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Lara Veylit

# Causes and consequences of body growth variation in hunted wild boar populations

**NTNU**  
Norwegian University of Science and Technology  
Thesis for the Degree of  
Philosophiae Doctor  
Faculty of Natural Sciences  
Department of Biology



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Trondheim, February 2021

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# Preface

This thesis is certainly not only my work, but really a product of years of supervision and guidance from various people I would like to thank wholeheartedly. First and foremost, I would like to thank my supervisors and collaborators, Marlène Gamelon, Bernt-Erik Sæther, Jean-Michel Gaillard, and Eric Baubet. I was ridiculously lucky to have such an amazing group help me develop as a scientist-remerci à vous og tusen takk. I have too many scientific mentors and friends to count or mention across the globe from before my time at NTNU-thank you for all the opportunities you provided me and your belief in me. Thank you to members of the LBBE for welcoming me to your group in Lyon. I appreciate all the times we spent in the french sunshine eating baguettes. The community at the CBD both past and present have not only been my colleagues but also friends. Thank you all for the coffee breaks and nights out exploring Trondheim.

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# Summary

The life of an organism can be described as its birth, growth, reproduction, and death. There is a high variation in the life history of individuals; some individuals may grow at a faster rate or produce fewer offspring than others. Body growth is a particularly interesting life-history trait as it is linked to body size in adulthood, reproductive success, and longevity. Understanding how and why body growth varies among populations and between individuals is crucial for understanding how populations respond to environmental variation. However, studies of free ranging populations often focus on reproduction and survival rather than body growth due to the rarity of high quality longitudinal data (i.e. multiple measurements of individuals throughout life). Therefore, body growth is a relatively poorly studied fitness-related trait.

In this thesis, we took advantage of data from individual long-term monitoring studies of wild boar (*Sus scrofa*) in several European populations to explore the causes and the consequences of body growth variation at the individual- and population-levels. Using wild boar as a study species was important for several reasons. As a widespread species across different habitats, we had the opportunity to compare body growth patterns across contrasting environments. Wild boar are also an emblematic game species, making it possible to study body growth in populations subject to varying hunting pressures. Understanding how harvesting may shape growth patterns is especially vital as the distribution and abundance of this species increases throughout Europe. This work was also motivated by wild boar's social importance; wild boar account for substantial economic damage and may be a reservoir of disease. A better understanding of sources (i.e. causes) of variation in body growth of wild boar and how they influence the dynamics of populations (i.e. consequences) may be used to inform and improve their management.

Our first aim was to quantify and compare body growth early in life (until about 6 months of age) across three populations of wild boars that contrasted in terms of habitat quality and hunting pressures. We assessed the relative roles of environmental covariates (e.g. temperature) and individual-level differences in determining early-life growth rates. We found that individual plasticity in body growth rates in early-life, not environmental conditions at birth, explained high variation in body growth rates across time in both sexes. Then, we focused on one population that was monitored for more than 30 years to test whether, as expected under the current life history theory, fast early-life growth

entailed a survival cost. Indeed, an increase in energy allocation to growth early in life should come at a cost of another trait (e.g. survival) resulting in life history trade-offs. Using capture-mark-recapture-recovery data and multistate models, we found that fast early-life growth did not entail a physiological cost as would be expected. Then, we broadened our focus to lifetime growth trajectories (i.e. not only early-life growth) to quantify growth trajectories across two populations in contrasting environments. We analysed whether body growth trajectories and related parameters (e.g., body mass in adulthood) varied at the individual level, between sexes, and across populations using growth functions that encompass the expected range of growth shapes. We found context-dependent body growth; the shape of body growth varied between environments, sexes, and across individuals. Finally, using multistate models, we assessed the role of acorns, an important food resource, on the probability for a female to move from a given body mass class to another within a year (i.e. growth transitions). We also assessed the effects of acorns on stage-specific reproduction and survival. These analyses were performed on three populations. Then, these demographic rates were integrated into a stage-structured population model allowing us to estimate the effects of acorns on the growth rates of the three contrasting populations. We found that acorn availability positively influences body growth. The positive relationship between acorn availability and body growth may be associated with faster population growth rates from our population-level analyses.

While we focused on wild boar as a case study, this thesis improves our general knowledge on the causes and consequences of body growth variation in the wild.



# List of papers

- I **Veylit, L.**, Sæther, B.-E., Gaillard, J.-M., Baubet, E., Gamelon, M. (2020). How do conditions at birth influence early-life growth rates in wild boar? *Ecosphere*, 11(7), e03167.
- II **Veylit, L.**, Sæther, B.-E., Gaillard, J.-M., Baubet, E., Gamelon, M. (2020). Grow fast at no cost: no evidence for a mortality cost for fast early-life growth in a hunted wild boar population. *Oecologia*, 192(4), 999.
- III **Veylit, L.**, Sæther, B.-E., Gaillard, J.-M., Baubet, E., Gamelon, M. Evidence for context-, sex- and cohort-specific lifetime growth in a wild mammal. *Submitted manuscript*.
- IV Gamelon M., Touzot, L., Baubet E., Cachelou, J., Focardi S., Franzetti B., Nivois E., **Veylit L.**, and Sæther B.E. Effects of pulsed resources on the dynamics of seed consumer populations: a comparative demographic study in wild boar. *In press, Ecosphere*.

## Declaration of contributions

Papers I & II: LV, MG, and JMG designed the studies. EB provided the data. LV analysed the data with input from JMG and MG. LV wrote the first draft of the manuscript, which was reviewed and commented on by all coauthors.

Paper III: LV, MG, and JMG designed the studies. EB provided the data. LV analysed the data with input from JMG and MG. LV, MG, and JMG wrote the manuscript, which was reviewed and commented on by all coauthors.

Paper IV: MG designed the study. LT, MG, and JC analysed the data. EB, SF, BF, EN provided data. MG wrote the manuscript, which was reviewed and commented on by all coauthors.

# Introduction

The life of organisms can be simplified down to traits relating to individual fitness such as survival, somatic (i.e., body) growth, and reproduction (Roff, 1992; Stearns, 1992). Variation across fitness-related traits occurs due to individual-level differences in ability to acquire resources from the environment (e.g., food) and allocate these resources to these fitness-related traits (van Noordwijk and de Jong, 1986). Energy must be budgeted as the amount of resources that can be acquired by a given individual is limited (Williams, 1966; Cody, 1966). Trade-offs between life-history traits are observed as resources allocated to one life-history trait reduces the amount of resources available for another trait. For example, an increase in allocation of resources to body growth may be associated with a reduced lifespan due to a reduced amount of resources allocated to somatic maintenance costs (Rollo, 2002). Negative covariations between competing life-history traits are therefore common as no “Darwinian demon” exists that can maximize all fitness-related traits (Law, 1979). However, trade-offs are not always observed. For example, individuals of high quality (e.g., with positive correlations between fitness related traits; Wilson and Nussey, 2010) consistently outperform others by optimizing the acquisition and allocation of resources. High quality individuals thus outperform lower quality individuals in factors related to fitness such as higher survival and breeding probability (in kittiwakes *Rissa tridactyla* Cam and Monnat, 2000). Individual-level heterogeneity can thus partially or completely mask negative covariation between fitness-related traits at the population level as high quality individuals outperform low quality individuals (e.g., positive correlations between survival and reproduction in *Ovis canadensis*; Hamel et al. 2009; reproduction and body growth in *Macropus giganteus* G  lin et al., 2016; see Bleu et al., 2016 for review of reproductive costs). Therefore, while trade-offs are expected to be theoretically observed, empirical tests are needed to explore the relationships between fitness-related traits.

Body growth, one fitness-related trait, has a strong impact on an individual’s performance throughout life (Roff, 1992; Dmitriew, 2011). For example, body growth rate is related to time to reach maturity and size in adulthood (Day and Rowe, 2002; Galbraith et al., 1989). In the past, body growth was expected to be physiologically maximized regardless of the environment due to the advantages conferred by a large body size/mass (Ricklefs, 1969). However, observed body growth rates during development are usually

lower than the physiological maximum (Abrams and Rowe, 1996; Case, 1978; Dmitriew, 2011). Indeed, body growth rates are also not always rapid as individuals may experience poor environmental conditions (Arendt, 1997; Gotthard et al., 1994). Body growth trajectories are thus highly responsive to changes in ecological conditions such as population density and available food resources, leading to variability within and between populations over time (Monro and Marshall, 2014). Accelerated early-life growth may also entail costs later in life (e.g., smaller litter sizes; Auer et al., 2010, reduced lifetime; Inness and Metcalfe, 2008; Lee et al., 2013). Therefore, while fast body growth was previously expected to be favored, empirical studies have found body growth rates throughout life to be optimized according to resource availability and physiological costs of body growth. Environmental conditions experienced early in life may even carry late-life effects. Favorable conditions (low competition for resources, high resource availability) experienced early in life confer advantages to individuals throughout life such as longer lifetimes and faster growth rates in early-life. These “silver spoon effects” (Grafen, 1988) may result in cohort-level variation in body growth rates, reproductive success, and survival later in life (Descamps et al., 2008; Plard et al., 2015). Harvesting (i.e., fishing, hunting) may also favor fast body growth through shifting a populations’ position towards the fast end of the slow-fast continuum, a well-established axis of variation in life-history tactics (Gaillard et al., 2005; Bielby et al., 2007). In fisheries, the removal of certain individuals from populations has been established to act as a selective pressure (Trippel, 1995; Rowell, 1993), leading to faster body growth rates, younger age-at-maturity, and smaller size-at-age in many populations (Law, 2000; Stokes and Law, 2000; Conover and Munch, 2002). Similarly, in ungulate species, a high hunting pressure may theoretically induce a faster pace-of-life, characterized by early maturity, rapid body growth, high fecundity, and shortened lifetimes (Jeschke and Kokko, 2009). Due to the relative rarity of long term data with repeated body mass measurements of individuals from early-life through adulthood and particularly of harvested populations (Festa-Bianchet et al., 2017), there are few studies analysing how body growth trajectories vary across time and space (i.e., between populations) for a single species. Understanding the causes of variation in body growth among individuals in populations subject to contrasting environments and the consequences for population dynamics is thus needed.

# Aims

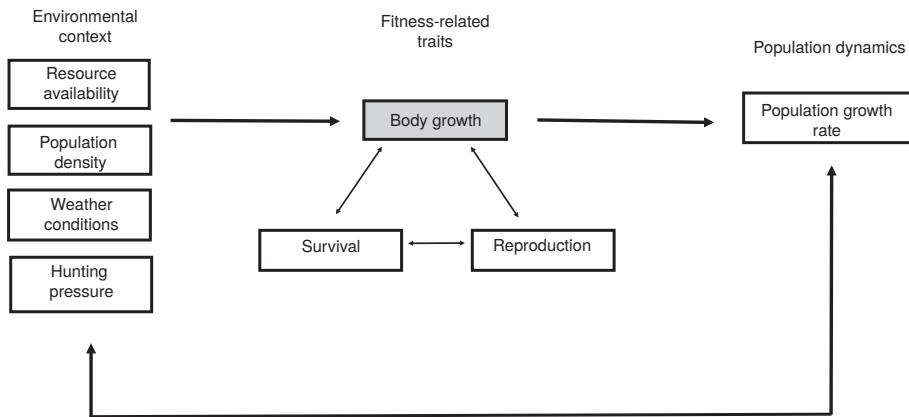
In this thesis, we seek to address the causes (e.g., environmental variation) and consequences (at both the individual and population level) of body growth variation in a free-ranging harvested species. To do this, we used unique long term individually based data of European wild boar (*Sus scrofa*) populations subject to contrasting environments in terms of hunting pressures and food availability.

1. What causes variation in body growth over space and time (papers I, III, IV)?

In paper I, we analysed the effect of environmental conditions at birth (e.g. temperature) on early-life growth rates (up to 6 months of age) in three wild boar populations living in contrasting environments (see Figure 1). In paper III, we broadened our focus to body growth trajectories throughout life (not only early-life) by fitting standard growth models to data for two populations in different environments (one population in a high quality habitat for wild boar with a high hunting pressure, one population in a low quality habitat for wild boar with a low hunting pressure). In paper IV, we explored how the availability of an important food resource for wild boar, acorns, influenced survival, reproduction and body growth, of females in three contrasting populations.

2. What are consequences for variation in body growth over space and time (papers II & IV)?

In paper II, we asked whether there was a consequence for fast early-life growth in terms of mortality. To answer this, we analysed the covariation between early-life growth rate and mortality probability by cause (i.e. hunting and non-hunting related mortality). In paper IV, we determined how body mass-specific demographic responses (i.e. survival, growth, reproduction) to the availability of acorns influenced generation time and population growth rate in three populations subject to contrasting environmental contexts. We were therefore able to determine whether changes to body growth due to resource availability influenced population dynamics.



**Figure 1:** Summary figure of conceptual ideas discussed in this thesis. We benefited from unique individual long-term monitoring of three wild boar populations to explore how environmental context influences body growth in early-life (paper I). Then, we tested for a trade-off between growth and survival. Specifically, in one population, we tested whether fast early-life growth entailed a survival cost (paper II). We then quantified lifetime body growth trajectories of two populations in different environmental contexts (paper III). Finally, we assessed the effects of resource availability (acorns) on the growth rate of three populations via their effects on growth, survival and reproduction (paper IV).

# Methods

## Study species

Wild boar are a widespread species (found on every continent except Antarctica; Barrios-Garcia and Ballari, 2012). Throughout Europe, the distribution and number of wild boars have expanded at an unprecedented rate. This increase in number has been linked to a combination of wild boar's high reproductive capability for a large ungulate, land abandonment, climatic changes, and changes to agricultural practices (Massei and Genov, 2004). This increase in population numbers has caused economic concerns due to disturbed landscapes as well as trampling on and eating crops (Barrios-Garcia and Ballari, 2012). Wild boar are also a reservoir for pathogens that are transmissible to humans (although direct transmission to humans is rare) and livestock (see Meng et al., 2009 for a review of wild boar disease transmission). Wild boar are hunted throughout Europe to control populations. In wild boar populations, mortality is largely due to hunting rather than natural predators (see Gamelon, 2020 for review of mortality causes of wild boar). For example, in an Italian population, predation only accounted for 1.9% of overall mortality while poaching and hunting accounted for 97.1% of mortality (Merli et al., 2017). However, the number of hunters is stable or declining across Europe (Massei and Genov, 2004). In addition, the effectiveness of hunting practices as a tool to manage population growth is unclear. Indeed, a high hunting pressure has been linked to adaptive responses in wild boar, such as a faster population turnover (Servanty et al., 2011) and earlier birth dates (Gamelon et al., 2011), favoring high population growth rates despite high hunting pressures.

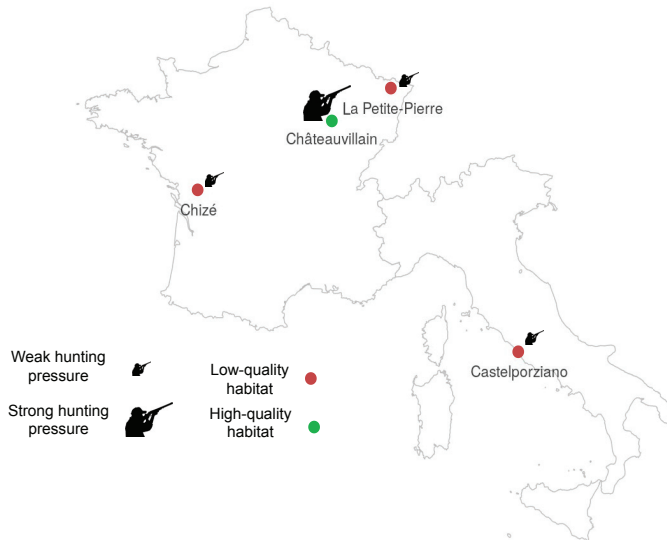
Wild boar is a long-lived ungulate species (lifespan of up to 13 years; see Gamelon et al., 2014). European wild boar can produce up to 14 offspring in a single litter (Frauen-dorf et al., 2016; Servanty et al., 2007). Wild boar may attain sexual maturity at as young as 1 year of age (Servanty et al., 2009; Gamelon et al., 2011). Wild boar exhibit strong sexual dimorphism (Pépin, 1991), with males reaching a much larger weight in adulthood than females. While wild boar preferentially feed on vegetable foods such as acorns, beechnuts, chestnuts, pine seeds, olives, and seeds, they are omnivorous with other important food sources including earthworms and crops (Schley and Roper, 2003; Baubet et al., 2004). Their variable diet makes wild boar highly adaptable to many habitats.

The type of resources available to mothers plays an important role in reproductive allocation and offspring growth. For example, reproductive allocation increased with acorn availability (Gamelon et al., 2017; Touzot et al., 2020). Acorns are rich in lysine, an essential component of high-quality milk which is associated with offspring growth (Yang et al., 2000; Gamelon et al., 2017). In adulthood, natural survival decreases with age (i.e., actuarial senescence) in lightly hunted populations (Gamelon et al., 2014). In heavily hunted populations, individuals rarely live long enough to be impacted by senescence. Due to greater susceptibility to adverse environmental conditions as well as competition for mates, adult male mortality risk is higher than for females (Toigo and Gaillard, 2003). In addition, males are particularly vulnerable to hunting mortality when they are solitary as subadults and adults (Merli et al., 2017). Wild boar are thus subject to age- and sex-specific mortality.

## Study areas and data collection

The data reported in this thesis are based on three populations of wild boar in France and one in Italy (Figure 2 for study areas). For the population located in Châteauvillain forest (“Châteauvillain”, 48.02°N, 4.56°E), oak (*Quercus petraea*, 41% of forest cover) and beech (*Fagus sylvatica*, 30% of forest cover) dominate the 11,000 ha site, resulting in high availability of seeds for wild boar to feed on. Pulsed resources (i.e. beechnut and acorn) are frequently available due to masting events (Servanty et al., 2011; Gamelon et al., 2017; Touzot et al., 2020). During temporally varying masting events, synchronized seed production within tree species lead to abundant food resource availability for wild boar (Silvertown, 1980). In the Réserve Biologique Intégrale at Chizé (“Chizé”; 46.05°N, 0.25°W), productivity of the forest is low and summer droughts are frequent (Gaillard et al., 2003). Therefore, high quality forage is scarce. Approximately 40% of the 2,614 ha reserve is covered by rich habitat for wild boar (i.e., oak *Quercus* spp. and hornbeam *Carpinus betulus*). In the 2,674 ha La Petite-Pierre National Hunting and Wildlife Reserve (“La Petite-Pierre”; 48.50°N, 7.00°E) located in the Vosges mountains, food resources for wild boar are scarce. The forest is composed of beech, *Fagus sylvatica*, and coniferous species as well as poorly diversified vegetation of low nutritive quality (Pellerin et al., 2010; Storms et al., 2008). At the Castelporziano Preserve (“Castelporziano”; 41°44N, 12°24E), situated approximately 20 km southeast of Rome, Italy, summers are dry and droughts are common (Servanty et al., 2011; Focardi et al., 2008). Châteauvillain is a high-quality habitat for wild boar due to the high percentage of seed producing trees in this area while Chizé, La Petite-Pierre, and Castelporziano are low-quality habitat for wild boar due to the lower percentage cover of seed producing trees.

Capture-mark-recapture-recovery (CMRR) data for wild boar was collected in all four study areas (see Figure 3 for data collection periods in a given year). Individuals

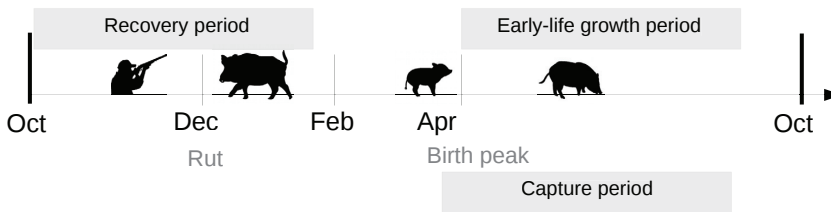


**Figure 2:** The study sites of La Petite-Pierre (papers I & IV), Chizé (papers I, & III), Châteauvillain (papers I, II, III & IV), France and Castelporziano (paper IV), Italy. Resource quality for wild boar for each site and the strength of the hunting pressure are shown.

were captured in traps, marked, then released between March and September. Sex, date, and body mass to the nearest 0.1 kg were recorded for each individual at capture or recovery (i.e., recovered from the forest after being hunted). During the recovery period (October-February), individuals were hunted or translocated. Hunters are able to easily approximate wild boar age/mass from a distance due to highly visible traits. Juveniles are striped until 4 months of age, then as subadults have a reddish coat until approximately 30 kg (Moretti, 2014). Adults of both sexes have dark colored coats. Females remain in their matrilineal social groups while male are solitary, making sex determination straightforward. Differences in management strategy and population size at the local level led to site-specific differences in hunting pressure. In Châteauvillain, each weekend during the recovery period drive hunts are organized. Hunters are posted to ambush wild boar as beaters and dogs flush them from brush (Vajas et al., 2020). Hunting is highly effective in this area and not oriented towards any specific age or body mass class (> 40% mortality of all size and age-classes; Toïgo et al., 2008; Gamelon et al., 2011). While a restriction is in place on the hunting of large females (63 kg live mass; Gamelon et al., 2012) with a paid penalty, adult females are still hunted although at a lower rate than other age/size classes. Recovery rates from hunting are very high (approximately 100%) thanks to the involvement of the French Office of Biodiversity (OFB) as data



is collected in cooperation with hunters. Information on the cause of death outside of hunting was not available, apart from rare automobile collisions. In La Petite-Pierre and Castelporziano wild boar were only weakly hunted during the recovery period to control population size. In Chizé, managers either translocate or hunt individuals during the recovery period.



**Figure 3:** A schematic representation of the wild boar life cycle and data collection. The peak birth month is April, followed by the early-life growth period for juveniles (approximately 6 months in length) which coincides with the capture period (from March through September, although it varies slightly between study areas). The period when individuals are recovered from hunting or translocation (October-February) co-occurs with the rut in December.

## Statistical methods

### *Multistate models*

We analyzed CMRR data using multistate models (Arnason, 1973; Brownie et al., 1993) to calculate the annual probability of an individual moving from one state (e.g., alive) to another (e.g. alive, dead by hunting) when there is imperfect detection. Expansions of multistate models have been used to calculate unobserved states (e.g., dead by natural causes). Indeed, during the capture-mark-recapture period and later during the hunting season, individuals may be not detected (not seen), seen alive, or they may be killed by hunting and recovered from the forest. Individuals are in four states: (1) alive, (2) dead by hunting, (3) dead by non-hunting related causes, and (4) already dead the previous year, the absorbing state. The multi-state framework thus allows estimating transition probabilities from one state to another, and thus mortality probabilities, in particular hunting related and non-hunting related mortalities, while accounting for imperfect detection. In papers II & IV, we used multi-state CMRR models to calculate mortality probabilities of marked individuals. In paper II, we calculated age-specific

mortality probabilities using the program E-SURGE (multi-Event SURvival Generalized Estimation; Choquet et al., 2009) for the heavily hunted population in Châteauvillain. Age classes corresponded to juveniles ( $< 1$  year of age), subadults (1-2 years of age), and adults ( $> 2$  years of age). We added early-life growth rates as a covariate to test whether higher early-life growth rates were associated with higher mortality. In paper IV, analyses were implemented in JAGS (Just Another Gibbs Sampler) for three populations (Châteauvillain, La Petite-Pierre, and Castelporziano). While in paper II we used an age-structured model to relate mortality by cause to early-life growth rate, in paper IV we used a size-structured model to calculate cause-specific mortality. In both papers II & IV, we took advantage of the expanded multistate framework to calculate the probability of natural mortality, a hidden state as we did not have data on this mortality cause.

### *Demographic models*

In paper IV, we estimated demographic rates (mortality probabilities, transition between body mass classes, litter size, and proportion of reproductive females) in three populations (La Petite-Pierre, Châteauvillain and Castelporziano). Demographic rates were calculated for three body mass classes (i.e., small, medium, large) which were defined separately for each population due to differences between body mass distributions across study populations. Then, the demographic rates were integrated into two stage-structured population models (one for each condition of resource availability; during which acorns are available and when acorns were unavailable). From the population models, we were able to estimate  $\lambda$  (population growth rate) and  $T$  (generation time as defined as the mean age of mothers at childbirth) for both resource conditions in each population. We then performed a LTRE (Life Table Response Experiment) to calculate the relative contribution of each demographic rate to  $\lambda$  in each condition of acorn availability and classical elasticity analyses.

### *Linear and nonlinear mixed models*

In paper I, we estimated the interactive effects of temperature, precipitation levels, and number of removed individuals at the time of birth on early-life growth rates using data from three study areas: La Petite-Pierre, Châteauvillain, and Chizé. To do so, we used linear mixed-effects models; early-life growth rate was the response variable, temperature, precipitation levels, and number of removed individuals at the time of birth were included as explanatory covariates and year of birth was included as a random intercept in the model due to repeated measures of early-life growth rate within a year.

In paper III, we fit standard nonlinear growth models (forms of the Gompertz, logistic, and monomolecular equations) to data relating body mass to time elapsed since the first capture for both sexes at Chizé and Châteauvillain. Indeed, the shape of lifetime body

growth of mammals using repeated mass measurements over time is often well described using nonlinear functions (Zullinger et al., 1984). Using these standard growth equations, we also estimated the associated body growth parameters:  $k$  the relative growth rate,  $t_0$  the inflection point (for Gompertz and logistic models),  $A$ , the asymptotic body mass,  $I$ , the body mass at first capture (monomolecular model), and  $E(W)$  body mass at time  $t+1$  (see Table 1 for equations used to describe body growth). We tested for a fixed cohort effect on adult body mass  $A$  in addition to individual-level random effects of shape parameters (i.e.  $A$ ,  $k$ ,  $t_0$  for Gompertz and logistic models;  $A$  and  $k$  for monomolecular models).

