

HIGH HUNTING PRESSURE SELECTS FOR EARLIER BIRTH DATE: WILD BOAR AS A CASE STUDY

Marlène Gamelon,^{1,2,3} Aurélien Besnard,^{1,4} Jean-Michel Gaillard,^{5,6} Sabrina Servanty,^{7,8,9} Eric Baubet,^{10,11} Serge Brandt,^{2,12} and Olivier Gimenez^{1,13}

¹Centre d'Ecologie Fonctionnelle et Evolutive, Unité Mixte de Recherche 5175, campus CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France

²Office National de la Chasse et de la Faune Sauvage, 2 Bis Rue des Religieuses, BP 19, 52120 Châteauvillain, France

³E-mail: marlene.gamelon@univ-lyon1.fr

⁴E-mail: aurelien.besnard@cefe.cnrs.fr

⁵Laboratoire de Biométrie et Biologie Evolutive, Unité Mixte de Recherche 5558, Université Claude Bernard Lyon I, 43 Bd du 11 novembre 1918, 69622 Villeurbanne Cedex, France

⁶E-mail: jean-michel.gaillard@univ-lyon1.fr

⁷USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, Maryland 20708–4039

⁸Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, 1484 Campus Delivery, Fort Collins, Colorado 80523–1484

⁹E-mail: sab.servanty@free.fr

¹⁰Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés Sangliers, Montfort 01330 Birieux, France

¹¹E-mail: eric.baubet@oncfs.gouv.fr

¹²E-mail: serge.brandt@oncfs.gouv.fr

¹³E-mail: olivier.gimenez@cefe.cnrs.fr

Received January 6, 2011

Accepted May 10, 2011

Data Archived: Dryad doi:10.5061/dryad.rn1ns

Exploitation by humans affects the size and structure of populations. This has evolutionary and demographic consequences that have typically been studied independent of one another. We here applied a framework recently developed applying quantitative tools from population ecology and selection gradient analysis to quantify the selection on a quantitative trait—birth date—through its association with multiple fitness components. From the long-term monitoring (22 years) of a wild boar (*Sus scrofa*) population subject to markedly increasing hunting pressure, we found that birth dates have advanced by up to 12 days throughout the study period. During the period of low hunting pressure, there was no detectable selection. However, during the period of high hunting pressure, the selection gradient linking breeding probability in the first year of life to birth date was negative, supporting current life-history theory predicting selection for early births to reproduce within the first year of life with increasing adult mortality.

KEY WORDS: Birth timing, elastogram, exploited populations, population dynamics, selection gradient analyses, *Sus scrofa*.

Humans, by exploitation through hunting, fishing, or agriculture, affect the size and structure of populations over time (exploited populations *sensu* Lebreton 2005). The demographic consequences of human exploitation are well established and generally involve increasing extinction risk (Keane et al. 2005; Hilton-Taylor 2000; Johnson et al. 2010). However, human exploitation can also induce evolutionary consequences for populations and species (Darimont et al. 2009). For example, Andersen and Brander (2009) estimated that the expected evolutionary rates of change induced by fisheries ranged from 0.1% to 0.6% per year and were higher for reproductive traits. Similarly, Coltman et al. (2003) found that high-intensity trophy harvest selected for individuals with smaller horn size and body mass, leading to declines in individual breeding values.

Because of perceived operational differences in timescales, evolutionary and ecological processes have typically been studied independent of one another. Traditionally, evolution is assumed to be too slow to leave a signature in ecological dynamics (Slobodkin 1961) so that ecologists mostly ignore evolutionary dynamics whereas evolutionary biologists mostly ignore ecological processes (Metcalf and Pavard 2007). However, recent studies have shown that ecological and evolutionary processes can occur at the same time scale (Pelletier et al. 2007; Ozgul et al. 2009, 2010; see Pemberton 2010 for a review). Many organisms can undergo evolution over just a few generations (Carroll et al. 2007; Parmesan 2006; Visser 2008; Dunn and Winkler 1999), exploited populations making no exception (Darimont et al. 2009). In this context, an approach linking both demographic and evolutionary processes is required to allow the identification of pathways through which the focal trait changes over time, so that managers would be able to establish appropriate management strategies.

Lande (1982) and Van Tienderen (2000) have shown that selection and population dynamics can be related by coupling projection matrix models commonly used in population demography and analyses of selection gradients often performed by evolutionary ecologists. Such a direct link is justified because the population growth rate measures the average individual fitness (Fisher 1930). Although appealing, this approach has been thus far applied only occasionally (Smekens and Van Tienderen 2001; Coulson et al. 2003) and never to our knowledge in the context of exploited populations.

We used this approach to quantify selection on reproductive phenology of birth dates in a wild boar (*Sus scrofa scrofa*) population intensively monitored for 22 years by the French National Game and Wildlife Agency (ONCFS) and subject to highly contrasting hunting regimes throughout the study period. The timing of births plays indeed a determinant role in population dynamics of large mammals living in temperate areas (Gaillard et al. 2000), where births are generally highly synchronized (Rutberg 1987) likely in response to stabilizing selection. Birth date affects the

likelihood of survival in at least two ways: being born too early may result in lowered survival if birth date does not coincide with favorable environmental conditions, and similarly, being born too late may also result in lowered survival if a newborn's growth rate cannot compensate for a reduced period of growth before the first winter. Likewise, late birth may also delay the onset of sexual maturity (see e.g., Festa-Bianchet 1988a for bighorn sheep, Gaillard et al. 1993 for roe deer *Capreolus capreolus*, Lomas and Bender 2007 for mule deer *Odocoileus hemionus*). Here, we aimed to test whether a high hunting pressure leads to a selection pressure for earlier births that would allow females to reach sexual maturity earlier (Darimont et al. 2009) and then to give birth at a younger age as recently reported in that population (Servanty et al. 2009).

Material and Methods

STUDY AREA AND WILD BOAR MANAGEMENT

We studied a wild boar population located in northeastern France in the 11,000 ha forest of Châteauvillain-Arc-en-Barrois. The study site is administratively divided into two parts: a core area that covers 8500 ha of national forest and a 2500 ha surrounding area of private or communal forest. These forests are mainly composed by oak (*Quercus petraea*), beechnut (*Fagus sylvatica*), and hornbeam (*Carpinus betulus*). The climate is intermediate between continental and oceanic. From 1981 to 2003, mean annual rainfall was 74.4 ± 8.6 mm, and average monthly temperatures ranged from $2.34 \pm 2.06^\circ\text{C}$ in January to $18.6 \pm 1.58^\circ\text{C}$ in August (Météo-France).

Population size of wild boar at this site was estimated to be between 1200 and 1500 individuals over the course of the study. Major sources of wild boar mortality include starvation, diseases, and collisions with vehicles. Adult wild boars have no natural predators in the study area but are hunted each year between October and February. Hunting pressure varied markedly throughout the study period. Between the years 1981–1982 to 1985–1986, an average of 180 (± 69) individuals were removed each year, corresponding to a rather weak hunting pressure on the population, along with a low proportion of individuals less than 1 year of age harvested. Between the years 1986–1987 to 2003–2004, an average of 463 (± 224) wild boars were removed each year, corresponding to a much higher hunting pressure (Toïgo et al. 2008), along with a marked increase in the proportion of individuals aged between 6 months and 1 year harvested (Fig. 1). Harvest regulations for females varied between these two periods; females with a dressed body mass of ≥ 50 kg were protected between the 1986–87 and 2003–2004 hunting seasons. Harvest regulations for males did not vary between the two time periods.

DATA COLLECTION

Between 1981 and 2004, capture–mark–recapture–recovery (CMRR) data were collected annually (Williams et al. 2002).

