g. Matschke 1964). Sagitally cut ovaries were examined to observe (i) the presence of Graafian follicle, which indicated that females were in oestrus and/or (ii) the presence of *corpora lutea*, which indicated a recent ovulation (Fernández-Llario *et al.* 2004). Finally, the presence of embryos or foetuses in the reproductive tract clearly indicated that females were pregnant. The reproductive status of each female was then classified into two categories: reproductive (either in oestrus, having ovulated or pregnant) vs. nonreproductive (no oestrus, no ovulation and no foetus).

Age was estimated according to tooth eruption and replacement patterns (Baubet *et al.* 1994) by distinguishing three age classes: (i) juvenile (less than 1 year of age), (ii) yearling (between 1 and 2 years of age) and (3) adult (older than 2 years of age).

Each year, food availability was measured indirectly through diet composition, using the analysis of stomach contents throughout the year and notably during the hunting period (Brandt *et al.* 2006). Wild boar are opportunistic omnivores, but their diet is primarily composed of vegetation, and, when available, oak and beech mast is highly preferred to any other food resources, namely compared to agricultural crops (Schley & Roper 2003). We distinguished four categories of years (Supporting Information, Table S1): (i) years with high oak mast production, when acorns represented 75–90% of stomach contents during the hunting season, (ii) years with medium oak mast production, when acorns represented 50–65% of stomach contents, (iii) years with high beech mast production, when beechnuts represented 65–85% and (iv) years with no mast production, when maize was the preferred item (15–55%) and with acorn or beechnut representing less than 3% (see Bieber & Ruf 2005 for a similar approach).

Climatic data were obtained from Météo France (Villiers-le-Sec's weather station for temperatures and Châteauvillain's weather station for precipitations). As weather may affect both quality and abundance of food and thereby influence the timing of reproduction, we tested the influence of mean spring and summer temperatures and precipitations on the proportions of females breeding. Mean spring temperatures and precipitations were calculated from April to June when climatic conditions influence plant growth in temperate forests (Geisser & Reyer 2005), and thereby affect the availability and quality of forage during lactation (when the energetic requirements peak; Oftedal 1985). We calculated mean summer temperatures and precipitations from July to September when climatic conditions affect vegetation phenology and when females show a seasonal inhibition of reproduction (Mauget 1982). During our study period, precipitations and temperatures varied a lot from year to year (Fig. 1).

DATA ANALYSIS

We tested whether between-individual differences in the onset of oestrus were generated by differences in age, dressed body mass, month of year, mast production during current and previous years, and/or changes in climatic conditions. As the proportion of female breeding and its variation are strongly age specific in large herbivores (Gaillard *et al.* 2000), we performed separate analyses for each age class (i.e. juvenile, yearling and adult females) to assess the responses of the proportion of female breeding to observed variations in climate and resources. To test for a possible interaction of mast production during current and previous years, we built a synthetic variable (referred to as MIXTURE hereafter) that included feeding conditions in both current and previous years (Supporting Information, Table S1).

Females shot in October and February were not included. Indeed, as hunting did not occur every year during those months, the sample size of females killed per age class and per year was too small to be included. The analyses were thus restricted to November, December and January.

The response variable (i.e. the reproductive status of a given female) was binomially distributed. We thus fitted generalized linear models with a logit link function in an ANCOVA-like procedure (see Festa-Bianchet *et al.* 1998 for details). Model selection was based both on the Akaike Information Criterion corrected for small sample size (AICc) and Akaike weights (AICc weights) to compare the relative performance of the tested models (Burnham & Anderson 2002). The model with the lowest AICc was selected as the best one. When the evidence ratio (i.e. the ratio between AICc weights, Burnham & Anderson 2002) between competitive models was low, the parsimony criterion was used and the simplest model retained (Burnham & Anderson 2002).

We broke down the analysis into two steps to avoid over-parameterized models. We first tested for effects of dressed body mass, month of the hunting season and MIXTURE, together with their possible interactions and then, we tested for the additional effects of temperature and rainfall in spring and summer. Residual deviance was consistently less than the associated numbers of degrees of freedom, so we had no indication of over dispersion (McCullagh & Nelder 1989). We also checked whether the selected model fitted well our data by performing a test on the Pearson residuals (McCullagh & Nelder 1989). We measured the explanatory power of the selected model as the proportion of deviance explained, as recommended by Schemper (1990). All analyses were performed with R 1.7.1 (R Development Core Team 2004).

To rank wild boar along the capital–income breeding continuum, we started from a general model including the effects of body mass and month of hunting as well as their interactions. We performed this analysis on the whole data set (i.e. including all age classes). We then added either the effect of current and/or previous resources. We quantified in each case the proportion of total deviance that was accounted for by these factors.