Table 1: Equations used to describe body growth trajectories in paper III.

Model	E(W)
Gompertz	$Ae^{-e^{-k(t-t_0)}}$
Logistic	$\frac{A}{1 + e^{-k(t-t_0)}}$
Monomolecular	$A + (I - A) e^{-e^{kt}}$

# Results and discussion

## 1. What causes variation in body growth over space and time (papers I, III, IV)?

In paper I, we assessed the influence of conditions at birth on wild boar populations at La Petite-Pierre, Chizé, and Châteauvillain. Specifically, the effect of interactions between the number of removed individuals (which may be interpreted biologically as either a proxy for population density or a reduction in population density for the next year), temperature, and precipitation during birth were quantified for populations found in low and high quality environments. We found conditions at birth that are expected to increase in frequency with global climatic changes were positively associated with faster early-life growth rates. Indeed, warmer, drier springs were positively related to early-life growth rates in La Petite-Pierre and Châteauvillain. As warmer springs are linked to more frequent masting events, we may expect faster early-life growth during these conditions to be related to mast availability. This has important implications as faster early-life growth rates may lead to reaching the threshold size for reproduction more quickly (Servanty et al., 2009), shortening the time to reach reproduction, and thus leading to faster population turnover. In all three sites, early-life growth rates also increased with the number of removed individuals. When the number of removed individuals is interpreted biologically as a proxy for population density, in high density environments wild boar exhibited faster early-life growth rates. This may be a consequence of a density-dependent litter size effect. Following this interpretation, at high densities mothers must compete for resources leading to lighter mothers producing smaller litters (a phenomenon observed across taxa from great tits *Parus major*, Both et al., 2000; to gray wolves, *Canis lupus* Sidorovich et al., 2007). Mothers are able to allocate more resources per offspring in smaller litters, and thus offspring exhibit faster early-life growth rates. Further, we differentiated the relative roles of individual-level plasticity and cohort effects. Individual-level plasticity rather than conditions at birth was found to explain most of the observed variations in early-life growth rates in these three populations. From the results of paper I, we thus demonstrated that although conditions at birth that are expected to occur more frequently are as-

sociated with faster early-life growth rates, individual-level plasticity plays a larger role in determining variation in wild boar early-life growth rates.

In paper III, we tested for the effect of environmental context on the full lifetime body growth trajectories in Châteauvillain and Chizé. We found that body growth curves of wild boar varied between sexes, individuals, and according to environmental context. We expected wild boar body growth to be well described by the Gompertz function as it has been used to describe domestic pig body growth (Ceron et al., 2020) and is generally used to describe body growth for altricial species (Gaillard et al., 1997; Zullinger et al., 1984). Indeed, in resource-rich Châteauvillain, the Gompertz function best described body growth in both sexes. However, in resource-poor Chizé, the monomolecular function best described body growth in females while in males the logistic model performed best. In addition, we observed high heterogeneity in body growth shapes and metrics (growth parameters; e.g. asymptotic body mass) among individuals within a population. This variation both across individuals and between populations indicates a flexibility in body growth shape in wild boar which may be partially attributable to wild boar ranking intermediate on the altricial-precocial continuum. Although wild boar are altricial for an ungulate species following some criteria (e.g. shorter gestation period compared to similarly sized ungulates; remain in nests during early-life due to dependence on mothers for food provisioning and thermoregulation; see Derrickson, 1992), wild boar also possess traits common to precocial species (born with their eyes open and with teeth). Thus, wild boar may also exhibit a monotonically decreasing growth rate from birth onwards (as is described by the monomolecular function), which is observed in precocial species. Further, we observed a cohort effect on adult body mass in both study areas. This finding is consistent with resource conditions at birth influencing body growth through development (i.e., McCance, 1962; Douhard et al., 2013). These long-lasting effects of conditions at birth in the form of a cohort effect may be explained by a silver spoon effect (Grafen, 1988). When comparing between study areas, we also found higher sexual size dimorphism in Châteauvillain than Chizé. As males are more susceptible than females to resource limitation in species under strong sexual selection (also see LeBlanc et al. 2001), this finding was unsurprising. In paper III, we demonstrated that variation in body growth is due to developmental mode (intermediate ranking on altricial-precocial continuum), environmental effects (conditions at birth) and sex.

In paper IV, we tested whether the availability of acorns influenced body mass-specific vital rates in three study areas (Châteauvillain, La Petite-Pierre, and Castelporziano). We calculated the probability of different body mass (i.e., small, medium, large) females surviving, growing, and reproducing when acorns

were and were not available. In Châteauxvillain and Castelporziano, we observed a higher probability of growing to a larger body mass in the presence of acorns for small females and a higher proportion of breeding females. Wild boar in resource rich environments (Châteauxvillain) utilized current acorns while wild boar in poor environments stored resources acquired when acorns were available the previous year. This indicated that wild boar females in Châteauxvillain displayed more of an income breeder tactic than wild boars in the resource poor site that exhibited a breeding tactic closer to the capital breeder end of the capital-income breeder tactic (Jönsson, 1997). Resource availability thus influences allocation strategies to body growth and reproduction differently according to environmental context. From the results from paper IV, we demonstrated that acorn availability influences body growth differently according to environmental context and differently according to female body mass class.

## 2. **What are consequences for variation in body growth over space and time (papers II–IV)?**

In paper II, consistent with energy budgeting theory, we expected to observe a trade-off between early-life growth and natural mortality across individuals (Cody, 1966), i.e. a positive relationship between early-life growth and mortality. Similarly, we expected faster growing individuals to experience a higher hunting probability due to modified habitat use (Creel and Christianson, 2008; Stamps, 2007). We did not find evidence for a cost of growing fast on survival in Châteauxvillain. These findings indicated that variation in body growth rates early in life did not influence survival later in life. For subadult males, however, we even found a negative relationship between early-life growth rate and non-hunting related mortality. Subadult males that lost weight early in life were therefore more likely to emigrate or die of natural causes (e.g., starvation, disease).

In paper IV, we highlighted the importance of resource conditions on population growth rates and generation time across populations of wild boar. In the high-quality habitat (Châteauxvillain), we found high population growth rates in years when acorns were available due to a higher proportion of younger breeding females. In one resource poor site (Castelporziano), acorn availability was similarly associated with higher population growth rates, although this was due to a higher proportion of older, larger females reproducing and of females growing to a larger size. In the other poor-quality habitat, acorn availability did not strongly influence population growth rate, however females were more likely to grow to a larger size. While in both Châteauxvillain and Castelporziano, acorn availability was associated with a lower generation time, in La Petite-Pierre acorn availability was not strongly linked to generation time. Thus, in paper IV, we demonstrated that acorn availabil-

ity may be associated with faster body growth, higher breeding proportion, faster population turnover and higher population growth rates as a consequence (although these relationships are context-dependent).

# Conclusions and prospects

Following Dobzhansky's famous quote "nothing in biology makes sense except in the light of evolution," in the anthropocene, nothing in ecology makes sense except in the light of human-induced change. Therefore, we would like to consider the results of this thesis in the context of a global climatic change and human exploitation of populations. Here, we focused on body growth of a species that is found across environments of varying quality and is also widely hunted. We demonstrated that wild boar body growth rates will likely increase under predicted climate change scenarios (in warm and dry springtimes, see paper I, due to more frequent masting events Touzot et al., 2020 and thus acorn availability, see paper IV). This increase in body growth rates may lead to increased population growth rates and population turnover (paper IV). This increase in population growth must also be considered in the context of the hunting pressure acting on populations. We did not find that fast early-life growth was related to a higher hunting or natural mortality (paper II), suggesting in heavily hunted populations faster development may be favored as individuals do not survive long enough to pay a cost in later-life (i.e., Lemaître et al., 2015). Indeed, hunting may indirectly select for a faster pace-of-life, although there is currently little evidence of this phenomenon in ungulate species (Festa-Bianchet, 2017). However, in light of our findings of high individual-level heterogeneity in body growth rates and trajectories (i.e., high phenotypic plasticity in early-life growth rates paper I, individual-level differences in lifetime body growth trajectories in paper III), it may be difficult to observe whether hunting selects for faster development due to high individual-level variation in body growth. Our ability to record individual-level heterogeneity across populations was only possible due to the availability of high-quality individual-based data on this species in differing environments. The use of similar data on other harvested species provides a fruitful avenue of research into comparing body growth variation across species.



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# Paper I





## How do conditions at birth influence early-life growth rates in wild boar?

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**Abstract.** Weather conditions and population density individuals experience at birth influence their life-history traits and thereby population dynamics. Early-life individual growth is a key fitness-related trait; however, how it is affected by such conditions at birth remains to be explored. Taking advantage of long-term monitoring of three wild boar (*Sus scrofa*) populations living in contrasting ecological contexts, we assess how weather conditions (temperature and precipitation) and the number of removed individuals at birth influence early-life growth rates. We found that the number of individuals removed before the early-growth period had a positive effect on early-life growth rate across sites. This might be interpreted as a density-dependent response involving an increase in food availability per capita that favors faster growth. Alternatively, if the number of removed individuals increases with population density, this result might be attributable to decreasing litter sizes at high density, leading mothers to allocate more resources to individual offspring, which favors higher juvenile growth rates. Early-life growth rates also increased with spring-time temperature and decreasing precipitation. Thus, early-life growth is expected to increase in response to warmer and drier springs, which should become more frequent in the future under current climate change. We found that conditions at birth explained very little among-year variation in early-life growth rates (i.e., weak cohort effects) and that within-year variation in early-life growth rates was more likely caused by strong individual differences.

**Key words:** cohort effects; conditions at birth; individual growth; repeatability analysis; *Sus scrofa*.

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### INTRODUCTION

Life-history traits are shaped by the environmental conditions (e.g., population density, weather conditions) individuals experience at birth (Lindström 1999, Gaillard et al. 2000, Monaghan 2008). These conditions at birth do not affect natural populations independently of each other, as weather conditions generally interact with density-dependent effects. Indeed, the

negative effect of bad weather conditions is expected to be more evident near the carrying capacity (e.g., *Ovis aries* Coulson 2001 and *Halobaena caerulea* Barbraud and Weimerskirch 2003). For example, bad weather conditions (rain-on-snow events) reduce food availability for Svalbard reindeer (*Rangifer tarandus*), which leads to decreased fecundity and survival. The negative effect of bad weather conditions on vital rates is stronger at high population densities, leading to

population crashes (Hansen et al. 2019). While there are an increasing number of studies focused on the combined effects of weather and density on vital rates (survival, fecundity; see Portier et al. 1998, Gamelon et al. 2017b, Layton-Matthews et al. 2020 for case studies), how early-life growth is influenced by the interplay between weather conditions and density has yet to be explored.

The rate of body size growth early in life is a key life-history trait that influences asymptotic size, reproductive success, and longevity (Metcalfe and Monaghan 2001, Hamel et al. 2016). Early-life growth rates (hereafter called ELGR) are known to be plastic (Dmitriew 2011) and to vary across latitudinal clines (e.g., Conover and Present 1990 for countergradient variation) as well as among cohorts. Juveniles born in a year with low population density and good weather conditions may have faster growth rates (potentially with fitness advantage throughout life, see “silver spoon effects”) over those born in a year characterized by high density and poor weather conditions. The strength of these cohort effects can be more pronounced in poor environments, as observed in roe deer *Capreolus capreolus* (Pettorelli et al. 2006). Differences in individual ability to acquire (van Noordwijk and de Jong 1986) and allocate (Cody 1966, Descamps et al. 2016) resources may also account for individual-level variance in ELGR. The susceptibility of ELGR to environmental conditions at birth is thus expected to vary both within and across populations.

Taking advantage of long-term individual monitoring of three wild boar (*Sus scrofa*) populations in contrasting ecological contexts, we assessed how the interplay between the number of removed individuals and weather conditions at birth shapes ELGR. We expected the lowest ELGRs to occur under poor weather conditions in resource-poor sites. We also decomposed the variation in ELGR to assess the relative role of cohort effects and among-individual differences.

## MATERIALS AND METHODS

### Data collection

The study was conducted in three sites where the size of wild boar populations is mostly controlled by harvesting (i.e., hunting and/or

removal of individuals). The first site is the 11,000 ha forest of Châteauvillain in northeastern France (48.02° N, 4.56° E), characterized by a climate intermediate between continental and oceanic. Châteauvillain is considered resource rich as the study area is dominated by oak *Quercus* spp. (41%) and beech *Fagus sylvatica* (30%) (Servanty et al. 2009) that produce acorns and beechnuts, respectively, which offers a regular high-quality forage availability to wild boar (Servanty et al. 2011, Gamelon et al. 2017a). The second site is the 2614 ha Réserve Biologique Intégrale at Chizé in southwestern France (46.05° N, 0.25° W), characterized by mild winters and often warm and dry summers. Productivity of the forest is low as the soil in this site is shallow and calciferous and summer droughts are frequent (Gaillard et al. 2003b). Chizé is considered as a resource-poor habitat for ungulates (Gaillard et al. 2003a, Douhard et al. 2013), with the richest habitat for wild boar (oak *Quercus* spp. and hornbeam *Carpinus betulus*) covering approximately 40% of the reserve (Toïgo et al. 2006). The third site is the 2674 ha national reserve at La Petite Pierre located in the Vosges mountains (48.50° N, 7.00° E) and is characterized by a mixture of continental and oceanic climates, with cool summers and mild winters. The forest is evenly composed by beech, *F. sylvatica*, and coniferous species (mainly silver fir *Abies alba*, Norway spruce *Picea abies*, and Scots pine *Pinus sylvestris*, Hamann et al. 1997). La Petite Pierre is also considered as a resource-poor forest because the soil is acidic and therefore not highly fertile, which leads to poorly diversified vegetation of low nutritive quality for ungulates (Storms et al. 2008, Pellerin et al. 2010).

In all three sites, a capture–mark–recapture–recovery program has allowed capturing, marking using traps, and then releasing a large number of wild boars each year between March and September (Fig. 1). Sex, date, and body mass to the nearest 0.1 kg are recorded for each individual caught, and multiple captures (alive and dead when shot by hunters) are available. This allowed estimating ELGR (in g/d) for individuals with repeated measurements by assuming linear growth until a body mass of 20 kg (about 6 months of age) was reached (as supported by previous analyses, see Gaillard et al. 1992, Veylit et al. 2020). We retained measurements taken

more than seven days apart for each individual. Analyses were conducted on 991 individuals (516 males, 475 females) at Châteauvillain between 1983 and 2016, 742 individuals (365 males, 377 females) at Chizé between 2003 and 2016, and 523 individuals (238 males, 285 females) at La Petite Pierre between 2008 and 2017.

As weather conditions at birth may influence ELGR, we considered cumulative precipitation (in mm) and mean temperature (in °C) in April when the birth peak occurs (Appendix S1: Fig S1). Weather data were obtained from Météo France (Beauvoir sur Niort weather station for Chizé; stations in Villiers le sec, Chaumont-ville, and Chaumont-Semoutiers for Châteauvillain; Phalsbourg for La Petite Pierre). The number of removed individuals (i.e., the annual number of individuals killed or translocated) during the hunting season (October–February) may also influence ELGR in spring (from April). Both weather conditions and the number of removed individuals differed among study sites (Appendix S1: Fig. S2, Table S1).

#### Statistical analysis

Early-life growth rate was entered as the response variable in linear mixed models with year of birth as a random intercept to account for repeated measurements of ELGR within a year. Temperature and precipitation in April and the number of removed individuals were included as continuous covariates, in interaction with the study site, which was included as a categorical

factor. As the correlations between weather conditions and the number of removed individuals were consistently below 0.7 (Appendix S1: Table S2), no collinearity problems occurred and we included these covariates in the same model (following Dormann et al. 2013's recommendations). To test for the interactive effect of weather and the number of removed individuals, precipitation and temperature were included as covariates in interaction with the number of removed individuals and study site. We also tested for a different effect of temperature on ELGR at different precipitation levels. Sex was included as a categorical factor. Year of birth was included as a continuous variable to test for a possible linear temporal trend in ELGR. We tested all derived models.

We then partitioned the variance in ELGR into within-year (i.e., differences among individuals) and between-year variances and estimated the repeatability ( $R$ ) of ELGR in a given year as:

$$R = \frac{V_{BY}}{(V_{BY} + V_{WY})}$$

where  $V_{BY}$  is the between-year variance in ELGR, and  $V_{WY}$  the within-year variance (Nakagawa and Schielzeth 2010). First, we estimated  $R$  from a model including only year as a random factor to calculate the ratio of within- and between-year variances in ELGR. Then, from the model retained based on Akaike's information criterion, corrected for sample sizes ( $AIC_c$ ; Anderson and Burnham 2002), we included the fixed effects to calculate the repeatability in ELGR after

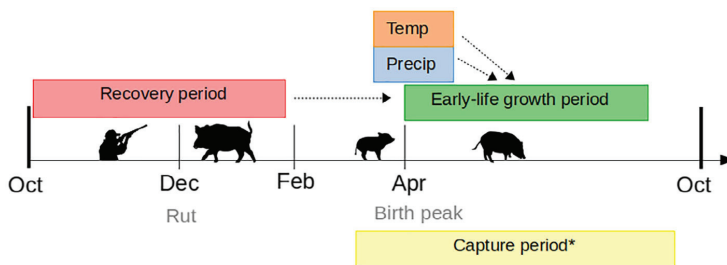


Fig. 1. Wild boar life cycle. Data on the number of removed individuals are collected during the hunting season (October–February) coinciding with the rut and gestation periods. Weather variables (temperature and precipitation) that influence early-life growth rates were collected during the birth peak, in April, and the period of early-life growth coincides with the capture period (which may vary slightly between sites).

controlling for fixed effects. When  $AIC_c$  values of two competing models were within two units, we retained the simplest model (i.e., the model with the fewest parameters) to satisfy parsimony rules.

Analyses were conducted in R v. 3.6.0 using the nlme package (v. 3.1-140, Anderson and Burnham 2002, Pinheiro et al. 2019). Associated 95% confidence intervals for model estimates were calculated using the delta method (Powell 2007). Repeatability and associated standard errors (SE) were estimated from 1000 bootstrap iterations using rptR (v. 0.9.22, Stoffel et al. 2017).

## RESULTS

Early-life growth rates fluctuated over the study period in all sites (Appendix S1: Fig. S3). Average ELGR were estimated to be  $79.62 \pm 49.84$  g/d in Châteauvillain,  $27.62 \pm 49.09$  g/d in Chizé, and  $57.01 \pm 39.90$  g/d in La Petite Pierre. ELGR was affected by sex, weather conditions at birth, number of removed individuals the winter before the early-life growth period, and interactions between these effects and study site. The same analysis conducted on each site separately allowed for a simpler interpretation of complex interactive effects.

In Châteauvillain, following the rules of parsimony, the model (Table 1) included a weak sex effect with males growing slightly faster than females (by  $8.10 \pm 2.94$  g/d, Table 2). This model also included an interaction between temperature and the number of removed individuals, such that ELGR increased with temperature at a greater rate when the number of removed individuals was higher (Fig. 2A). Growth rate repeatability from the model including the random effect of year was 0.23 (SE: 0.05). After controlling for fixed effects,  $R$  was 0.14 (SE: 0.04) and the fixed effects in the model (i.e., sex, number of removed individuals, and temperature) explained 9.30% (SE: 0.04) of the phenotypic variance in early-life growth rates. The selected model performed much better than the constant model ( $\Delta AIC_c = 16.04$ ).

In Chizé, the selected model included a weak positive effect of the number of removed individuals on ELGR ( $0.21 \pm 0.11$  Table 2, Fig. 2B). Growth rate repeatability within a year was 0.28 (SE: 0.10). When controlling for fixed effects, it

was 0.21 (SE: 0.08) and the number of removed individuals explained only 3.30% (SE: 0.03) of the observed phenotypic variance in early-life growth rates. Indeed, the selected model only slightly outperformed the constant model ( $\Delta AIC_c = 1.73$ ), indicating weak support for an influence of conditions at birth on early-life growth rates at Chizé.

In La Petite Pierre, the selected model included an interaction between temperature and precipitation (Table 2, Fig. 2C). At high precipitation levels, temperature had virtually no effect on ELGR, whereas at low precipitation levels, ELGR increased with April temperature. Temperature also had a positive effect on ELGR ( $0.28 \pm 0.05$ , Table 2). Growth rate repeatability within a year was 0.16 (SE: 0.07). After controlling for fixed effects, it was close to 0 (SE: 0.01). The fixed effects in the model (i.e., the number of removed individuals, precipitation, and temperature) explained 15.10% (SE: 0.03) of the phenotypic variance in ELGR, indicating a very low repeatability in ELGR after controlling for fixed effects. The best model substantially outperformed the constant model ( $\Delta AIC_c = 15.09$ ).

## DISCUSSION

Using three populations of wild boar exposed to contrasting ecological contexts, we examined the interactive effects of environmental conditions at birth on juvenile growth. More specifically, we assessed the effects of temperature and precipitation in April. These weather conditions at birth may directly affect ELGR by inducing thermoregulation costs (Vetter et al. 2015). As piglets are born without extensive energy stores, they are expected to be vulnerable to weight loss during cold weather (see Le Dividich and Noblet 1983 in domestic pigs). Temperature and precipitation in April may also indirectly affect ELGR through resource availability. Thus, evidence is accumulating that spring conditions may influence fruit production such as oak seeds (acorns; Caignard et al. 2017, Schermer et al. 2019), a major food resource for wild boar. Therefore, warm springs are expected to be associated with higher seed production and higher food availability for the wild boar, allowing a higher allocation to body mass (Gamelon et al. 2017a) and growth. Here,

Table 1. Model selection based on AIC<sub>c</sub> showing the 10 best models for each site and the constant model.

Site	NR	T	P	Sex	Year	NR × T	NR × P	T × P	df	AIC <sub>c</sub>
Châteauvillain	X	X	X	X		X			8	10,439.45
	X	X		X		X			7	<b>10,439.47</b>
	X	X	X	X		X	X		9	10,440.99
	X	X	X	X		X		X	9	10,441.16
	X	X		X	X	X			8	10,441.37
	X	X	X	X	X	X			9	10,441.41
	X	X	X	X		X	X	X	10	10,442.76
	X	X	X	X	X	X	X		10	10,442.77
	X	X	X	X	X	X			10	10,443.15
	X	X	X	X	X	X	X	X	11	10,444.62
									3	10,455.51
Chizé	X	X	X			X		X	8	7789.81
	X	X				X			6	7789.87
	X	X	X			X			7	7790.12
	X								4	<b>7790.58</b>
	X	X	X			X	X	X	9	7790.94
	X	X	X		X	X			8	7791.02
	X	X	X			X	X		8	7791.12
	X	X	X		X	X	X		9	7791.15
	X	X							5	7791.38
	X	X	X		X	X		X	9	7791.48
									3	7792.31
La Petite Pierre	X	X	X					X	7	<b>5267.17</b>
	X	X	X				X	X	8	5267.67
	X	X	X			X		X	8	5268.28
	X	X	X		X			X	8	5269.21
	X	X	X	X				X	8	5269.23
	X	X	X			X	X	X	9	5269.61
	X	X	X	X			X	X	9	5269.71
	X	X	X		X		X	X	9	5269.73
	X	X	X		X	X		X	9	5270.11
	X	X	X	X		X		X	9	5270.32
									3	5282.26

Note: Effects of sex (*Sex*), annual trend (*Year*), mean temperature (*T*), and cumulative precipitation (*P*) in April, and number of removed individuals (*NR*) on wild boar ELGR, at Châteauvillain, Chizé, and La Petite Pierre, France. Selected models are indicated in bold. AIC<sub>c</sub>, Akaike's information criterion, corrected for sample sizes.

we found that April temperature had a positive effect on ELGR in Châteauvillain and La Petite Pierre. Moreover, the average ELGR was higher in Châteauvillain, where wild boar have access to abundant food resources (Servanty et al. 2011, Gamelon et al. 2017a), than in Chizé and La Petite Pierre where fruit production was lower as the soil quality in these sites is poor. In addition to seeds, earthworms constitute an important food resource for wild boar (Baubet et al. 2003, 2004). Interestingly, we did not find evidence for higher ELGR under cold and wet conditions when earthworm emergence is higher. Rather, ELGR increased with warm and dry conditions in La Petite Pierre (Fig. 2C).

While most size dimorphic ungulates exhibit sex-specific maternal allocation (Byers and Moodie 1990), which leads to sex-specific ELGR, wild boar is a rare example of an ungulate species with similar early-life growth rates for both sexes. Indeed, in accordance with previous work (Gaillard et al. 1992, Veylit et al. 2020), we found no support for ELGR being sex-specific for the populations at Chizé and La Petite Pierre. In Châteauvillain, a sex-specific ELGR was detected but the effect size was very weak.

For the three sites, we consistently found low-to-moderate (as defined by Nakagawa and Schielzeth 2010) within-year repeatability of ELGR (ranging from 0.16 to 0.28), which

Table 2. Effects of mean temperature ( $T$ ), cumulative precipitation in April ( $P$ ), number of removed individuals ( $NR$ ) as well as sex ( $Sex$ , with “ $M$ ” referring to males) on early-life growth rate at Châteauvillain, Chizé, and La Petite Pierre, France.

