

Effects of pulsed resources on the dynamics of seed consumer populations: a comparative demographic study in wild boar

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Abstract. Mast seeding is a well-known example of pulsed resources in terrestrial ecosystems. Despite the large literature available so far on the effects of mast seeding on the dynamics of seed consumer populations, it remains unknown whether heterogeneity in demographic responses to mast seeding exists both within a population of consumers and among consumer populations. Here, we fill this knowledge gap by assessing the effects of acorn production (i.e., oak mast) on all stage-specific demographic rates (i.e., survival, growth, reproduction) in several consumer populations. From long-term capture–mark–recapture data collected in three wild boar populations in Europe and detailed information on annual acorn production, we quantified the effects of acorn production on body mass-specific demographic rates in these populations. We then built a body mass-structured population model for each population and assessed the effect of acorn production on generation time—the mean age of mother at childbirth—and population growth rate using a combination of prospective and retrospective demographic analyses. Within populations, acorn production had a positive effect on reproduction (proportion of breeding females) and growth of small-sized females. Survival remained buffered against environmental variation, in accordance with the demographic buffering hypothesis. Thus, all stage-specific demographic rates were not influenced in the same way by acorn production. In turn, higher reproduction and growth probabilities involved higher population growth rates and shorter generation times. Despite these common demographic responses to mast seeding among populations, we highlighted marked among-population variation in the magnitude of these responses. Also, while populations inhabiting resource-rich environments took advantage of current acorn conditions, populations under resource-poor environments stored and allocated acorns produced the preceding year to reproduction indicating contrasting breeding tactics along the capital–income continuum. Our results suggest heterogeneity in demographic responses to mast seeding, within and among populations. This is an important finding for our understanding of the effects of mast seeding on the dynamics of seed consumer populations.

Key words: acorn production; generation time; population growth rate; prospective analysis; retrospective analysis; *Sus scrofa*; ungulates.

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INTRODUCTION

Pulsed resources, that display a high variation in their availability, are widespread in many terrestrial and aquatic ecosystems (Ostfeld and Keesing 2000, Yang et al. 2008). Mast seeding, which is characterized by intermittent production of large seed crops synchronized at the tree population level (Ostfeld and Keesing 2000), constitutes a well-known example of pulsed resource in terrestrial ecosystems. Empirical evidence is accumulating that mast seeding and thus fluctuations in food resource availability may in turn influence the dynamics of seed consumer populations through its effects on survival, growth, reproduction, or immigration (Ostfeld and Keesing 2000, Holt 2008, Yang et al. 2008, Bogdziewicz et al. 2016). For instance, beechnut production (i.e., beech mast) has a positive effect on reproductive output and lifetime reproductive success of edible dormouse (*Glis glis*; Bieber and Ruf 2009) as well as on local recruitment and immigration rate of great tit (*Parus major*; Grøtan et al. 2009).

Due to marked differences in fruiting dynamics at both temporal and spatial scales, one can expect heterogeneity in demographic responses to mast seeding among populations. Surprisingly, until now, despite the large literature available on the effects of mast seeding on the population dynamics of seed consumers (reviewed in Ostfeld and Keesing 2000, Holt 2008, Yang et al. 2008, Bogdziewicz et al. 2016), few studies have investigated the effects of mast seeding on multiple populations, that is, at the intraspecific level (see Table 1 for a review). Furthermore, among the available studies, most of them have focused on rodents and very few on large mammals.

At the intrapopulation level, one can expect individuals to exhibit contrasting demographic responses to mast seeding depending on their (st)age. Indeed, there is growing evidence that individual heterogeneity in response to environmental fluctuations exists. Hence, Coulson et al. (2001) showed that survival of young and older individuals specifically was dependent on North Atlantic Oscillation and rainfall at the end of the winter in a Soay sheep (*Ovis aries*) population. Similarly, Hansen et al. (2019) showed that senescent individuals were the most sensitive to

increasing frequency of rain-on-snow events in a Svalbard reindeer (*Rangifer tarandus platyrhynchus*) population. Likewise, age-dependent effects of climate have been highlighted on Black-browed Albatrosses (*Thalassarche melano-phris*; Pardo et al. 2013). Among the comparative studies shown in Table 1, to the best of our knowledge, none has assessed the effect of mast seeding on all (st)age-specific demographic rates (i.e., survival, reproduction, growth across the life cycle). Assessing whether differences in demographic responses to fluctuating mast seeding occur between populations and within a population could undoubtedly offer new insights on demographic patterns observed across time and space *in natura*. Different conservation/management strategies could in fine be implemented for several populations of a focal species, if they have contrasting demographic responses to mast seeding.

Wild boar (*Sus scrofa*) is a widely distributed ungulate species worldwide (Massei and Genov 2004) that displays an unusual life history strategy among ungulates (Focardi et al. 2008). Despite its large size, wild boar exhibits a high fecundity, as they can produce up to 14 piglets per litter (Gamelon et al. 2013) and reproduce in their first year of life (Servanty et al. 2009). Wild boar preferentially feeds on acorns, the most common example of pulsed resources in temperate forest ecosystems (Caignard et al. 2017, Touzot et al. 2018, Schermer et al. 2019) during autumn–winter. Previous studies have shown that the long-term asymptotic population growth rate λ of wild boar populations and home range dynamics are dependent on the presence or absence of acorn production (Parsons 1962, Jędrzejewska et al. 1997, Bieber and Ruf 2005, Zeman et al. 2016, Bisi et al. 2018, Touzot et al. 2020, Vetter et al. 2020). However, none of these studies has assessed the effects of acorn production on all demographic rates (i.e., survival, growth, reproduction for all stages of the life cycle) on populations experiencing various ecological contexts. Whether populations exhibit common demographic responses to acorn production and whether, within a population, all individuals respond in the same way to acorn production remains to be carefully explored. Answering this question is of major importance to gain a good understanding of the effects of

Table 1. Summary of the comparative studies exploring an effect of mast seeding on the dynamics of multiple consumer populations.