Results

We collected data on 1666 females. Previous and current resources accounted for similar proportion of deviance (7·74% and 7·36% respectively) when we added one or the other to the global model which included the effects of dressed body mass, month of hunting and their interactions. Including the effect of MIXTURE led to reduce slightly the size of our data set (1518 vs. 1666 individuals), but the inclusion of the variable MIXTURE strongly improved the model fit (AIC = 1279·9 when MIXTURE was included vs. AIC = 1614·0 when only the effects of past and present resources were considered). We then tested different models including only the variable MIXTURE that combined previous and current resources for each age class.

JUVENILE FEMALES

The selected model included interactive effects among body mass, month of hunting and MIXTURE (Table 1a). When testing for climatic effects, the final selected model included both spring and summer temperature and spring rainfall

(Table 1a) and accounted for 41·3% of the observed deviance in the proportion of females breeding.

The body mass effect

The proportion of females breeding increased with body mass (slope of 0·226 ± 0·056 on a logit scale) and throughout the hunting season (slope increased by 0·024 ± 0·058 in December and by 0·107 ± 0·061 in January, logit scale; Fig. 2). The effect of body mass on the proportion of females breeding also depended on food availability and climatic conditions. Under average climatic conditions less than 20% of juveniles were typically breeding in January, when they weighed between 20 and 25 kg dressed mass, but when a year without fructification followed an average acorn year (AAN) the proportion of juvenile females breeding increased by up to 40% (Fig. 3). No juvenile weighing less than 19 kg bred: the threshold body mass above which they breed thus occurred between 33·3% and 40% of the mean observed female's adult body mass. A mean threshold among ungulate species studied so far occurred at 75·48% (±12·36) of the adult mass (Table 2).

The effects of climate and resources

The effect of MIXTURE on the proportion of females breeding suggested the occurrence of a time-lag in the onset of breeding in relation to available resources (Fig. 2). For instance, three times more juvenile females are breeding in November and December in a beechnut year following an average acorn year (AAB) than in an average acorn year following a beechnut year (BAA; Fig. 2). Proportion of females breeding increased when temperature and rainfall in spring were lower than the average. For a mean dressed mass of 28·4 kg and for instance, when an acorn year followed a year with no fructification (NA), 81·76% bred whereas 72% bred when climatic conditions in spring were higher than the average (Fig. 4). Moreover high temperature in summer had a positive effect on proportion of females breeding: 82·2% bred against 70·99% when temperature was less than average (Fig. 4).

YEARLING FEMALES

The selected model included the effects of dressed body mass, month of hunting, MIXTURE and of the interaction between body mass and MIXTURE (Table 1b). When looking for climatic influences, the final selected model included temperatures and precipitations in both spring and summer and accounted for 42·2% of the observed deviance in the proportion of yearling females breeding (Table 1b).

The body mass effect

As in juveniles, body mass had a positive effect (slope of 0·16 ± 0·039 on a logit scale) and the proportion of females

Table 1. Model selection for proportions of females breeding during the study period: 1983–2005