Site	Parameter	Slope $\pm$ SE	Standardized slope $\pm$ SE
Châteauvillain	$Sex$ ( $M$ )	$8.10 \pm 2.94$	$8.10 \pm 2.94$
	$NR$	$-0.33 \pm 0.10$	$-3.69 \pm 4.06$
	$T$	$-20.10 \pm 9.06$	$7.01 \pm 3.81$
	$T \times NR$	$0.03 \pm 0.01$	$10.86 \pm 3.48$
Chizé	$NR$	$0.21 \pm 0.11$	$9.46 \pm 4.82$
	$P$	$4.95 \pm 0.93$	$-18.29 \pm 4.03$
	$T$	$26.79 \pm 4.35$	$4.23 \pm 2.00$
	$NR$	$0.28 \pm 0.05$	$9.83 \pm 1.86$
La Petite Pierre	$P \times T$	$-0.55 \pm 0.10$	$-18.25 \pm 3.41$

Note: Coefficients are shown for unstandardized and standardized covariates (i.e., normalized). SE, standard error.

indicates high among-individual variation. The proportion of variance in ELGR explained by the environmental covariates was generally low, ranging from 3.30% for Chizé to 15.10% for La Petite Pierre. Environmental conditions thus explain a small proportion of the variance in ELGR and it is likely that strong individual differences account for such a high within-year variation in ELGR (Niemelä and Dingemans 2017, Renaud et al. 2019). As wild boar are closer to income breeders along the capital-income breeder continuum (Servanty et al. 2009, Gamelon et al. 2017a), current conditions are expected to influence maternal body condition and offspring ELGR. Differences in milk quality provisioned to offspring for ELGR are thus dependent on what resources mothers are able to acquire (Gamelon et al. 2017a) and provision to offspring. Therefore, differences in ELGR among individuals within a year likely originated from contrasting maternal attributes (e.g., mass, age, litter size) to acquire and allocate resources.

In all three sites, there was a positive relationship between the number of removed individuals and ELGR. The number of removed individuals may be interpreted biologically in two ways. A high number of individuals removed during winter (October–February) may reduce the number of individuals in the population in the following spring (from April onwards; Fig. 1). In this case, the observed positive relationship between ELGR and number of removed

individuals may be interpreted as a density-dependent response that involved an increase in food availability per capita favoring a faster growth. Alternatively, under specific management strategies (e.g., if the removal rate is constant over years), the number of removed individuals may be interpreted as a proxy for the population density (Cattadori et al. 2003, Flanders-Wanner et al. 2004). In that case, the positive relationship between ELGR and the number of removed individuals may be related to a confounding effect of density-dependent response of litter size. At high densities, mothers usually produce smaller litters because of stronger competition for resources to allocate to reproduction (Stefan and Krebs 2001 in snowshoe hares *Lepus americanus*, Both et al. 2000 in great tits *Parus major*, and Sidorovich et al. 2007 in gray wolves *Canis lupus*). In many species, smaller litters have both higher survival (Lack 1947) and juvenile growth (Rödel et al. 2008 in rabbits and rats). Indeed, in domesticated pigs, mass gain between birth and weaning was negatively related to litter size (Andersen et al. 2011). At high densities, females may thus produce fewer higher quality offspring (Sinervo et al. 2000). We expected these density-dependent responses to be stronger in the resource-poor sites than in Châteauvillain, which is characterized by high resource availability. Additional data will be needed to reliably estimate population density in each of the three sites (St. Clair 2012) and to discriminate between the two biological interpretations.

We detected an effect of interacting conditions at birth on ELGR in two populations. In Châteauvillain, the positive effect of temperature on ELGR was stronger at higher numbers of removed individuals. In La Petite Pierre, ELGR increased with temperature, but only at low precipitation levels. This positive association between April temperature and growth may also be linked to decreased litter size at high temperatures, as observed in a German wild boar population (Frauendorf et al. 2016) and to increased maternal provisioning to individual offspring. However, in all sites the effects of conditions at birth are largely overshadowed by individual-level variation in ELGR. Therefore, strong phenotypic plasticity rather than environmental conditions at birth appears to drive variation in wild boar ELGR.



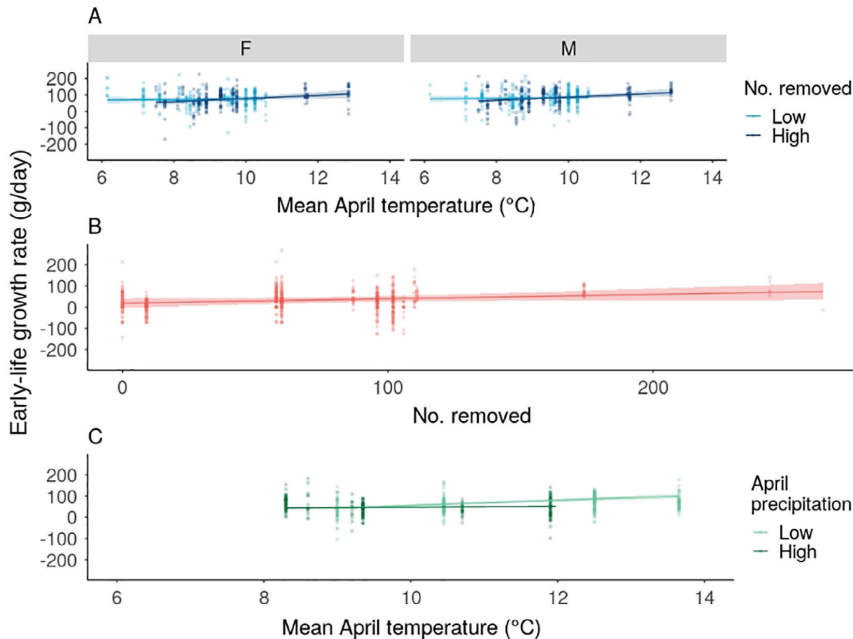


Fig. 2. Early-life growth rate vs. environmental variables for three populations of wild boar. At Châteauvillain (A), early-life growth rates are shown as a function of April temperature for females (F) and males (M), at the 25% ("Low", light blue) and 75% quantiles ("High", dark blue) for the number of removed individuals. At Chizé (B), early-life growth rates are shown as a function of the number of removed individuals, and at La Petite Pierre (C), early-life growth rates are shown as a function of April temperatures at the 25% ("low", light green) and 75% quantiles ("high", dark green) April precipitation levels. Regression lines are reported with associated 95% confidence intervals from the selected models (Tables 1, 2).

Here, we found that various environmental conditions at birth (e.g., temperature, number of individuals removed) may explain a small part of the observed phenotypic variance in ELGR in wild boar. Thus, individuals are able to respond plastically to different environmental conditions to a small extent. In particular, wild boar born in conditions that are expected to increase in frequency with global climatic change (e.g., warmer and drier springs) grow more quickly in early life. Increasing ELGR may shorten the time to reach the threshold size for reproduction and lead to reproduction at earlier ages, at least for females (Servanty et al. 2009). This shortening in generation time may ultimately accelerate the population turnover, with potential important

implications throughout Europe as wild boar populations are already increasing in size and distribution (Massei et al. 2015). Importantly, environmental conditions at birth explained only very little among-year variation in ELGR and strong individual differences likely induced high within-year variation in ELGR.

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### SUPPORTING INFORMATION

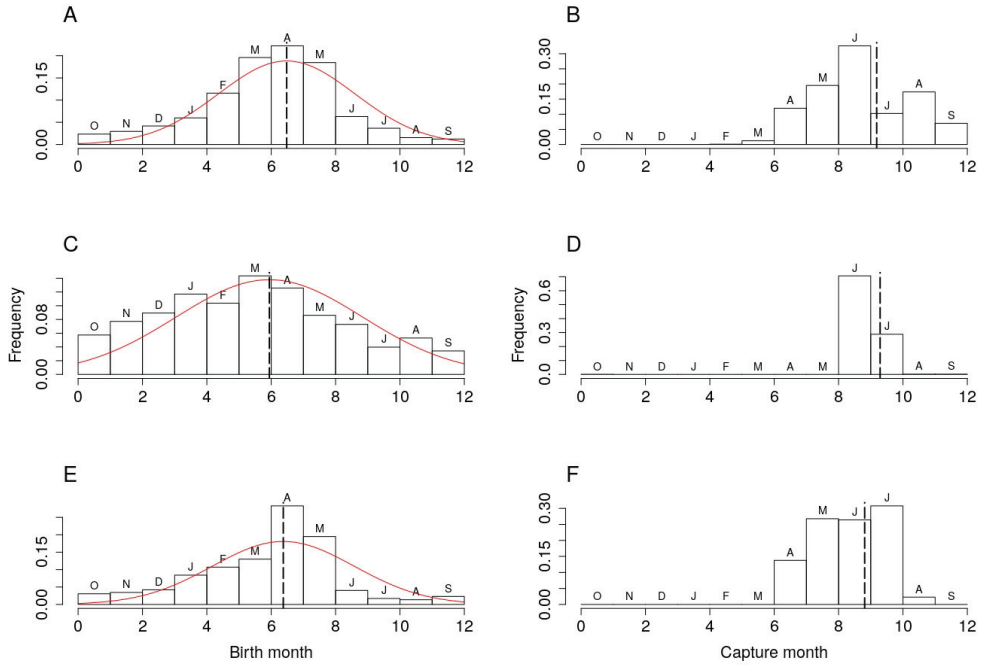
Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3167/full>

## Appendix S1

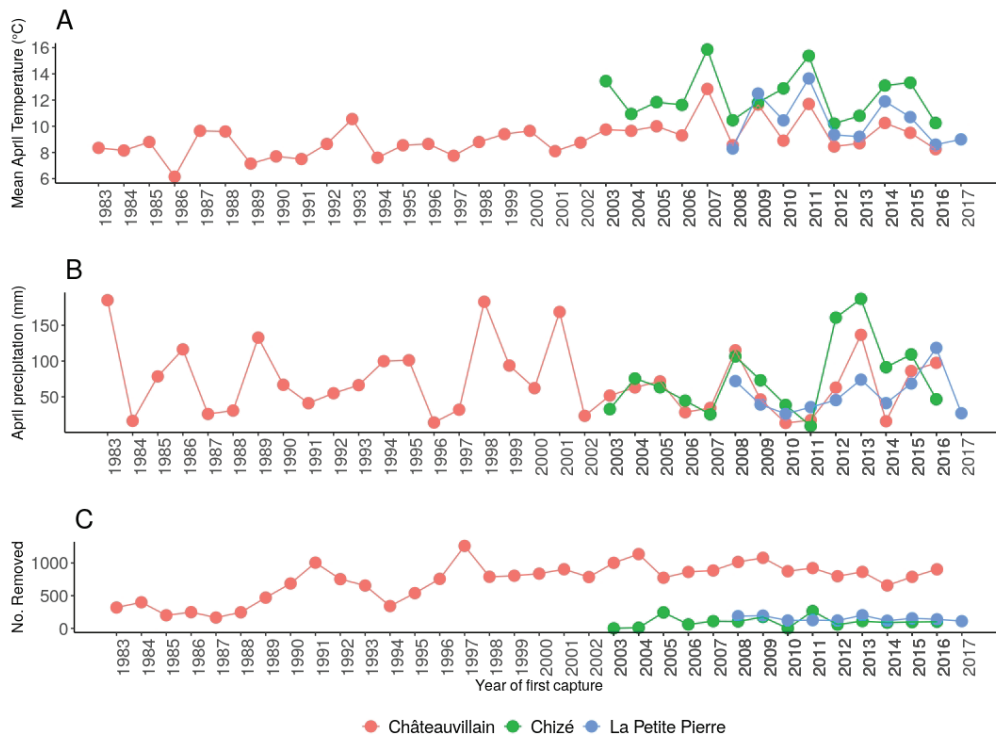
“How do conditions at birth influence early-life growth rates in wild boar?”

by

Lara Veylit, Bernt-Erik Sæther, Jean-Michel Gaillard, Eric Baubet, and Marlène Gamelon



**Figure S1:** Months of birth (A,C,E) and capture (B,D,F) for wild boars at Châteauvillain (A,B), Chizé (C,D), and La Petite Pierre (E,F). The dashed line represents the mean capture/birth month. The first letter of the month of capture/birth are given above the given frequency. Birth dates were back calculated using weight at first capture and individual growth rate, assuming a linear juvenile growth rate and birth weight of 1kg. Negative and null early-life growth rates were set to the mean for a given sex at a given site.



**Figure S2:** Mean April temperature (A) (in °C), cumulative April precipitation (B) (in mm), and number of removed individuals (C) across study years for Châteauvillain (red), Chizé (green), and La Petite Pierre (blue), France.

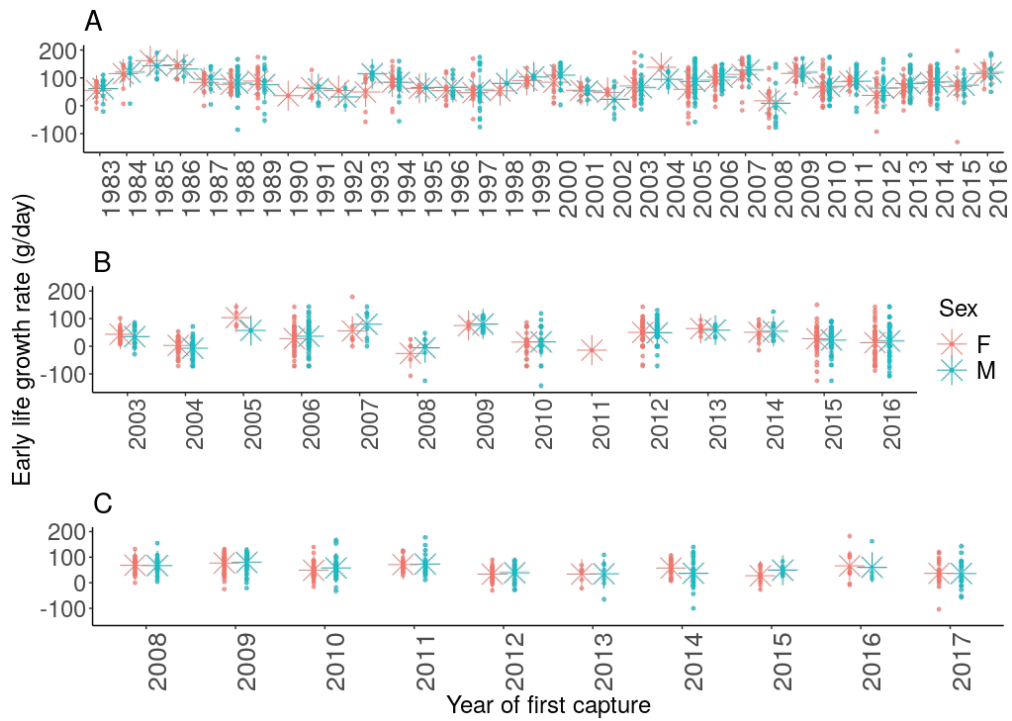
**Table S1:** Mean and standard deviation mean April temperature (in °C) ( $T$ ), cumulative April precipitation (in mm) ( $P$ ), and number of removed individuals ( $NR$ ) across study years for Châteauvillain, Chizé, and La Petite Pierre, France.

	T	P	NR
Châteauvillain	$9.03 \pm 1.34$	$71.56 \pm 48.85$	$727.18 \pm 282.07$
Chizé	$12.28 \pm 1.81$	$75.99 \pm 51.15$	$101.50 \pm 80.94$
La Petite Pierre	$10.37 \pm 1.81$	$54.76 \pm 28.63$	$146.80 \pm 35.19$



**Table S2:** Pearson product-moment correlation values and associated  $p$ -values (in brackets) for mean temperature ( $T$ ) and cumulative precipitation ( $P$ ) in April, and number of removed individuals ( $NR$ ) at Châteauvillain, Chizé, and La Petite Pierre, France.

Châteauvillain		
	T	P
P	-0.39 (0.02)	...
NR	0.27 (0.12)	-0.15 (0.40)
Chizé		
	T	P
P	-0.60 (0.02)	...
NR	0.24 (0.41)	-0.12 (0.67)
La Petite Pierre		
	T	P
P	-0.51 (0.13)	...
NR	-0.12 (0.74)	0.38 (0.28)



**Figure S3:** Early-life growth rates across years (mean annual values are indicated by stars) for males (blue) and females (red) at Châteauvillain (A), Chizé (B), and La Petite Pierre (C).

## Paper II





# Grow fast at no cost: no evidence for a mortality cost for fast early-life growth in a hunted wild boar population

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## Abstract

From current theories on life-history evolution, fast early-life growth to reach early reproduction in heavily hunted populations should be favored despite the possible occurrence of mortality costs later on. However, fast growth may also be associated with better individual quality and thereby lower mortality, obscuring a clear trade-off between early-life growth and survival. Moreover, fast early-life growth can be associated with sex-specific mortality costs related to resource acquisition and allocation throughout an individual's lifetime. In this study, we explore how individual growth early in life affects age-specific mortality of both sexes in a heavily hunted population. Using longitudinal data from an intensively hunted population of wild boar (*Sus scrofa*), and capture–mark–recapture–recovery models, we first estimated age-specific overall mortality and expressed it as a function of early-life growth rate. Overall mortality models showed that faster-growing males experienced lower mortality at all ages. Female overall mortality was not strongly related to early-life growth rate. We then split overall mortality into its two components (i.e., non-hunting mortality vs. hunting mortality) to explore the relationship between growth early in life and mortality from each cause. Faster-growing males experienced lower non-hunting mortality as sub-adults and lower hunting mortality marginal on age. Females of all age classes did not display a strong association between their early-life growth rate and either mortality type. Our study does not provide evidence for a clear trade-off between early-life growth and mortality.

**Keywords** Capture–mark–recapture analysis · Covariation in life-history traits · Early-life growth · Exploited population

## Introduction

Harvesting acts as a strong selective pressure for early reproduction (Conover and Munch 2002; Festa-Bianchet 2003; Proaktor et al. 2007). High body growth rates allow individuals to reach the threshold size for reproduction early in life (Ricklefs 1969; Gadgil and Bossert 1970). As a consequence, fast early-life growth could be selected for in intensively hunted populations. However, fast early-life growth might be associated with some mortality costs. Following the principle of allocation (Cody 1966), fast early-life growth comes at the expense of other life-history traits such as somatic maintenance (Rollo 2002; Metcalfe and Monaghan 2003). An immediate natural mortality cost that may result from fast early-life growth can come in the form of reduced immune function in mammals (McDade 2005; but see Cheynel et al. 2019). Faster-growing individuals may thus experience higher natural mortality than slower-growing counterparts due to physiological costs associated with fast early-life growth. However, differences in individual

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quality in both resource acquisition and allocation may partially or completely mask trade-offs between life-history traits (van Noordwijk and de Jong 1986; Hamel et al. 2009; Wilson and Nussey 2009).

High-quality individuals (where quality is referred to as a positive covariation among performance traits that maximize lifetime reproductive success; see Wilson and Nussey 2009) exhibit secondary traits and behaviors that allow both high survival and high reproduction within their environmental context. Individuals of high quality are better able to acquire resources and thereby their probability of dying from natural causes is reduced compared to low-quality individuals (Bérubé et al. 1999; Blums et al. 2005). Therefore, high-quality individuals with fast early-life growth are expected to be those with lower natural mortality, and thus we expect a negative relationship between early-life growth and natural mortality for high-quality individuals. The resulting relationship between early-life growth and mortality may therefore be driven by a resource allocation trade-off and/or heterogeneity in individual quality.

The type of covariation among life-history traits is context dependent, with factors such as sex and age influencing their relationship. Predation risk modifies how populations seek out resources, for example by changing home range sizes, foraging time, or habitat selection (Creel and Christianson 2008). Behavioral effects of hunting can be stronger than those induced by non-human predators (see Proffitt et al. 2009 for an example of wolves and human predation on elk *Cervus elaphus*). Hunting may therefore influence how individuals acquire and allocate resources as well as the characteristics of a high-quality individual. For example, individuals that exhibit risky behavior and acquire more resources have higher early-life growth rates and are able to reproduce at a younger age than more cautious and slower-growing peers. However, when exposed to a high hunting pressure, bolder individuals may then face a higher probability of being harvested (Biro et al. 2006; Stamps 2007). Therefore, although faster early-life growth may be advantageous in some contexts, this faster growth schedule may come at an increased hunting risk. In the case of a hunted population, the highest-quality individuals are those able to acquire the highest amount of resources while also avoiding hunters. High-quality individuals therefore minimize predation risk when acquiring resources (Festa-Bianchet 1988 in bighorn sheep *Ovis canadensis*; Altendorf et al. 2001 in mule deer *Odocoileus hemionus*; Verdolin 2006 for a meta-analysis).

Changes to habitat use in response to hunting disturbance may differ between sexes (Saïd et al. 2012) and across age classes (Ciuti et al. 2012). Moreover, there is compelling evidence for differential allocation to early-life growth between males and females, resulting in different mortality costs for each sex. In polygynous species displaying strong sexual size

dimorphism, males usually grow faster than females (e.g., red deer *Cervus elaphus* Clutton-Brock et al. 1982; but see Byers and Moodie 1990). We can thus expect mortality costs of growing fast to differ between sexes in species subjected to a strong sexual size dimorphism. The difference in natural mortality costs between sexes for fast early-life growth is expected to reflect the time to reach sexual maturity. The sex that reaches sexual maturity at a younger age is therefore expected to pay a cost at a younger age than the sex that displays a prolonged early-life growth. Thus, differences such as age and sex could influence the relationship between early-life growth rate and different mortality types (i.e., natural mortality vs. hunting mortality) in hunted populations.

The scarce empirical evidence available for a relationship between early-life growth and survival in harvested populations generally indicates that growing fast entails a cost, although there are notable exceptions (Table 1, Appendix S1). It is noteworthy that some studies have failed to detect a relationship between early-life growth and survival (e.g., Bergeron et al. 2008; Bonenfant et al. 2009), while others have found positive relationships (Chambellant et al. 2003; Beauplet et al. 2005; Nuñez et al. 2015). In these studies, high individual quality (with traits such as a heavy weight at birth) was strongly related to fast early-life growth and lower mortality rates. While investigating the potential effect of growing fast on survival in harvested populations, it is important to consider that most of the studies did not distinguish among the causes of mortality (Table 1, Appendix S1). Mortality from hunting and non-hunting causes were generally pooled as “overall mortality” (e.g., Loehr et al. 2007; Jorgensen and Holt 2013; but see Bonenfant et al. 2009). Moreover, all studies dealing with harvested populations only focused on one sex (Table 1, Appendix S1), preventing an assessment of between-sex differences (e.g., Robinson et al. 2006). A study linking early-life growth and age-specific mortality rates for individuals who experienced two types of mortality (natural and hunting) in males and females would allow further understanding of the mortality costs of fast early-life growth.

Taking advantage of a unique long-term monitoring study of an intensively hunted population of wild boar (*Sus scrofa*), we aimed to assess both whether early-life growth is associated with subsequent mortality and whether sex and mortality cause influenced this potential association. We first looked for the relationship between early-life growth rate and overall mortality in both sexes. Then, we explored the relationship between early-life growth rate and cause-specific mortality in both sexes. In a highly dimorphic and polygynous species such as wild boar (Toïgo et al. 2008), we could expect sex-specific differences in the strength of the relationship between early-life growth rate and natural mortality. In particular, wild boar males and females start growing at the same rate, but females stop growing well before

**Table 1** Studies linking early-life growth rates to survival (non-exhaustive list)

Species	Order	References	Effect		Study type	Exploited
			Males	Females		
Bighorn sheep <i>Ovis canadensis</i>	Artiodactyla	Bonenfant et al. (2009)	(0)	NA	Field	Yes
Dall sheep <i>Ovis dalli</i>	Artiodactyla	Loehr et al. (2007)	(−)	NA	Field	Yes
Stone sheep <i>Ovis dalli stonei</i>	Artiodactyla	Douhard et al. (2016)	(−)	NA	Field	Yes
Alpine ibex <i>Capra ibex ibex</i>	Artiodactyla	Toïgo et al. (2013)	(0) <sup>a</sup>	NA	Field	No
Alpine ibex <i>Capra ibex ibex</i>	Artiodactyla	Bergeron et al. (2008)	(0)	NA	Field	No
Chamois <i>Rupicapra rupicapra</i>	Artiodactyla	Bleu et al. (2014)	NA	(−)	Field	No
Chamois <i>Rupicapra rupicapra</i>	Artiodactyla	Corlatti et al. (2017)	(0)	(0)	Field	No
Chamois <i>Rupicapra rupicapra</i>	Artiodactyla	Corlatti et al. (2017)	(−)	(±) <sup>b</sup>	Field	Yes
European mouflon <i>Ovis orientalis</i>	Artiodactyla	Kavčić et al. (2019)	(−)	NA	Field	Yes
Subantarctic fur seal <i>Arctocephalus tropicalis</i>	Carnivora	Chambellant et al. (2003)	(+)	(0)	Field	No
Subantarctic fur seal <i>Arctocephalus tropicalis</i>	Carnivora	Beauplet et al. (2005)	(+)	(+)	Field	No
Three-spined stickleback <i>Gasterosteus aculeatus</i>	Gasterosteiformes	Lee et al. (2012)	(−)	(−)	Experimental	No
Speckled wood butterfly <i>Pararge aegeria</i>	Lepidoptera	Gotthard et al. (1994)	(−)	(−)	Experimental	No
Perch <i>Perca fluviatilis</i>	Perciformes	Metcalfe and Monaghan (2003) and Craig (1980)	(−)	NA	Field	No
European plaice <i>Pleuronectes platessa</i>	Pleuronectiformes	Jorgensen and Holt (2013)	NA	(−)	Theoretical model	Yes
Rhesus Macaques <i>Macaca mulatta</i>	Primates	Núñez et al. (2015)	(+)	(+)	Experimental	No
Wild type mice <i>Muridae Mus</i>	Rodentia	Rollo (2002)	(−)	(−)	Experimental	No
Norway rats <i>Rattus norvegicus</i>	Rodentia	Rollo (2002)	(−)	(−)	Experimental	No
Tasmanian snow skinks <i>Niveoscincus mircolepidotus</i>	Squamata	Olsson and Shine (2002)	(−)	(−)	Experimental	No

We reported if early-life growth had a positive (+), negative (−), no (0), or untested (NA) effect on survival. The literature survey was performed using ISI Web of Science and Google Scholar using combinations of the keywords “early-life growth rate,” “juvenile growth rate,” “trade-off,” “survival,” “mortality,” “growth–lifespan trade-off,” “growth–survival trade-off,” and “growth–mortality trade-off.” In addition, the bibliographies of relevant papers were used to search for studies to include in the review. These terms were kept broad as the relationship between early-life growth and survival can be analyzed in a study but not be its focus. Only studies performed on animal species were retained. The search was conducted in February 2020. For more precise information from each paper detailing the trade-off, see Appendix S1

<sup>a</sup>Early-life growth was not related to survival until late life, when early horn growth incurred a survival cost

<sup>b</sup>The culling regime and hunter preference determined survival patterns in the two harvested populations

males (Gaillard et al. 1992). Also, wild boar females exhibit a lower threshold body mass for reproduction than other species of large herbivores (Servanty et al. 2009). We thus expect females to pay a natural mortality cost at a younger age than males, which display a prolonged growth period. As the hunting pressure is strong in this system, we expect high hunting mortality for individuals regardless of sex, age, or early-life growth rate.