Consumer species	Tree species	Demographic parameters	Populations	References
Great tit (<i>Parus major</i>)	Beech species (<i>Fagus sylvatica</i>)	+ Local recruitment + Immigration	5	Grøtan et al. (2009)
Flying squirrel (<i>Pteromys volans</i>)	Birch (<i>Betula</i> spp.) Alder (<i>Alnus</i> spp.)	+ Lifetime reproductive success + Longevity	2	Hoset et al. (2017)
Flying squirrel (<i>P. volans</i>)	Alder (<i>Alnus</i> spp.)	+ Fecundity	2	Hoset et al. (2017)
Flying squirrel (<i>P. volans</i>)	Food abundance in the following year: Birch (<i>Betula</i> spp.) Alder (<i>Alnus</i> spp.)	0 Production of summer litters	2	Selonen and Wistbacka (2016)
Flying squirrel (<i>P. volans</i>)	Food abundance in the preceding year: Birch (<i>Betula</i> spp.) Alder (<i>Alnus</i> spp.)	+ Production of summer litters	2	Selonen and Wistbacka (2016)
Eurasian red squirrel (<i>Sciurus vulgaris</i>)	Food abundance in the preceding year: Scots (<i>Pinus sylvestris</i>), Corsican pine (<i>Pinus nigra</i>), chestnut (<i>Castanea sativa</i>), oak (<i>Quercus</i> spp.), beech (<i>F. sylvatica</i>), hornbeam (<i>Carpinus betulus</i>), hazel (<i>Coryllus avellana</i>)	+ Proportion of females producing spring litters 0 Summer litter size 0 Proportion of females producing a summer litter 0 Summer population growth rate	3	Boutin et al. (2006)
Eurasian red squirrel (<i>S. vulgaris</i>)	Food abundance in the following year: Scots (<i>P. sylvestris</i>), Corsican pine (<i>P. nigra</i>), chestnut (<i>C. sativa</i>), oak (<i>Quercus</i> spp.), beech (<i>F. sylvatica</i>), hornbeam (<i>C. betulus</i>), hazel (<i>C. avellana</i>)	0 Proportion of females producing spring litters + Summer litter size + Proportion of females producing a summer litter + Summer population growth rate	3	Boutin et al. (2006)
Eurasian red squirrel (<i>S. vulgaris</i>)	Coniferous site: Scots pine (<i>P. sylvestris</i>) and Corsican pine (<i>P. nigra</i>) vs. Deciduous site: English oak (<i>Quercus robur</i>) and beech (<i>F. sylvatica</i>)	+ Number of litters + Litter size (old females) + Probability of producing a litter (young and old females)	2	Wauters and Dhondt (1995)
Red squirrels (<i>Tamiasciurus hudsonicus</i>)	White spruce (<i>Picea glauca</i>)	+ Population growth rate + Litter size 0 Parturition date + Offspring survival	2	McAdam et al. (2019)
Eastern chipmunks (<i>Tamias striatus</i>)	Beech (<i>F. grandifolia</i>) and red maple (<i>Acer rubrum</i>)	+ Proportion of females in summer estrus	3	Tissier et al. (2020)
Edible dormouse (<i>Glis glis</i>)	Beech (<i>F. sylvatica</i>)	+ Number of juveniles + Pre-hibernation body mass of adults + Body mass of adults at emergence from hibernation	2	Fietz et al. (2005)
Edible dormouse (<i>G. glis</i>)	Beech species (<i>F. sylvatica</i>) in the "forest" vs. less energy-rich food availability (e.g., fleshy fruits) in the "grove" and "hedge"	Forest vs. Grove/Hedge: + Reproductive output – Yearly survival probability of adults – Lifespan + Lifetime reproductive success	3 subpopulations (connected by (e) migration)	Bieber and Ruf (2009)
Edible dormouse (<i>G. glis</i>)	Food abundance in the previous year: Beech (<i>F. sylvatica</i>)	– Survival	2	Ruf et al. (2006)
Edible dormouse (<i>G. glis</i>)	Food abundance in the current year: Beech (<i>F. sylvatica</i>)	+ Reproduction	2	Ruf et al. (2006)

(Table 1. Continued.)

Consumer species	Tree species	Demographic parameters	Populations	References
Stoat (<i>Mustela erminea</i>)	Food abundance in the current year: Beech (<i>Nothofagus</i>)	+ Reproductive success	3	Wittmer et al. (2007)
Stoat (<i>M. erminea</i>)	Food abundance in the previous year: Beech (<i>Nothofagus</i>)	– Survival – Fertility	3	Wittmer et al. (2007)
American black bear (<i>Ursus americanus</i>)	Hard mast species (e.g., white oak <i>Quercus alba</i> , chestnut oak <i>Quercus prinus</i>)	0 Litter size – Missed reproductive opportunities	2	Bridges et al. (2011)
Wild boar (<i>Sus scrofa</i>)	Food abundance in the previous year: Beech (<i>F. sylvatica</i>) and oak (<i>Quercus petraea</i>) vs. Mediterranean oak (<i>Quercus ilex</i> , <i>Quercus cerris</i> , <i>Quercus frainetto</i>)	Beech (<i>F. sylvatica</i>) and oak (<i>Q. petraea</i>): + Juvenile body mass + Number of <i>corpora lutea</i> of juveniles + Litter size of juveniles Mediterranean oak (<i>Q. ilex</i> , <i>Q. cerris</i> , <i>Q. frainetto</i>): + Adult body mass + Number of <i>corpora lutea</i> of adults + Litter size of adults	2	Gamelon et al. (2017)
Wild boar (<i>S. scrofa</i>)	Food abundance in the current year: Beech (<i>F. sylvatica</i>) and oak (<i>Q. petraea</i>) vs. Mediterranean oak (<i>Q. ilex</i> , <i>Q. cerris</i> , <i>Q. frainetto</i>)	Beech (<i>F. sylvatica</i>) and oak (<i>Q. petraea</i>) and Mediterranean oak (<i>Q. ilex</i> , <i>Q. cerris</i> , <i>Q. frainetto</i>): + Adult body mass + Number of <i>corpora lutea</i> of adults + Litter size of adults	2	Gamelon et al. (2017)

Notes: Displayed are the primary consumer species, the tree species, the demographic parameters influenced by mast seeding with the sign of this effect, the number of populations included in the analysis, and the reference of the study. Note that experimental studies are not shown in this table.

mast seeding at both the intraspecific and intrapopulation levels.

Here, we took advantage of a long-term monitoring of three wild boar populations in France and Italy and explored how acorn production influences their demography. First, detailed information on annual acorn production was available in these populations allowing us to split the years in two categories: years of acorn production vs. scarce acorn production. Second, long-term detailed individual-based data (i.e., capture–mark–recapture data and hunting bags) in all wild boar populations allowed us to estimate stage-specific demographic rates (reproduction, survival, growth) and therefore population growth rate as well as generation time under the two regimes of acorn production. Third, for each population, we determined the demographic rates with the greatest potential to affect the population growth rate λ under the two conditions of acorn availability (years of acorn production vs. scarce acorn production) using a combination

of prospective and retrospective analyses (Horvitz et al. 1997, Caswell 2001, respectively). Prospective analyses include elasticity analyses and evaluate how a proportional change in a demographic rate would influence the population growth rate λ (de Kroon et al. 1986), under the two conditions of acorn availability. Retrospective analyses consist in life-table response experiment (LTRE) analyses that decompose the observed difference in λ under the two conditions of acorn availability into the relative contributions of each demographic parameter (Caswell 1989, 2010).

MATERIALS AND METHODS

Study areas

The data come from two long-term study sites in France (Châteauvillain and La Petite Pierre) and one site in Italy (Castelporziano; Fig. 1 and Table 2). In the fenced site at Castelporziano, dispersal/emigration outside the study area was not