Tested models	AICc	ΔAICc	AICc weights	Evidence ratio
(a) *Model selection for juvenile females. The selected model accounted for 41·3% of observed variation*				
First step: model selection without climatic data				
Logit (proportions of females breeding) = W + M + MIXTURE + W × M + M × MIXTURE + W × MIXTURE	702·92	0	0·630	
Logit (proportions of females breeding) = W + M + MIXTURE + W × M + M × MIXTURE	705·08	2·16	0·214	2·94
Logit (proportions of females breeding) = W + M + MIXTURE + M × MIXTURE + W × MIXTURE	706·37	3·45	0·112	5·61
Logit (proportions of females breeding) = W + M + MIXTURE + M × MIXTURE	708·35	5·43	0·042	15·1
Logit (proportions of females breeding) = W + M + MIXTURE + W × M + W × MIXTURE	714·27	11·35	0·002	315
Selected model: (1): Logit (proportions of females breeding) = W + M + MIXTURE + W × M + M × MIXTURE + W × MIXTURE				
Second step: model selection with climatic data				
(1) + Tspring + Rspring + Tsummer	692·70	0·00	0·29	
(1) + Rspring + Tsummer	693·68	0·98	0·18	1·63
(1) + Tsummer	694·19	1·49	0·14	2·11
(1) + Tspring + Rspring + Rsummer + Tsummer	694·53	1·83	0·12	2·50
(1) + Tspring + Tsummer	695·23	2·53	0·08	3·54
(1) + Rspring + Rsummer + Tsummer	695·69	2·99	0·07	4·46
(1) + Rsummer + Tsummer	695·58	2·88	0·07	4·22
(1) + Tspring + Rsummer + Tsummer	696·35	3·65	0·05	6·20
Final model: Logit (proportions of females breeding) = W + M + MIXTURE + W × M + M × MIXTURE + W × MIXTURE + Tspring + Rspring + Tsummer				
(b) *Model selection for yearling females. The selected model accounted for 42·2% of observed variation*				
First step: model selection without climatic data				
Logit (proportions of females breeding) = W + M + MIXTURE + W × MIXTURE	449·06	0·000	0·432	
Logit (proportions of females breeding) = W + M + MIXTURE + W × M + W × MIXTURE	450·18	1·120	0·247	1·751
Logit (proportions of females breeding) = W + M + MIXTURE	451·33	2·270	0·139	3·111
Logit (proportions of females breeding) = W + M + MIXTURE + W × M	452·38	3·320	0·082	5·259
Logit (proportions of females breeding) = W + M + MIXTURE + M × MIXTURE + W × MIXTURE	453·22	4·160	0·054	8·004
Logit (proportions of females breeding) = W + M + MIXTURE + M × MIXTURE	455·17	6·110	0·020	21·221
Logit (proportions of females breeding) = W + M + MIXTURE + W × M + M × MIXTURE + W × MIXTURE	455·305	6·245	0·019	22·703
Logit (proportions of females breeding) = W + M + MIXTURE + W × M + M × MIXTURE	457·24	8·180	0·007	59·740
Selected model: (1): Logit (proportions of females breeding) = W + M + MIXTURE + W × MIXTURE				
Second step: model selection with climatic data				
(1) + Tspring + Rspring + Rsummer + Tsummer	430·75	0·00	0·97	
(1) + Tspring + Rspring + Tsummer	438·11	7·36	0·02	39·65
Final selected model: Logit (proportions of females breeding) = W + M + MIXTURE + W × MIXTURE + Tspring + Rspring + Rsummer + Tsummer				
(c) *Model selection for adult females. The selected model accounted for 51·2% of observed variation*				
First step: global model without climatic data				
Logit (proportions of females breeding) = W + M + MIXTURE	238·315	0·00	0·36	
Logit (proportions of females breeding) = W + M + MIXTURE + W × M	238·67	0·35	0·31	1·19
Logit (proportions of females breeding) = W + M + MIXTURE + W × MIXTURE	239·50	1·19	0·20	1·81
Logit (proportions of females breeding) = W + M + MIXTURE + W × M + W × MIXTURE	241·29	2·97	0·08	4·43
Logit (proportions of females breeding) = M + MIXTURE	242·96	4·65	0·04	9
Logit (proportions of females breeding) = W + M + MIXTURE + M × MIXTURE	246·86	8·55	0·01	36

Table 1. (Continued)

Tested models	AICc	ΔAICc	AICc weights	Evidence ratio
Selected model: (1): Logit (proportions of females breeding) = W + M + MIXTURE				
Second step: model selection with climatic data				
(1) + Tspring + Rspring + Rsummer + Tsummer	206·61	0·00	0·80	
(1) + Tspring + Rsummer + Tsummer	210·27	3·66	0·13	6·23
(1) + Tspring + Tsummer	212·11	5·50	0·05	16
(1) + Tspring + Rspring + Tsummer	213·68	7·07	0·02	40
Selected model: Logit (proportions of females breeding) = W + M + MIXTURE + Tspring + Rspring + Rsummer + Tsummer				

For each model (numbers in brackets), the table gives the terms included in the model, the AICc, the ΔAICc, the AICc weights and the evidence ratio for models with ΔAICc < 10. We only notified here the tested models that have an AICc weight > 0·000 and the selected model at each step of the analysis is indicated. W = dressed mass; M = month of hunting; A = age class; MIXTURE = combination of the resources for the current year and the previous year (see Supporting Information, Table S1).
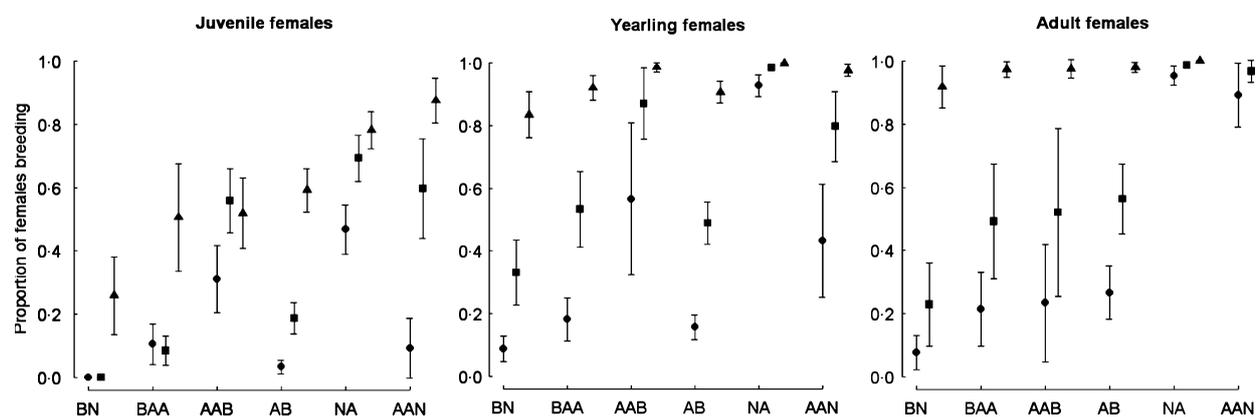