## Materials and methods

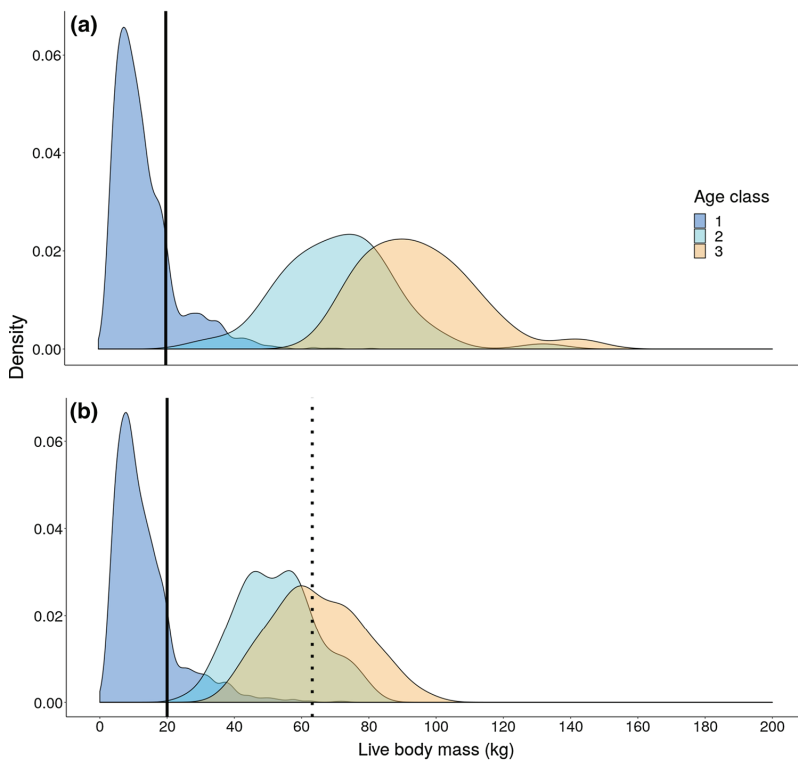
### Study area and data collection

We analyzed data collected from a long-term study of a hunted wild boar population located in the Châteauvillain-Arc-en-Barrois forest. The 11,000 ha forest is located in north-eastern France (45°02'; 4°55' E) and is characterized by a climate intermediate between continental and oceanic. Capture-mark-recapture data were collected annually between March and September from 1983 to 2017. Individuals weighing less than 20 kg (i.e., juveniles < 1 year of age) were captured using traps, marked, and released (Fig. 1). Sex, date, and body mass to the nearest 0.1 kg were

recorded for each individual. Individuals were recaptured after at least 1 week has passed since the previous capture event. Therefore, all body mass measurements were more than 7 days apart. These data were collected for 516 males and 475 females.

Starvation, disease, and vehicle collisions accounted for most non-hunting mortality in this population. As only 5 out of 992 individuals died from vehicle collisions in our dataset, non-hunting mortality is a good proxy of natural mortality. Hunting was the main source of mortality (Gamelon et al. 2011). While wild boars have been growing in numbers appreciably throughout Europe during the last decades, they are managed at a local scale. At Châteauvillain-Arc-en-Barrois, wild boars are harvested by drive hunts between October and February each year during the study period. Each weekend during the hunting period, drive hunts are organized. Ambush hunters are posted around a given area and wait for wild boars startled by beaters and dogs (Saïd 2012; Vajas et al. 2020). Wild boars are killed when they are flushed out of the hunted plot. In that respect, hunting is not oriented toward any specific age or body mass class. However, large females are protected from hunters who have to pay a penalty when shooting females over 50 kg (dressed body mass, Gamelon et al. 2012), which corresponds to about 63 kg live body mass (Fig. 1b).

**Fig. 1** The distribution (displayed as kernel density estimates) of (a) male and (b) female body mass of individual wild boar in relation to age class. Age class one corresponds to birth to 1 year of age (i.e., juveniles), age class two corresponds to one to 2 years of age (i.e., subadults), and age class three corresponds to individuals older than 2 years of age (i.e., adults). Individuals included in the analysis were captured for the first time in their first year of life (age class one) and were captured at least twice with a live body mass measurement of or below 20 kg (this body mass threshold is indicated by the black solid lines) to estimate their early-life growth rate. Females at or above 63 kg (i.e., with a dressed body mass at or above 50 kg, see Gamelon et al. 2012) were protected by a hunting restriction (black dotted line)





Such a hunting regulation did not exist for males. Due to the unique life history of wild boar, the protected threshold size for hunting (63 kg) is reached as early as 2 years of age by most females (see Fig. 1). Thanks to the social structure of wild boar as well as strong phenotypic differences between sexes and ages, hunters can easily assess sex and approximate body mass, and thus avoid shooting the largest females (Gamelon et al. 2012). Indeed, wild boars live in matrilineal social groups and males are solitary (Kaminski et al. 2005), making the determination of sex straightforward. Also, a female group is led by a large sow (generally weighing more than 63 kg), followed by juveniles that are markedly smaller. They are striped until 4 months of age and then wear a reddish coat until they reach about 30 kg. This makes the determination of body mass straightforward. As a consequence, because of the high hunting pressure and the hunting restriction on large females, a large proportion of individuals less than 1 year of age is shot in that population (between 60 and 80%, see Fig. 1 in Gamelon et al. 2011). Live and dressed body mass (recorded after removing the digestive system, heart, lungs, liver, reproductive tract, and blood) as well as sex was recorded for each hunted wild boar. When live body mass information was not collected, the dressed body mass was converted to live body mass using the established relationship between these metrics (see Gamelon et al. 2017). Emigration was not expected to contribute to non-hunting mortality as wild boar emigration is very low (except for subadult males, see Truvé and Lemel 2003; Keuling et al. 2010). Hereafter, we define year in relation to the hunting season, from October 1 in a given year to October 1 the next year.

### Estimating early-life growth rate

Wild boar included in the analysis had at least two recorded live body mass measurements below 20 kg as juveniles (Fig. 1), in the first few months of life. The number of times an individual was captured was not strongly related to its early-life growth rate (Pearson correlation coefficient between the number of captures and early-life growth rate = 0.19,  $p$  value  $\leq 0.01$ ). Although statistically significant, the relationship was weak because only 4% of the variation in the early-life growth rate observed across wild boars was accounted for by differences in the number of times these individuals were captured. As growth rates are linear in the first 6 months of life in wild boar (Gaillard et al. 1992), we estimated the early-life growth rate ( $G_i$ ) of each individual as:

$$G_i = \frac{W_n - W_1}{T_{\text{elapsed}}},$$

where  $W_n$  is the last recorded body mass (in grams) at either last recapture or recovery (at or below a live body mass of 20 kg),  $W_1$  is the body mass at first capture (in grams) and

$T_{\text{elapsed}}$  is the number of days elapsed between the two measurements. We checked the assumption that early-life growth rates are effectively linear by comparing this method to a second method that used the average of growth rates early in life (see Appendix S2), which had a weaker assumption of linearity. It is noteworthy that the two methods produced highly similar early-life growth rate estimates (see Appendix S2, Fig. S2).

### Estimating overall mortality

We estimated the overall mortality probability using capture–mark–recapture–recovery (CMRR) analysis (Lebreton et al. 2009). Noticeably, emigration is very low for this species, as females are sedentary, except for subadult males that leave matrilineal groups and disperse to live alone (Truvé and Lemel 2003; Keuling et al. 2010). Overall mortality is thus “apparent” and includes both the probability of dying and the probability of dispersing/emigrating for subadult males, whereas it mostly represents true mortality for females and males of other ages. Analyses were performed for males and females separately. First, we tested the goodness of fit (GOF; Pradel et al. 2005) of these models using U-CARE (Choquet et al. 2009). As mortality rates are slightly age specific in wild boar (Gamelon et al. 2011; Toigo et al. 2008), we distinguished three age classes: juveniles (less than 1 year olds), subadults (between 1 and 2 years old), and adults (more than 2 years old) (Fig. 1). We did not look for further age dependence in adult wild boar because the oldest male was only 5 years of age and the oldest female was 8 years of age in our dataset, likely as a consequence of the intensive hunting pressure (Toigo et al. 2008). We explored whether overall mortality differed among age classes. For the analysis, we define  $p$  as the probability of live individuals to be recaptured (i.e., the probability for an individual to be recaptured in a trap), and  $r$  as the probability of individuals shot by hunters to be recovered (i.e., the probability for an individual to be recovered by the hunters when killed). As capture and recovery protocols were kept constant throughout the study period (Gamelon et al. 2011),  $p$  and  $r$  were assumed to be constant over time, as done in Gamelon et al. (2011, 2012). Consistent with previous studies for this population,  $p$  was generally low (see results). This indicates that an individual captured at year  $t$  has a low probability to be recaptured at year  $t + 1$ . There was no evidence for contrasting recapture rates between ages, which are consistently very low. To test the assumption of a constant recapture probability  $p$  throughout the study period, we compared mortality estimates with constant and time-varying  $p$ . Models with a time-varying  $p$  struggled to produce estimates for  $p$  due to low sample size. However, mortality estimates for models with constant and time-varying recapture rates  $p$  were highly similar for all models

(results not shown here). We therefore did not consider different recapture rates over years and among age classes. On the contrary,  $r$  was very high, approaching 1 (see results). Such a high recovery rate was due to the involvement of the French National Agency for Wildlife and Hunting (OFB) that collected all the wild boar shot in cooperation with hunters. Thus, most of the individuals killed by hunters were then collected and identified if they were previously marked. We therefore did not expect recovery rates to differ over years and among age classes.

We used the Akaike information criterion corrected for small sample size (AICc, Burnham and Anderson 2002) to compare the candidate models used to assess whether overall mortality differed among age classes. When AICc values of two competing models were within two units, we retained the simplest model (i.e., the model with the fewest parameters) to satisfy parsimony rules.

### Estimating cause-specific mortality

CMRR analyses (Lebreton et al. 2009) were used to estimate cause-specific mortality by performing the joint analysis of recaptures of live individuals and recoveries of hunted individuals (Schaub and Pradel 2004). Individuals were considered to be in one of four states: (1) “alive”, (2) “dead by hunting”, (3) “dead by non-hunting causes”, and (4) “already dead”, the absorbing state. States (3) and (4) were not observable because information was only available for individuals that were shot by hunters. All individuals in states (2) and (3) at year  $t$  moved to the absorbing state (4) at  $t+1$  (see Appendix S3 for event matrices). Thus, hunting mortality corresponded to the transition from the state “alive” (1) at year  $t$  to the state “dead by hunting” (2) at year  $t+1$  and non-hunting mortality corresponded to the transition from the state “alive” (1) at year  $t$  to the state “dead by non-hunting causes” (3) at year  $t+1$  (see Appendix S3 and Gamelon et al. 2011 for transition and event matrices). As wild boar are sedentary, non-hunting mortality represents the true probability of dying from non-hunting causes, except for subadult males for which non-hunting mortality represents both the probability of dying from non-hunting causes and the probability of dispersing/emigrating. To ensure all probabilities fell within the range [0–1], we used a generalized (multinomial) logit-link function. As done for overall mortality,  $p$  and  $r$  were assumed to be constant over time and we explored whether cause-specific mortalities differed among age classes using AICc for model comparison.

### Linking early-life growth rate and mortality

To explore the effect of early-life growth on overall mortality, we included growth rate as an individual covariate to the best model with the selected age structure. Early-life growth

rate was thus treated as a continuum in the analyses and entered as a continuous variable. As all age classes exhibit the same overall mortality for males (see results), we tested an effect of early-life growth rate on overall mortality with all ages pooled together. For females, age class 1 (juveniles) has a different overall mortality than older individuals (see results). Similarly, we assessed the effect of early-life growth on both hunting and non-hunting mortality by including the growth rate as a continuous individual covariate in the selected model that distinguished between the causes of mortality.

In addition to considering growth rate as a continuous variable, we considered it as a categorical variable. We thus split the male and female datasets into 15 classes of early-life growth rates, each class including approximately 32 individuals (see Appendix S4 for minimum and maximum early-life growth rates for each categorical class in g/day). We then estimated overall mortality and cause-specific mortality for each class of early-life growth rate by entering growth rate as a categorical variable. To further explore the age-specific mortality of individuals that experienced negative early-life growth rates, models with mortality estimated for individuals with either a negative or a positive growth rate were used. Early-life growth rate was included as a categorical variable to estimate age-specific mortalities for individuals in one class that had a negative to zero early-life growth or greater than zero early-life growth rate in a separate class.

All analyses were performed using the program E-SURGE (Choquet et al. 2009).

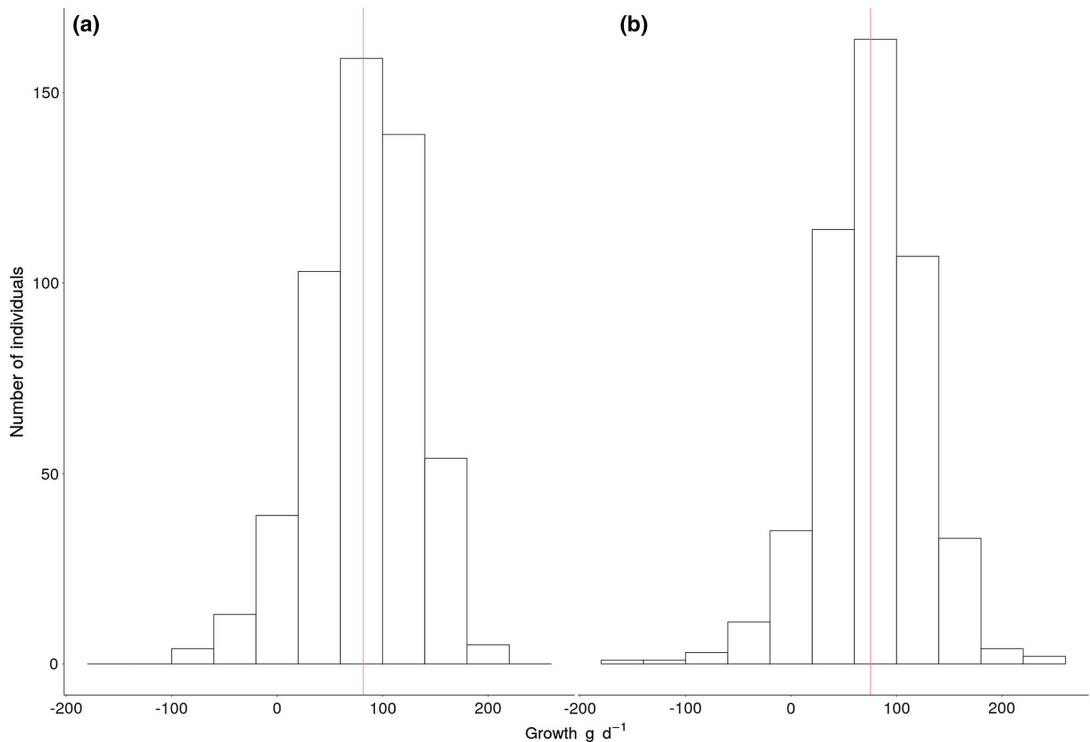
## Results

### Early-life growth rate

The average early-life growth rate was 82.67 g/day (max = 214.29 g/day, min = - 86.21 g/day) for males and 76.29 g/day (max = 226.19 g/day, min = - 170.00 g/day) for females (Fig. 2). It is notable that some individuals had negative growth rates.

### Linking early-life growth rate to overall mortality

The GOF test did not detect any lack of fit (global test for males:  $P=0.20$ ,  $df=62$ ; for females:  $P=0.20$ ,  $df=79$ ). For males, the selected model without including growth indicated constant rates of overall mortality across age classes, with an estimated overall mortality rate of 0.71 (SE: 0.02) (Table 2A, males, M1). From this model, the recapture probability was 0.27 (SE: 0.03) and the recovery rate was 0.72 (SE: 0.02). We found no evidence that mortality differs among age classes (Table 2A, males, M5,  $\Delta$ AICc of 3.22), which suggests similar mortality rates across age



**Fig. 2** Distribution of early-life growth rates (i.e., for individuals weighing up to 20 kg) for (a) male and (b) female wild boar at Châteauvillain-Arc-en-Barrois. Red vertical lines indicate the average growth rate for each sex

classes. Adding the growth rate as an individual covariate to the selected model, we found that early-life growth rate and overall mortality were negatively associated, indicating that fast-growing males had lower mortality marginal on age (Fig. 3a). From the models with negative vs. positive early-life growth as a categorical variable, the youngest and oldest males with negative early-life growth rates had the highest probability of dying (juvenile  $M=0.92$ , SE: 0.05; adult  $M=0.99$ , SE: 0.02), whereas subadults with negative early-life growth rates had the lowest ( $M=0.52$ , SE: 0.35; stars, Fig. 3a). Juvenile and adult males with positive growth rates had a lower probability of dying across age classes (juvenile  $M=0.70$ , SE: 0.02; subadult  $M=0.68$ , SE: 0.05; adult  $M=0.75$ , SE: 0.07) than males with negative early-life growth rates.

For females, the selected model revealed a higher overall mortality for juveniles than for subadults and adults (Table 2A, females, M3). The mortality estimates were 0.74 (SE: 0.02) for juvenile and 0.58 (SE: 0.03) for older (i.e., subadult and adult) females from the best model without including the growth rate covariate. The recapture probability was 0.43 (SE: 0.04) and the recovery rate was 0.71 (SE: 0.02). This model performed

slightly better than the model that included age-specific mortality rates (Table 2A, females, M5,  $\Delta\text{AICc}=1.45$ ), and much better than a model with constant mortality across age classes (Table 2A, Females, M1,  $\Delta\text{AICc}=12.59$ ). Adding the growth rate as an individual covariate to the selected model, early life-growth rate was weakly related to overall mortality rate across age classes (Fig. 3b). From the models with early-life growth as a categorical variable that was either negative or positive, juveniles and adults with negative early-life growth rates had similarly high probabilities of experiencing mortality (stars, Fig. 3b). Females with positive early-life growth rates had similar mortality probabilities (juvenile  $M=0.74$ , SE: 0.02; subadult  $M=0.56$ , SE: 0.05; adult  $M=0.60$ , SE: 0.06) as females with negative early-life growth rates (juvenile  $M=0.71$ , SE: 0.10; subadult  $M=0.47$ , SE: 0.19; adult  $M=0.68$ , SE: 0.19) across age classes.

### Linking early-life growth rate to cause-specific mortality

For males, the best cause-specific mortality model included a high hunting mortality  $Mh$  of 0.59 (SE: 0.02) for all age

**Table 2** Model selection for overall mortality (A) and cause-specific mortality (B) in wild boar

Model name	Model notation	$Np$	Biological meaning	AICc for males	AICc for females
<b>A</b>					
M1	M(1&2&3)	3	Same overall mortality for age classes 1, 2 and 3	<b>1512.43</b>	1548.44
M2	M(1&3, 2)	4	Same overall mortality for age classes 1 and 3; different for age class 2	1513.92	1540.30
M3	M(1&2, 3)	4	Same overall mortality for age classes 1 and 2; different for age class 3	1514.01	1547.80
M4	M(1, 2&3)	4	Same overall mortality for age classes 2 and 3; different for age class 1	1514.41	<b>1535.85</b>
M5	M(1, 2, 3)	5	Different overall mortalities for age classes 1, 2, and 3	1515.65	1537.30
<b>B</b>					
M1	Mh(1&2&3), Mn(1&3, 2)	5	The same hunting mortalities for age classes 1, 2, and 3; different non-hunting mortalities for age class 2 than 1 and 3	<b>1503.49</b>	1549.67
M2	Mh(1&2&3), Mn(1,2,3)	6	The same hunting mortalities for age classes 1, 2, and 3; different non-hunting mortalities for age classes 1, 2, and 3	1504.77	1551.20
M3	Mh(1&2, 3), Mn(1, 2, 3)	7	The same hunting mortalities for age classes 1 and 2, and a different hunting mortality for age class 3; different non-hunting mortalities for age classes 1, 2, and 3	1505.05	1551.31
M4	Mh(1, 2&3), Mn(1, 2, 3)	7	The same hunting mortalities for age classes 2 and 3, and a different hunting mortality for age class 1; different non-hunting mortalities for age classes 1, 2, and 3	1505.06	1539.77
M5	Mh(1&2, 3), Mn(1&3, 2)	6	Different hunting mortalities for age class 3 than age classes 1 and 2; different non-hunting mortalities for age class 2 than age classes 1 and 3	1505.42	1551.93
M6	Mh(1&3, 2), Mn(1&3, 2)	6	The same hunting mortalities for age classes 1 and 3, and a different hunting mortality for age class 2; different non-hunting mortality for age class 2 than 1 and 3	1505.43	1541.89
M7	Mh(1, 2&3), Mn(1&3, 2)	6	The same hunting mortalities for age classes 2 and 3, and a different hunting mortality for age class 1; different non-hunting mortality for age class 2 than 1 and 3	1505.80	1539.79
M8	Mh(1, 2, 3), Mn(1, 2, 3)	8	Different hunting mortalities for age classes 1, 2, and 3; different non-hunting mortalities for age classes 1, 2, and 3	1506.42	1541.23
M9	Mh(1&3, 2), Mn(1, 2, 3)	7	The same hunting mortalities for age classes 1 and 3 and a different hunting mortality for age class 2; A different non-hunting mortality for age classes 1, 2, and 3	1506.54	1543.73
M10	Mh(1, 2, 3), Mn(1&3, 2)	7	Different hunting mortalities for age classes 1, 2 and 3; A different non-hunting mortality for age class 2 than for 1 and 3	1506.80	1541.36
M11	Mh(1&2, 3), Mn(1, 2&3)	6	The same hunting mortalities for age classes 1 and 2, a different hunting mortality for age class 3; A different non-hunting mortality for age classes 2 and 3 than 1	1510.27	1552.23
M12	Mh(1&2&3), Mn(1, 2&3)	5	The same hunting mortalities for age classes 1, 2, and 3; A different non-hunting mortality for age class 1 than for 2 and 3	1510.29	1550.42
M13	Mh(1, 2, 3), Mn(1, 2&3)	7	Different hunting mortalities for age classes 1, 2 and 3; The same non-hunting mortality for age classes 2 and 3 and a different non-hunting mortality for age class 1	1511.93	1541.23
M14	Mh(1, 2&3), Mn(1, 2&3)	6	Different hunting mortalities for age classes 2 and 3 than age class 1; The same non-hunting mortality for age classes 2 and 3 and a different non-hunting mortality for age class 1	1512.24	1537.76
M15	Mh(1&2&3), Mn(1&2&3)	4	The same hunting mortalities for age classes 1, 2, and 3; The same non-hunting mortalities for age classes 1, 2, and 3	1512.43	1548.43

**Table 2** (continued)

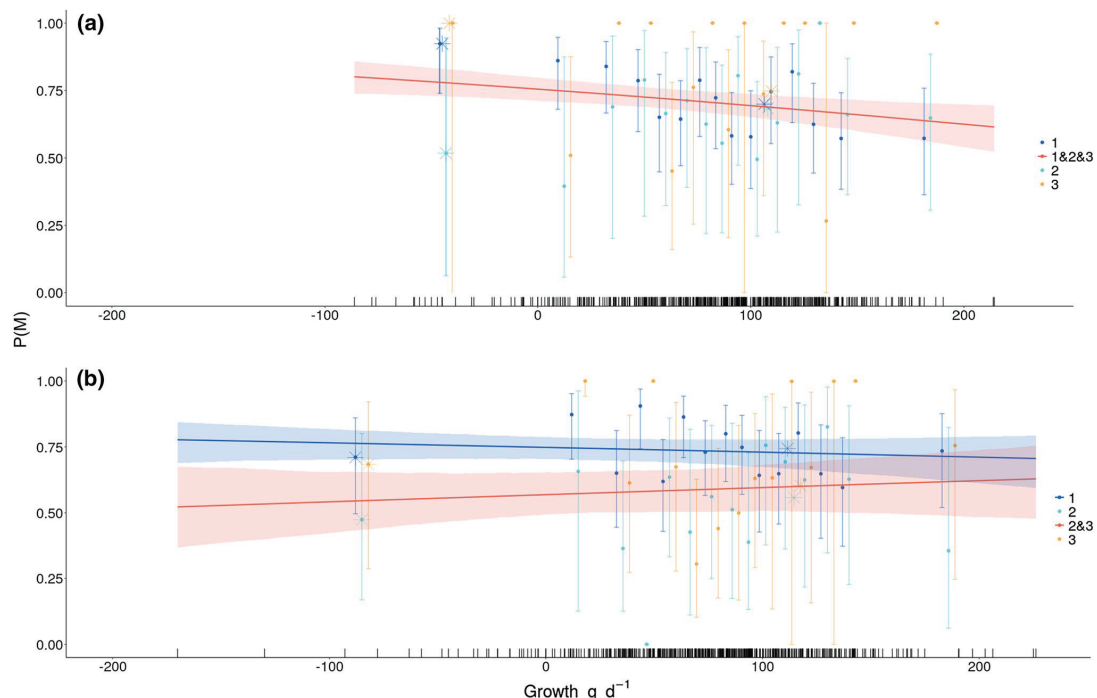
Model name	Model notation	<i>Np</i>	Biological meaning	AICc for males	AICc for females
M16	Mh(1&3, 2), Mn(1, 2&3)	6	The same hunting mortalities for age classes 1 and 3 and a different hunting mortality for age class 2. The same non-hunting mortality for age classes 2 and 3 and a different non-hunting mortality for age class 1	1512.60	1543.73
M17	Mh(1&3, 2), Mn(1&2&3)	5	The same hunting mortalities for age classes 1 and 3 and a different hunting mortality for age class 2. The same non-hunting mortality for age classes 1, 2, and 3	1513.07	1541.89
M18	Mh(1&2&3), Mn(1&2, 3)	5	The same hunting mortalities for age classes 1, 2, and 3. Different non-hunting mortality for age classes 1 and 2 than age class 3	1513.09	1549.65
M19	Mh(1&2, 3), Mn(1&2, 3)	6	Different hunting mortalities for age classes 1 and 2 than age class 3. Different non-hunting mortality for age classes 1 and 2 than age class 3	1514.37	1549.56
M20	Mh(1, 2, 3), Mn(1&2&3)	6	Different hunting mortalities for age classes 1, 2, and 3. The same non-hunting mortality for age classes 1, 2, and 3	1514.51	1539.22
M21	Mh(1&3, 2), Mn(1&2, 3)	6	The same hunting mortalities for age classes 1 and 3 and a different hunting mortality for age class 2. The same non-hunting mortality for age classes 1 and 2 and a different non-hunting mortality for age class 3	1514.92	1543.74
M22	Mh(1&2, 3), Mn(1&2&3)	5	A different hunting mortality for age class 3 than for age classes 1 and 2. The same non-hunting mortality for age classes 1, 2, and 3	1515.13	1549.86
M23	Mh(1, 2&3), Mn(1&2&3)	5	A different hunting mortality for age class 1 than 2 and 3. The same non-hunting mortality for age classes 1, 2, and 3	1515.32	<b>1537.79</b>
M24	Mh(1, 2, 3), Mn(1&2, 3)	7	Different hunting mortalities for age classes 1, 2, and 3. The same non-hunting mortality for age classes 1 and 2 and a different non-hunting mortality for age class 3	1516.48	1541.23
M25	Mh(1, 2&3), Mn(1&2, 3)	6	A different hunting mortality for age class 1 than for age classes 2 and 3. The same non-hunting mortality for age classes 1 and 2 and a different non-hunting mortality for age class 3	1516.48	1539.80

Displayed are models relating age classes to overall mortality (*M*), hunting mortality (*Mh*), and non-hunting mortality (*Mn*). Age classes are denoted as 1 for juveniles, 2 for subadults, and 3 for adults. Pooled age classes are indicated with ‘&’ between them. ‘*Np*’ indicates the number of biological parameters. ‘Biological meaning’ explains the ‘Model notation’ in biologically relevant terms. When two models had close AICc values ( $\Delta\text{AICc} < 2$ ), the most parsimonious model was selected. The selected models are indicated in bold

classes (Table 2B, males, M1). Non-hunting mortality *Mn* was 0.07 (SE: 0.02) for juveniles and adults, and 0.38 (SE: 0.08) for subadults (Table 2B, males, M1). The recapture probability was 0.24 (SE: 0.03) and the recovery rate was 0.91 (SE: 0.02). We found no support for constancy in both non-hunting mortality and hunting mortality across age classes (Table 2B, males, M15,  $\Delta\text{AICc} = 8.94$ ).