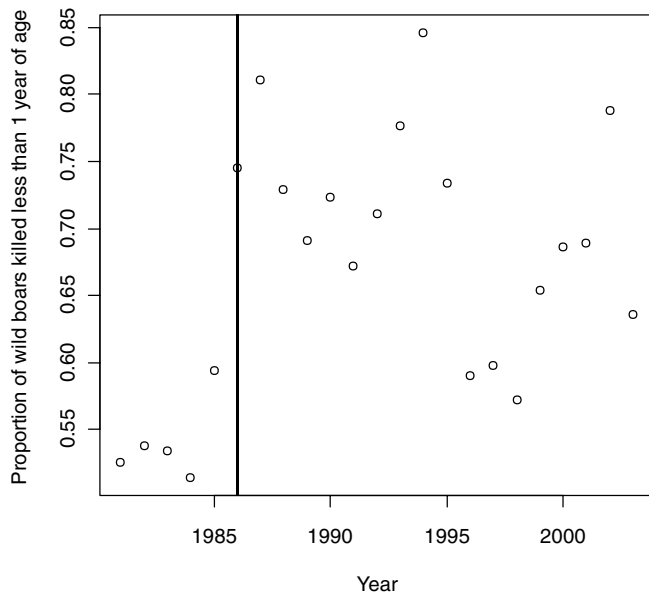


Figure 1. Proportion of wild boars less than 1 year of age killed each year from the season 1981–1982 to the season 2003–2004. The two periods corresponding to two different hunting pressures are separated by the solid line.

Individuals were captured from March to September of each year using traps, marked and released in their environment. We only included animals marked as juveniles (i.e., less than 1 year of age) in our analyses. For each capture event, we recorded date of capture, weight at capture, and for first captures, sex of the individual. Based on tooth-eruption pattern, the youngest animals trapped were 3 months of age and had thus survived the neonatal period for which we do not have reliable survival estimates (Toïgo et al. 2008). The fate of known individuals was determined through a mark recovery program adopted by hunters in the region, and date of death recorded. Although the date at death was known for all individuals that were shot (recoveries), no information was available for individuals that died from natural causes or from hunting without being recovered corresponding to crippling loss. During those years, 1890 juveniles were marked (991 males and 899 females), of these 238 were recaptured at least once and 1204 were recovered.

In addition to CMRR data, we collected data on female reproductive status based on examination of the reproductive tracts of 676 juvenile females. Sagittally cut ovaries were examined for the presence of Graaf follicles indicating that females were in oestrus or the presence of corpora lutea indicating a recent ovulation (Fernandez-Llario et al. 2004). Uteri were examined for the presence of embryos or fetuses. We assigned each female to one of two reproductive categories: reproductive (i.e., sexually mature) versus nonreproductive (i.e., sexually immature). We recorded the dressed body mass, absent the digestive system, heart, lungs, liver, reproductive tract, and blood of each female.

ASSESSING TEMPORAL TRENDS IN BIRTH DATE

Birth date was estimated by (A) using the weight of a juvenile at first capture or at death for a hunted juvenile (less than 1 year of age) females (B) assuming birth weight equals 1 kg (Baubet et al. 2009) and (C) using a linear model to predict individual growth rate over the first months of life (Gaillard et al. 1992). Individual growth rate depends on environmental conditions, in particular food availability. We thus considered a different growth rate depending on mast production in a given year that corresponds to $110 \text{ g}\cdot\text{d}^{-1}$ when mast production is high, and to $125 \text{ g}\cdot\text{d}^{-1}$ when mast production is low (Servanty et al., unpubl. data). For these analyses, we did not use the calendar year, but rather define year based on seasonality of mast production and corresponding levels of food availability. Mast production in autumn of one year will benefit an individual born in spring of the subsequent year. Using data from our assessment of reproductive status, we determined the earliest birth date for wild boar was November 12. For analyzing CMRR data, we estimated birth date as the “number of days until the 12th of November.” We considered classes spanning 15 days to attenuate spurious effects due to the approximation of birth dates and because wild boar have low synchrony of birth dates thus allowing us to account for many fortnights. Thus, an individual that was born on the 1st of October had a birth date of -2 because it was born the second fortnight before the 12 November.

The variation in hunting intensity between the two periods allowed us examining the selective pressure corresponding to the change of harvesting on birth dates. The fortnight of birth was related to year (linear effect) using a logistic regression. Moreover, by using an ANCOVA, we tested for a period-specific temporal trend in birth date due to the hunting pressure, by including a linear effect of year to account for a possible climatic change over the study. All analyses were performed with R 2.10.1 (R Development Core Team 2009).

ESTIMATING MORTALITY

CMRR data were analyzed using multistate capture–recapture models (Lebreton et al. 2009 for a review) to estimate mortality probabilities. The multistate approach allowed the joint analysis of recaptures of live individuals and recoveries of hunted individuals to separate natural mortality from mortality due to harvest (Schaub and Pradel 2004). We considered four states to describe the fate of an individual: (1) the individual was alive; (2) the individual had just died from hunting; (3) the individual had just died from a natural cause, and (4) the individual was already dead. The state “dead from a natural cause” was not observable because no information was available for individuals that did not die from hunting. The state “already dead” was not observable either but brought together all the dead individuals. The transition probability for moving from the state “alive” at time t to the

state “dead from hunting” at time $t+1$ is the mortality probability due to hunting (Mh); similarly, the transition probability for moving from the state “alive” at time t to the state “dead from a natural cause” at time $t+1$ is the natural mortality probability (Mn) (see Appendix S1). The annual survival probability (S) is the complement of the overall mortality probability, i.e., $S = 1 - Mh - Mn$. Once a wild boar was classified as dead, it could not return to the state “alive” so this transition was set to 0. To ensure that all probabilities were estimated within the interval $[0, 1]$ and summed to 1, we used a generalized (or multinomial) logit link function (e.g., Choquet 2008). Regarding the observation process, if an individual was alive, it could be recaptured (respectively not recaptured) with probability p (respectively $1 - p$); if an individual has just died from hunting, it could be recovered (respectively not recovered) with probability r (respectively $1 - r$) (see Appendix S1). We analyzed males and females separately because in wild boars, sexual dimorphism in size is important and harvest regulations differ between the sexes. Both capture and tag recovery protocols were constant over the course of the study, thus recapture and recovery probabilities were assumed to be constant over time. We used a Z -test to evaluate whether sex had an effect on recapture and recovery probabilities (Lebreton et al. 1992).

We tested different hypotheses regarding the mortality parameters. First, we assessed whether the probability of being harvested increased with age (Toïgo et al. 2008) by modeling an age-specific mortality due to hunting (i.e., a three age-class model). Second, as juveniles generally are more vulnerable to environmental factors than yearlings (individuals between 1 and 2 years of age) or adults (individuals older than 2 years) (Gaillard et al. 2000), we fitted models including age-specific natural mortality. Third, we considered a model in which the two mortality causes were age-specific. Fourth, we tested whether the mortality probability was the same between the two periods by considering a model in which natural mortality and mortality due to hunting were constant over the study period. Fifth, we tested whether natural mortality was different between the two periods. Sixth, we expected mortality to be higher during the period of more intensive harvest pressure; we therefore fitted a model in which mortality due to hunting was different between the two periods. Lastly, we assessed whether an increase of hunting pressure could influence the two mortality causes; this was achieved by fitting a model in which natural mortality and mortality due to hunting differed between periods.

To compare among the various competing models, we used the Akaike’s information criterion (Burnham and Anderson 2002) corrected for small sample size (AICc). The model with the lowest AICc was selected as the best one. These analyses were implemented in E-SURGE (Choquet et al. 2009).