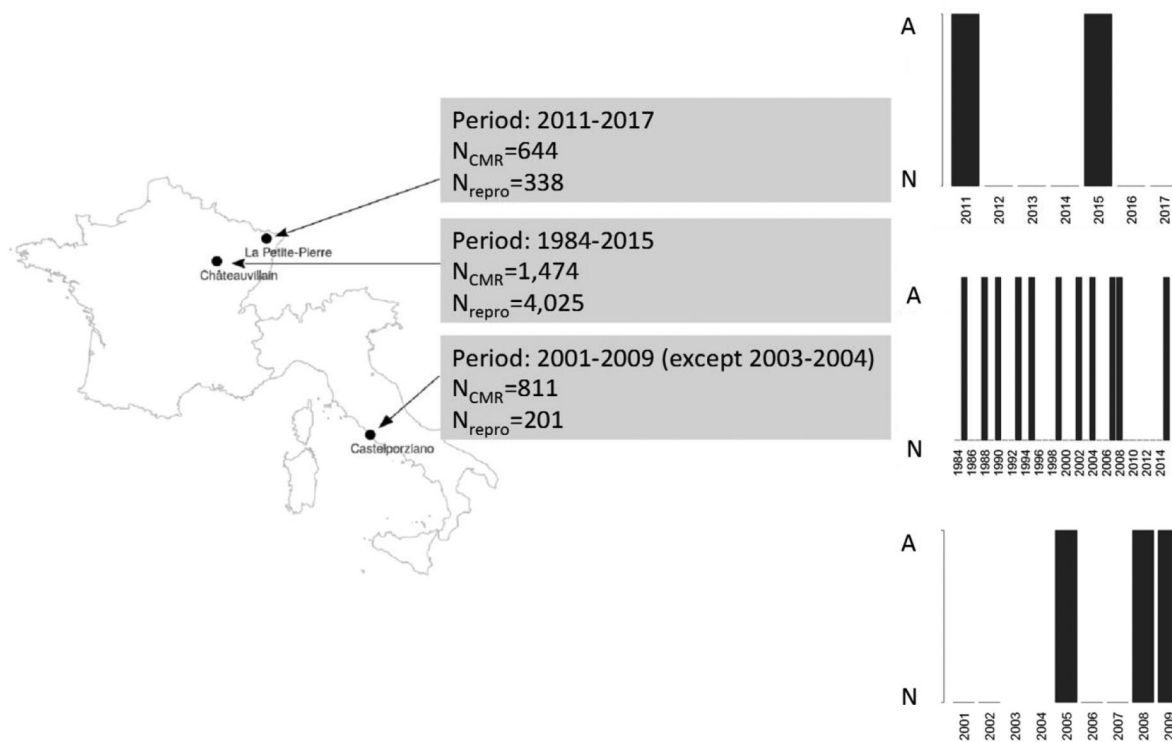


Fig. 1. Location of the three sites included in this study where the effect of acorn production on wild boar population dynamics was investigated. Displayed are the number of marked females as part of capture–recapture programs (N_{CMR}), the number of harvested females for which reproductive status has been assessed (N_{repro}), the study period, and the sequence of acorn production (years of scarce acorn production [N] and of acorn production [A]) during the studied period.

existent. In open sites at Châteauvillain and La Petite Pierre, we assumed no immigration and emigration as the probability for female wild boar dispersing is generally very low (Truvé and Lemel 2003, Keuling et al. 2010). In all sites, populations are subjected to hunting each year between October and February.

Acorn data collection

As acorn fall begins in early autumn in temperate oak forests, hereafter, we defined year from 1st October at year t to 30th September at year $t + 1$. In Châteauvillain, the absence of experimental design to collect acorns directly from the oak trees (see e.g., Touzot et al. 2018) or to measure growth characteristics (e.g., age of the trees, crown width, volume; see e.g., Kim et al. 2016) prevented us for obtaining any direct estimates of acorn production on this site. However, acorn production was measured annually indirectly

based on diet composition obtained from the analysis of stomach contents of harvested wild boars during the hunting season (see Brandt et al. 2006, Servanty et al. 2009, Gamelon et al. 2017, Touzot et al. 2020 for similar approaches). We identified two categories of years depending on the quantity of acorns found in the stomachs: years of acorn production (A) when acorns represented 50–90% of stomach contents; otherwise, the years were considered as scarce acorn production (N ; Fig. 1).

In other sites (Castelporziano and La Petite Pierre), acorn production was measured annually directly with seed traps (using the ground plot counting method, see Touzot et al. 2018). Between October and February, which corresponds to the period of acorn fall (Touzot et al. 2018), traps of 1 m² were placed under oak tree at about two-thirds the distance between the trunk and the canopy margin, where acorn

Table 2. Three sites included in this study where the effect of acorn production on wild boar population dynamics was investigated.

Study sites	Description	Climate	Forest composition
Châteauvillain	11,000-ha open forest	Between continental and oceanic	<i>Quercus petraea</i> and <i>Fagus sylvatica</i>
Castelporziano	6000-ha fenced preserve	Mediterranean (dry summers and rainfall mainly in autumn)	<i>Quercus ilex</i> , <i>Quercus cerris</i> , <i>Quercus frainetto</i> , <i>Carpinus orientalis</i>
La Petite Pierre	2674-ha open reserve	Between continental and oceanic	<i>Fagus sylvatica</i> , <i>Quercus petraea</i> and coniferous species (<i>Abies alba</i> , <i>Picea abies</i> , <i>Pinus sylvestris</i>)

Note: Displayed are the study sites (see also Fig. 1), a description of the areas, climate, and forest composition for each site.

production is the highest. Up to 50 traps were distributed within the site. Each year, an acorn production index was calculated as the average number of acorns collected per trap (see Focardi et al. 2008, Gamelon et al. 2017, Barrere et al. 2020 for further information about the protocol). For consistency, as done in Châteauvillain, we identified two categories of years depending on the quantity of acorns collected in the traps: years of acorn production (*A*) when acorns represented more than 50% of the maximum index obtained during the study period; otherwise, the years were considered as scarce acorn production (*N*; Fig. 1).

Demographic data collection

From March to September, capture–mark–recapture–recovery (CMRR) data were collected annually in all sites (see Fig. 1 for information on the years included in the analyses). During those periods, we captured female wild boar using traps, marked them with numbered ear-tags, and released them in their environment (see Fig. 1 for information on site-specific number of females monitored). Later, they were recaptured alive in traps, and/or recovered dead from hunting. For each capture and recovery event, the date and the individual's weight were recorded by researchers/field assistants. Weight measurements of live individuals during captures were converted into dressed body mass (i.e., body mass without digestive tract, heart, lungs, liver, reproductive tract, and blood; see Gamelon et al. 2017 for a similar approach) whereas dressed body masses were directly recorded on individuals killed by hunters.

In addition to CMRR data, our research team collected data on reproductive status based on examination of the reproductive tracts of females

harvested during the hunting season (see Fig. 1 for information on site-specific number of females for which reproductive status has been assessed). From sagittally cut ovaries, we defined each female as reproductive (i.e., presence of *corpora lutea*/pregnant) or non-reproductive (i.e., absence of *corpora lutea*/not pregnant). We used these data to estimate the annual proportion of breeding females (BP). For harvested females that were pregnant, we recorded the number of fetuses present in the uteri to evaluate litter size (LS).

Life cycle and stage-structured population model

We built a stage-structured population model by considering three classes of (dressed) body mass: small, medium, and large females. The definition of these classes differed among sites. In Châteauvillain, the small class brings together females <30 kg, the medium class corresponds to females weighting between 30 and 50 kg and the large class brings together females >50 kg (see Gamelon et al. 2012 for a description of these body mass classes). At La Petite Pierre, the three classes of body mass were <25 kg (small females), 25–45 kg (medium females), and >45 kg (large females). At Castelporziano, wild boar was significantly lighter than in the French sites, and the three classes of body mass were <8 kg (small females), 8–22 kg (medium females), and >22 kg (large females).