Fig. 2. Effects of months and of the combination of resource availability [MIXTURE: for instance AB means that the current year is a beechnut year (B) whereas the year before was an acorn year (A), see Supporting Information, Table S1] on the proportion of reproductive females (mean ± 1 SE) during 3 months (November: circles, December: squares and January: triangles). Predicted means for each age class are corrected by the mean observed dressed mass in each age class (i.e. 61 kg for adults, 47·3 kg for yearlings and 28·4 kg for juveniles) and by the mean observed climatic conditions according to the selected model for each age class (see Table 1). We thus displayed the 'average' climatic conditions that influence each age class to reproduce.

breeding increased over time: for a mean dressed mass of 47·3 kg, 7·99, 30·87 and 81·88% bred in November, December and January respectively (Fig. 2). However, the relationship between body mass and the proportion of females breeding was less pronounced in yearlings than in juveniles. This is likely due to the fact that most females (80–100%) were in oestrus independently of their body mass at the end of the hunting season (Fig. 2).

The effects of climate and resources

The effect of MIXTURE on the proportion of females breeding was more pronounced in yearlings than in juveniles, indicating a delayed oestrus in yearlings (Fig. 2). For instance, more yearling females were breeding in November and December when an average acorn mast year was followed either by a beechnut mast year (AAB) or by no fructification (AAN) than when a beechnut mast year was followed by an average acorn mast year (BAA) (Fig 2). As observed in juve-

niles, when temperature and rainfall in spring were higher than the average the proportion of females breeding decreased whereas when rainfall and temperature in summer were higher than the average the proportion of females in oestrus increased (Fig. 4).

ADULT FEMALES

The selected model only included the main effects of body mass, month of hunting and MIXTURE (Table 1c). When looking for climatic influences on the proportions of females breeding, the final selected model included temperatures and precipitations during both spring and summer and accounted for 51·2% of the observed deviance in the proportion of adult females breeding (Table 1c).

Unlike younger females, more than 90% (i.e. between 92% and 100%) of adult females entered in oestrus before the end of the hunting season (Fig. 2). As in yearlings, the proportions of adult females breeding were lower when
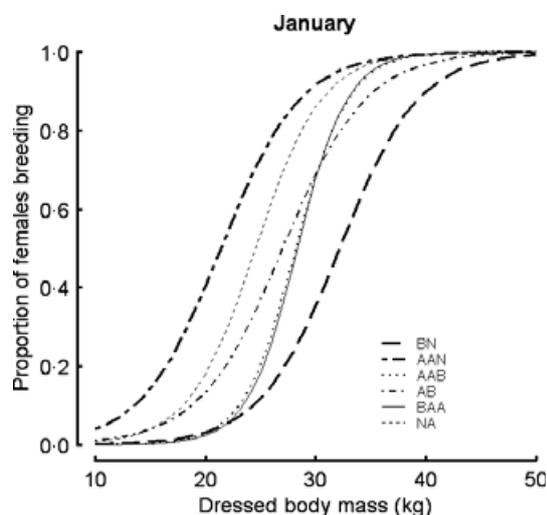
Fig. 3. Proportion of juvenile females breeding in January in relation to dressed mass and to the combination of resource availability (MIXTURE; see the legend of the Fig. 2 and Supporting Information, Table S1). Predicted curves are corrected for the mean spring rainfall (i.e. 219·75 mm), the mean observed spring temperature (i.e. 12·82 °C) and for the mean observed summer temperature (i.e. 17·29 °C).

temperature and rainfall in spring were higher than the average, and higher when temperature and rainfall in summer were higher than the average (Fig. 4). We also

found delayed effects of food availability on breeding status (Fig. 2).

Discussion

Some main findings emerge from this study: as expected (i) the threshold body mass to reproduce for the first time occurred at a much lower body mass in this heavily hunted population of wild boar than in similar-sized ungulates studied so far (i.e. only one third of adult body mass vs. about 80%); (ii) heavier females became reproductive in higher proportions than lighter females, and the proportions of females breeding increased throughout the hunting season and (iii) the proportions of females breeding and the timing of oestrus varied in relation to both food resources and climate.