SELECTION GRADIENTS ON BIRTH DATE THROUGH MORTALITY PARAMETERS

We linked fitness components (i.e., natural mortality and mortality due to hunting) with birth date to evaluate the effect of an early or a late birth date on the two mortality causes. Relying on the best model from the previous analyses, we incorporated the date of birth as an individual covariate to assess a linear effect of birth date on natural mortality and mortality due to hunting. The logistic-like regression coefficients we obtained from the CMRR analyses could not be used directly in the equations modeling the micro-evolutionary change of birth date, but the selection gradients obtained from a linear regression approach can be substituted. Adapting the approach proposed by Janzen and Stern (1998), we transformed the regression coefficients (slopes and intercepts) to obtain approximate selection gradients. The expressions of natural mortality (Mn) and mortality due to hunting (Mh), considered as functions of birth date, were derived for each individual. The average of these derivatives for all the individuals was the average selection gradient (β) on birth date through the mortality probability (Janzen and Stern 1998)

$$\beta = \frac{1}{N} \sum_{i=1}^N \left. \frac{\partial M(x_i)}{\partial x_i} \right|_{x_i}$$

where N is the number of individuals, x_i the birth date of individual i and M stands for Mn or Mh . We used a nonparametric bootstrap procedure to obtain confidence intervals for the selection gradients and their significance (Davison and Hinkley 1997) because average selection gradients are functions of estimated parameters (slopes and intercepts) that are subject to uncertainty (measured as SE).

SELECTION GRADIENTS ON BIRTH DATE THROUGH REPRODUCTIVE PARAMETERS

About half of all juveniles gave birth at one year, whereas more than 90% yearlings and adults gave birth annually (Servanty et al. 2009). Because variation in breeding probabilities (BP s) of yearling and adult females was low, we assumed that birth date does not influence BP of yearlings and adults. We thus only used reproductive data from juvenile females. To assess an effect of birth date on BP of juveniles, we fitted logistic regressions with possible additional effects of period and year on either the intercept or the slope (implemented in R 2.10.1, R Development Core Team 2009), using AICc for model selection (Burnham and Anderson 2002). We used a similar procedure as that for mortality gradients to obtain selection gradients on birth date through BP , together with their confidence intervals.

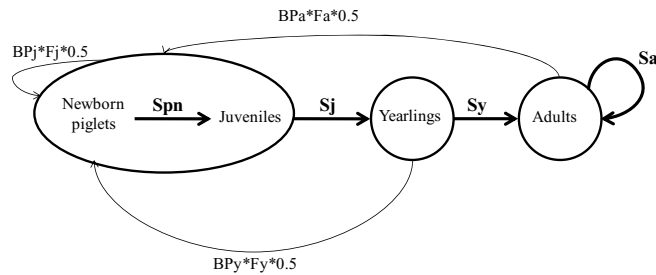


Figure 2. Wild boar (*Sus scrofa scrofa*) life cycle. *Spn*, *Sj*, *Sy*, and *Sa* are, respectively, postnatal, juvenile, yearling, and adult survival probabilities. *BPj*, *BPy*, and *BPa* are breeding probabilities for the three age classes juvenile, yearling, and adult. *Fj*, *Fsa*, and *Fa* are fecundities (the mean number of piglets produced) for juvenile, yearling, and adult. The sex ratio is 0.5.

MATRIX MODELING

Fitness components (*Mh*, *Mn*, and *BP*) were integrated in a two-sex age-structured population model (Caswell 2001) for each period separately (see Appendix S2). We considered a prebreeding census model and three age-classes based on the wild boar life cycle (Fig. 2): juveniles (*j*) (1-year old), yearlings (*y*) (2-year old) and adults (*a*) (older than 2 years of age). Sex-specific survival parameters (*m* for males and *f* for females) included juvenile overall survival (i.e., survival after taking into account both natural and hunting mortalities: $Sj = 1 - Mhj - Mnj$), yearling survival (*Sy*) and adult survival (*Sa*). Recruitment rate per age-class was obtained as the product of the age-specific proportion of breeding females (juvenile: 51%; yearling: 90%; adult: 97%, Servanty et al. 2009), the mean number of juveniles produced per age-class (juvenile: 3.88; yearling: 5.40; adult: 6.36, Servanty et al. 2011), the postnatal survival (i.e., from birth to weaning) based on expert opinion (0.75), and the survival of the considered age-class. We assumed a balanced sex ratio at birth.

The proportional change in population growth rate resulting from a hypothetical proportional change in matrix elements was quantified by calculating elasticities. Elasticity of a_{11} , which is the value of the matrix element in row 1 and column 1, is defined as $\frac{\partial \log \lambda}{\partial \log a_{11}}$ (de Kroon et al. 2000; Caswell 2001) and was calculated for each period.

The elasticities of matrix elements were used to calculate elasticities of fitness components, that is the proportional change in population growth rate resulting from a hypothetical proportional change in demographic parameters (juvenile *BP* and natural mortality probability, mortality probability due to hunting in each age-class and each sex). For a given fitness component, we summed all its elasticities on the pathways where we found it to obtain the total effect of this fitness component (Coulson et al. 2003).

Matrix modeling and the calculation of elasticities were performed with program ULM (Legendre and Clobert 1995).

LINKING SELECTION GRADIENTS WITH ELASTICITIES OF FITNESS COMPONENTS: THE ELASTOGRAM

Selection gradients and elasticities of fitness components were connected in a path diagram also called an elastogram (Van Tienderen 2000) to estimate the proportional change in population growth rate resulting from a hypothetical proportional change in birth date. The elastogram incorporates all paths between the trait (birth date) and the population growth rate (Fig. 3). Elasticity of birth date via a specific pathway, or rather fitness component, is given by the product of the selection gradient for the trait on a fitness component and the elasticity of the fitness component of population growth rate (Coulson et al. 2003). For example, elasticity of birth date via pathway no. 1 (see Fig. 3) is the product of the selection gradient through *BPjf* and elasticity of *BPjf*. Selection on birth date is calculated as the sum of the product of all pathways between the trait and population growth rate.

OBSERVED VERSUS EXPECTED RESPONSE TO SELECTION

To validate the model, we compared the observed response to selection with the response expected from our model. More specifically, we estimated an additive genetic variance for which the observed response to selection was equal to the expected response. The observed response was estimated as the temporal trend in birth date over the study period, which is the slope of the regression of birth date on time in years. Expected response to selection (*ER*) was obtained by multiplying the evolvability by selection on birth date (Coulson et al. 2003). Selection on the trait, estimated for each period, allows the calculation of total selection over the study period. Evolvability was estimated using generation time (estimated at 2.3 years in this population; Servanty et al. 2011), number of years of the studied period, and additive genetic variation (*Va*) (Coulson et al. 2003):

$$ER = \frac{22 \times Va}{2.3} \times \text{total selection}$$

Because no information was available on the additive genetic variation in birth dates of wild boar, we evaluated the expected response to selection. We checked the value of additive genetic variation for which observed and expected responses to selection were equal.

Results

BIRTH DATES

Births occurred throughout the year but there was a marked peak in the 10th fortnight (i.e., mid-April) (Fig. 4). Birth dates occurred 12 days earlier in 2003–2004 than 22 years before (slope = -0.038 , SE: 0.003, $P = 0.003$). The ANCOVA showed marked