Females from body mass class *j* may reproduce with a probability BP_j and produce LS_j juveniles that may survive with a probability Spn (Fig. 2). Then, females may remain in the same body mass class with a probability π_{iO} for juveniles, p_{SS} for small females, p_{MM} for medium females, and p_{LL} for large females. Alternatively, they can move in heavier body mass

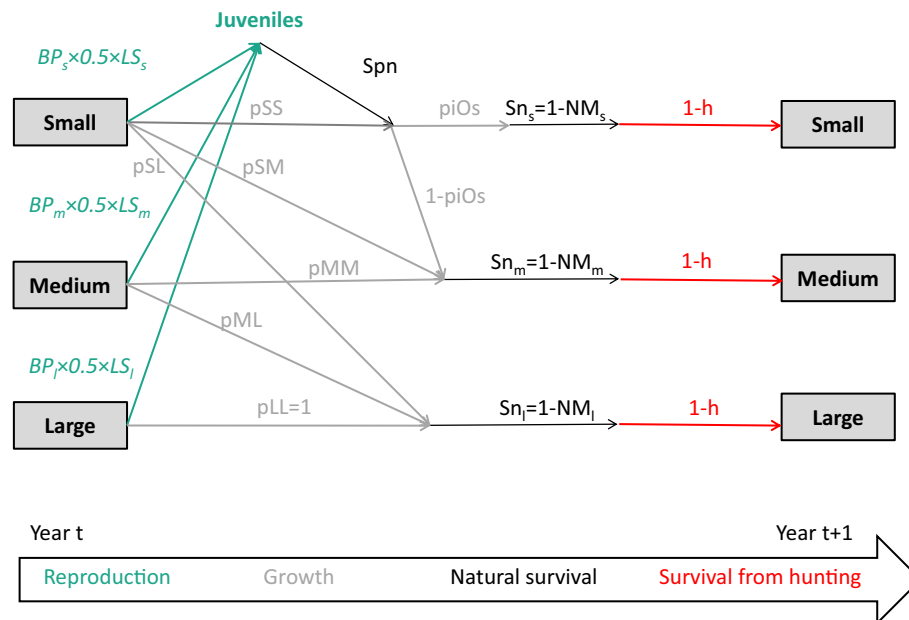


Fig. 2. Wild boar life cycle. We assumed a balanced sex ratio at birth. Postnatal survival Spn and the probability for juveniles to remain in the small class $piOs$ were set to 0.75 and 0.60, respectively. See Table 3 and Fig. 4 for the meaning and the estimated parameters.

classes with probabilities $1 - piOs$, pSM (i.e., from small to medium), pSL (i.e., from small to large), or pML (i.e., from medium to large; Fig. 2). From March to September, females may survive from natural causes of death (e.g., disease) with a probability $S_{n_j} = 1 - NM_j$ (with NM_j being the natural mortality), and from October to February, they may survive from hunting with a probability $1 - h_j$ (see Table 3 for the list of the demographic parameters and their biological meaning in bold). Importantly, the values of the parameters shown on the life cycle (Fig. 2) possibly differ according to the conditions of acorn availability (i.e., A and N) which is what we aimed to assess, and also differ between populations. For instance, in Châteauvillain, all females can reproduce whereas only females in the large body mass class can reproduce at Castelporziano (i.e., $BP_s = BP_m = 0$; see Appendix S1 for the stage-structured population matrix).

Estimating annual survival and transition probabilities between body mass classes

All the parameters in the stage-structured population model (Fig. 2) were estimated from

CMRR data, except postnatal survival Spn ($= 0.75$) and the probability for juveniles to remain in the small body mass class $piOs$ ($= 0.60$) that were estimated by expert opinion (Gamelon et al. 2012, Touzot et al. 2020). For all study areas, we analyzed CMRR data using a multistate model (see Lebreton et al. 2009 for a review) that allows annual natural mortality ($NM_{j,t}$) to be estimated separately from annual hunting mortality ($HM_{j,t}$) for each body mass class j . The model has already been fully described in previous works (Gamelon et al. 2012, Touzot et al. 2020) but we provide here a brief overview of its structure.

Each year, the status of a female was described using 10 states. States 1, 2, and 3 were for individuals captured alive in the traps in the small, medium, and large body mass classes, respectively. States 4, 5, and 6 were for individuals just killed by hunters and recovered, again in the three body mass classes, respectively. States 7, 8, and 9 (unobservable) were for individuals that just died from natural causes, again in the three body mass classes, respectively. State 10 (unobservable) was for individuals already dead (from hunting or natural causes the previous

Table 3. Model selection results.

Models	Châteauvillain	Castelporziano	La Petite Pierre
Natural mortality for small NM_s			
Constant	×	×	×
Acorn production t			
Acorn production $t - 1$			
Natural mortality for medium NM_m			
Constant	×	×	×
Acorn production t			
Acorn production $t - 1$			
Natural mortality for large NM_l			
Constant	×	×	×
Acorn production t			
Acorn production $t - 1$			
Probability of remaining in the small class pSS			
Constant	×	×	
Acorn production t			
Acorn production $t - 1$			×
Probability of transitioning from the small to the medium class pSM			
Constant	×		×
Acorn production t		×	
Acorn production $t - 1$			
Probability of transitioning from the small to the large class pSL			
Constant	×		×
Acorn production t		×	
Acorn production $t - 1$			
Probability of transitioning from the medium to the large class pML			
Constant	×	×	×
Acorn production t			
Acorn production $t - 1$			
Proportion of small reproductive females BP_s			
Constant	×		
Acorn production t			
Acorn production $t - 1$			
Proportion of medium reproductive females BP_m			
Constant			
Acorn production t	×		×
Acorn production $t - 1$			
Proportion of large reproductive females BP_l			
Constant			×
Acorn production t	×		
Acorn production $t - 1$		×	
Litter size of small LS_s			
Constant	×		
Acorn production t			
Acorn production $t - 1$			
Litter size of medium LS_m			
Constant	×		×
Acorn production t			
Acorn production $t - 1$			
Litter size of large LS_l			
Constant	×	×	×
Acorn production t			
Acorn production $t - 1$			

Notes: The first column indicates the models tested with the response variables (in bold) and the explanatory variables. For each population, the best models retained are indicated with a cross.

year) and was simply an absorbing state. The multistate model allows the transitions between states from one year to the next to be estimated. In other words, all the transitions probabilities between body mass classes (Fig. 2) were estimated annually. In addition, annual probability to be killed by hunters ($HM_{j,t}$) or to die from natural causes ($NM_{j,t}$) was estimated for each body mass class j . Noticeably, because the probability of female wild boar dispersing is generally very low (Truvé and Lemel 2003, Keuling et al. 2010), the estimates of natural mortality probabilities ($NM_{j,t}$) were assumed to correspond to true natural mortality probabilities. As derived parameters, we estimated natural survival ($Sn_{j,t}$) as $1 - NM_{j,t}$ and the proportion of individuals removed yearly by hunting as $h_{j,t} = HM_{j,t} / (1 - NM_{j,t})$. Recapture and recovery probabilities were considered body mass- and time-dependent. All these parameters (i.e., natural mortality, hunting mortality, transition probabilities between body mass classes) were estimated using the multistate model fitted within a Bayesian framework using Markov Chain Monte Carlo (MCMC) simulations. We ran three independent chains of 25,000 MCMC iterations, with a burn-in of 8,000 iterations thinning every fifth observation, resulting in 5,000 posterior samples for each chain and thus in 15,000 posterior samples in total. Convergence was assessed using the Brooks and Gelman diagnostic ($\hat{R} < 1.05$; Brooks and Gelman 1998). The analyses were implemented using JAGS (Plummer 2003) version 4.3.0 called from R version 3.4.3 (R Development Core Team 2017) with package rjags (Plummer 2016; see Appendix S2 for the code used to fit the multistate model).