Most yearlings and adult females (90–100%) showed active reproduction each year at the end of the hunting season, irrespective of dressed body mass, the food resource availability or climatic conditions. While previous studies have reported a high reproductive output in female wild boar (Mauget 1982; Groot Bruinderink, Hazebroek & Van Der Voot 1994; Massei, Genov & Staines 1996), we clearly showed here that once sexual maturity has been reached, nearly every female attempts to reproduce each year whatever the environmental conditions (Fig. 4). Wild boar females seem thus to follow a more risky life-history tactic than other similar-sized ungulate females such as bighorn

Table 2. Body mass at first reproduction and adult body mass for 11 ungulate species

Species	Body mass (kg) at first reproduction	Adult body mass (kg)	% of the asymptotic size	Study site	Reference
Roe deer (*Capreolus capreolus*)	18·1	21·2	85·4	France	Gaillard *et al.* 1992
Reindeer (*Rangifer tarandus*)	34·3[a]	44·70[a]	76·7	Norway (North Ottadalen)	Reimers *et al.* 2005;
	63·455	71·3	89	Norway (Riast/ Hylling)	Weladji *et al.* 2002
Red deer (*Cervus elaphus*)	47[a]	67·2[a]	69·9	Belgium	Bertouille & De
	45[a]	60[a]	75	France	Crombrugghe 2002; Bonenfant *et al.* 2002
Mouflon (*Ovis gmelini musimon* Blyth 1841)	15·5[a]	21 kg[a]	73·8	France	Garel *et al.* 2005
Alaskan Moose (*Alces alces gigas* Miller 1899)	340	450	75·55	Alaska	Schwartz & Hundertmark 1993
Moose (*Alces alces*)	120[a]	180[a]	66·7	Sweden	Sand 1996;
	140[a]	178[a]	78·65	Norway	Sæther *et al.* 1996;
	150[a]	180[a]	83·33	Norway	Solberg *et al.* 2004
Bison (*Bison bison* L.)	325–375	424	76·65–88·44 Mean: 82·545	USA	Green & Rothstein 1991
Mountain goat (*Oreamnos americanus*)	62–66	72–75	86·1–88 Mean: 87·05	Canada	Côté & Festa-Bianchet 2001
Fallow deer (*Dama dama*)	32	42	76·2		Langbein & Putman 1992
Bighorn sheep (*Ovis canadensis*)	**26**	**55**	**47·27**	**Canada**	**Jorgenson *et al.* 1993 Festa-Bianchet *et al.* 1995**
Wild boar (*Sus scrofa scrofa*)	20–25[a]	61[a]	32·79–40·98 Mean: 36·89	France	Gaillard *et al.* 1993; this study