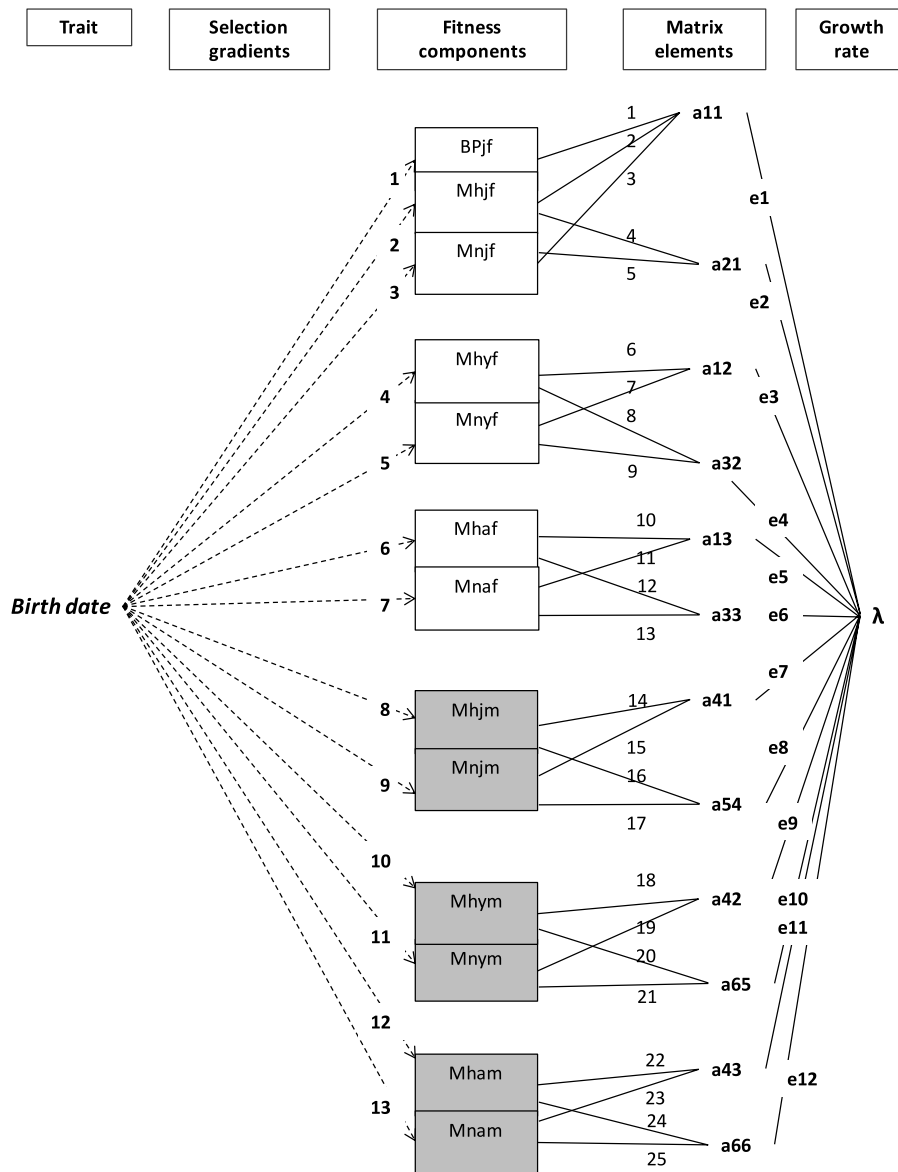


Figure 3. Elastogram. Selection gradients in dotted lines are numbered from 1 to 13 in the left of the elastogram and link the trait, that is birth date, with fitness components [BP = breeding probability; Mh = mortality due to hunting and Mn: natural mortality for male (m) and female (f), juvenile (j), yearling (y) and adult (a)]. Dark components are male ones. Each fitness component is located in one or several matrix elements (Appendix S2). Mhjf for example, is in the matrix element a21 (2nd row and 1st column) and in the matrix element a11. Each of these matrix elements has an elasticity (e) on population growth rate λ . Selection can thus operate via 25 paths numbered from 1 to 25 in the right of the elastogram.

interactive effects between hunting period and time on birth dates ($P = 2.88 \times 10^{-05}$). During the period of low hunting pressure, the annual birth date decreased through time at a rate of -0.480 (SE: 0.127) day per year. During the period of high hunting pressure, the rate of annual change of birth date reduced by -0.020 (SE: 0.017) day per year, leading to an almost constant birth date over time (Fig. 5). However, birth date in a given year was much earlier during the high hunting period than during the low hunting one (difference in intercept of 913.010 (SE: 217.818)).

MORTALITY PARAMETERS

For males, the best model included among age-class differences but not between-period differences in both mortality due to hunting and natural mortality ($\Delta AICc = 33.736$) (Table 1A). Probability of being harvested was high and increased with age, from 0.376 (SE: 0.026) for juveniles, to 0.421 (SE: 0.049) for yearlings, and 0.758 (SE: 0.038) for adults. We estimated natural mortality of juveniles at 0.094 (SE: 0.053), of yearlings at 0.347 (SE: 0.069), and of adults at 0.001 (SE: 0.001). Consequently, annual survival

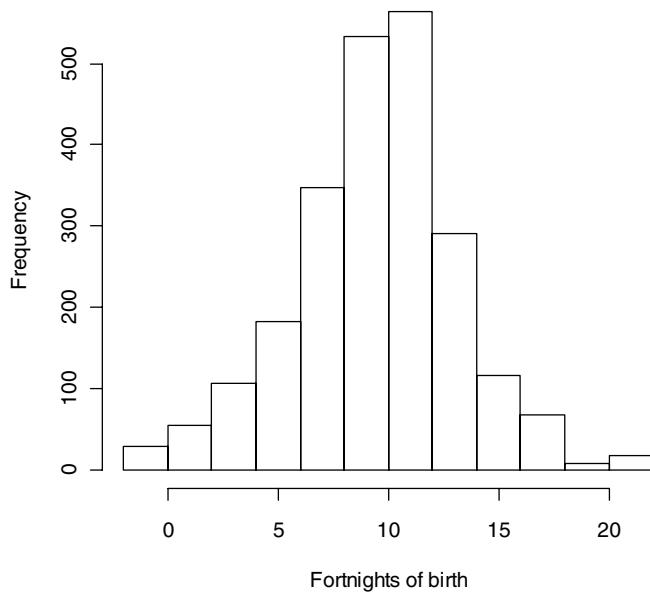


Figure 4. Distribution of fortnights of birth of all individuals during the studied period, that is from the season 1981–1982 to 2003–2004. Fortnight number 0 is the first fortnight of November, fortnight number 10 is the first one of April and fortnight number 20 is the second one of August.

was estimated at 0.530 for juveniles, 0.232 for yearlings, and 0.241 for adults. Recapture probability for males was estimated at 0.130 (SE: 0.016) and recovery probability was estimated at 0.958 (SE: 0.051).

For females, the best model included between-period differences in both mortality due to hunting and natural mortality but not difference among age classes ($\Delta\text{AICc} = 13.97$). This model was better supported by the data than the model incorporating the same mortality probabilities between periods ($\Delta\text{AICc} = 6.958$) (Table 1A). Mortality due to hunting increased from 0.333 (SE: 0.030) during the weakly hunted period to 0.452 (SE: 0.018) during the highly hunted period. Natural mortality was estimated to be 0.138 (SE: 0.025) during the first period and to be 0.115 (SE: 0.011) during the second period. Annual survival was estimated to be 0.529 during the first period and at 0.432 during the second period. Recapture probability for females was estimated at 0.211 (SE: 0.017) and recovery probability was estimated at 0.798 (SE: 0.013).

When comparing the difference between males and females, the recapture probability for females was higher ($z = 3.552$, $P = 0.0002$), whereas recovery probability was higher for males ($z = 3.047$, $P = 0.001$).