Estimating demographic parameters for each condition of acorn availability

The multistate model was used to estimate annual natural mortality probabilities ($NM_{j,t}$) and annual transition probabilities between body mass classes for each population. Once these were estimated, linear regressions were used to examine whether they were constant over years, depended on acorn production (discrete factor with two modalities: N and A) at year t (i.e., the current year) or at year $t - 1$ (i.e., the previous year). The following regression models were used (illustration with $NM_{j,t}$):

$$\text{logit}(NM_{j,t}) = \gamma_j \quad (1)$$

$$\text{logit}(NM_{j,t}) = \gamma_j + \beta_j \text{Acorn}_t \quad (2)$$

$$\text{logit}(NM_{j,t}) = \gamma_j + \beta_j \text{Acorn}_{t-1} \quad (3)$$

where γ are the intercepts and β are the regression coefficients for each body mass class j . These regressions were fit for each posterior sample (15,000 in total for each population) and the best model was retained using Akaike information criterion (Burnham and Anderson 2002). Among the 15,000 posterior samples, we computed the probability that Eqs. 1, 2, or 3 corresponded to the retained model. For instance, among the 15,000 posterior samples, a probability P (Eq. 1 retained) $> P$ (Eq. 3 retained) $> P$ (Eq. 2 retained) would indicate that annual natural mortality probabilities ($NM_{j,t}$) were best supported by a constant model (Eq. 1) rather than explained by previous or current acorn conditions. On the contrary, a probability P (Eq. 2 retained) $> P$ (Eq. 1 retained) $> P$ (Eq. 3 retained) would indicate that annual natural mortality probabilities ($NM_{j,t}$) were best explained by current acorn conditions (Eq. 2). Once the model providing the best fit among the 15,000 posterior samples was selected, it was fitted to each of the 15,000 posterior samples and the distribution of 15,000 values for NM_j was recorded for each condition of acorn production. We thus obtained the posterior distribution of each parameter (i.e., mean natural mortality NM_j , mean transition probability from one body mass class to another) for each body mass class j (i.e., small, medium, and large) and the conditions of acorn availability (i.e., A and N ; see Fig. 3 for a schematic showing the different analytical steps).

Similarly, for reproductive parameters, we assessed whether the probabilities to participate to reproduction $BP_{j,t}$ and the litter sizes $LS_{j,t}$ depended on acorn production (at year t or $t - 1$) or were constant over years. Regressions were fit within a Bayesian framework. For $LS_{j,t}$ we used a Poisson distribution. We ran three independent chains of 25,000 MCMC iterations, with a burn-in of 8,000 iterations thinning every 5th observation, resulting in 5,000 posterior samples for each chain and thus in 15,000 posterior samples in total. Convergence was assessed

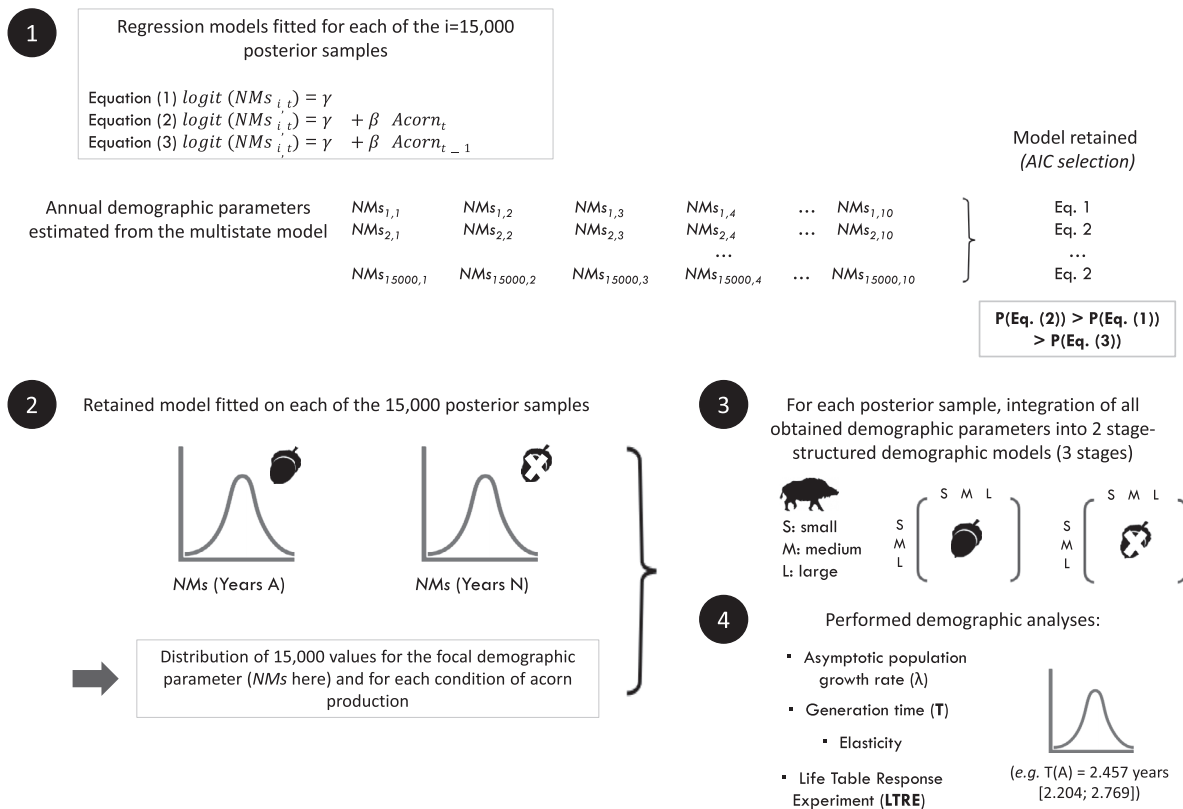


Fig. 3. Schematic summary of the different analytical steps. Example with natural mortality of small females, NMs_s .

using the Brooks and Gelman diagnostic ($\hat{R} < 1.05$; Brooks and Gelman 1998). We selected the best model using the Widely Applicable Information Criterion with the *loo* package (Vehtari et al. 2017). The posterior distribution of 15,000 values for $BP_{j,t}$ and $LS_{j,t}$ was recorded for each condition of acorn production.

Retrospective/prospective demographic analyses

For each posterior sample (15,000 in total for each population), the estimated demographic rates (mortality probabilities, transitions between body mass classes, reproductive parameters) were integrated into two stage-structured population models, one for each condition of acorn production (A and N ; see Appendix S1). Note that the proportion of individuals removed by hunting, h , was set to its average value across all body mass classes and categories of acorn production (posterior means [95% credible intervals]: $h = 0.478$ [0.442; 0.509] in Châteauvillain,

0.180 [0.100; 0.317] in Castelporziano and 0.452 [0.417; 0.483] in La Petite Pierre). This ensured that the mean population size estimated from the past observed sequence of acorn production was fairly stable over time (i.e., $\lambda = 1$) and that we really assessed the demographic responses to acorn production, not to changes in hunting pressure over years. We then calculated the asymptotic population growth rate λ (i.e., the dominant eigenvalue of the matrix) as well as the generation time T , for each condition of acorn production (A and N). The generation time corresponds to the weighted mean age of mothers in a population having reached its asymptotic regime (Gaillard et al. 2005). We estimated T as the inverse of the summed elasticity of the recruitment parameters (i.e., proportion of reproductive females or litter size) obtained across the three body mass classes (Brooks and Lebreton 2001). From the 15,000 estimates of λ and T , we computed the mean of the posterior distribution

and the 95% CRI of λ and T . Finally, we estimated the elasticity of λ to each demographic rate, i.e., the proportional change in λ obtained when changing a given demographic rate by a small amount (e.g., 1%), using the *popbio* package (Stubben and Milligan 2007) in R version 3.4.3 (R Development Core Team 2017). We computed the mean of the posterior distribution and the 95% CRI of each elasticity among the 15,000 posterior samples. Lastly, to measure the contribution of each demographic rate to the observed changes in λ between conditions of acorn production, we performed a LTRE analysis. Such analysis consists in multiplying the difference observed for a given demographic parameter between the two treatments (e.g., here years A and N) by its elasticity (equation from Caswell 2001):

$$\lambda^{(A)} = \sum_{k=1}^K (x_k^{(A)} - x_k^{(N)}) \cdot \sum_{ij} \frac{\partial \lambda}{\partial a_{ij}} \cdot \frac{\partial a_{ij}}{\partial x_k}$$

By doing so, we directly estimate the percentage of change in λ explained by the difference observed in terms of demographic response to various conditions a food resource availability (see Fig. 3 for a schematic showing the different analytical steps).