When the individual covariate representing early-life growth was added to the best model, we found a negative association between early-life growth rate and hunting mortality for males (Fig. 4a, red curve), indicating that fast-growing males early in life had lower hunting mortality rates at all ages than slower-growing counterparts. Similarly, we found that faster-growing males had a lower non-hunting mortality rate as subadults than slower-growing individuals (Fig. 4b, light blue line). However, for juvenile and adult males, there

was no evidence of a relationship between early-life growth rate and non-hunting-related mortality (Fig. 4b, red line). Among individuals exhibiting a negative early-life growth rate, adults faced the highest probability of being hunted (juvenile *Mh* = 0.68, SE: 0.11, subadult *Mh* = 0.50, SE: 0.36, adult *Mh* = 0.99, SE: 0.06; stars, Fig. 4a), while juveniles had the highest probability of dying from non-hunting mortality (juvenile *Mn* = 0.26, SE: 0.11, subadult *Mn*  $\leq 0.01$ , SE: 0.11, adult *Mn*  $\leq 0.01$ , SE: 0.05; stars, Fig. 4b). Males with positive early-life growth rates had a lower probability of being hunted across age classes than males with negative early-life growth rates. Among individuals exhibiting positive growth rates, juveniles *Mn* = 0.09, SE: 0.07) and adults (*Mn*  $\leq 0.01$ , SE:  $< 0.01$ ) had a very low probability of dying from non-hunting mortality, while subadults had a higher probability (*Mn* = 0.44, SE: 0.09). Males with positive early-life



**Fig. 3** Age-specific (1, 2, 3) overall mortality  $P(M)$  as a function of early-life growth rate (in  $g/day$ ) for **(a)** male and **(b)** female wild boar in Châteauvillain-Arc-en-Barrois. The points depict the mortality estimates and associated 95% confidence intervals for each class of early-life growth rates from models with early-life growth rate included as a categorical variable. The lines show estimates from the selected models with early-life growth rate as a continuous individual

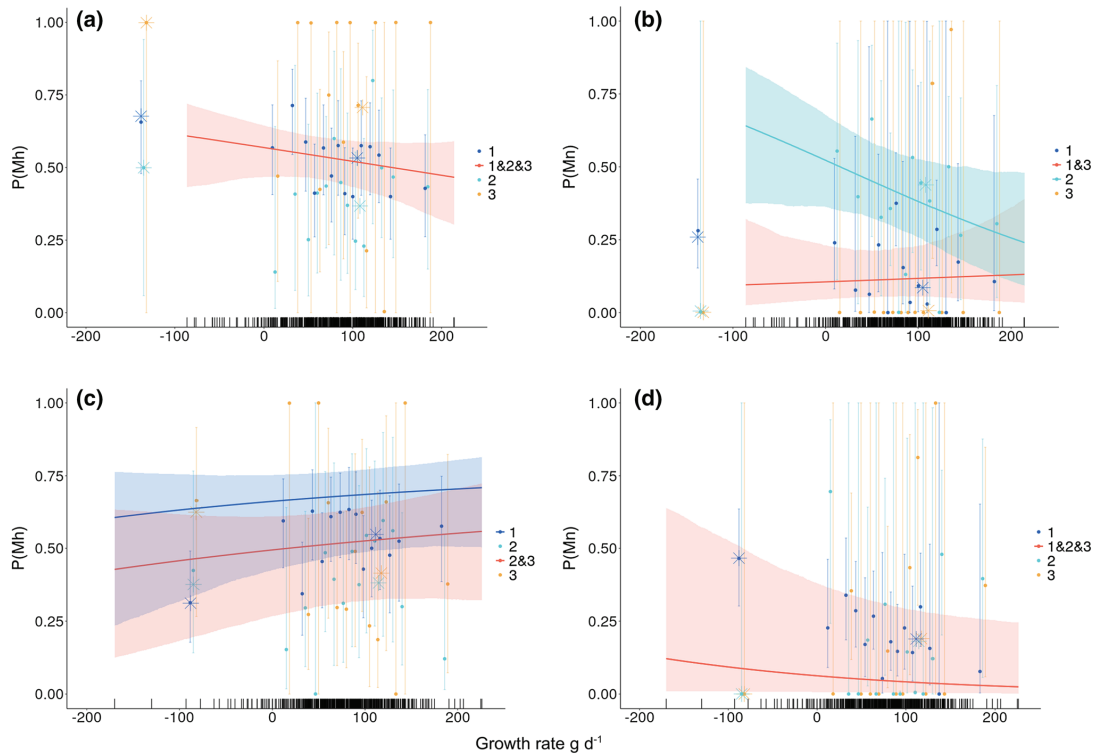
covariate (see Table 2A) and associated 95% confidence intervals. The rug plot shows the respective distributions of early-life growth rates for each sex. The stars depict age-specific mortality estimates from models with either negative to zero early-life growth rates or positive early-life growth rates. The estimates from the categorical models are plotted against the median value in the range of early-life growth rates for a given bin

growth rates always had a lower probability of being hunted (juvenile  $Mh=0.53$ , SE: 0.06, subadult  $Mh=0.37$ , SE: 0.06, adult  $Mh=0.71$ , SE: 0.08) across age classes than males with negative early-life growth rates.

For females, two models had nearly the same AICc values (Table 2B, females, M14 and M23,  $\Delta AICc=0.03$ ) for cause-specific mortality. The selected model (Table 2B, females, M22), chosen following the rules of parsimony, indicated that hunting mortality  $Mh$  was 0.73 (SE: 0.13) for juveniles and 0.56 (SE: 0.18) for older females (i.e., subadults and adults). The non-hunting mortality ( $Mn$ ) estimate for all females was 0.01 (SE: 0.11). The recapture probability was 0.43 (SE: 0.04) and the recovery rate 0.73 (SE: 0.15). The models including constant hunting and non-hunting mortality rates across age classes performed very poorly (Table 2B, Females, M15,  $\Delta AICc=14.01$ ).

When the individual covariate representing early-life growth was added to the best model, we found that early-life growth rate was weakly related to both hunting and

non-hunting-related mortalities. Thus, hunting mortality (Fig. 4c, dark blue and red lines) and non-hunting mortality (Fig. 4d, red line) did not appear to strongly depend on early-life growth rate (see Appendix S5 for slope and intercept estimates of the selected models on either the logit scale (for overall mortality) or generalized logit scale (for cause-specific mortality)). Females with a negative early-life growth rate were most likely to die from hunting as adults ( $Mh=0.63$ , SE: 0.20, stars, Fig. 4c) and experienced non-hunting mortality as juveniles ( $Mn=0.47$ , SE: 0.09; stars, Fig. 4d). Subadults ( $Mn \leq 0.01$ , SE:  $< 0.01$ ) and adults ( $Mn \leq 0.01$ , SE:  $< 0.01$ ) with negative early-life growth rates were very unlikely to die from non-hunting mortality. Females with positive early-life growth rates across age classes (juvenile  $Mh=0.55$ , SE: 0.02, subadult  $Mh=0.38$ , SE: 0.05, adult  $Mh=0.41$ , SE: 0.06) had a higher hunting mortality probability than juvenile ( $Mh=0.30$ , SE: 0.08) and subadult ( $Mh=0.38$ , SE: 0.18) females with negative early-life growth rates. Females with positive growth rates across



**Fig. 4** Age-specific hunting mortality (**a** and **c**;  $P(M_h)$ ) and non-hunting mortality (**b**, and **d**;  $P(M_n)$ ) as a function of early-life growth rate (in g/day) for (**a** and **b**) male and (**c** and **d**) female wild boar in Châteauvillain-Arc-en-Barrois. The points depict the mortality estimates and 95% confidence intervals from a model for each class of early-life growth rates included as a categorical variable. The lines correspond to mortality estimates for each age class included in the

selected models with early-life growth rate as a continuous variable (see Table 2B) and associated 95% confidence intervals. The rug plot shows the distributions of early-life growth rates for each sex. The stars depict age-specific mortality estimates from models with either negative to zero early-life growth rates or positive early-life growth rates. The estimates from the categorical models are plotted against the median value in the range of early-life growth rates for a given bin

age classes had a very low probability of dying from non-hunting mortality (juvenile  $M_n = 0.19$ , SE: 0.02, subadult  $M_n = 0.18$ , SE: 0.07, adult  $M_n = 0.19$ , SE: 0.06) compared to juveniles with negative early-life growth rates.

## Discussion

Our approach is unique among studies linking early-life growth to mortality in harvested populations because it accounts for possible confounding effects of age, sex, and cause-specific mortality (i.e., non-hunting vs. hunting mortality). Classical approaches would have only tested for a relationship between early-life growth rate and overall mortality in both sexes. If we had only followed this approach without splitting mortality into its causes, we would have simply found that the fastest-growing males experienced

lower overall mortality than their slower-growing counterparts (see Fig. 3a). However, in our population, hunting mortality accounted for most of the overall mortality compared to non-hunting mortality. Consequently, overall mortality models usually fitted in survival analyses of hunted vertebrate populations do not accurately depict how age-specific hunting versus non-hunting mortality is related to other life-history traits (Lebreton 2005; but see Schaub and Pradel 2004; Brodie et al. 2013; or Koons et al. 2014 who used cause-specific mortality models to assess different natural and human-related sources of mortality). Here, from the cause-specific models, we show that male juveniles and adults as well as females of all age classes display a very weak relationship between early-life growth rate and non-hunting-related mortality. Indeed, only the non-hunting mortality of subadult males was strongly related to early-life growth rate. In particular, slow-growing males exhibited the

highest non-hunting mortality at age two. At this age, they disperse from their natal area and face increased mortality risks (Truvé and Lemel 2003). It should be noted that non-hunting-related mortality includes emigration. Therefore, the strong negative relationship between male subadult non-hunting-related mortality and early-life growth rate may be due to slow-growing males being more likely to die of non-hunting-related causes as subadults. Alternatively, males that grow slowly early in life may be more likely to disperse as subadults, and likely to acquire more resources. Splitting mortality into its causes is thus recommended to gain an understanding of the underlying mechanisms shaping the covariation between life-history traits when mortality can be mostly attributable to one cause (e.g., harvesting).

In addition, for males, hunting probability was negatively related to early-life growth rate (Fig. 4a). Further, from the models with negative and positive early-life growth rates, males with positive early-life growth rates had a lower probability of being hunted than those with a negative early-life growth rate for every age class. Therefore, we found that faster-growing males were less likely to be hunted than slower-growing individuals. This provides support for the hypothesis that males with high growth rates are also more able to evade being hunted, and are possibly of higher quality (similar to Festa-Bianchet 1988; Altendorf et al. 2001). However, we did not find strong evidence of a relationship between early-life growth rate and hunting mortality for females. Females that grew quickly had a slightly higher probability to be hunted than females that grew slowly (Fig. 4c). We therefore found no detectable evidence that individual ability to grow quickly early in life reduced hunting probability for females (i.e., faster-growing individuals had a lower probability of being hunted).

Some studies have reported a positive relationship between early-life growth and mortality (see Table 1). Our expectation in this population characterized by a high hunting pressure was that fast-growing females, in addition to allocating a large amount of resources to growth, would reach the threshold body mass to reproduce earlier than slower growing juveniles. We expected that earlier reproduction would then lead to an increase in non-hunting-related mortality costs. Indeed, fast-growing females consistently reach sexual maturity earlier than slower growing counterparts in most vertebrate species (e.g., Enberg et al. 2012 in fish; Flom et al. 2017 in humans). In the studied population, females only need to reach about 37% of their adult body mass to reproduce for the first time (Servanty et al. 2009) within their first year of life (Gamelon et al. 2011). We did not find evidence of a positive relationship between early-life growth and non-hunting mortality in females. As fast early-life growth did not increase the probability that wild boar experienced non-hunting mortality, we did not find evidence that fast early-life growth leads to higher non-hunting

mortality. Note, however, that because of the high hunting pressure in this system, we assessed the costs of fast early-life growth at young ages. We tested for potential negative effects of fast growth rates on mortality at ages 0–1, 2, and 3 or more, whereas growth costs might occur much later in life. Indeed, in response to the high hunting pressure, only a few individuals were likely to die from non-hunting causes during adulthood, which explains the large confidence intervals in the estimates of non-hunting mortality of adults (Fig. 4). Also, we did not find a strong negative relationship between early-life growth and non-hunting mortality, so our results did not support the individual quality hypothesis (e.g., faster-growing individuals are less likely to die of starvation or disease). Most previous studies dealing with harvested populations did not distinguish among causes of mortality and generally did not explore such relationships between early-life growth and mortality in both sexes. Our study proves that disentangling mortality causes is important when the hunting pressure is strong in a population, as males and females can exhibit different responses.

There is increasing evidence that human exploitation induces rapid evolutionary changes in populations, which results in shortening the time between birth and first reproduction. While effects of harvest-induced changes to early-life growth rates are well documented in fisheries (Law 2000; Dunlop et al. 2009; Enberg et al. 2011), they remain largely unexplored in hunted mammals (see Table 1). This distinction is important as fish are indeterminate growers, and experience more flexibility in the age/size at maturity and therefore have a much greater variability in the individual relationship linking body size and reproduction than mammals. In many species, there is extensive evidence that a strong harvesting pressure can increase body growth rates, which allows reaching the threshold body size/mass for reproduction earlier (see Kuparinen and Festa-Bianchet 2017 for a review of evolutionary effects of harvesting). Noticeably, individuals might simply reproduce at smaller sizes, with unaffected body growth rates. Previous work on wild boar linked a high hunting pressure with a lower threshold body mass for reproduction and earlier birth dates, which stimulate high reproductive rates within the first year of life (Servanty et al. 2009; Gamelon et al. 2011). Thus, it is likely that harvest-induced selection in wild boar has resulted in a reduction of the size threshold for reproduction rather than an increase of early-life growth rate. Here, we were not able to demonstrate that early-life growth rate was linked to non-hunting mortality, rather we observed a weak or null relationship between these life-history traits (except in the case of subadult males). In particular, we found no evidence that fast-growing females that reach the mass/size threshold for reproduction at younger ages exhibit higher mortality costs than slow-growing individuals. However, males that grew quickly also were less likely to be hunted, indicating that



heterogeneity in individual quality may influence the covariation between early-life growth rate and hunting mortality. Comparing early-life growth rates in an experimental population where the hunting pressure is manipulated could provide further insight into whether hunting indeed increases early-life growth rates, offering promising avenues for research.

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**Author contribution statement** LV and MG performed the analyses. MG, LV, and J.-M. G wrote the manuscript. EB collected the data. B.-E. S and EB provided editorial advice.

**Data Availability** The data used in our analysis will be made available upon publication of this study.

## Compliance with ethical standards

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

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Supplementary Materials for the article:

“Grow fast at no cost: hunted wild boar do not pay a mortality cost  
for fast early-life growth”

Appendix S1: Specific information from the literature linking early-life growth to survival

Species	Reference	Effect		Quote demonstrating trade-off
		Males	Females	
Bighorn sheep	Bonenfant et al. 2009	(0)	NA	"Growing large horns early in life is not related to any consistent survival costs."
Dall sheep	Loehr et al. 2007	(-)	NA	"We found a negative relationship between horn growth rate and longevity for natural mortality in areas with little or no hunting."
Stone sheep	Douhard et al. 2016	(-)	NA	"A decline in harvest age with rapid early horn growth was more marked in the high than in the low hunting area."
Alpine ibex	Toigo et al. 2013	(0) <sup>1</sup>	NA	"(...) early horn growth did not negatively influence survival over most of the lifetime, indicating that males do not invest in horn growth at survival costs at least until 12 years of age."
Alpine ibex	Bergeron et al. 2008	(0)	NA	"Our results suggest that males with fast-growing horns early in life were able to grow longer horns without any apparent longevity cost."
Chamois	Bleu et al. 2014	NA	(-)	"(...) the best-fitting model included a negative effect of early horn growth on yearly survival of 8-12 years old females."

<sup>1</sup>Early-life growth was not related to survival until late life, when early horn growth incurred a survival cost.

<sup>2</sup>The culling regime and hunter preference determined survival patterns in the two harvested populations.

Species	Reference	Effect		Quote demonstrating trade-off
		Males	Females	
Chamois	Corlatti et al. 2017	(0)	(0)	"Within the protected population, under pressure of sexual/natural selection, we found statistically non-significant negative trade-offs between early horn growth and survival in both males and females."
Chamois	Corlatti et al. 2017	(-)	(+/-) <sup>2</sup>	"(...) selection on early horn growth of culled individuals showed diametrically opposed sex-biased patterns, depending on the culling regime and hunters' preferences."
European mouflon	Kavčić et al. 2019	(0)	(0)	"The mean age at death of rams with rapid early horn growth (> 50 cm) was 3.86 years, while it was 4.64 years for rams with slower early horn growth (≤ 50 cm)."
Three-spined stickleback	Lee et al. 2012	(-)	(-)	"These results demonstrate the growth-lifespan trade-off."
Subantarctic fur seals	Chambellant et al. 2003	(+)	(0)	"..the GR <sub>60</sub> value for male pups which survived to weaning is higher than for pups that died...The relationship between GR <sub>60</sub> and SR <sub>L</sub> was found to be not significant in female pups."
Subantarctic fur seals	Beauplet et al. 2005	(+)	(+)	"We detected a significant positive relationship between pup preweaning growth rate and individual post-weaning survival and interestingly, this effect was greater for males than for females."
Speckled wood butterfly	Gotthard et al. 1994	(-)	(-)	"(...) the results of the longevity study indicate that a shorter life span may represent a cost of high growth rates (...)"

Species	Reference	Effect		Quote demonstrating trade-off
		Males	Females	
Perch	Metcalfe & Monaghan 2003; Craig 1980	(-)	NA	"(...) the average early growth rate of a year-class is the strongest predictor of its subsequent adult mortality rate, with those year-classes exhibiting the fastest early growth having the shortest life expectancy"
European plaice	Jorgensen et al. 2013	NA	(-)	"Fish tend to take more risk to accelerate growth prior to maturation, despite increased mortality"
Rhesus Macaques	Núñez et al. 2015	(+)	(+)	"For the heaviest and fastest-growing juveniles, this can mean a five to ten-fold decrease in hazard"
Wild type and Norway rats	Rollo 2002	(-)	(-)	"Peak body mass (which reflects juvenile growth rates) was negatively associated with longevity within both species."
Tasmanian snow skinks	Olsson & Shine 2002	(-)	(-)	"When later released into the wild, the individuals that grew more rapidly as neonates experienced much higher mortality than did slower-growing conspecific"

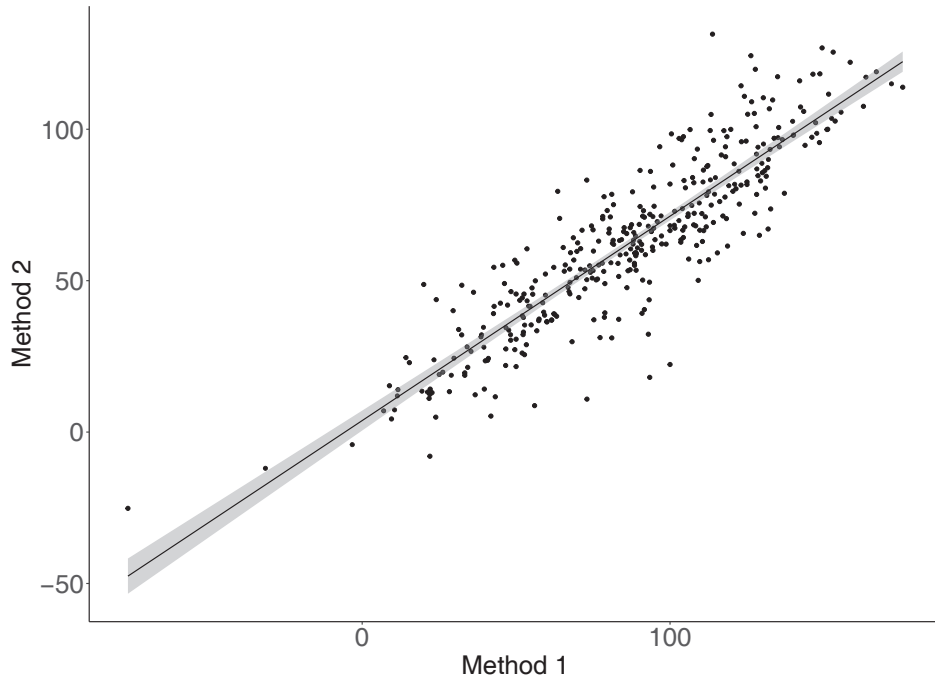
## Appendix S2: Growth rate calculation: testing the assumption of linearity of growth rates

Individual early-life growth rates for 516 males and 475 females were included in the analysis. These rates were calculated using an alternative method (Method 2), which does not have as strict an assumption of linearity as Method 1 (outlined in the text). Instead of estimating growth rate from the first and the last body mass measurements (Method 1) and requiring 2 body mass measurements, we took into account all the successive body mass measurements such as:

$$G_i = \frac{\sum_{j=1}^n \frac{W_{(j+1)} - W_j}{T_{(j+1)} - T_j}}{C} \quad (1)$$

where the sum of each recorded body mass ( $W$ ) subtracted by the body mass measurement recorded at the previous capture event is then divided by the time that elapsed between the two captures in days ( $T$ ) divided by the number of captures ( $C$ ). This method thus uses the average of successive individual growth rates from the first capture to the last measure of the wild boar when their weight was less than 20 kg (what we have defined as the period of early-life growth; see Gaillard et al. 1992). These two methods for calculating individual growth rates ( $G_i$ ) of individuals captured at least 3 times were compared using a linear regression. The sample size for the two methods were therefore different (Method 1  $N = 991$ , Method 2  $N = 377$ ) as Method 2 required one capture more than Method 1. The relationship between the methods provided a  $R^2$  of 0.79 indicating a very good match between growth rates estimated with Method 1 and Method 2. Method 1 was chosen for our analysis as it was comparable to Method 2 and allows for the inclusion of more individuals in the analysis (for Method 2, the number of males = 208 and females = 169). Using Method 2, for males, the average early-life growth rate was 64.69 g/day (minimum = -25.19 g/day, maximum = 131.41 g/day) and for females, it was 59.77 g/day (minimum = -11.96 g/day, maximum = 119.80).