SELECTION GRADIENTS ON BIRTH DATE THROUGH MORTALITY PARAMETERS

For males, birth date was incorporated in the model including age-dependent natural and hunting mortalities. We assumed that the

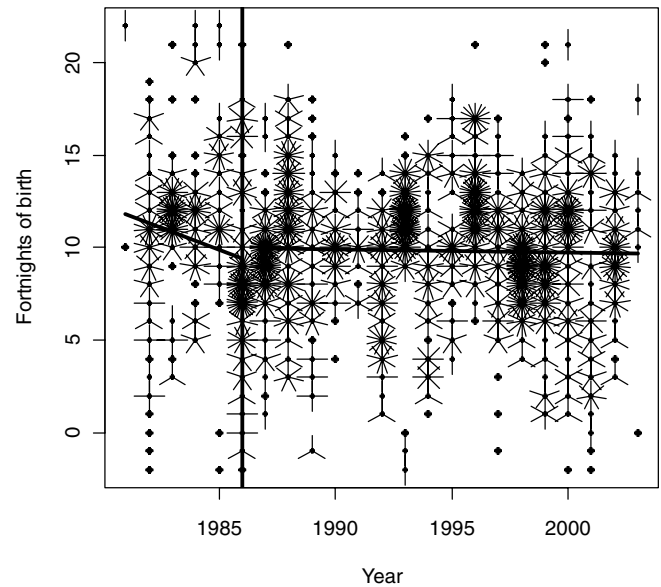


Figure 5. Linear effect of year (solid lines) for the weakly hunted period (slope: -0.480 , SE: 0.127) and for the highly hunted period (slope: -0.020 , SE: 0.017). The two periods corresponding to two different hunting pressures are separated by the vertical solid line. One petal of a flower corresponds to one point, that is the number of individuals born the same fortnight and the same year.

selection gradients through male mortality parameters were the same irrespective of period because no period effect was detected. Selection gradients were estimated to be -0.006 (SE: 0.007) for Mh and 0.002 (SE: 0.013) for Mn for juveniles, -0.002 (SE: 0.011) for Mh and 0.010 (SE: 0.013) for Mn for yearlings, and 0.003 (SE: 0.011) for Mh and -0.002 (SE: 0.006) for Mn for adults. No selection gradient was significantly different from 0. For females, birth date was incorporated into the model having period-specific hunting and natural mortalities. For the low hunting intensity period, selection gradients did not differ from 0 in any case and were estimated to be 0.011 (SE: 0.010) for Mh and -0.005 (SE: 0.012) for Mn . For the high hunting intensity period, selection gradients were estimated to be 0.006 (SE: 0.010) for Mh and -0.003 (SE: 0.014) for Mn . Again, no selection gradient was significantly different from 0.

SELECTION GRADIENTS ON BIRTH DATE THROUGH REPRODUCTIVE PARAMETERS

Over the study period, BP in the first year of life was affected by birth date, year, period, and interactions between birth date and period and between period and year. The same analysis conducted on each period separately allowed a simpler interpretation of these complex interactions. The best model for the weakly hunted period showed that BP for juveniles was influenced by year (linear effect) (Table 1B) but not birth date (slope = 0.060; SE: 0.160). However, the most parsimonious model showed that BP in the

first year of life was constant ($\Delta AICc = 0.266$). Consequently, there was no detectable selection gradient on birth date through *BP* in the first period. On the other hand, the best model for the highly hunted period showed that *BP* was influenced by birth date (Table 1B). The later the birth date, the lower the *BP* (slope = -0.137 ; SE: 0.040). In this period, the selection gradient on birth date through juvenile *BP* was estimated to be -0.026 and differed significantly from 0 (SE: 0.006; $P < 0.05$). A delay of one fortnight in birth date translated into a 2.6% decrease in the *BP*.

CALCULATION OF ELASTICITIES

The population growth rate was calculated for each period. It was estimated at 1.215 during the weakly hunted period and at

1.0 during the highly hunted period. Elasticities were similar between periods (Table 2A). Overall survival of juvenile females, including both natural mortality and mortality due to hunting, had the highest elasticity. Population growth rate was most sensitive to changes in juvenile female survival. For instance, an increase of 10% in juvenile female survival led to an increase of 3% in the population growth rate. As expected when the number of males is not limiting female breeding, the elasticities of matrix elements involving male fitness components were quasi null. Total elasticities of fitness components were obtained from elasticities of matrix elements for each period (Table 2B). In the weakly hunted period, the elasticity of *BP* for juvenile females was positive. A 10% *BP* increase led to a 1.4% population growth rate increase.

Table 1. Model selection results. Displayed are the number of parameters (*Np*) and difference in *AICc* between each tested model and the best model ($\Delta AICc$); for (A) effects of period (*P*), age-classes (3a for juvenile, yearling, and adult), on survival probability (*S*, including mortality due to hunting *Mh* and natural mortality *Mn*) for males (*M*) and females (*F*). *AICc* of the best models are 3256.119 (males) and 3349.988 (females); and for (B) effects of birth date and year depending on period on breeding probability in the first year of life (*BP*) via logistic regression models. *AICc* of the best models are 37.137 (weakly hunted period) and 470.902 (highly hunted period).

Model	Biological meaning	<i>Np</i>	$\Delta AICc$
A			
M			
<i>S(Mh)_3a - (Mn)_3a</i>	<i>Mh</i> and <i>Mn</i> depend on three age-classes	8	0
<i>S(Mh)_3a - (Mn)</i>	<i>Mh</i> depends on three age-classes- <i>Mn</i> constant	6	9.239
<i>S(Mh)_P - (Mn)_P</i>	<i>Mh</i> and <i>Mn</i> depend on period	6	33.736
<i>S(Mh)_P - (Mn)</i>	<i>Mh</i> depend on period- <i>Mn</i> constant	5	35.888
<i>S(Mn)_P - (Mh)</i>	<i>Mn</i> depend on period- <i>Mn</i> constant	5	42.085
<i>S(Mn)_3a - (Mh)</i>	<i>Mn</i> depends on three age-classes- <i>Mh</i> constant	6	45.087
<i>S</i>	<i>Mn</i> and <i>Mh</i> constant	4	45.204
F			
<i>S(Mh)_P - (Mn)_P</i>	<i>Mh</i> and <i>Mn</i> depend on period	6	0
<i>S(Mh)_P - (Mn)</i>	<i>Mh</i> depends on period- <i>Mn</i> constant	5	0
<i>S</i>	<i>Mn</i> and <i>Mh</i> constant	4	6.958
<i>S(Mn)_P - (Mh)</i>	<i>Mn</i> depends on period- <i>Mh</i> constant	5	8.679
<i>S(Mn)_3a - (Mh)</i>	<i>Mn</i> depends on three age-classes- <i>Mh</i> constant	6	10.284
<i>S(Mh)_3a - (Mn)</i>	<i>Mh</i> depends on three age-classes- <i>Mn</i> constant	6	12.472
<i>S(Mh)_3a - (Mn)_3a</i>	<i>Mh</i> and <i>Mn</i> depend on three age-classes	8	13.97
B			
Weakly hunted period			
<i>BP</i> (year)	<i>BP</i> depends on year	3	0
<i>BP</i> (constant)	<i>BP</i> constant	2	0.266
<i>BP</i> (birth date)+year	<i>BP</i> depends on birth date, year (additive)	4	1.463
<i>BP</i> (birth date)	<i>BP</i> depends on birth date	3	2.127
<i>BP</i> (birth date)×(year)	<i>BP</i> depends on birth date, year (interaction)	5	2.946
Highly hunted period			
<i>BP</i> (birth date)	<i>BP</i> depends on birth date	3	0
<i>BP</i> (birth date)+(year)	<i>BP</i> depends on birth date, year (additive)	4	1.830
<i>BP</i> (birth date)×(year)	<i>BP</i> depends on birth date, year (interaction)	5	3.640
<i>BP</i> (constant)	<i>BP</i> constant	2	10.656
<i>BP</i> (year)	<i>BP</i> depends on year	3	12.646

Table 2. Elasticities depending on the period of (A) matrix elements with for example a_{21} corresponding to matrix element in row 2 and column 1 (see Appendix S2); (B) fitness components in females (mortality due to hunting Mh, natural mortality Mn) for juveniles (j), yearlings (y), and adults (a), and breeding probability (BP) (male components elasticities are not indicated here because they are quasi null). Highest elasticities (positive and negative) are in bold.