RESULTS

Effects of acorn production on stage-specific demographic parameters

We found that within a population, all stage-specific demographic rates were not similarly influenced by acorn production (Fig. 4, Table 3). Indeed, at Châteauvillain, 62% of the posterior

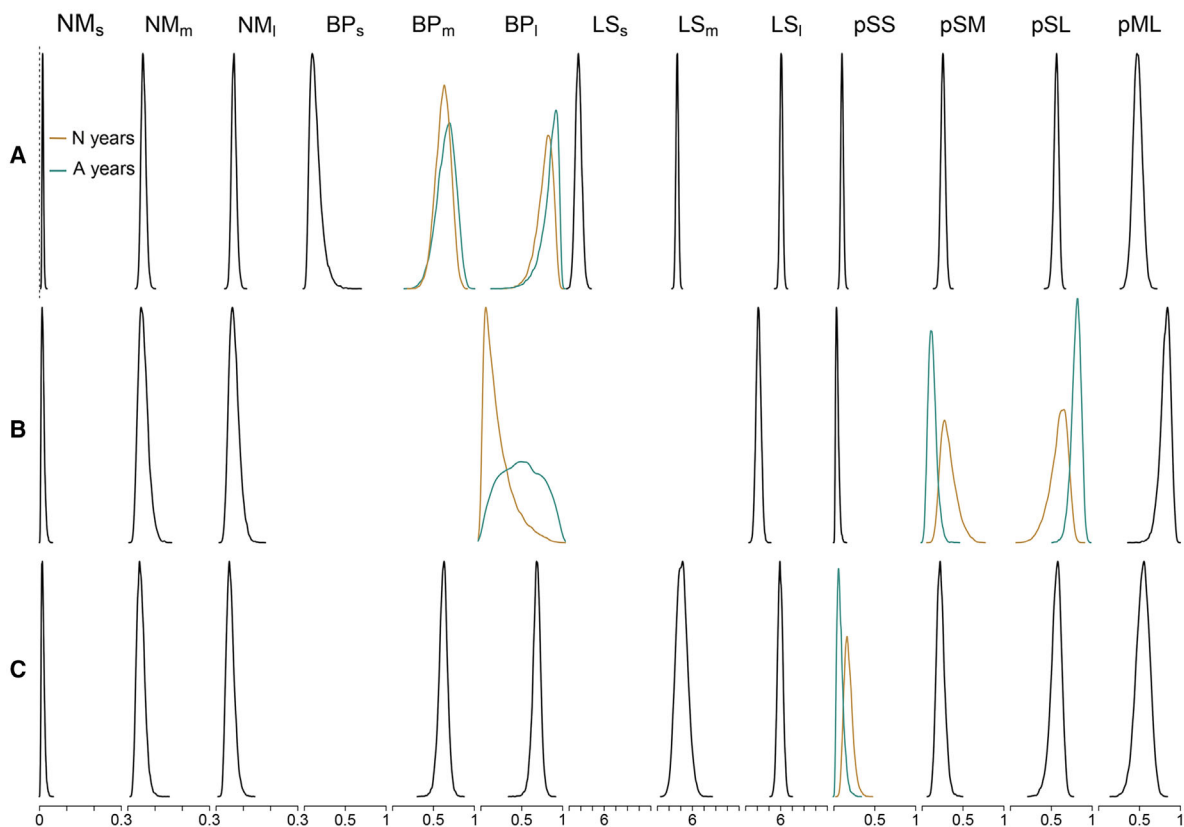


Fig. 4. Columns show the posterior distributions of the demographic parameters in the three wild boar populations (in rows) in (A) Châteauvillain, (B) Castelporziano, and (C) La Petite Pierre. Parameters in orange correspond to years of scarce acorn production (N), in blue to years of acorn production (A) while parameters in black are the same in both A and N years. See Table 3 and Fig. 2 for the meaning of the parameters.

samples indicated that annual natural mortality probabilities for small females (NM_s) were best supported by a constant model (Eq. 1) rather than explained by current (Eq. 2, 25%) or previous (Eq. 3, 13%) acorn conditions. The same pattern was found at La Petite Pierre (P [Eq. 1 retained] = 58%; P [Eq. 2 retained] = 21% and P [Eq. 3 retained] = 21%) and at Castelporziano (P [Eq. 1 retained] = 52%; P [Eq. 2 retained] = 23% and P [Eq. 3 retained] = 25%). Similarly, for the three populations, annual natural mortality probabilities for medium and large females (NM_m and NM_l) were best supported by a constant model, indicating that natural mortality did not depend on acorn conditions, irrespective of the body mass class (Fig. 4, Table 3). For the three populations, natural mortality was low for all body mass classes (Fig. 4). Likewise, litter size was independent on acorn production (Fig. 4, Table 3). However, the proportion of breeding females and the probability of small females entering a heavier body mass class during the year were the main parameters responding to an increase in acorn availability (Fig. 4, Table 3). In the populations of Châteauvillain and Castelporziano, the proportion of breeding females (BP_i) was positively influenced by acorn production (Fig. 4). In Châteauvillain, this positive effect of acorn production on the proportion of breeding females was significant for medium and large females only, not for small females. In Castelporziano, the probability of small females entering a heavier body mass class during the year (pSM and pSL) also increased in relation to acorn production.

In addition to highlighting marked differences in demographic responses to acorn production within a population, we found contrasting demographic responses among populations in terms of magnitude of these responses (Fig. 4) and of drivers. In particular, depending on the populations, either past (year $t - 1$) or current (year t) conditions of acorn production may influence demographic rates. In Châteauvillain, current acorn conditions mattered for the proportion of breeding females in the medium and large body mass classes, whereas conditions the previous year influenced this proportion in Castelporziano (Table 3). Importantly, current conditions also appeared to be important in Castelporziano through their immediate effect on the transition

probability of small females entering a heavier body mass class during the year (for the transition pSM from small to medium P [Eq. 1 retained] = 26%; P [Eq. 2 retained] = 39% and P [Eq. 3 retained] = 34%; for the transition pSL from small to large P [Eq. 1 retained] = 34%; P [Eq. 2 retained] = 43% and P [Eq. 3 retained] = 23%). In La Petite Pierre, only past conditions mattered: a year of acorn production was followed by a lower probability to remain in the small body mass class pSS (Fig. 4; P [Eq. 1 retained] = 35%; P [Eq. 2 retained] = 20% and P [Eq. 3 retained] = 46%).