**Figure S2:** Linear relationship between growth rates calculated using two methods. Method 1 assumes growth rate is linear in early life and can be applied when only two measures of body mass are available. Growth rates from Method 1 were used in the analyses. Method 2 is an average of growth rates for a given individual and requires at least three measurements and weakens the assumption that early-life growth rate is linear





### Appendix S3: Matrices for overall and cause-specific mortality models

#### *Overall mortality models*

Matrix showing transition probabilities from time  $t$  (rows) to time  $t+1$  (columns) for overall mortality models. Three states were considered ( $A$  or alive,  $M$  or overall mortality, and  $D$  or already dead at time  $t+1$ ).

$$\begin{array}{c} A \quad M \quad D \\ A \begin{pmatrix} 1-M & M & 0 \\ M & 0 & 1 \\ D & 0 & 1 \end{pmatrix} \\ M \\ D \end{array}$$

Matrix showing recapture ( $p$ ) and recovery ( $r$ ) probabilities from time  $t$  (rows) to time  $t+1$  (columns) for overall mortality models. Three states were considered ( $ND$  or not detected,  $A$  or alive, and  $M$  or dead). Individuals not seen (0) could be recaptured ( $p$ ) or recovered ( $r$ ) at time  $t+1$  unless they were already dead ( $D$ ).

$$\begin{array}{c} ND \quad A \quad M \\ A \begin{pmatrix} 1-p & p & 0 \\ M & 1-r & 0 & r \\ D & 1 & 0 & 0 \end{pmatrix} \\ M \\ D \end{array}$$

#### *Cause-specific mortality models*

Transition matrix showing cause-specific mortality probabilities from time  $t$  (rows) to time  $t+1$  (columns). Transitions for the four given states ( $A$ , or alive,  $Mh$  for hunting mortality,  $Mn$  for non-hunting mortality, and  $D$  for already dead at time  $t+1$ ) are given.

$$\begin{array}{c}
A \quad M_h \quad M_n \quad D \\
A \left( \begin{array}{cccc}
1 - M_h - M_n & M_h & M_n & 0 \\
0 & 0 & 0 & 1 \\
0 & 0 & 0 & 1 \\
0 & 0 & 0 & 1
\end{array} \right) \\
M_h \\
M_n \\
D
\end{array}$$

The events matrix for the probability of being recaptured ( $p$ ) or recovered ( $r$ ) at time  $t+1$  (columns) given the state at time  $t$  (rows).

$$\begin{array}{c}
ND \quad A \quad M_h \\
A \left( \begin{array}{ccc}
1 - p & p & 0 \\
1 - r & 0 & r \\
1 & 0 & 0 \\
1 & 0 & 0
\end{array} \right) \\
M_h \\
M_n \\
D
\end{array}$$

**Appendix S4: Growth rate classes for models including early-life growth rate as a categorical variable**

Table S4

Class	Males	Females	Sample size males	Sample size females
1	-86.21-0	-170.00-0	33	32
2	3.01-25.00	3.07-30.00	37	37
3	25.16-43.16	31.58-40.98	35	32
4	45.28-54.74	41.06-52.00	34	35
5	55.17-64.29	52.04-61.54	34	33
6	65.16-75.00	62.11-70.97	37	41
7	75.12-82.96	71.31-81.82	34	40
8	83.33-90.00	82.14-89.66	33	33
9	90.74-97.78	90.14-96.88	39	34
10	98.15-107.89	97.10-105.88	35	28
11	108.33-116.67	106.06-113.46	33	32
12	117.50-127.55	114.07-125.00	35	30
13	128.07-136.96	125.68-134.02	35	30
14	137.14-153.58	135.16-143.86	35	21
15	154.41-214.29	146.30-226.19	28	26

## Appendix S5: Intercept and slope estimates for the selected models

**Table S5:** Overall (A) and cause-specific (B) mortality. Displayed are the intercept and slope estimates for the selected models (see Figs. 2 and 3) on the logit and generalized logit scales for overall and cause-specific mortality estimates, respectively. Age classes are denoted as one for juveniles (up to one year of age), two for subadults (one to two years old), and three for adults (more than two years old). Pooled age classes are indicated with “&” between them. M indicates overall mortality estimates, *Mh* indicates estimates for hunting mortality *Mn* indicates non-hunting mortality estimates, and SE indicates the associated Standard Error. Bolded values do not include zero in the confidence interval.

Model Name	Age Class	Intercept	Slope
A			
<u>Males</u>			
	<b>M(1&amp;2&amp;3)</b>	<b>0.93 (SE: 0.10)</b>	<b>-0.27 (SE: 0.10)</b>
<u>Females</u>			
	M(1)	<b>1.06 (SE: 0.12)</b>	<b>-0.11 (SE:0.12)</b>
	M(2&3)	<b>0.31 (SE: 0.15)</b>	<b>0.13 (SE:0.15)</b>
B			
<u>Males</u>			
	Mh(1&2&3)	<b>0.44 (SE: 0.11)</b>	<b>-0.17 (SE:0.11)</b>
	Mn(1&3)	-1.13 (SE: 0.37)	<0.01 (SE: 0.32)
	Mn(2)	<b>0.66 (SE: 0.25)</b>	<b>-0.60 (SE: 0.26)</b>
<u>Females</u>			
	Mh(1)	<b>0.89 (SE: 0.19)</b>	<b>0.05 (SE:0.14)</b>
	Mh(2&3)	<b>0.20 (SE: 0.21)</b>	<b>0.07 (SE:0.19)</b>
	Mn(1&2&3)	-1.59 (SE: 1.13)	-0.45 (SE:0.35)

# Paper III

This paper is awaiting publication and is not included in NTNU Open



## Paper IV





1 **Effects of pulsed resources on the dynamics of seed consumer populations:**  
2 **A comparative demographic study in wild boar**

3

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20

21 **Abstract**

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

45 responses to mast seeding, within and among populations. This is an important finding for our  
46 understanding of the effects of mast seeding on the dynamics of seed consumer populations.

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48 **Keywords:** acorn production, generation time, population growth rate, prospective analysis,  
49 retrospective analysis, *Sus scrofa*, ungulate

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## 66 INTRODUCTION

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

78 Due to marked differences in fruiting dynamics at both temporal and spatial scales, one  
79 can expect heterogeneity in demographic responses to mast seeding among populations.  
80 Surprisingly, until now, despite the large literature available on the effects of mast seeding on  
81 the population dynamics of seed consumers (reviewed in Ostfeld and Keesing, 2000; Holt,  
82 2008; Yang et al., 2008; Bogdziewicz et al., 2016), few studies have investigated the effects of  
83 mast seeding on multiple populations, i.e. at the intraspecific level (see table 1 for a review).  
84 Furthermore, among the available studies, most of them have focused on rodents and very few  
85 on large mammals.

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87 **Table 1.** Summary of the comparative studies exploring an effect of mast seeding on the dynamics of multiple consumer populations. Displayed  
88 are the primary consumer species, the tree species, the demographic parameters influenced by mast seeding with the sign of this effect, the number  
89 of populations included in the analysis and the reference of the study. Note that experimental studies are not shown in this table.

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<b>Consumer species</b>	<b>Tree species</b>	<b>Demographic parameter</b>	<b>Populations</b>	<b>Reference</b>
Great tit ( <i>Parus major</i> )	Beech species ( <i>F. sylvatica</i> )	+ Local recruitment + Immigration	5 populations	(Grøtan et al. 2009)
Flying squirrel ( <i>Pteromys volans</i> )	Birch ( <i>Betula spp.</i> ) Alder ( <i>Alnus spp.</i> )	+ Lifetime reproductive success + Longevity	2 populations	(Hoset et al. 2017)
Flying squirrel ( <i>Pteromys volans</i> )	Alder ( <i>Alnus spp.</i> )	+ Fecundity	2 populations	(Hoset et al. 2017)

Flying squirrel ( <i>Pteromys volans</i> )	Food abundance in the following year: Birch ( <i>Betula spp.</i> ) Alder ( <i>Alnus spp.</i> )	0 Production of summer litters	2 populations	(Selonen and Wistbacka 2016)
Flying squirrel ( <i>Pteromys volans</i> )	Food abundance in the preceding year: Birch ( <i>Betula spp.</i> ) Alder ( <i>Alnus spp.</i> )	+ Production of summer litters	2 populations	(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 spp.</i> ), 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 populations	(Boutin et al. 2006)

Eurasian red squirrel ( <i>Sciurus vulgaris</i> )	Food abundance in the following year: Scots ( <i>Pinus sylvestris</i> ), Corsican pine ( <i>Pinus nigra</i> ), chestnut ( <i>Castanea sativa</i> ), oak ( <i>Quercus spp.</i> ), beech ( <i>F. sylvatica</i> ), hornbeam ( <i>Carpinus betulus</i> ), hazel ( <i>Coryllus avellana</i> )	0 Proportion of females producing spring litters + Summer litter size + Proportion of females producing a summer litter + Summer population growth rate	3 populations	(Boutin et al. 2006)
Eurasian squirrel ( <i>Sciurus vulgaris</i> )	Coniferous site: Scots pine ( <i>Pinus sylvestris</i> ) and Corsican pine ( <i>Pinus nigra</i> ) vs. Deciduous site: English oak ( <i>Quercus robur</i> ) and beech ( <i>Fagus sylvatica</i> )	+ Number of litters + Litter size (old females) + Probability of producing a litter (young and old females)	2 populations	(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 populations	(McAdam et al. 2019)

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Eastern chipmunks ( <i>Tamias striatus</i> )	Beech ( <i>F. grandifolia</i> ) and red maple ( <i>Acer rubrum</i> )	+ Proportion of females in summer oestrus	3 populations	(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 populations	(Fietz et al. 2005)
Edible dormouse ( <i>Glis 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>Glis glis</i> )	Food abundance in the previous year:	- Survival	2 populations	(Ruf et al. 2006)

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Beech (*Fagus sylvatica*)

Edible dormouse ( <i>Glis glis</i> )	Food abundance in the current year:	+ Reproduction	2 populations	(Ruf et al. 2006)
	Beech ( <i>Fagus sylvatica</i> )			
Stoat ( <i>Mustela erminea</i> )	Food abundance in the current year:	+ Reproductive success	3 populations	(Wittmer et al. 2007)
	Beech ( <i>Nothofagus</i> )			
Stoat ( <i>Mustela erminea</i> )	Food abundance in the previous year:	- Survival	3 populations	(Wittmer et al. 2007)
	Beech ( <i>Nothofagus</i> )	- Fertility		
American black bear ( <i>Ursus americanus</i> )	Hard mast species (e.g. white oak <i>Q. alba</i> , chestnut oak <i>Q. prinus</i> )	0 Litter size - Missed reproductive opportunities	2 populations	(Bridges et al. 2011)
Wild boar ( <i>Sus scrofa</i> )	Food abundance in the previous year:	Beech ( <i>F. sylvatica</i> ) and oak ( <i>Q. petraea</i> ):	2 populations	(Gamelon et al. 2017)

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<p>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>)</p>	<ul style="list-style-type: none"> <li>+ Juvenile body mass</li> <li>+ Number of corpora lutea of juveniles</li> <li>+ Litter size of juveniles</li> </ul> <p>Mediterranean oak (<i>Q. ilex</i>, <i>Q. cerris</i>, <i>Q. frainetto</i>):</p> <ul style="list-style-type: none"> <li>+ Adult body mass</li> <li>+ Number of corpora lutea of adults</li> <li>+ Litter size of adults</li> </ul>	<p>(Gamelon et al. 2017)</p>
<p>Wild boar (<i>Sus scrofa</i>)</p> <p>Food abundance in the current year:</p> <p>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>)</p>	<p>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>):</p> <ul style="list-style-type: none"> <li>+ Adult body mass</li> <li>+ Number of corpora lutea of adults</li> <li>+ Litter size of adults</li> </ul>	<p>2 populations</p>

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93           At the intrapopulation level, one can expect individuals to exhibit contrasting  
94 demographic responses to mast seeding depending on their (st)age. Indeed, there is growing  
95 evidence that individual heterogeneity in response to environmental fluctuations exists. Hence,  
96 Coulson et al. (2001) showed that survival of young and older individuals specifically was  
97 dependent on North Atlantic Oscillation and rainfall at the end of the winter in a Soay sheep  
98 (*Ovis aries*) population. Similarly, Hensen et al. (2019) showed that senescent individuals were  
99 the most sensitive to increasing frequency of rain-on-snow events in a Svalbard reindeer  
100 (*Rangifer tarandus platyrhynchus*) population. Likewise, age-dependent effects of climate  
101 have been highlighted on Black-browed Albatrosses (*Thalassarche melanophris*) (Pardo et al.  
102 2013). Among the comparative studies shown in table 1, to the best of our knowledge, none  
103 has assessed the effect of mast seeding on all (st)age-specific demographic rates (i.e. survival,  
104 reproduction, growth across the life cycle). Assessing whether differences in demographic  
105 responses to fluctuating mast seeding occur between populations and within a population could  
106 undoubtedly offer new insights on demographic patterns observed across time and space *in*  
107 *natura*. Different conservation/management strategies could *in fine* be implemented for several  
108 populations of a focal species, if they have contrasting demographic responses to mast seeding.

109           Wild boar (*Sus scrofa*) is a widely distributed ungulate species worldwide (Massei and  
110 Genov 2004) that displays an unusual life history strategy among ungulates (Focardi et al.  
111 2008). Despite its large size, wild boar exhibits a high fecundity, as they can produce up to 14  
112 piglets per litter (Gamelon et al. 2013) and reproduce in their first year of life (Servanty et al.  
113 2009). Wild boar preferentially feeds on acorns, the most common example of pulsed resources  
114 in temperate forest ecosystems (Caignard et al. 2017, Touzot et al. 2018, Schermer et al. 2019)  
115 during autumn-winter. Previous studies have shown that the long-term asymptotic population  
116 growth rate  $\lambda$  of wild boar populations and home range dynamics are dependent on the presence

117 or absence of acorn production (Parsons 1962, Jedrzejewska et al. 1997, Bieber and Ruf 2005,  
118 Zeman et al. 2016, Bisi et al. 2018, Touzot et al. 2020, Vetter et al. 2020). However, none of  
119 these studies has assessed the effects of acorn production on all demographic rates (i.e. survival,  
120 growth, reproduction for all stages of the life cycle) on populations experiencing various  
121 ecological contexts. Whether populations exhibit common demographic responses to acorn  
122 production and whether, within a population, all individuals respond in the same way to acorn  
123 production remains to be carefully explored. Answering this question is of major importance  
124 to gain a good understanding of the effects of mast seeding at both the intraspecific and  
125 intrapopulation levels.

126         Here, we took advantage of a long-term monitoring of three wild boar populations in  
127 France and Italy, and explored how acorn production influences their demography. First,  
128 detailed information on annual acorn production was available in these populations allowing  
129 us to split the years in two categories: years of acorn production vs. scarce acorn production.  
130 Second, long-term detailed individual-based data (i.e. capture-mark-recapture data and hunting  
131 bags) in all wild boar populations allowed us to estimate stage-specific demographic rates  
132 (reproduction, survival, growth) and therefore population growth rate as well as generation  
133 time under the two regimes of acorn production. Third, for each population, we determined the  
134 demographic rates with the greatest potential to affect the population growth rate  $\lambda$  under the  
135 two conditions of acorn availability (years of acorn production vs. scarce acorn production)  
136 using a combination of prospective and retrospective analyses (Horvitz et al., 1997; Caswell,  
137 2001, respectively). Prospective analyses include elasticity analyses and evaluate how a  
138 proportional change in a demographic rate would influence the population growth rate  $\lambda$  (de  
139 Kroon et al. 1986), under the two conditions of acorn availability. Retrospective analyses  
140 consist in life-table response experiment (LTRE) analyses that decompose the observed

141 difference in  $\lambda$  under the two conditions of acorn availability into the relative contributions of  
142 each demographic parameter (Caswell 1989, 2010).

143

## 144 **MATERIALS AND METHODS**

### 145 **Study areas**

146 The data come from two long-term study sites in France (Châteauvillain and La Petite  
147 Pierre) and one site in Italy (Castelporziano) (Fig. 1 and table 2). In the fenced site at  
148 Castelporziano, dispersal/emigration outside the study area was not existent. In open sites at  
149 Châteauvillain and La Petite Pierre, we assumed no immigration and emigration as the  
150 probability for female wild boar dispersing is generally very low (Truvé and Lemel 2003,  
151 Keuling et al. 2010). In all sites, populations are subjected to hunting each year between  
152 October and February.

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162 **Table 2:** Three sites included in this study where the effect of acorn production on wild boar  
 163 population dynamics was investigated. Displayed are the study sites (see also Fig. 1), a  
 164 description of the areas, climate and forest composition for each site.

Study site	Description	Climate	Forest composition
Châteauvillain	11,000 ha open forest	Between continental and oceanic	<i>Quercus petraea</i> and <i>Fagus sylvatica</i>
Castelporziano	6,000 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	2,674 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> )

165

## 166 **Acorn data collection**

167 As acorn fall begins in early autumn in temperate oak forests, hereafter, we defined year  
 168 from 1<sup>st</sup> October at year  $t$  to 30<sup>th</sup> September at year  $t+1$ . In Châteauvillain, the absence of  
 169 experimental design to collect acorns directly from the oak trees (see e.g. Touzot et al. 2018)  
 170 or to measure growth characteristics (e.g. age of the trees, crown width, volume) (see e.g. Kim  
 171 et al. 2016) prevented us for obtaining any direct estimates of acorn production on this site.  
 172 However, acorn production was measured annually indirectly based on diet composition  
 173 obtained from the analysis of stomach contents of harvested wild boars during the hunting

174 season (see Brandt et al. 2006, Servanty et al. 2009, Gamelon et al. 2017, Touzot et al. 2020  
175 for similar approaches). We identified two categories of years depending on the quantity of  
176 acorns found in the stomachs: years of acorn production (A) when acorns represented 50-90%  
177 of stomach contents; otherwise, the years were considered as scarce acorn production (N) (Fig.  
178 1).

179 In other sites (Castelporziano and La Petite Pierre), acorn production was measured  
180 annually directly with seed traps (using the ground plot counting method, see Touzot et al.  
181 2018). Between October and February, which corresponds to the period of acorn fall (Touzot  
182 et al. 2018), traps of 1m<sup>2</sup> were placed under oak tree at about two-thirds the distance between  
183 the trunk and the canopy margin, where acorn production is the highest. Up to fifty traps were  
184 distributed within the site. Each year, an acorn production index was calculated as the average  
185 number of acorns collected per trap (see Focardi et al. 2008, Gamelon et al. 2017, Barrere et  
186 al. 2020 for further information about the protocol). For consistency, as done in Châteauvillain,  
187 we identified two categories of years depending on the quantity of acorns collected in the traps:  
188 years of acorn production (A) when acorns represented more than 50% of the maximum index  
189 obtained during the study period; otherwise, the years were considered as scarce acorn  
190 production (N) (Fig. 1).

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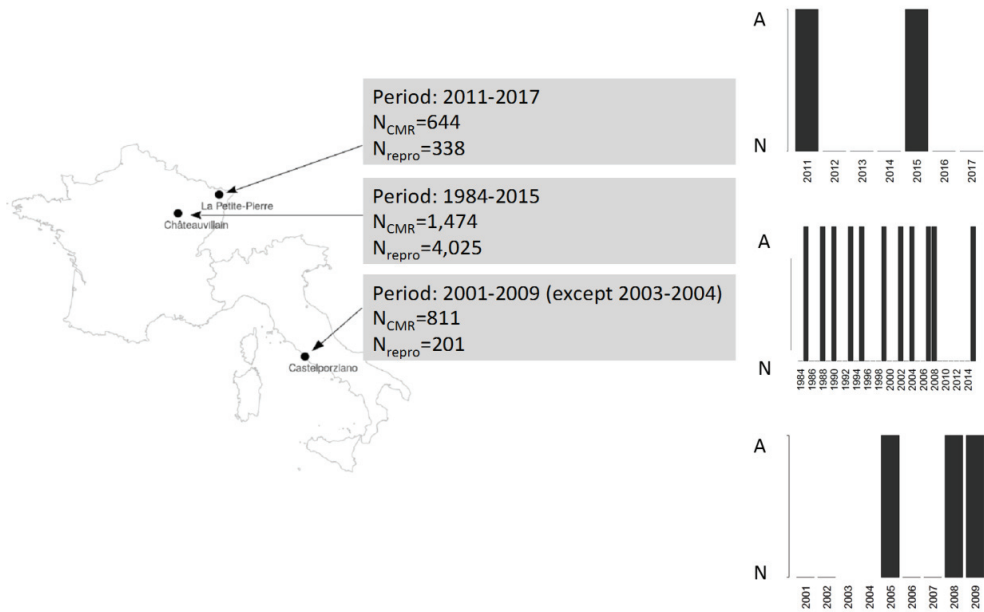
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198 **Figure 1.** Location of the three sites included in this study where the effect of acorn production  
 199 on wild boar population dynamics was investigated. Displayed are the number of marked  
 200 females as part of capture-recapture programs ( $N_{CMR}$ ), the number of harvested females for  
 201 which reproductive status has been assessed ( $N_{repro}$ ), the study period, as well as the sequence  
 202 of acorn production (years of scarce acorn production (N) and of acorn production (A)) during  
 203 the studied period.

204

### 205 **Demographic data collection**

206 From March to September, capture-mark-recapture-recovery (CMRR) data were  
 207 collected annually in all sites (see Fig. 1 for information on the years included in the analyses).  
 208 During those periods, we captured female wild boar using traps, marked them with numbered  
 209 ear-tags and released them in their environment (see Fig. 1 for information on site-specific  
 210 number of females monitored). Later, they were recaptured alive in traps, and/or recovered



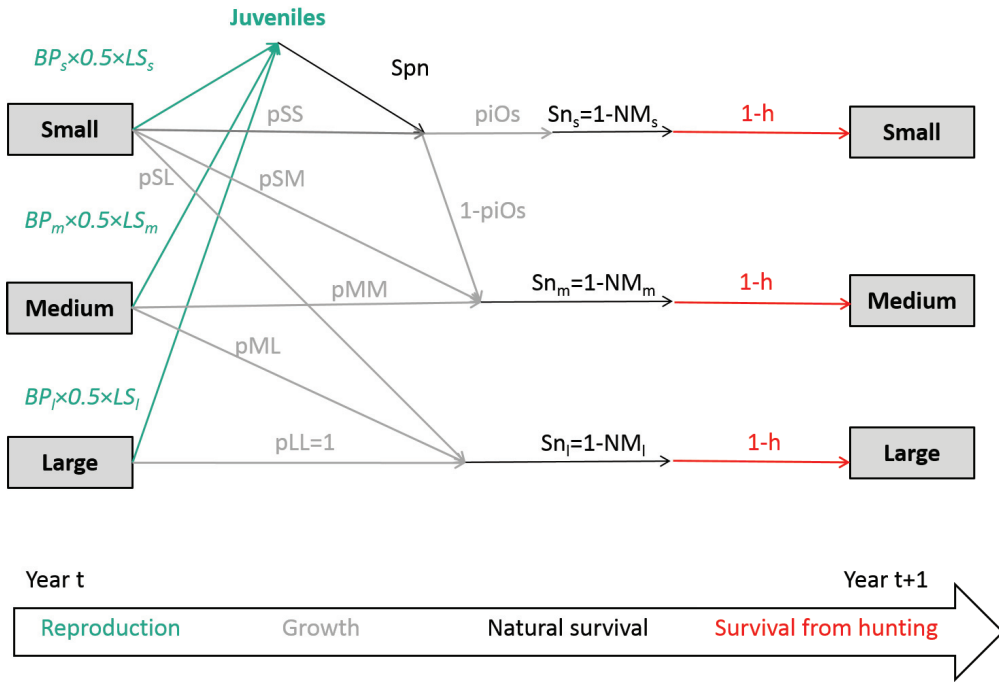
211 dead from hunting. For each capture and recovery event, the date and the individual's weight  
212 were recorded by researchers/field assistants. Weight measurements of live individuals during  
213 captures were converted into dressed body mass (i.e. body mass without digestive tract, heart,  
214 lungs, liver, reproductive tract and blood) (see Gamelon et al. 2017 for a similar approach)  
215 whereas dressed body masses were directly recorded on individuals killed by hunters.

216 In addition to CMRR data, our research team collected data on reproductive status based  
217 on examination of the reproductive tracts of females harvested during the hunting season (see  
218 Fig. 1 for information on site-specific number of females for which reproductive status has  
219 been assessed). From sagittally cut ovaries, we defined each female as reproductive (i.e.  
220 presence of *corpora lutea* / pregnant) or non-reproductive (i.e. absence of *corpora lutea* / not  
221 pregnant). We used these data to estimate the annual proportion of breeding females (*BP*). For  
222 harvested females that were pregnant, we recorded the number of fetuses present in the uteri to  
223 evaluate litter size (*LS*).

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## 225 **Life cycle and stage-structured population model**

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



236

237 **Figure 2.** Wild boar life cycle. We assumed a balanced sex ratio at birth. Postnatal survival  
 238  $Spn$  and the probability for juveniles to remain in the small class  $piOs$  were set to 0.75 and  
 239 0.60, respectively. See table 3 and figure 4 for the meaning and the estimated parameters.

240

241 Females from body mass class  $j$  may reproduce with a probability  $BP_j$  and produce  $LS_j$   
 242 juveniles that may survive with a probability  $Spn$  (Fig. 2). Then, females may remain in the  
 243 same body mass class with a probability  $piOs$  for juveniles,  $pSS$  for small females,  $pMM$  for  
 244 medium females and  $pLL$  for large females. Alternatively, they can move in heavier body mass  
 245 classes with probabilities  $1-piOs$ ,  $pSM$  (i.e. from small to medium),  $pSL$  (i.e. from small to  
 246 large) or  $pML$  (i.e. from medium to large) (Fig. 2). From March to September, females may  
 247 survive from natural causes of death (e.g. disease) with a probability  $Sn_j=1-NM_j$  (with  $NM_j$

248 being the natural mortality) and from October to February, they may survive from hunting with  
249 a probability  $l-h_j$  (see table 3 for the list of the demographic parameters and their biological  
250 meaning in bold). Importantly, the values of the parameters shown on the life cycle (Fig. 2)  
251 possibly differ according to the conditions of acorn availability (i.e. A and N) which is what  
252 we aimed to assess, and also differ between populations. For instance, in Châteauvillain, all  
253 females can reproduce whereas only females in the large body mass class can reproduce at  
254 Castelporziano (i.e.  $BP_s=BP_m=0$ ) (see Appendix S1 for the stage-structured population matrix).