A	Elasticity	
	Weakly hunted period	Highly hunted period
Matrix elements		
a11	$e_1=0.142$	0.142
a21	$e_2=0.299$	0.299
a12	$e_3=0.151$	0.151
a32	$e_4=0.147$	0.147
a13	$e_5=0.147$	0.147
a33	$e_6=0.113$	0.113
$a_{41}/a_{54}/a_{42}/a_{65}/a_{43}/a_{66}$	$e_8=e_9=e_{10}=e_{11}=e_{12}=0$	0
B		
Fitness components		
BPj	0.142	0.142
Mhj	-0.277	-0.461
Mnj	-0.115	-0.117
Mhy	-0.188	-0.313
Mny	-0.078	-0.080
Mha	-0.164	-0.273
Mna	-0.068	-0.069

The population growth rate during the period of low intensity hunting was most sensitive to a given change in mortality due to hunting for juveniles. A 10% mortality due to hunting for juvenile increase led to a 2.8% population growth rate decrease. During the period of high-intensity hunting, the population growth rate was most sensitive to mortality due to hunting for juveniles. In this period, a 10% mortality increase due to hunting for juvenile females led to a 4.6% population growth rate decrease.

LINKING SELECTION GRADIENTS WITH ELASTICITIES OF FITNESS COMPONENTS

For each period, selection via different pathways (Fig. 3) was estimated from selection gradients and elasticities of fitness components. In the first period (Fig. 6A), selection varied among pathways. Most pathways describing the elasticities of population growth rate with respect to birth date were negative, suggesting an advantage of being born earlier. Pathways associated with mortality due to hunting for each age-class (i.e., pathways number 2, 4, 6, 8, 10, and 12) had the highest elasticity. In the second period (Fig. 6B), selection also varied among pathways. Most pathways describing the elasticities were negative, again suggesting an advantage of being born earlier. Pathways associated with mortality due to hunting for each age-class (i.e., pathways num-

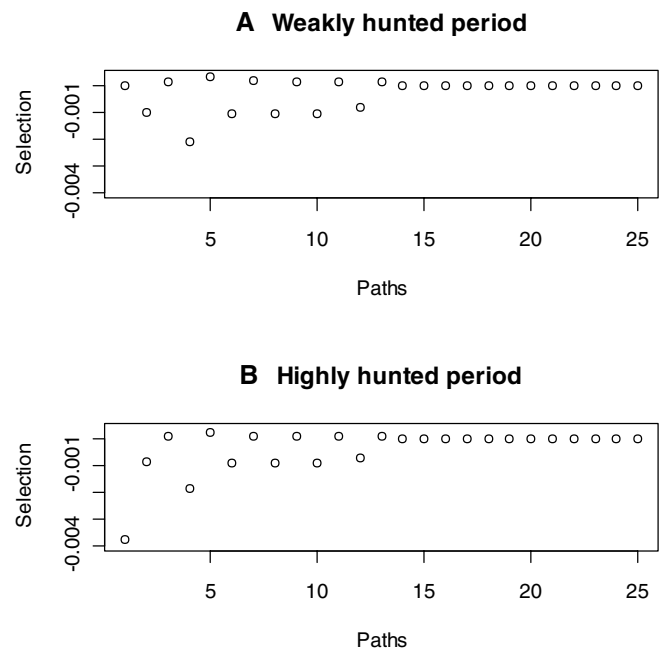


Figure 6. Selection on birth date via the different paths (see Elastogram Fig. 3 for the meaning of path numbers) during (A) the weakly hunted period, and during (B) the highly hunted period. The first path of the highly hunted period is associated with juvenile female breeding probability and has the highest elasticity.

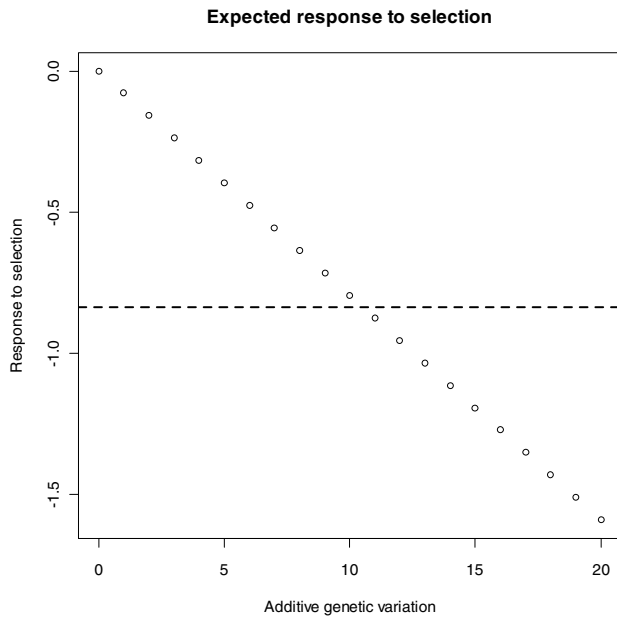


Figure 7. Expected response to selection over the study as a function of a range of possible values for additive genetic variation. The dotted line is the observed response to selection (-0.836). Expected response to selection and observed response are equal for an additive genetic variation estimated at 10.524.

ber 2, 4, 6, 8, 10, and 12) had again a high elasticity but pathway associated with juvenile female BP (i.e., pathway no. 1) had the highest one. The elastogram (Fig. 3) linking selection gradients to fitness components, to matrix elements, and finally to population growth rate showed an increasing total selection on birth date from the weakly hunted period (-0.006) to the highly hunted period (-0.009). A 10% increase of mean birth date during the weakly hunted period, with individuals born on average 15 days later, led to a 0.06% population growth rate decrease, while the same increase of mean birth date during the highly hunted period led to a 0.09% population growth rate decrease.

OBSERVED VERSUS EXPECTED RESPONSE TO SELECTION

The observed response to selection over the whole study period was estimated to be -0.038 (SE: 0.003) fortnight per year, giving a response to selection of -0.836 fortnight over the 22 years of the study, corresponding to a decrease in birth date of 12 days over that period. The expected response to selection oscillated between -1.6 and 0 depending on the values of additive genetic variation (Fig. 7). The expected and observed response to selection was matching for $Va = 10.524$.

Discussion

Several studies have shown that exploitation has strong evolutionary consequences (Allendorf and Hard 2009; Fenberg and

Roy 2008). Here, we found a selection for early birth dates of wild boar subject to high hunting pressure, which allows juvenile females to grow for longer and thereby to reach the threshold size for giving birth at one year of age. This result was achieved by applying quantitative tools from population ecology and selection gradient analysis (Coulson et al. 2010) using a procedure developed by Van Tienderen (2000; see also Coulson et al. 2003 for an application to red deer *Cervus elaphus*). Overall, we provide here the first application of this framework to exploited populations. This approach allows studying selection possibly operating via multiple fitness components, whereas selection gradients are generally calculated using only a single fitness component (Kingsolver et al. 2001). In particular, we have paid particular attention to estimate mortality rates and selection gradients while accounting for the issue of detectability less than one (Gimenez et al. 2006; 2009). If ignored, imperfect detection may lead to flawed inference about evolutionary studies and mark–recapture models provide appropriate tools to cope with this issue (Gimenez et al. 2008).

During the highly hunted period, BP in the first year of life increased when birth dates occurred earlier, indicating a benefit for female wild boar to give birth early. Such a positive association between birth date and primiparity has been repeatedly reported in populations of large herbivores (Sadleir 1987). In wild boar like in other ungulates (Gaillard et al. 2000), females have to reach a threshold body mass (27–33 kg) before breeding for the first time although this threshold is much lower in wild boar than in similar-sized species (Servanty et al. 2009). Threshold body mass in wild boar was reached earlier in the year when individuals were born early, allowing them to give birth at one year. On the contrary, when born late, individuals reached the threshold body mass only after the breeding season and thus had to breed the next season.