Overall effects of acorn production on demography: retrospective/prospective analyses

Because in Châteauvillain, only current conditions influenced demographic parameters, we integrated the estimated demographic rates (Fig. 4) into two stage-structured population models (Appendix S1), one for each conditions of acorn production (i.e., N vs. A). We found that in years of scarce acorn production, the population size tended to decrease ($\lambda = 0.990$, 95% CRI [0.946; 1.034]), whereas it tended to increase by 1.7% per year of acorn production ($\lambda = 1.017$, 95% CRI [0.940; 1.089]; Fig. 5). Retrospective analysis (LTRE) revealed that the observed difference in λ under the two conditions of acorn availability mainly occurred through the effect of acorns on the proportion of breeding in the large class (BP_i ; Fig. 5). The generation time was lower during years of acorn production ($T = 2.457$ yr, 95% CRI [2.204; 2.769]) than when acorns were scarce ($T = 2.502$ yr, 95% CRI [2.247; 2.777]; Fig. 5). Thus, in presence of acorns, the mean age of mothers at childbirth was 0.045 yr (i.e., 16 d) younger than in absence of acorns. Irrespective of acorn conditions, prospective analyses showed that the highest elasticity was found for the natural survival of large females indicating that this demographic parameter had the highest contribution to λ (Fig. 6).

In Castelporziano, both past and current acorn conditions influenced demographic parameters. Therefore, we integrated the estimated demographic rates (Fig. 4) into four stage-structured population models (Appendix S1) corresponding to the succession of years of acorn production and years of scarce production (i.e., AA , NN , AN , NA). Two successive years of scarce acorn

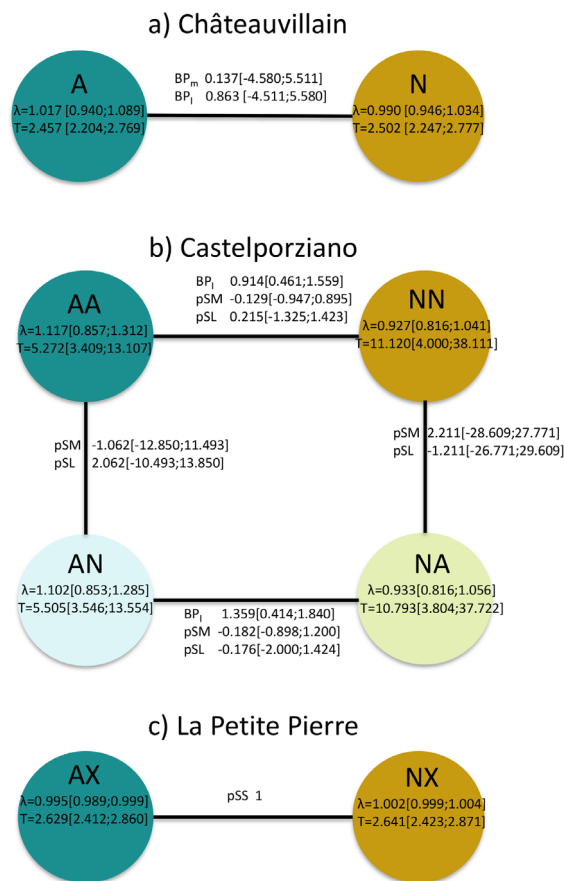


Fig. 5. Prospective analysis (LTRE): Decomposition of the difference in population growth rate λ under various conditions of acorn production (A, years of acorn production; N, years of scarce acorn production) for the three wild boar populations. T corresponds to generation time (in years). Mean posterior distributions together with their 95% CRI are reported. See Table 3 and Fig. 2 for the meaning of the parameters.

production (NN) led to a decrease of the population growth rate ($\lambda = 0.927$, 95% CRI [0.816; 1.041]) whereas one year of acorn production followed by another year of acorn production (AA) was associated with an increasing population growth rate ($\lambda = 1.117$, 95% CRI [0.857; 1.312]; Fig. 5). As expected, retrospective analysis indicated that the observed difference in λ between AA years and NN years resulted from changes in the proportion of breeding females and the transition probability of small females entering a heavier body mass class during the year. However, the proportion of breeding females in the

large class (BP_i) mostly explained the observed difference in λ (Fig. 4). Because the proportion of breeding females was responsible for most of the difference in λ and because this parameter was influenced by past acorn production, a year of scarce acorn production followed by a year of acorn production (NA) induced similar demographic responses than NN years, whereas a year of acorn production followed by a year of scarce acorn production (AN) provided similar results than AA years (Figs. 5, 6). The generation time was lower in AA (and AN) years than in NN (and NA) years (e.g., $T = 5.272$ yr, 95% CRI [3.409; 13.107] vs. 11.120 yr, 95% CRI [4.000; 38.111]) indicating that in AA and AN years, the mean age of mothers at childbirth was almost 5.848 yr younger than in NN and NA years. Prospective analysis showed that, as observed in Châteauvillain, the highest elasticity was for the natural survival of large females, irrespective of acorn conditions (Fig. 6).

At La Petite Pierre, only acorn conditions the preceding year (at $t - 1$) influenced demographic parameters the current year (year X at t , see Table 3). Therefore, we integrated the estimated demographic rates (Fig. 5) into two stage-structured population models (i.e., NX vs. AX). Years of scarce acorn production (years N) were followed, the next year (NX), by a population growth rate of $\lambda = 1.002$, 95% CRI [0.999; 1.004]. Years of acorn production (years A) were followed by a population growth rate of 0.995, 95% CRI [0.989; 0.999] the next year (AX). The small difference in λ under the two conditions of acorn availability only occurred through the effect of acorns on the probability for small females to remain in this body mass class during the year (pSS; Fig. 5). Indeed, following a year of acorn production (AX years), the probability for small females to remain in the small class was slightly lower than after a year of scarce acorn production (Fig. 4). In other words, females were more likely to move into a larger body mass class after a year of acorn production (pSM and/or pSL). Nevertheless, these transition probabilities (pSM and pSL) were not significantly influenced by acorn production (Table 3, Fig. 4) suggesting that the effect of acorn production on pSS was almost negligible from a biological viewpoint. This explains why in overall, acorn production has only little effect on population growth rate and