### 255 **Estimating annual survival and transition probabilities between body mass classes**

256 All the parameters in the stage-structured population model (Fig. 2) were estimated  
257 from CMRR data, except postnatal survival  $Spn$  ( $=0.75$ ) and the probability for juveniles to  
258 remain in the small body mass class  $piOs$  ( $=0.60$ ) that were estimated by expert opinion (see  
259 Gamelon et al. 2012, Touzot et al. 2020). For all study areas, we analysed CMRR data using a  
260 multistate model (see Lebreton et al. 2009 for a review) that allows annual natural mortality  
261 ( $NM_{j,t}$ ) to be estimated separately from annual hunting mortality ( $HM_{j,t}$ ) for each body mass  
262 class  $j$ . The model has already been fully described in previous works (see Gamelon et al. 2012,  
263 Touzot et al. 2020) but we provide here a brief overview of its structure.

264 Each year, the status of a female was described using ten states. States 1, 2 and 3 were  
265 for individuals captured alive in the traps in the small, medium and large body mass classes,  
266 respectively. States 4, 5 and 6 were for individuals just killed by hunters and recovered, again  
267 in the three body mass classes, respectively. States 7, 8 and 9 (unobservable) were for  
268 individuals that just died from natural causes, again in the three body mass classes, respectively.  
269 State 10 (unobservable) was for individuals already dead (from hunting or natural causes the  
270 previous year) and was simply an absorbing state. The multistate model allows the transitions  
271 between states from one year to the next to be estimated. In other words, all the transitions

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

### 289 **Estimating demographic parameters for each condition of acorn availability**

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

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

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

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

299 where  $\gamma$  are the intercepts and  $\beta$  are the regression coefficients for each body mass class  $j$ . These  
 300 regressions were fit for each posterior sample (15,000 in total for each population) and the best  
 301 model was retained using Akaike Information Criterion (Burnham and Anderson 2002).  
 302 Among the 15,000 posterior samples, we computed the probability that Eqn. (1), Eqn. (2) or  
 303 Eqn. (3) corresponded to the retained model. For instance, among the 15,000 posterior samples,  
 304 a probability  $P(\text{Eqn. (1) retained}) > P(\text{Eqn. (3) retained}) > P(\text{Eqn. (2) retained})$  would indicate  
 305 that annual natural mortality probabilities ( $NM_{j,t}$ ) were best supported by a constant model  
 306 (Eqn. 1) rather than explained by previous or current acorn conditions. On the contrary, a  
 307 probability  $P(\text{Eqn. (2) retained}) > P(\text{Eqn. (1) retained}) > P(\text{Eqn. (3) retained})$  would indicate  
 308 that annual natural mortality probabilities ( $NM_{j,t}$ ) were best explained by current acorn  
 309 conditions (Eqn. 2). Once the model providing the best fit among the 15,000 posterior samples  
 310 was selected, it was fitted to each of the 15,000 posterior samples and the distribution of 15,000  
 311 values for  $NMs$  was recorded for each condition of acorn production. We thus obtained the  
 312 posterior distribution of each parameter (i.e. mean natural mortality  $NM_j$ , mean transition  
 313 probability from one body mass class to another) for each body mass class  $j$  (i.e. small, medium  
 314 and large) and the conditions of acorn availability (i.e. A and N) (see Fig. 3 for a schematic  
 315 showing the different analytical steps).

316 Similarly, for reproductive parameters, we assessed whether the probabilities to  
 317 participate to reproduction  $BP_{j,t}$  and the litter sizes  $LS_{j,t}$  depended on acorn production (at year  
 318  $t$  or  $t-1$ ) or were constant over years. Regressions were fit within a Bayesian framework. For  
 319  $LS_{j,t}$ , we used a Poisson distribution. We ran three independent chains of 25,000 MCMC  
 320 iterations, with a burn-in of 8,000 iterations thinning every 5<sup>th</sup> observation, resulting in 5,000

321 posterior samples for each chain and thus in 15,000 posterior samples in total. Convergence  
322 was assessed using the Brooks and Gelman diagnostic ( $R' < 1.05$ ) (Brooks and Gelman 1998).  
323 We selected the best model using the Widely Applicable Information Criterion (WAIC) with  
324 the *loo* package (Vehtari et al. 2017). The posterior distribution of 15,000 values for  $BP_{j,t}$  and  
325  $LS_{j,t}$  was recorded for each condition of acorn production.

326

### 327 **Retrospective/prospective demographic analyses**

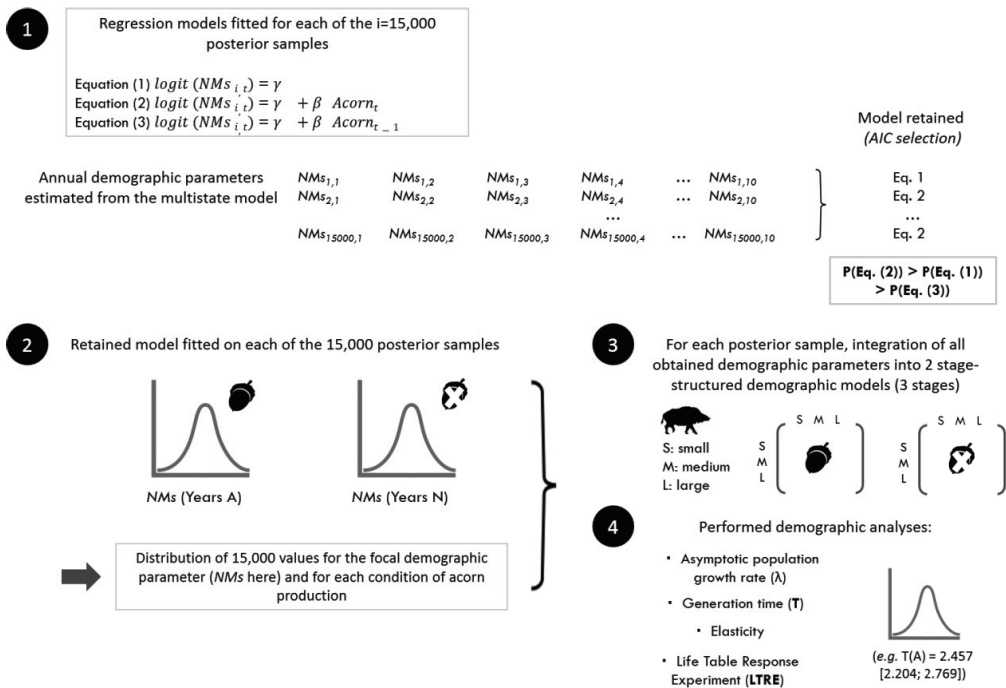
328 For each posterior sample (15,000 in total for each population), the estimated  
329 demographic rates (mortality probabilities, transitions between body mass classes,  
330 reproductive parameters) were integrated into two stage-structured population models, one for  
331 each condition of acorn production (A and N) (see Appendix S1). Note that the proportion of  
332 individuals removed by hunting,  $h$ , was set to its average value across all body mass classes  
333 and categories of acorn production (posterior means [95% credible intervals]:  $h=0.478$  [0.442;  
334 0.509] in Châteauvillain, 0.180 [0.100; 0.317] in Castelporziano and 0.452 [0.417; 0.483] in  
335 La Petite Pierre). This ensured that the mean population size estimated from the past observed  
336 sequence of acorn production was fairly stable over time (i.e.  $\lambda=1$ ) and that we really assessed  
337 the demographic responses to acorn production, not to changes in hunting pressure over years.  
338 We then calculated the asymptotic population growth rate  $\lambda$  (i.e., the dominant eigenvalue of  
339 the matrix) as well as the generation time  $T$ , for each condition of acorn production (A and N).  
340 The generation time corresponds to the weighted mean age of mothers in a population having  
341 reached its asymptotic regime (Gaillard et al. 2005). We estimated  $T$  as the inverse of the  
342 summed elasticity of the recruitment parameters (i.e. proportion of reproductive females or  
343 litter size) obtained across the three body mass classes (Brooks and Lebreton 2001). From the  
344 15,000 estimates of  $\lambda$  and  $T$ , we computed the mean of the posterior distribution and the 95%

345 CRI of  $\lambda$  and  $T$ . Finally, we estimated the elasticity of  $\lambda$  to each demographic rate, i.e. the  
 346 proportional change in  $\lambda$  obtained when changing a given demographic rate by a small amount  
 347 (e.g. 1%), using the popbio package (Stubben and Milligan 2007) in R version 3.4.3 (R  
 348 Development Core Team 2017). We computed the mean of the posterior distribution and the  
 349 95% CRI of each elasticity among the 15,000 posterior samples. Lastly, to measure the  
 350 contribution of each demographic rate to the observed changes in  $\lambda$  between conditions of acorn  
 351 production, we performed a LTRE analysis. Such analysis consists in multiplying the  
 352 difference observed for a given demographic parameter between the two treatments (e.g. here  
 353 years A and N) by its elasticity (equation from Caswell (2001)):

354

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

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



358

359 **Figure 3.** Schematic summary of the different analytical steps. Example with natural mortality of small  
360 females,  $NMs$ .

361

## 362 RESULTS

### 363 Effects of acorn production on stage-specific demographic parameters

364 We found that within a population, all stage-specific demographic rates were not  
365 similarly influenced by acorn production (Fig. 4, table 3). Indeed, at Châteauvillain, 62% of  
366 the posterior samples indicated that annual natural mortality probabilities for small females  
367 ( $NMs$ ) were best supported by a constant model (Eqn. 1) rather than explained by current (Eqn.  
368 2, 25%) or previous (Eqn. 3, 13%) acorn conditions. The same pattern was found at La Petite  
369 Pierre ( $P(\text{Eqn. (1) retained})=58\%$ ;  $P(\text{Eqn. (2) retained})=21\%$  and  $P(\text{Eqn. (3) retained})=21\%$ )  
370 and at Castelporziano ( $P(\text{Eqn. (1) retained})=52\%$ ;  $P(\text{Eqn. (2) retained})=23\%$  and  $P(\text{Eqn. (3) retained})=25\%$ )



371 retained)=25%). Similarly, for the three populations, annual natural mortality probabilities for  
 372 medium and large females ( $NM_m$  and  $NM_l$ ) were best supported by a constant model, indicating  
 373 that natural mortality did not depend on acorn conditions, irrespective of the body mass class  
 374 (Fig. 4, table 3). For the three populations, natural mortality was low for all body mass classes  
 375 (Fig. 4). Likewise, litter size was independent on acorn production (Fig. 4, table 3). However,  
 376 the proportion of breeding females and the probability of small females entering a heavier body  
 377 mass class during the year were the main parameters responding to an increase in acorn  
 378 availability (Fig. 4, table 3). In the populations of Châteauvillain and Castelporziano, the  
 379 proportion of breeding females ( $BP_j$ ) was positively influenced by acorn production (Fig. 4).  
 380 In Châteauvillain, this positive effect of acorn production on the proportion of breeding females  
 381 was significant for medium and large females only, not for small females. In Castelporziano,  
 382 the probability of small females entering a heavier body mass class during the year ( $pSM$  and  
 383  $pSL$ ) also increased in relation to acorn production.

384

385 **Table 3.** Model selection results. The first column indicates the models tested with the response  
 386 variables (in bold) and the explanatory variables. For each population, the best models retained  
 387 are indicated with a cross.

Models	Châteauvillain	Castelporziano	La Petite Pierre
<b>Natural mortality for small <math>NMs</math></b>			
Constant	X	X	X
Acorn production t			
Acorn production t-1			
<b>Natural mortality for medium <math>NM_m</math></b>			
Constant	X	X	X
Acorn production t			
Acorn production t-1			
<b>Natural mortality for large <math>NM_l</math></b>			
Constant	X	X	X

Acorn production t  
Acorn production t-1

**Probability of remaining in the small class  $p_{SS}$**

Constant X X  
Acorn production t  
Acorn production t-1 X

**Probability of transitioning from the small to the medium class  $p_{SM}$**

Constant X X  
Acorn production t X  
Acorn production t-1

**Probability of transitioning from the small to the large class  $p_{SL}$**

Constant X X  
Acorn production t X  
Acorn production t-1

**Probability of transitioning from the medium to the large class  $p_{ML}$**

Constant X X X  
Acorn production t  
Acorn production t-1

**Proportion of small reproductive females  $BPs$**

Constant X  
Acorn production t  
Acorn production t-1

**Proportion of medium reproductive females  $BPm$**

Constant  
Acorn production t X X  
Acorn production t-1

**Proportion of large reproductive females  $BPl$**

Constant X  
Acorn production t X  
Acorn production t-1 X

**Litter size of small  $LSs$**

Constant X  
Acorn production t  
Acorn production t-1

**Litter size of medium *LSm***

Constant	X		X
Acorn production t			
Acorn production t-1			

**Litter size of large *LSl***

Constant	X	X	X
Acorn production t			
Acorn production t-1			

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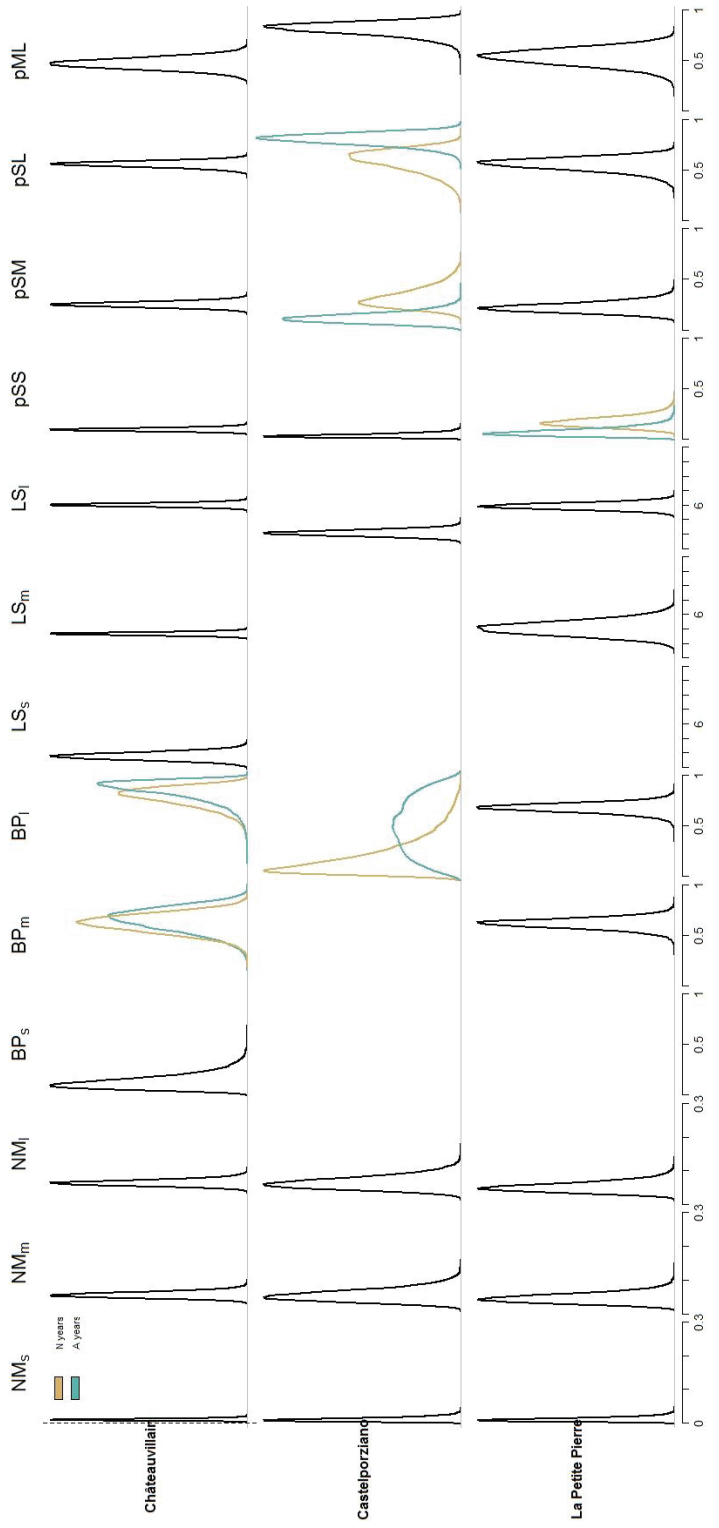
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394 **Figure 4.** Columns show the posterior distributions of the demographic parameters in the three wild boar populations (in rows). Parameters in  
 395 yellow correspond to years of scarce acorn production (N), in blue to years of acorn production (A) while parameters in black are the same in both  
 396 A and N years. See table 3 and figure 2 for the meaning of the parameters

397 In addition to highlighting marked differences in demographic responses to acorn  
398 production within a population, we found contrasting demographic responses among  
399 populations in terms of magnitude of these responses (see Fig. 4) and of drivers. In particular,  
400 depending on the populations, either past (year  $t-1$ ) or current (year  $t$ ) conditions of acorn  
401 production may influence demographic rates. In Châteauvillain, current acorn conditions  
402 mattered for the proportion of breeding females in the medium and large body mass classes,  
403 whereas conditions the previous year influenced this proportion in Castelporziano (table 3).  
404 Importantly, current conditions also appeared to be important in Castelporziano through their  
405 immediate effect on the transition probability of small females entering a heavier body mass  
406 class during the year (for the transition  $p_{SM}$  from small to medium:  $P(\text{Eqn. (1) retained})=26\%$ ;  
407  $P(\text{Eqn. (2) retained})=39\%$  and  $P(\text{Eqn. (3) retained})=34\%$ ; for the transition  $p_{SL}$  from small to  
408 large:  $P(\text{Eqn. (1) retained})=34\%$ ;  $P(\text{Eqn. (2) retained})=43\%$  and  $P(\text{Eqn. (3) retained})=23\%$ ). In  
409 La Petite Pierre, only past conditions mattered: a year of acorn production was followed by a  
410 lower probability to remain in the small body mass class  $p_{SS}$  (Fig. 4) ( $P(\text{Eqn. (1) retained})=35\%$ ;  
411  $P(\text{Eqn. (2) retained})=20\%$  and  $P(\text{Eqn. (3) retained})=46\%$ ).

412

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

414 Because in Châteauvillain, only current conditions influenced demographic parameters,  
415 we integrated the estimated demographic rates (Fig. 4) into two stage-structured population  
416 models (Appendix S1), one for each conditions of acorn production (i.e. N vs. A). We found  
417 that in years of scarce acorn production, the population size tended to decrease ( $\lambda=0.990$ , 95%  
418 CRI [0.946; 1.034]), whereas it tended to increase by 1.7% per year of acorn production  
419 ( $\lambda=1.017$ , 95% CRI [0.940; 1.089]) (Fig. 5). Retrospective analysis (LTRE) revealed that the  
420 observed difference in  $\lambda$  under the two conditions of acorn availability mainly occurred through

421 the effect of acorns on the proportion of breeding in the large class ( $BP_l$ ) (Fig. 5). The  
422 generation time was lower during years of acorn production ( $T=2.457$  years, 95% CRI [2.204;  
423 2.769]) than when acorns were scarce ( $T=2.502$  years, 95% CRI [2.247; 2.777]; Fig. 5). Thus,  
424 in presence of acorns, the mean age of mothers at childbirth was 0.045 years (i.e. 16 days)  
425 younger than in absence of acorns. Irrespective of acorn conditions, prospective analyses  
426 showed that the highest elasticity was found for the natural survival of large females indicating  
427 that this demographic parameter had the highest contribution to  $\lambda$  (Fig. 6).

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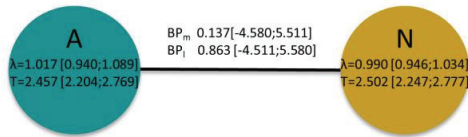
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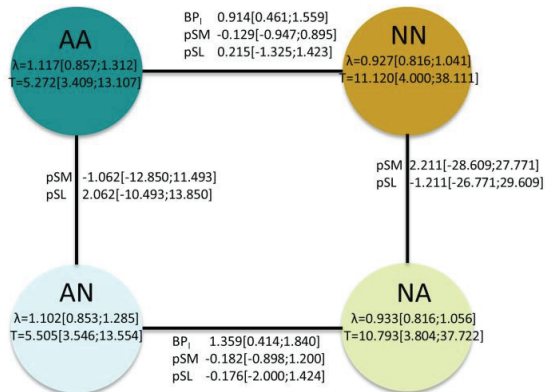
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a) Châteauvillain



b) Castelporziano



c) La Petite Pierre



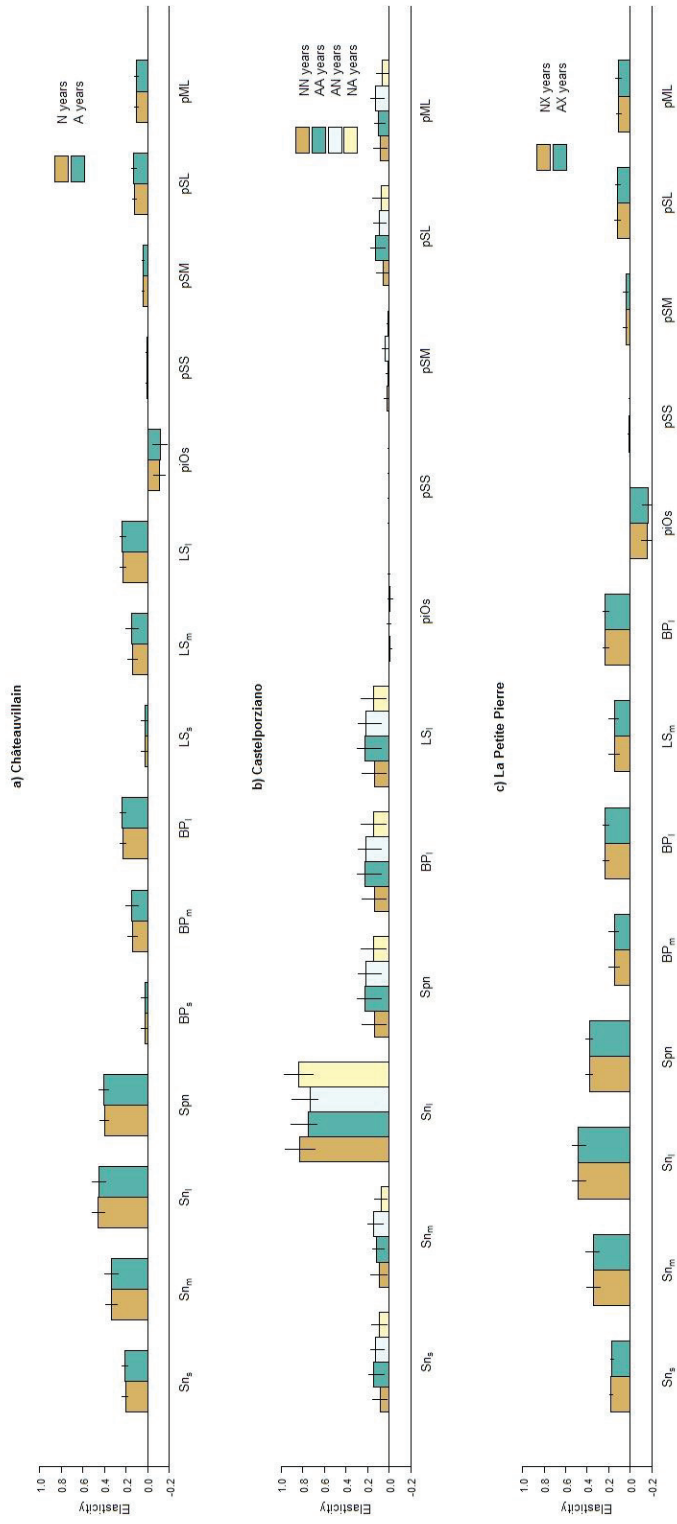
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442 **Figure 5.** Prospective analysis (LTRE): Decomposition of the difference in population growth rate  $\lambda$   
 443 under various conditions of acorn production (A: years of acorn production; N: years of scarce acorn  
 444 production) for the three wild boar populations. T corresponds to generation time (in years). Mean  
 445 posterior distributions together with their 95% CRI are reported. See table 3 and figure 2 for the meaning  
 446 of the parameters.

447

448 In Castelporziano, both past and current acorn conditions influenced demographic  
449 parameters. Therefore, we integrated the estimated demographic rates (Fig. 4) into four stage-  
450 structured population models (Appendix S1) corresponding to the succession of years of acorn  
451 production and years of scarce production (i.e. AA, NN, AN, NA). Two successive years of  
452 scarce acorn production (NN) led to a decrease of the population growth rate ( $\lambda=0.927$ , 95%  
453 CRI [0.816; 1.041]) whereas one year of acorn production followed by another year of acorn  
454 production (AA) was associated with an increasing population growth rate ( $\lambda=1.117$ , 95% CRI  
455 [0.857; 1.312]) (Fig. 5). As expected, retrospective analysis indicated that the observed  
456 difference in  $\lambda$  between AA years and NN years resulted from changes in the proportion of  
457 breeding females and the transition probability of small females entering a heavier body mass  
458 class during the year. However, the proportion of breeding females in the large class ( $BP_l$ )  
459 mostly explained the observed difference in  $\lambda$  (Fig. 4). Because the proportion of breeding  
460 females was responsible for most of the difference in  $\lambda$  and because this parameter was  
461 influenced by past acorn production, a year of scarce acorn production followed by a year of  
462 acorn production (NA) induced similar demographic responses than NN years, whereas a year  
463 of acorn production followed by a year of scarce acorn production (AN) provided similar  
464 results than AA years (Fig. 5 and Fig. 6). The generation time was lower in AA (and AN) years  
465 than in NN (and NA) years (e.g.  $T=5.272$  years, 95% CRI [3.409; 13.107] vs. 11.120 years,  
466 95% CRI [4.000; 38.111]) indicating that in AA and AN years, the mean age of mothers at  
467 childbirth was almost 5.848 years younger than in NN and NA years. Prospective analysis  
468 showed that, as observed in Châteauvillain, the highest elasticity was for the natural survival  
469 of large females, irrespective of acorn conditions (Fig. 6).