Mortality due to hunting was very high for both sexes and higher than natural mortality, which confirms the pattern generally observed in hunted adult animals (Festa-Bianchet 2003). In males, the mortality rates were identical between the two periods corresponding to the fact that shooting rules did not change between periods. However there were differences among age-classes, the probability of being harvested increasing from juveniles to adults. Mortality due to hunting was the highest for adult males. This might be because hunters prefer shooting an individual alone, easily identifiable as a male, to avoid shooting in a group and thus pay a tax if they kill a female with dressed body mass higher than 50 kg. Natural mortality was different among age-classes, with the highest one for yearlings. This result can be explained by the fact that yearling males often disperse from their natal area (Truvé and Lemel 2003, Mauget et al. 1984) and are faced with increased mortality risk due to collisions with vehicles in particular.

In females, mortality rates were the same among the three age-classes but were different between periods of contrasting

hunting pressure. Nevertheless, all age-classes taken together, mortality due to hunting in females was lower than for males when the hunting rule protects females (see also Toïgo et al. 2008). However, one female of two did not survive between two consecutive years, which corresponds to a huge mortality for an ungulate (Toïgo and Gaillard 2003).

The elasticity analysis we performed on wild boar was expected to give similar results to those obtained for other large mammals, that is the highest elasticity for adult survival (Brault and Caswell 1993; Gaillard et al. 2000). In ungulate females, adult survival is generally high (Toïgo and Gaillard 2003), and females skip a reproductive event instead of jeopardizing their own survival (environmental canalization of adult survival sensu Gaillard and Yoccoz 2003). In the wild boar, elasticities for males were quasi null showing females drive the population demography. In fact, when the number of males is not limiting female breeding, male survival has no influence on the population growth rate (see Gaillard et al. 2003 for a discussion). Nevertheless, we showed that a variation in juvenile female survival had an effect twice as big on population growth rate as the same variation in any other parameter. More precisely, juvenile female mortality from hunting had the highest negative elasticity. An increase in mortality due to hunting in juvenile stage had a higher negative effect on population growth rate than the same variation on any other parameter. Moreover, the fitness component having the highest positive elasticity is the juvenile female *BP*; population growth rate increased the most when juvenile breeding probability increased. Juvenile survival and juvenile breeding are thus the two main parameters driving the demography of this population (see also Servanty et al. 2011). This pattern is usually observed in small mammals that have a short life span leading to early breeding in their life. A recent study (Servanty et al. 2011) showed that a weakly hunted population of wild boar had the typical demographic pattern observed in other long-lived species, that is, a population growth rate most sensitive to adult survival, a higher growth rate and a longer generation time (3.70 years in a weakly hunted population vs. 2.30 years in Châteauvillain) than observed in our population. This uncommon demographic pattern present in wild boar is likely shaped by high hunting pressure (Toïgo et al. 2008) that greatly reduces wild boar survival and puts a selective pressure favoring an earlier age and a decreased threshold body mass at primiparity (Servanty et al. 2009).

The critical role of juvenile parameters in hunted wild boar populations was confirmed by the study of selection gradients. Indeed, the only gradient we detected was through juvenile female breeding probability during the highly hunted period. There was a clear directional selection over the studied period for an earlier birth date, mainly via juvenile female reproduction. During the highly hunted period, early birth dates were selected for, allowing an early primiparity that increased population growth rate. For

example, an individual born on the 10 November had a breeding probability in the first year of life estimated at 50%, whereas an individual born on the 30 June had a breeding probability estimated at 11.4%. Individuals that reproduced from their first year of life, that is individuals that were born early in the year, could produce offspring, whereas 50% of those not born early will be hunted and not produce offspring in the next year. This discrepancy between individuals born early versus late within the same year led to a marked difference in lifetime reproductive success because wild boar life span in this population was much reduced by the low survival caused by heavy hunting. However, early breeding could lead to reproductive costs in terms of future survival (Hamel et al. 2010, see for instance Moyes et al. 2006 in red deer). Nevertheless, such reproductive costs are not expected to be counter-selected in the studied population where most females only have one or two reproductive attempts on average.

We showed a selection through increasing juvenile breeding probability that led to an advance of birth dates estimated at 12 days over the 22 years study period. These earlier birth dates could be caused by hunting or environmental conditions. In many nonexploited populations, the mean breeding date has advanced by up to several days and hunting could not be responsible for this phenological advance (Parmesan 2006). In red deer for example, mean birth date was 10 days earlier than before and contrary to our study was linked to climate change (Coulson et al. 2003). In the case of wild boar, earlier birth dates were mainly affected by the hunting pressure. Selection could favor plasticity on birth dates, allowing a female breeding early or late in the season depending on hunting pressure. For example, the stress generated by hunting could favor early birth as observed in populations suffering a high level of predation (Krebs et al. 1995; Boonstra et al. 1998). However, the between-period differences in the annual response of birth dates to exploitation showed an unexpected pattern: the response was very weak during the period of high hunting pressure. The high hunting pressure could have led to changes in the population structure by increasing the proportion of juveniles that reproduce early. As first breeders generally give birth later in the season than experienced breeders in ungulate populations (see e.g., Festa-Bianchet 1988b), the average birth date should be delayed when an increased proportion of juveniles give birth. If we assume that the observed response to selection is a microevolutionary response to hunting pressure, the comparison between observed and expected response led to an estimate of additive genetic variation at 10.524. This value is close to the phenotypic variation value estimated at 14.039, which is consistent with a microevolutionary response. Consequently, the low response to selection during the high hunting period might also involve the fact that an evolutionary limit on birth dates has been reached by the lack of genetic variation, as recently demonstrated in laboratory conditions (Hine et al. 2011). Although our additive genetic variance estimation was based on

strong assumptions, our genetic variance was high and accounted for a large part of the phenotypic variation. We are thus inclined to favor the first hypothesis (i.e., a change in age structure caused by hunting). A definite answer would require genealogical data with pedigrees allowing the decomposition of phenotypic variability in genetic versus environmental sources via quantitative genetic tools (Pemberton 2010).

We demonstrated that exploitation intensity and management have both demographic and evolutionary consequences. From a demographic point of view, the increase of hunting pressure had led to a decrease of population growth rate, from 1.215 to 1. From an evolutionary point of view, selection on early birth dates allows the population to adapt to this high hunting pressure.

ACKNOWLEDGMENTS

We are grateful to all those who helped capturing and marking wild boar, as well as those who helped collecting harvested wild boars, particularly P. Van den Bulck and G. Corbeau. We are grateful to the Office National des Forêts and to F. Jehlé, who allowed us to work on the study area. We thank A. Charmantier, T. Coulson, and one anonymous referee for their helpful comments that markedly improved our article. We warmly thank E. Bean for correcting our English. This work was supported by an ANR-JCJC grant, “Towards Capture–Recapture Mixed Models” (ANR-08-JCJC-0088–01).