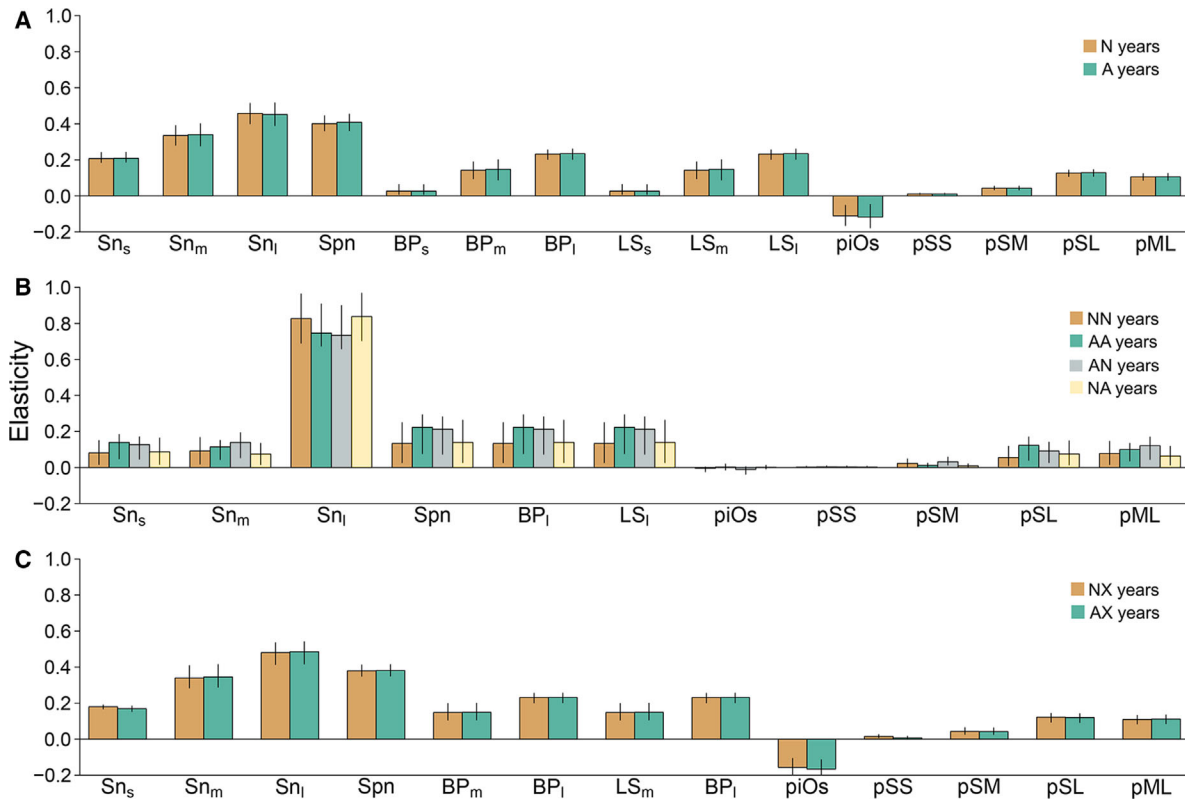


Fig. 6. Retrospective analysis: Elasticity of demographic rates for the three wild boar populations (A) Châteauvillain, (B) Castelporziano, and (C) La Petite Pierre, according to acorn production (A, years of acorn production; N, years of scarce acorn production). Mean posterior distributions together with their 95% CRI are reported. See Table 3 and Fig. 2 for the meaning of the parameters.

generation time in La Petite Pierre. The generation time was indeed 2.641 yr, 95% CRI [2.423; 2.871] in NX years and 2.629 yr, 95% CRI [2.412; 2.860] in AX years indicating that mean age of mothers at childbirth was somewhat similar under the two conditions of acorn availability (Fig. 5). Again, irrespective of the acorn conditions, prospective analysis revealed that natural survival of large females had the highest elasticity (Fig. 6).

DISCUSSION

Our goal was to investigate whether variation in demographic responses to acorn production exists both within and among populations. Using two complementary approaches, retrospective and prospective analyses, we found some common responses to acorn production among

populations: higher breeding probability and/or transition probability from the small body mass class to larger ones, resulting in higher population growth rate and shorter generation time. Despite these similarities, we also found some marked differences both within and among populations. Within populations, acorn production mainly influenced reproductive parameters of medium and large females and growth of small females (i.e., transitions between small mass class and heavier ones). Among populations, these demographic responses differed in magnitude. In turn, the magnitude of the resulting changes in population growth rates and generation times in response to acorn production was strongly population-specific.

Irrespective of acorn conditions, the generation time was longer in the Italian population (Castelporziano) than in the French populations

(Châteauvillain and La Petite Pierre). Generation time is a metric that ranks species on the slow–fast continuum, a major axis of variation in life history tactics in mammals (Gaillard et al. 2005, 2016, Bielby et al. 2007, Jeschke and Kokko 2009). This continuum contrasts fast species characterized with a short lifespan and the production of many offspring early in life to slow species with opposite characteristics. Therefore, the French populations consistently displayed a shorter generation time (about 2.5 yr) indicating a faster turnover. This accelerated pace of life has been interpreted as a demographic response to the high hunting pressure, where individuals are able to reallocate resources to reproduction to compensate for reduced survival (Servanty et al. 2011, Kapota and Saltz 2018). Other studies have pointed out the presence of reproductive compensation of harvest losses due to the diversion of resources from survival to reproduction in polytocous species such as feral pigs (Hanson et al. 2009), black bears *Ursus americanus* (Freedman et al. 2003) or Tasmanian devils *Sarcophilus harrisi* (Jones et al. 2008). With a generation time of about 10 yr in absence of acorns in Italy, wild boar displayed a generation time which is comparable to similar-sized ungulates that usually have a generation time longer than 6 yr (Servanty et al. 2011). Strikingly, in response to acorn production, generation time became shorter indicating that acorn production favored a faster turnover.

Our demographic analyses revealed that adult survival S_n remained high, as expected among ungulates where the average natural adult survival probability often exceeds 0.95 in females (Gaillard et al. 2000), exhibited the highest elasticity, and was independent on acorn production. These findings are in accordance with the demographic buffering hypothesis (Morris and Doak 2004, Hilde et al. 2020), positing that the demographic parameter with the strongest effect on the population growth rate (S_n in our case) should be buffered/canalized against environmental conditions. In contrast, acorn production positively influenced the proportion of breeding females BP and/or transition probability from the small to heavier body mass classes (pSM, pSL). At Châteauvillain, current acorn conditions were allocated to reproduction whereas resources from acorns produced the preceding year were

stored and then allocated to reproduction at Castelporziano (Fig. 4). This result indicates that wild boars in Châteauvillain, a resource-rich environment, displayed an income breeding tactic whereas at Castelporziano, a resource-poor environment, females were closer to the capital end of the capital–income continuum of breeding tactics (Jönsson 1997, Gamelon et al. 2017). In turn, an increase in BP and/or pSM, pSL positively influenced the population growth rate λ (Fig. 5). In populations characterized by this type of dynamics driven by environmental stochasticity, years of high resource availability are generally followed by strong density dependence leading populations to collapse (see Sæther et al. 2016 for a comparative study on birds). Because population sizes are regulated by harvest in the studied populations, carrying capacities are unlikely to be reached and the strength of density dependence should be negligible.

Thanks to long-term field studies of wild boar populations and fruiting dynamics in three sites in Europe, we assessed the effects of acorn production on all stage-demographic rates for populations under various ecological contexts. Our results provide evidence for heterogeneity in responses to mast seeding both within and among populations. This is an important finding, as most of the literature available so far on the effect of mast seeding on the dynamics of seed consumers has ignored (st)age-specific responses and has highlighted common demographic responses at the intraspecific level (Table 1). Wild boar, contrary to most of the species reported in Table 1, is influenced by the combined effects of mast seeding and hunting. To name just a few effects, hunting has been found to modify age/size structure in free-ranging populations (Kuparinen and Festa-Bianchet 2017). As responses to mast seeding are (st)age-specific (Fig. 4), hunting may influence populations' ability to respond to environmental variation (e.g., acorn production) and contrasting demographic responses to environmental variation are expected among populations with different harvest regimes. The question of potential interactions between environmental variation and harvest has received growing interest in marine ecology but little is known about the combined effects of environmental variation and hunting on terrestrial species (see Gamelon et al. 2019 for

a review). Our study shows that the lightly harvested population at Castelporziano was influenced by acorn production at a higher extent than the French populations (Châteauvillain and La Petite Pierre). In these latter populations, generation time was much shorter and hunting still remains the main driver of population dynamics (Toigo et al. 2008, Gamelon et al. 2011, Servanty et al. 2011). Noticeably, to the best of our knowledge, only two studies in the literature have investigated the effects of pulsed resources on harvested species (Table 1, see Bridges et al. 2011 for a study on black bear, see Gamelon et al. 2017 on wild boar). Gaining a good understanding on the combined effects of environmental variation (e.g., acorn production) and hunting is crucial to maintain sustainable harvest. This is particularly true in the current context of global changes where an increase in frequency of events of massive acorn production might be expected in response to warmer spring conditions (Caignard et al. 2017, Schermer et al. 2019). Exploring the expected effects of global warming, through its effect on pulsed resources, in combination with different hunting strategies, offers promising avenues of research.

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