The percentage of the asymptotic mass at which females reproduce for the first time is reported. On average, female ungulates reproduce at 75·48 ± 12·36% SD. ([a]) indicated that the body mass in the considered study was dressed mass. Bighorn sheep (in bold in the table) were excluded from the mean calculation since Festa-Bianchet *et al.* (1995) showed that body mass was not a good predictor of first reproduction. For this species, data were obtained from two different studies but they were carried out at the same study site
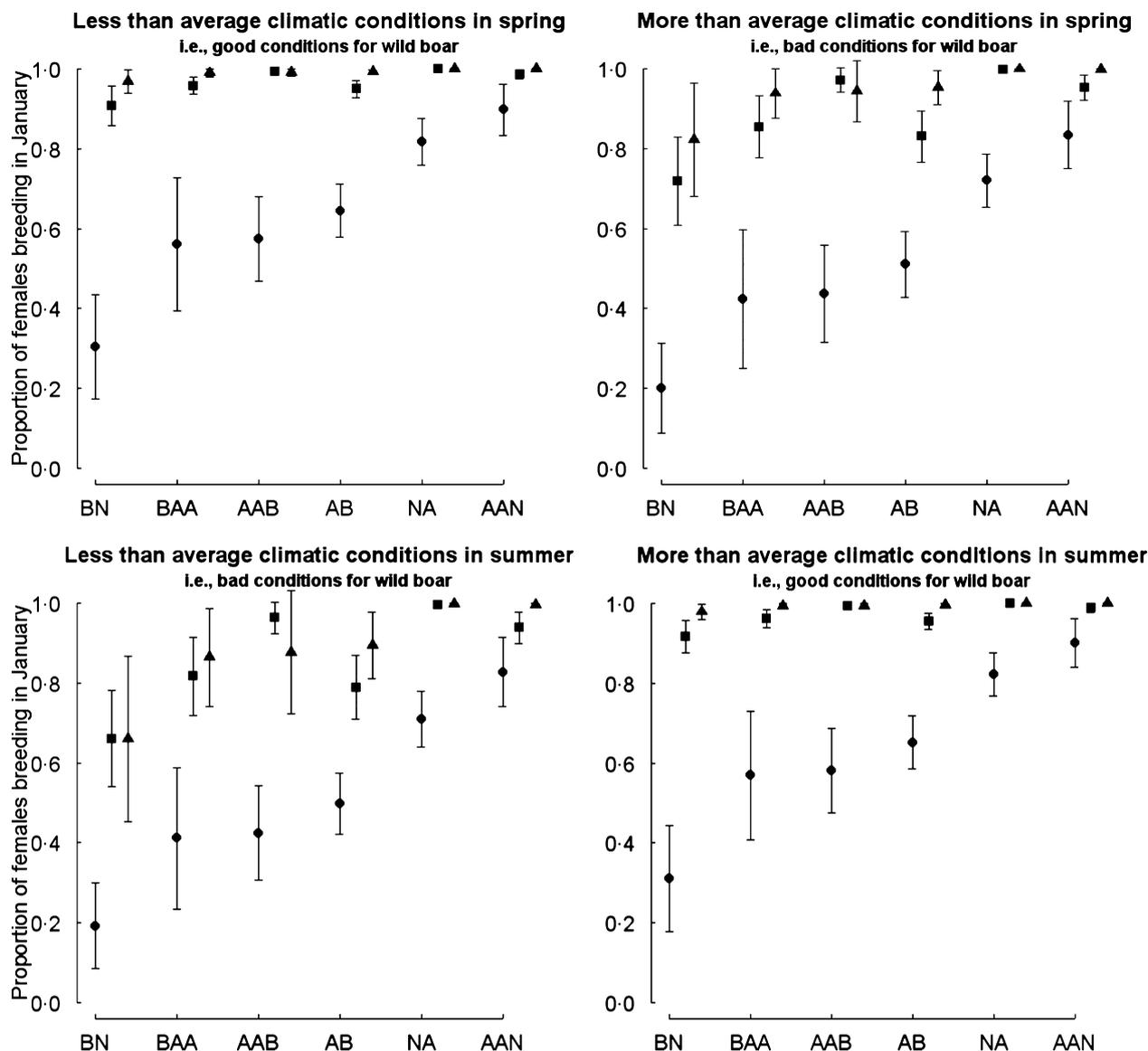
Fig. 4. Effects of climatic conditions on the proportion (mean $\pm$ 1 SE) of females breeding (juveniles: circles, yearlings: squares and adults: triangles) in January and in relation to the combination of food resources (MIXTURE; see the legend of the Fig. 2 and Supporting Information, Table S1). Predicted means for each age class are represented for the month of January and are corrected by the mean observed dressed mass in each age class (i.e. 61 kg for adults, 47·3 kg for yearlings and 28·4 kg for juveniles). Four conditions were represented: (i) less than average climatic conditions in spring (i.e. good climatic conditions for wild boar): observed first quartile of spring temperature (i.e. 12·33 °C) and rainfall (i.e. 184·1 mm) and mean climatic conditions in summer (i.e. 17·29 °C and 192·73 mm). (ii) More than average climatic conditions in spring (i.e. bad climatic conditions for wild boar): observed third quartile of spring temperature (13·13 °C) and rainfall (277·6 mm) and mean climatic conditions in summer (i.e. 17·29 °C and 192·73 mm). (iii) Less than average climatic conditions in summer (i.e. bad climatic conditions for wild boar): observed first quartile of summer temperature (16·57 °C) and rainfall (156·3 mm) and mean climatic conditions in spring (i.e. 12·82 °C and 219·75 mm). (iv) More than average climatic conditions in summer (i.e. good climatic conditions for wild boar) observed third quartile of summer temperature (17·62 °C) and rainfall (246·5 mm) and mean climatic conditions in spring (i.e. 12·82 °C and 219·75 mm).

sheep (*Ovis canadensis* Shaw 1804, Festa-Bianchet *et al.* 1998), mountain goat (*Oreamnos americanus* de Blainville 1816, Festa-Bianchet & Côté 2008) or reindeer/caribou (*Rangifer tarandus* L., Cameron 1994), which tend to skip reproduction when in poor conditions so to maximize their own survival (Gaillard & Yoccoz 2003). Moreover, while sexual maturity generally occurs between 2 (e.g. bighorn sheep) and 4 (e.g. mountain goat) years of age in similar-sized ungulates, a large proportion of juvenile wild boar can reproduce as early as at 1 year of age.