470

471 **Figure 6.** Retrospective analysis: Elasticity of demographic rates for the three wild boar populations, according to acorn production (A: years of

472 acorn production; N: years of scarce acorn production). Mean posterior distributions together with their 95% CRI are reported. See table 3 and

473 figure 2 for the meaning of the parameter.

474

475           At La Petite Pierre, only acorn conditions the preceding year (at  $t-1$ ) influenced  
476 demographic parameters the current year (year X at  $t$ , see table 3). Therefore, we integrated the  
477 estimated demographic rates (Fig. 5) into two stage-structured population models (i.e. NX vs.  
478 AX). Years of scarce acorn production (years N) were followed, the next year (NX), by a  
479 population growth rate of  $\lambda=1.002$ , 95% CRI [0.999; 1.004]. Years of acorn production (years  
480 A) were followed by a population growth rate of 0.995, 95% CRI [0.989; 0.999] the next year  
481 (AX). The small difference in  $\lambda$  under the two conditions of acorn availability only occurred  
482 through the effect of acorns on the probability for small females to remain in this body mass  
483 class during the year ( $p_{SS}$ ) (Fig. 5). Indeed, following a year of acorn production (AX years),  
484 the probability for small females to remain in the small class was slightly lower than after a  
485 year of scarce acorn production (Fig. 4). In other words, females were more likely to move into  
486 a larger body mass class after a year of acorn production ( $p_{SM}$  and/or  $p_{SL}$ ). Nevertheless, these  
487 transition probabilities ( $p_{SM}$  and  $p_{SL}$ ) were not significantly influenced by acorn production  
488 (see table 3, Fig. 4) suggesting that the effect of acorn production on  $p_{SS}$  was almost negligible  
489 from a biological viewpoint. This explains why in overall, acorn production has only little  
490 effect on population growth rate and generation time in La Petite Pierre. The generation time  
491 was indeed 2.641 years, 95% CRI [2.423; 2.871] in NX years and 2.629 years, 95% CRI [2.412;  
492 2.860] in AX years indicating that mean age of mothers at childbirth was somewhat similar  
493 under the two conditions of acorn availability (Fig. 5). Again, irrespective of the acorn  
494 conditions, prospective analysis revealed that natural survival of large females had the highest  
495 elasticity (Fig. 6).

496

497

498 **DISCUSSION**

499           Our goal was to investigate whether variation in demographic responses to acorn  
500 production exist both within and among populations. Using two complementary approaches,  
501 retrospective and prospective analyses, we found some common responses to acorn production  
502 among populations: higher breeding probability and/or transition probability from the small  
503 body mass class to larger ones, resulting in higher population growth rate and shorter  
504 generation time. Despite these similarities, we also found some marked differences both within  
505 and among populations. Within populations, acorn production mainly influenced reproductive  
506 parameters of medium and large females and growth of small females (i.e. transitions between  
507 small mass class and heavier ones). Among populations, these demographic responses differed  
508 in magnitude. In turn, the magnitude of the resulting changes in population growth rates and  
509 generation times in response to acorn production was strongly population-specific.

510           Irrespective of acorn conditions, the generation time was longer in the Italian population  
511 (Castelporziano) than in the French populations (Châteauvillain and La Petite Pierre).  
512 Generation time is a metric that ranks species on the slow-fast continuum, a major axis of  
513 variation in life history tactics in mammals (Gaillard et al. 2005, 2016, Bielby et al. 2007,  
514 Jeschke and Kokko 2009). This continuum contrasts fast species characterized with a short  
515 lifespan and the production of many offspring early in life to slow species with opposite  
516 characteristics. Therefore, the French populations consistently displayed a shorter generation  
517 time (about 2.5 years) indicating a faster turnover. This accelerated pace of life has been  
518 interpreted as a demographic response to the high hunting pressure, where individuals are able  
519 to reallocate resources to reproduction to compensate for reduced survival (Servanty et al.

520 2011, Kapota and Saltz 2018). Other studies have pointed out the presence of reproductive  
521 compensation of harvest losses due to the diversion of resources from survival to reproduction  
522 in polytocous species such as feral pigs (Hanson et al. 2009), black bears *Ursus americanus*  
523 (Freedman et al. 2003) or Tasmanian devils *Sarcophilus harrisii* (Jones et al. 2008). With a  
524 generation time of about 10 years in absence of acorns in Italy, wild boar displayed a generation  
525 time which is comparable to similar-sized ungulates that usually have a generation time longer  
526 than 6 years (Servanty et al. 2011). Strikingly, in response to acorn production, generation time  
527 became shorter indicating that acorn production favored a faster turnover.

528 Our demographic analyses revealed that adult survival  $S_n$  remained high, as expected  
529 among ungulates where the average natural adult survival probability often exceed 0.95 in  
530 females (Gaillard et al. 2000), exhibited the highest elasticity and was independent on acorn  
531 production. These findings are in accordance with the demographic buffering hypothesis  
532 (Morris and Doak 2004, Hilde et al. 2020), positing that the demographic parameter with the  
533 strongest effect on the population growth rate ( $S_n$  in our case) should be buffered/canalized  
534 against environmental conditions. In contrast, acorn production positively influenced the  
535 proportion of breeding females  $BP$  and/or transition probability from the small to heavier body  
536 mass classes ( $pSM$ ,  $pSL$ ). At Châteauvillain, current acorn conditions were allocated to  
537 reproduction whereas resources from acorns produced the preceding year were stored and then  
538 allocated to reproduction at Castelporziano (Fig. 4). This result indicates that wild boars in  
539 Châteauvillain, a resource-rich environment, displayed an income breeding tactic whereas at  
540 Castelporziano, a resource-poor environment, females were closer to the capital end of the  
541 capital-income continuum of breeding tactics (Jönsson, 1997; Gamelon et al., 2017). In turn,  
542 an increase in  $BP$  and/or  $pSM$ ,  $pSL$  positively influenced the population growth rate  $\lambda$  (Fig. 5).

543 In populations characterized by this type of dynamics driven by environmental stochasticity,  
544 years of high resource availability are generally followed by strong density dependence leading  
545 populations to collapse (see Sæther et al. 2016 for a comparative study on birds). Because  
546 population sizes are regulated by harvest in the studied populations, carrying capacities are  
547 unlikely to be reached and the strength of density dependence should be negligible.

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

566 and La Petite Pierre), for which generation time was much shorter and for which hunting likely  
567 remains the main driver of population dynamics (Toïgo et al. 2008, Gamelon et al. 2011,  
568 Servanty et al. 2011). Noticeably, to the best of our knowledge, only two studies in the literature  
569 has investigated the effects of pulsed resources on harvested species (table 1, see Bridges et al.  
570 2011 for a study on black bear, see Gamelon et al. 2017 on wild boar). Gaining a good  
571 understanding on the combined effects of environmental variation (e.g. acorn production) and  
572 hunting is crucial to maintain sustainable harvest. This is particularly true in the current context  
573 of global changes where an increase in frequency of events of massive acorn production might  
574 be expected in response to warmer spring conditions (Caignard et al. 2017, Schermer et al.  
575 2019). Exploring the expected effects of global warming, through its effect on pulsed resources,  
576 in combination with different hunting strategies, offers promising avenues of research.

577

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588

589 **AUTHOR CONTRIBUTIONS**

590 SF, BF, EB and EN provided access to the data. LT, JC and MG conducted the analyses and

591 MG wrote the manuscript with input from all coauthors.

592 **DATA AVAILABILITY STATEMENT**

593 The data used in our analysis will be made available upon publication of this study.

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791

1

## **Supplementary materials**

2 Effects of pulsed resources on the dynamics of seed consumer populations: A

3 comparative demographic study in wild boar

4

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6 Franzetti, Éveline Nivois, Lara Veylit and Bernt-Erik Sæther

7 **Appendix S1.** Body mass-structured population matrix used for the wild boar populations at  
8 Châteauvillain, Castelporziano and La Petite Pierre. Three body mass classes are considered  
9 (see main text for the definition of the body mass classes in each site). See figure 2 for a  
10 schematic representation of wild boar life cycle, table 3 for parameter definitions and figure 4  
11 for parameter values.

12

	Small	Medium	Large
Small	$BPs \times LSs \times 0.5 \times Spn \times piOs \times (1-NMs) \times (1-h) + pSS \times (1-NMs) \times (1-h)$	$BPm \times LSm \times 0.5 \times Spn \times piOs \times (1-NMs) \times (1-h)$	$BPl \times LSl \times 0.5 \times Spn \times piOs \times (1-NMs) \times (1-h)$
Medium	$BPs \times LSs \times 0.5 \times Spn \times (1-piOs) \times (1-NMm) \times (1-h) + pSM \times (1-NMm) \times (1-h)$	$BPm \times LSm \times 0.5 \times Spn \times (1-piOs) \times (1-NMm) \times (1-h) + pMM \times (1-NMm) \times (1-h)$	$BPl \times LSl \times 0.5 \times Spn \times (1-piOs) \times (1-NMm) \times (1-h)$
Large	$pSL \times (1-NMI) \times (1-h)$	$pML \times (1-NMI) \times (1-h)$	$(1-NMI) \times (1-h)$

13

14 **Appendix S2.** Code JAGS used to implement the multistate CMRR model (example with the  
15 wild boar population at Châteauvillain).

```
16  
17 #####  
18 # 0 - READ IN DATA  
19 #####  
20  
21 setwd("")  
22 mydata <- as.matrix(mydata) #Load CMRR data  
23  
24 #####  
25 # 1 - DATA MANIPULATION  
26 #####  
27  
28 # Data are in matrix "mydata", one female per row, with coding as follows:  
29 # 0 = female not observed;  
30 # 1 = female observed Small;  
31 # 2 = female observed Medium;  
32 # 3 = female observed Large;  
33 # 4 = female found dead Small;  
34 # 5 = female found dead Medium;  
35 # 6 = female found dead Large;  
36  
37 # Number of individuals  
38 n <- dim(mydata)[[1]]  
39  
40 # Number of capture occasions  
41 K <- dim(mydata)[[2]]  
42  
43 # compute date of first capture  
44 e <- NULL  
45 last <- NULL  
46 quid <- NULL  
47 for (i in 1:n){  
48   temp <- 1:K  
49   quid <- c(quid,(mydata[i,min(temp[mydata[i,]>=1])]))  
50   e <- c(e,min(temp[mydata[i,]>=1]))  
51 }  
52  
53 for (i in 1:n){  
54   temp <- 1:K  
55   mask = (mydata[i,]>=4)  
56   if (sum(mask)==1) {last <- c(last,temp[mask])}  
57   else {last <- c(last,K)}  
58 }  
59  
60 nyears <-26  
61  
62 #####  
63 # 2 - SPECIFY MODEL IN BUGS LANGUAGE  
64 #####  
65  
66 sink("cmrr.bug")  
67 cat("  
68   model{  
69  
70   #-----
```

```

71 # 1. Define the priors for the parameters
72 #-----
73
74 piVS ~ dunif(0,1)
75
76 for (t in 1:(nyears-1)){
77
78 # Dirichlet prior for survival probabilities
79 survS[1:7,t] ~ ddirch(alphaS[])
80 survM[1:5,t] ~ ddirch(alphaM[])
81 survL[1:3,t] ~ ddirch(alphaL[])
82
83 psiML[t] ~ dunif(0,1) # Transition from medium to large-sized body mass class (=pML=1-pMM)
84 pSMSL[1:3,t] ~ ddirch(transitionS[]) # Transitions from small to small, medium and large-sized body mass
85 classes (=pSS, pSM, pSL)
86
87 ppS[t] ~ dunif(0,1) # Recapture probability for small females (=ps)
88 ppM[t] ~ dunif(0,1) # Recapture probability for medium females (=pM)
89 ppL[t] ~ dunif(0,1) # Recapture probability for large females (=pL)
90
91 lIS[t] ~ dunif(0,1) # Recovery probability for small females (=rs)
92 lIM[t] ~ dunif(0,1) # Recovery probability for medium females (=rM)
93 lIL[t] ~ dunif(0,1) # Recovery probability for large females (=rL)
94
95 # Hunting mortality
96
97
98 pS[2,t] <- survS[2,t] # Small (=MHs)
99 pM[2,t] <- survM[2,t]+survS[3,t] # Medium (=MHM)
100 pL[2,t] <- survS[4,t]+survM[3,t]+survL[2,t] # Large (=MHL)
101
102
103 # Natural mortality
104
105 pS[3,t] <- survS[5,t] # Small (=NMs)
106 pM[3,t] <- survS[6,t]+survM[4,t] # Medium (=NMM)
107 pL[3,t] <- survS[7,t]+survM[5,t]+survL[3,t] # Large (=NML)
108
109
110 # Natural survival = 1-Natural mortality
111
112 pS[1,t] <- 1-pS[3,t]
113 pM[1,t] <- 1-pM[3,t]
114 pL[1,t] <- 1-pL[3,t]
115
116 # Proportion of hunted individuals h = Hunting mortality/Natural survival
117
118 h[1,t] <- pS[2,t]/pS[1,t] # Small
119 h[2,t] <- pM[2,t]/pM[1,t] # Medium
120 h[3,t] <- pL[2,t]/pL[1,t] # Large
121
122 }
123
124
125 #-----
126 # 2. Likelihood for capture-recapture-recovery data
127 #-----
128
129 # probabilities for each initial state
130

```



```
131 px0[1] <- piVS # Probability of being in initial state alive small
132 px0[2] <- 1 - piVS # Probability of being in initial state alive medium
133 px0[3] <- 0
134 px0[4] <- 0
135 px0[5] <- 0
136 px0[6] <- 0
137 px0[7] <- 0
138 px0[8] <- 0
139 px0[9] <- 0
140 px0[10] <- 0
141
142 po.init[1,1] <- 0
143 po.init[1,2] <- 1
144 po.init[1,3] <- 0
145 po.init[1,4] <- 0
146 po.init[1,5] <- 0
147 po.init[1,6] <- 0
148 po.init[1,7] <- 0
149
150 po.init[2,1] <- 0
151 po.init[2,2] <- 0
152 po.init[2,3] <- 1
153 po.init[2,4] <- 0
154 po.init[2,5] <- 0
155 po.init[2,6] <- 0
156 po.init[2,7] <- 0
157
158 po.init[3,1] <- 0
159 po.init[3,2] <- 0
160 po.init[3,3] <- 0
161 po.init[3,4] <- 1
162 po.init[3,5] <- 0
163 po.init[3,6] <- 0
164 po.init[3,7] <- 0
165
166 po.init[4,1] <- 0
167 po.init[4,2] <- 0
168 po.init[4,3] <- 0
169 po.init[4,4] <- 0
170 po.init[4,5] <- 1
171 po.init[4,6] <- 0
172 po.init[4,7] <- 0
173
174 po.init[5,1] <- 0
175 po.init[5,2] <- 0
176 po.init[5,3] <- 0
177 po.init[5,4] <- 0
178 po.init[5,5] <- 0
179 po.init[5,6] <- 1
180 po.init[5,7] <- 0
181
182 po.init[6,1] <- 0
183 po.init[6,2] <- 0
184 po.init[6,3] <- 0
185 po.init[6,4] <- 0
186 po.init[6,5] <- 0
187 po.init[6,6] <- 0
188 po.init[6,7] <- 1
189
190 po.init[7,1] <- 1
```

```

191 po.init[7,2] <- 0
192 po.init[7,3] <- 0
193 po.init[7,4] <- 0
194 po.init[7,5] <- 0
195 po.init[7,6] <- 0
196 po.init[7,7] <- 0
197
198 po.init[8,1] <- 1
199 po.init[8,2] <- 0
200 po.init[8,3] <- 0
201 po.init[8,4] <- 0
202 po.init[8,5] <- 0
203 po.init[8,6] <- 0
204 po.init[8,7] <- 0
205
206 po.init[9,1] <- 1
207 po.init[9,2] <- 0
208 po.init[9,3] <- 0
209 po.init[9,4] <- 0
210 po.init[9,5] <- 0
211 po.init[9,6] <- 0
212 po.init[9,7] <- 0
213
214 po.init[10,1] <- 1
215 po.init[10,2] <- 0
216 po.init[10,3] <- 0
217 po.init[10,4] <- 0
218 po.init[10,5] <- 0
219 po.init[10,6] <- 0
220 po.init[10,7] <- 0
221
222
223 for (t in 1:(nyears-1)){
224
225 # Probabilities of observations at a given occasion given states at this occasion
226
227 po[1,t,1] <- 1-ppS[t]
228 po[1,t,2] <- ppS[t]
229 po[1,t,3] <- 0
230 po[1,t,4] <- 0
231 po[1,t,5] <- 0
232 po[1,t,6] <- 0
233 po[1,t,7] <- 0
234
235 po[2,t,1] <- 1-ppM[t]
236 po[2,t,2] <- 0
237 po[2,t,3] <- ppM[t]
238 po[2,t,4] <- 0
239 po[2,t,5] <- 0
240 po[2,t,6] <- 0
241 po[2,t,7] <- 0
242
243 po[3,t,1] <- 1-ppL[t]
244 po[3,t,2] <- 0
245 po[3,t,3] <- 0
246 po[3,t,4] <- ppL[t]
247 po[3,t,5] <- 0
248 po[3,t,6] <- 0
249 po[3,t,7] <- 0
250

```

```

251 po[4,t,1] <- 1-lIS[t]
252 po[4,t,2] <- 0
253 po[4,t,3] <- 0
254 po[4,t,4] <- 0
255 po[4,t,5] <- lIS[t]
256 po[4,t,6] <- 0
257 po[4,t,7] <- 0
258
259 po[5,t,1] <- 1-lIM[t]
260 po[5,t,2] <- 0
261 po[5,t,3] <- 0
262 po[5,t,4] <- 0
263 po[5,t,5] <- 0
264 po[5,t,6] <- lIM[t]
265 po[5,t,7] <- 0
266
267 po[6,t,1] <- 1-lIL[t]
268 po[6,t,2] <- 0
269 po[6,t,3] <- 0
270 po[6,t,4] <- 0
271 po[6,t,5] <- 0
272 po[6,t,6] <- 0
273 po[6,t,7] <- lIL[t]
274
275 po[7,t,1] <- 1
276 po[7,t,2] <- 0
277 po[7,t,3] <- 0
278 po[7,t,4] <- 0
279 po[7,t,5] <- 0
280 po[7,t,6] <- 0
281 po[7,t,7] <- 0
282
283 po[8,t,1] <- 1
284 po[8,t,2] <- 0
285 po[8,t,3] <- 0
286 po[8,t,4] <- 0
287 po[8,t,5] <- 0
288 po[8,t,6] <- 0
289 po[8,t,7] <- 0
290
291 po[9,t,1] <- 1
292 po[9,t,2] <- 0
293 po[9,t,3] <- 0
294 po[9,t,4] <- 0
295 po[9,t,5] <- 0
296 po[9,t,6] <- 0
297 po[9,t,7] <- 0
298
299 po[10,t,1] <- 1
300 po[10,t,2] <- 0
301 po[10,t,3] <- 0
302 po[10,t,4] <- 0
303 po[10,t,5] <- 0
304 po[10,t,6] <- 0
305 po[10,t,7] <- 0
306
307 # Probabilities of states at a given occasion given states at the occasion before (see Appendix S1)
308
309 px[1,t,1] <- pSMSL[1,t]*survS[1,t]
310 px[1,t,2] <- pSMSL[2,t]*survS[1,t]

```

```

311 px[1,t,3] <- pSMSL[3,t]*survS[1,t]
312 px[1,t,4] <- survS[2,t]
313 px[1,t,5] <- survS[3,t]
314 px[1,t,6] <- survS[4,t]
315 px[1,t,7] <- survS[5,t]
316 px[1,t,8] <- survS[6,t]
317 px[1,t,9] <- survS[7,t]
318 px[1,t,10] <- 0
319
320 px[2,t,1] <- 0
321 px[2,t,2] <- (1-psiML[t])*survM[1,t]
322 px[2,t,3] <- psiML[t]*survM[1,t]
323 px[2,t,4] <- 0
324 px[2,t,5] <- survM[2,t]
325 px[2,t,6] <- survM[3,t]
326 px[2,t,7] <- 0
327 px[2,t,8] <- survM[4,t]
328 px[2,t,9] <- survM[5,t]
329 px[2,t,10] <- 0
330
331 px[3,t,1] <- 0
332 px[3,t,2] <- 0
333 px[3,t,3] <- survL[1,t]
334 px[3,t,4] <- 0
335 px[3,t,5] <- 0
336 px[3,t,6] <- survL[2,t]
337 px[3,t,7] <- 0
338 px[3,t,8] <- 0
339 px[3,t,9] <- survL[3,t]
340 px[3,t,10] <- 0
341
342 for (i in 4:10){
343   px[i,t,10] <- 1
344   for (j in 1:9){
345     px[i,t,j] <- 0
346   }
347 }
348
349 }
350
351 for (i in 1:N) # for each female
352 {
353
354   # Estimated probabilities of initial states are the proportions in each state at first capture occasion
355   alive[i,First[i]] ~ dcat(px0[1:10])
356   mydata[i,First[i]] ~ dcat(po.init[alive[i,First[i]],])
357
358   for (j in (First[i]+1):Last[i]) # loop over time
359   {
360
361     # State equations
362     # draw states at j given states at j-1
363     alive[i,j] ~ dcat(px[alive[i,j-1],j-1,])
364
365     # Observation equations
366     # draw observations at j given states at j
367     mydata[i,j] ~ dcat(po[alive[i,j],j-1,])
368
369   }
370

```

```

371   }
372
373   }
374
375   ",fill = TRUE)
376
377   sink()
378
379   #####
380   # 3 – DATA, INITIAL VALUES AND PARAMETERS MONITORED
381   #####
382
383   # data
384   mydatax <-
385   list(N=n,nyears=nyears,mydata=as.matrix(mydata+1),First=e,Last=last,alphaS=rep(1,7),alphaM=rep(1,5),alpha
386   L=rep(1,3),transitionS=rep(1,3))
387
388   alive = mydata
389
390   for (i in 1:n) {
391     for (j in 1:K) {
392       if (j < e[i]) {alive[i,j] <- NA}
393     }
394   }
395
396   for (i in 1:n) {
397     if (e[i] == K) 2+2
398     else {
399       for (j in (e[i]+1):K) {
400
401         if (alive[i,j]==0 & alive[i,j-1]==1 & sum(alive[i,j:K]==2)>0) {alive[i,j] <- 1}
402         if (alive[i,j]==0 & alive[i,j-1]==1 & sum(alive[i,j:K]==2)==0 & sum(alive[i,j:K]==6)==0 &
403         sum(alive[i,j:K]==3)==0) {alive[i,j] <- 1}
404
405         if (alive[i,j]==0 & alive[i,j-1]==1 & sum(alive[i,j:K]==3)>0) {alive[i,j] <- 2}
406         if (alive[i,j]==0 & alive[i,j-1]==1 & sum(alive[i,j:K]==3)==0 & sum(alive[i,j:K]==6)==0) {alive[i,j:K] <-
407         1}
408
409         if (alive[i,j]==0 & alive[i,j-1]==1 & sum(alive[i,j:K]==1)>0) {alive[i,j] <- 1}
410
411         if (alive[i,j]==0 & alive[i,j-1]==2 & sum(alive[i,j:K]==2)>0) {alive[i,j] <- 2}
412         if (alive[i,j]==0 & alive[i,j-1]==2 & sum(alive[i,j:K]==2)==0 & sum(alive[i,j:K]==6)==0) {alive[i,j] <- 2}
413
414         if (alive[i,j]==0 & alive[i,j-1]==2 & sum(alive[i,j:K]==3)>0) {alive[i,j] <- 2}
415
416         if (alive[i,j]==0 & sum(alive[i,j-1]==3)>0) {alive[i,j] <- 3}
417
418         if (alive[i,j]==0 & alive[i,j-1]==1 & sum(alive[i,j:K]==6)>0) {alive[i,j] <- 2}
419         if (alive[i,j]==0 & alive[i,j-1]==2 & sum(alive[i,j:K]==6)>0) {alive[i,j] <- 2}
420
421       }
422     }
423   }
424
425   for (i in 1:n) {
426     for (j in 1:K) {
427       if (mydata[i,j]==4 & j<K) {alive[i,(j+1):K] <- NA}
428       if (mydata[i,j]==5 & j<K) {alive[i,(j+1):K] <- NA}
429       if (mydata[i,j]==6 & j<K) {alive[i,(j+1):K] <- NA}
430     }

```

```

431 }
432
433
434
435 alive <- as.matrix(alive)
436
437 init1 <- list(alive=alive)
438 init2 <- list(alive=alive)
439
440 # concatenate list of initial values
441 inits <- list(init1,init2)
442
443 # specify the parameters to be monitored
444 parameters <- c("survS","survM","survL","pSMSL","psiML","piVS","ppS","ppM","ppL","IIS","IIM","IIL",
445 "pS","pM","pL","h")
446
447 #####
448 # 4 – RUN THE MODEL
449 #####
450
451 # load R package to call JAGS from R
452 library(rjags)
453
454 # run JAGS
455 jmodel <- jags.model("cmrr.bug", mydatax, inits, n.chains = 3, n.adapt = 8000)
456 jsample <- coda.samples(jmodel, parameters, n.iter=25000, thin = 5)
457
458 # save results
459 save(jsample,jmodel,file='cmr_boar.Rdata')
460
461

```

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