LITERATURE CITED

- Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc. Natl. Acad. Sci. USA* 106:9987–9994.
- Andersen, K. H., and K. Brander. 2009. Expected rate of fisheries-induced evolution is slow. *Proc. Natl. Acad. Sci. USA* 106:11657–11660.
- Baubert, E., S. Servanty, and S. Brandt. 2009. Tagging piglets at the farrowing nest in the wild: some preliminary guidelines. *Acta Silv. Lign. Hung.* 5:159–166.
- Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. *Ecol. Monogr.* 79:371–394.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444–1454.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer Verlag, New-York.
- Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. *Funct. Ecol.* 21:387–393.
- Caswell, H. 2001. Matrix population models. 2nd ed. Sinauer, MA.
- Choquet, R. 2008. Automatic generation of multistate capture–recapture models. *Can. J. Stat.* 36:1–15.
- Choquet, R., L. Rouan, and R. Pradel. 2009. Program E-SURGE: a software application for fitting multievent models. Pp. 845–865 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, eds. Modeling demographic processes in marked populations. Environmental and ecological statistics series. Volume 3. Springer-Verlag, New York.
- Coltman, D. W., P. O’Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Coulson, T., L. E. B. Kruuk, G. Tavecchia, J. M. Pemberton, and T. H. Clutton-Brock. 2003. Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution* 57:2879–2892.
- Coulson, T., S. Tuljapurkar, and D. Z. Childs. 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *J. Anim. Ecol.* 79:1226–1240.
- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmsers. 2009. Human predators outpace other agents of trait change in the wild. *Proc. Natl. Acad. Sci. USA* 106:952–954.
- Davison, A. C., and D. V. Hinkley. 1997. Bootstrap methods and their application. Cambridge Univ. Press, New York.
- de Kroon, H., J. van Groenendael, and J. Ehrlen. 2000. Elasticities: a review of methods and model limitations. *Ecology* 81:607–618.
- Dunn, P. O., and D. W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 266:2487–2490.
- Fenberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Mol. Ecol.* 17:209–220.
- Fernandez-Llario, P., A. Parra, E. R. Cerrato and J. Hermoso de Mendoza. 2004. Spleen size variations and reproduction in a Mediterranean population of wild boar (*Sus scrofa*). *Eur. J. Wild. Res.* 50:13–17.
- Festa-Bianchet, M. 1988a. Birth date and survival in bighorn lambs (*Ovis canadensis*). *J. Zool.* 214:653–651.
- . 1988b. Age-specific reproduction of bighorn ewes in Alberta, Canada. *J. Mamm.* 69:157–160.
- . 2003. Animal behavior and wildlife conservation. Festa-Bianchet, M., Appollonio, Island, Washington, DC 191–207.
- Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.
- Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.
- Gaillard, J. M., D. Pontier, S. Brandt, J. M. Jullien, and D. Allaine. 1992. Sex-differentiation in postnatal-growth rate—a test in a wild boar population. *Oecologia* 90:167–171.
- Gaillard, J. M., D. Delorme, J. M. Jullien, and D. Tatin. 1993. Timing and synchrony of births in roe deer. *J. Mammal.* 74:738–44.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31:367–393.
- Gaillard, J. M., A. Loison, and C. Toigo. 2003. Variation in life history traits and realistic population models for wildlife management. Pp. 115–132 in Festa-Bianchet, M. ed. The case of ungulates. Festa-Bianchet, M., Appollonio, Island, Washington, DC.
- Gimenez, O., R. Covas, C. R. Brown, M. D. Anderson, M. Bomberger Brown, and T. Lenormand. 2006. Nonparametric estimation of natural selection on a quantitative trait using mark–recapture data. *Evolution* 60:460–466.
- Gimenez, O., A. Viallefont, A. Charmantier, R. Pradel, E. Cam, C. R. Brown, M. D. Anderson, M. Bomberger Brown, R. Covas, and J. M. Gaillard. 2008. The risk of flawed inference in evolutionary studies when detectability is less than one. *Am. Nat.* 172:441–448.
- Gimenez, O., A. Grégoire, and T. Lenormand. 2009. Estimating and visualizing fitness surfaces using mark–recapture data. *Evolution* 63:3097–3105.
- Hamel, S., J. M. Gaillard, N. G. Yoccoz, A. Loison, C. Bonenfant, and S. Descamps. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecol. Lett.* 13:915–935.
- Hilton-Taylor, C. 2000. IUCN red list of threatened species. IUCN, Gland, Switzerland. xviii 61.
- Hine, E., K. McGuigan, and M. W. Blows. 2011. Natural selection stops the evolution of male attractiveness. *Proc. Natl. Acad. Sci. USA* 108:3659–3664.

- Janzen, F. J., and H. S. Stern. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution* 52:1564–1571.
- Johnson, P. J., R. Kinsky, A. J. Loveridge, and D. W. MacDonald. 2010. Size, raity and charisma: valuing African wildlife trophies. *Plos ONE* 5: e12866.
- Keane, A., M. D. Brooke, and P. J. K. McGowan. 2005. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). *Biol. Conserv.* 126:216–233.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* 157:245–261.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- Lande, R. 1982. A quantitative genetic theory of life-history evolution. *Ecology* 63:607–615.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62:67–118.
- Lebreton, J.-D. 2005. Dynamical and statistical models for exploited populations. *Aust. N. Z. J. Stat.* 47:49–63.
- Lebreton, J. -D., J. D. Nichols, R. J. Barker, R. Pradel, and J. A. Spende-low. 2009. Modeling individual animal histories with multistate capture-recapture models. *Adv. Ecol. Res.* 41:87–173.
- Legendre, S., and J. Clobert. 1995. ULM, a software for conservation and evolutionary biologists. *J. Appl. Stat.* 22:817–834.
- Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. *J. Wildl. Manage.* 71:884–894.
- Mauget, R., R. Campan, F. Spitz, M. Dardaillon, G. Janeau, and D. Pepin. 1984. Synthèse des connaissances actuelles sur la biologie du sanglier, perspectives de recherche. Symposium international sur le sanglier, les colloques de l'INRA 22:15–50.
- Metcalf, C. J. E., and S. Pavard. 2007. Why evolutionary biologists should be demographers. *Trends Ecol. Evol.* 22:205–212.
- Moyes, K., T. Coulson, B. J. T. Morgan, A. Donald, S. J. Morris, and T. H. Clutton-Brock. 2006. Cumulative reproduction and survival costs in female red deer. *Oikos* 115:241–252.
- Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* 325:464–467.
- Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466:482–485.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol., Evol. Syst.* 37:637–669.
- Pemberton, J. M. 2010. Evolution of quantitative traits in the wild: mind the ecology. *Philos. Trans. R. Soc. Lond. B* 365:2431–2438.
- Pelletier, F., T. Clutton-Brock, J. Pemberton, S. Tuljapurkar, and T. Coulson. 2007. The evolutionary demography of ecological change: linking trait variation and population growth. *Science* 315:1571–1574.
- R Development Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rutberg, A. T. 1987. Adaptive hypothesis of birth synchrony in ruminants: an interspecific test. *Am. Nat.* 130:692–710.
- Sadleir, R. M. F. S. 1987. Reproduction of female cervids. Pp *in* 123–144 C. M. Wemmer ed. *Biology and management of the cervidae*. Smithsonian Institution Press, Washington, DC.
- Schaub, M., and R. Pradel. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology* 85:930–938.
- Servanty, S., J. M. Gaillard, C. Toigo, S. Brandt, and E. Baubet. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *J. Anim. Ecol.* 78:1278–1290.
- Servanty, S., J. M. Gaillard, F. Ronchi, S. Focardi, E. Baubet, and O. Gimenez. 2011. Influence of harvesting pressure on demographic tactics: implications for wildlife management. *J. Appl. Ecol.* doi: 10.1111/j.1365-2664.2011.02017.x [Epub ahead of print].
- Slobodkin, L.B. 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York.
- Smekens, M. J., and P. H. van Tienderen. 2001. Genetic variation and plasticity of *Plantago coronopus* under saline conditions. *Acta Oecol.* 22: 187–200.
- Toigo, C., and J. M. Gaillard. 2003. Causes of sex-biased adult survival in ungulates: sexual dimorphism, mating tactic or environment harshness? *Oikos* 101:376–384.
- Toigo, C., S. Servanty, J. M. Gaillard, S. Brandt, and E. Baubet. 2008. Disentangling natural from hunting mortality in an intensively hunted wild boar population. *J. Wildl. Manage.* 72:1532–1539.
- Truvé, J., and J. Lemel. 2003. Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. *Wild. Biol.* 9:51–57.
- van Tienderen, P. H. 2000. Elasticities and the link between demographic and evolutionary dynamics. *Ecology* 81:666–679.
- Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B* 275:649–659.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, London.

Associate Editor: M. Blows

Supporting Information

The following supporting information is available for this article:

Appendix S1. Multistate capture–recapture models.

Appendix S2. Transition matrix.

Supporting Information may be found in the online version of this article.

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