Like reported for other ungulates (Table 2), young wild boar only reproduce when a threshold body mass has been reached. This threshold dressed body mass was between 20 and 25 kg (i.e. 26·8–33 kg live mass; Gaillard *et al.* 1993) in yearling females, and up to 80% of juveniles above the threshold showed reproductive activity in January (Fig. 3). This high proportion of juvenile females breeding may even be under-estimated as we did not have access to the reproduction of females during the non-hunting season. Indeed, a 2-year study showed that in three different parts of

Germany, only 30% of juvenile females showed active reproduction during the hunting season, whereas up to 60% were pregnant in the following March–April (Gethöffer, Sodeikat & Pohlmeyer 2007). However, the observed threshold mass above which juvenile females can reproduce is less than 40% of adult mass, which is very low compared to the observed average of 75% among ungulate species studied so far (Table 2). Two different explanations could account for such marked differences between our results and those reported for similar-sized ungulates. First, as wild boar exhibit very unusual combinations of life-history traits (i.e. large body mass and high fecundity; Focardi *et al.* 2008), the low threshold body mass we reported here might correspond to another life history characteristic of wild boar. Alternatively, the ecological context of the studied population might be involved. First the studied population faced with the most heavy hunting pressure ever measured for a large mammal (Toïgo *et al.* 2008), so that an early sexual maturity relative to full adult body mass might result from a selective pressure generated by hunting as commonly observed in fishes for instance (e.g. Conover & Munch 2002). Second, the studied population had a low population density and lived in a highly productive forest so that the per capita food resource was high, leading to high reproductive performance (Bonenfant *et al.* 2009). The available evidence so far collected in contrasted populations of wild boar tends to support an overwhelming influence of hunting. With the low life expectancy caused by the high risk of being shot, an increased reproductive effort early in life should be selected for only in intensively hunted populations (Festa-Bianchet 2003; Garel *et al.* 2007) provided that food resources will not be limiting as observed in the focal population (i.e. high frequency of mast years and low density). As expected the threshold body mass we reported here was lower than that observed in less intensively hunted populations of wild boar (Table 3). It is especially noteworthy that only wild boar females from Chambord (the only population with a high hunting pressure among the eight for which we got data) might had similar threshold body mass as we observed here. Moreover, the threshold body mass reported in intensively hunted populations was much lower than that measured on females captured in the wild as piglets and then raised in captivity and fed *ad libitum* [35 kg (i.e. 28 kg dressed mass); Pépin & Mauget 1989]. In this latter study, the authors tested for the effect of different plans of nutrition on growth and sexual maturity and found that sexual maturity was never reached before 20 months (Pépin & Mauget 1989). Those results clearly indicate that early reproduction at low body mass is not a species-specific trait of wild boar and support the widespread occurrence of marked among-population variation in the relationship between mass and reproduction (see e.g. Albon, Mitchell & Staines 1983 on red deer; Heard *et al.* 1997 on moose *Alces alces* L.). Available evidence therefore provide strong support for involving a response of wild boar to the high hunting pressure to account for both the high proportions of juvenile females breeding and the low threshold body

mass at which reproduction occurs in this heavily hunted population.

Interestingly, we observed little monthly variation in the proportion of juveniles breeding according to available resources, whereas a high variation in monthly proportions of females breeding occurred in yearlings and adults (Fig. 2). The timing of oestrus, as well as the marked influence of resource availability on the reproductive output in both the current and previous years may suggest the occurrence of reproductive costs on subsequent reproduction. Yearlings included both females that previously gave birth as juveniles and might thus have incurred some reproductive costs (Oftedal 1985) and females that did not previously reproduce and therefore had only allocated energy to growth and body reserves. Among adults, all females previously gave birth (i.e. they were all multiparous) and most of them had reproduced the previous year (i.e. no reproductive pause *sensu* Cameron 1994). Such high proportions of reproductive females each year indicate that females should have sufficient energy and nutrients to meet the high energetic costs of a reproductive attempt and often have to recover from this high energy expenditure before reproducing again (Gittleman & Thompson 1988). Thereby, the delay in the recovery of body condition is likely to be determined by the availability of food resources. Obviously, producing and rearing young may cause a negative energy balance among females that will not be totally compensated for by the end of the summer, the period during which females (i) have generally finished lactating and (ii) are in anoestrus. Moreover, as the observed variation in proportion of females breeding, accounted for by past and present resources was nearly equal (around 7·5%), wild boar could be ranked at an intermediate position on the capital–income continuum (e.g. Jönsson 1997). While comparable data on similar-sized ungulates are not available, the strong influence of body condition on reproductive output, the low fecundity, and the high average survival of offspring from birth to weaning reported for these species (see Gaillard *et al.* 2000 for a review), as well as their ranking close to the capital-breeder end of the continuum (e.g. Festa-Bianchet *et al.* 1998) are indicating that current resources around birthing time are much less influential than body reserves to shape their yearly reproductive success.

Feeding conditions during both current and previous years also influenced proportions of females breeding as juveniles. Environmentally-induced maternal effects (e.g. Mousseau & Fox 1998), might thus affect female reproductive output. As mast production is an unpredictable and pulsed resource (e.g. Ostfeld & Keesing 2000), the level of food in a given year is a poor predictor of the resources that juveniles will encounter at the time of their potential first reproduction in the following year. Mother–offspring similarity in mass growth when juvenile could be higher when available resources are limited as has been shown in red squirrels (*Tamiasciurus hudsonicus* Erxleben 1777) when spruce cones are limited (McAdam & Boutin 2003). Compensatory growth might thus explain how juvenile females could reach the threshold body mass to breed when facing low resources during a given year.

Table 3. Body mass and age at first reproduction of female wild boar in populations with contrasting hunting pressure

Studied area, Localization	Studied years (hunting season)	Hunting information	Reproduction	References
Chambord, France	*1986/87 to 1988/89*	*7·5–9·5 hunted wild boar/100 ha*	*In February, 16% (N = 4/25) of juvenile females weighing between 26·8 and 30 kg live mass (i.e. 20 and 24 kg dressed mass) were observed in oestrus*	*Unpublished data (ONCFS and Domaine National de Chambord)*
Châteauvillain, France	1983/84 to 2004/05	5·21 hunted wild boar/100 ha (±2·66, range: 0·64–9·27)	Threshold body mass between 26·8 and 33 kg live mass (i.e. 20 and 25 kg dressed mass)	This study
Valle Medio de l'Ebro, Zaragoza, Spain	*1994/95 to 2005/06*	*32% of hunted females are less than 1 year of age for an estimated density of less than 1 wild boar/100 ha (high hunting pressure) Observed life expectancy: 6 years*	*29·4% (N = 5/17) of juvenile females were pregnant The mean observed body mass in juveniles was 34·6 ± 9·7 kg*	*Herrero et al. 2008*
Grésigne, France	1978/79 to 1980/81	0·5–0·7 hunted wild boar/100 ha	No reproduction in juveniles although there was a good acorn mast in 1978	Pépin et al. 1987 Spitz et al. 1984
Regions of Trás-os-Montes, Beiras, Alentejo Portugal	*1999/00 and 2000/01*	*0·595 hunted females wild boar/ 100 ha (Beiras) 1·315 hunted females wild boar/ 100 ha (Alentejo)*	*In Beiras, a minimum threshold body mass of 33 kg live mass (i.e. 25 kg dressed mass) was observed in juveniles No reproduction was observed in juveniles in Alentejo*	*Fonseca et al. 2004*
Pirineo Occidental, Huesca, Spain	1990/91 to 1992/93	0·63 hunted wild boar/100 ha for an estimated density of 3·3 wild boar/ 100 ha (low hunting pressure) 30·7% of hunted females are less than 1 year of age Observed life expectancy: 10 years	6·7% (N = 1/15) of juvenile females were pregnant The mean observed body mass in juveniles was 24·6 ± 6·5 kg	Herrero et al. 2008

Populations facing high hunting pressure occur in italics. In Portugal, data are coming from females hunted by Montarias, a driven hunt with dogs. Montarias represents between 30% and 50% of the total hunting bag (C. Fonseca, pers. comm.).

Our results support the important role of climatic variation in determining females' reproductive performance, certainly acting trough their nutritional condition. The proportion of females breeding were positively influenced by (i) a less than average temperature and rainfall in spring through a longer period of high quality forage (Langvatn *et al.* 1996) and of storage in bulbous plants (Fenner 1998) and (ii) a rainy and hot summer through a longer vegetative growing season (Fenner 1998) and in the consumption of earthworm (Baubet, Ropert-Coudert & Brandt 2003; Fig. 4).

Conclusions

We showed that the timing of the oestrus of wild boar females is greatly influenced by environmental factors operating through climate and food resources. Furthermore, we showed that multiparous females can adjust the timing of their oestrus. Such a short-term adjustment induces a time delay in the reproduction (i.e. gestation does not start during the same month every year) so that both the timing of births and the duration of the growth period for juveniles should vary over years.

Our results showed that juveniles make a large contribution to the yearly recruitment, maybe as a result of the high hunting pressure faced by wild boar in the focal population. As most females are not living more than two or three breeding seasons, selective pressure should favour an increased reproductive effort early in life and so, juveniles should invest more in reproduction at the risk of reduced adult size or shorter lifespan (Festa-Bianchet 2003; Garel *et al.* 2007). As the generation time in our population was especially low (i.e. about 2 years, Gaillard, Vassant & Klein 1987) compared to what can be expected for similar sized large herbivore (e.g. 7 years, Gaillard *et al.* 2008), the selective advantage of reproducing yearly should be higher in wild boar than in similar-sized ungulates (see Stenseth & Dunlop 2009 for similar arguments). The low threshold mass we reported here, along with the short generation time, involves a high potential impact on population growth to changes in recruitment parameters. Reproducing early in life at low mass might be a response of wild boar to high hunting pressure.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Number of females for which we identified the reproductive status for each year (hunting season) and for each age class.

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