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How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study

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Abstract. Mast seeding in temperate oak populations shapes the dynamics of seed consumers and numerous communities. Mast seeding responds positively to warm spring temperatures and is therefore expected to increase under global warming. We investigated the potential effects of changes in oak mast seeding on wild boar population dynamics, a widespread and abundant consumer species. Using long-term monitoring data, we showed that abundant acorn production enhances the proportion of breeding females. With a body-mass-structured population model and a fixed hunting rate of 0.424, we showed that high acorn production over time would lead to an average wild boar population growth rate of 1.197 whereas non-acorn production would lead to a stable population. Finally, using climate projections and a mechanistic model linking weather data to oak reproduction, we predicted that mast seeding frequency might increase over the next century, which would lead to increase in both wild boar population size and the magnitude of its temporal variation. Our study provides rare evidence that some species could greatly benefit from global warming thanks to higher food availability and therefore highlights the importance of investigating the cascading effects of changing weather conditions on the dynamics of wild animal populations to reliably assess the effects of climate change.

Key words: climate change; climate projections; demographic population model; mast; population projections; resource budget model; spring temperatures; Sus scrofa.

INTRODUCTION

Numerous terrestrial and aquatic ecosystems depend on pulsed resources that display huge temporal and spatial variation in their availability (Ostfeld and Keesing 2000, Yang et al. 2008). Mast seeding, commonly defined as highly variable seed production over time that is spatially synchronized within tree populations (Silvertown 1980, Kelly 1994, Pearse et al. 2016), is one of the most widespread pulsed resources in terrestrial ecosystems (Ostfeld and Keesing 2000). These dramatic among-year fluctuations in seed production are known to affect population dynamics (Jones et al. 1998, Schmidt 2003), community dynamics (Ostfeld and Keesing 2000, Schmidt and Ostfeld 2008), and life-history strategies (Ergon et al. 2001, Gamelon et al. 2017*a*) of seed consumers (Bogdziewicz et al. 2016 for a review). For instance, juvenile survival of Eastern chipmunk (*Tamias striatus*) is positively influenced by beech seed production (Bergeron et al. 2011), and both American (*Tamiasciurus hudsonicus*) and Eurasian (*Sciurus vulgaris*) tree squirrels benefit from additional reproductive opportunities after a mast seeding event (Boutin et al. 2006).

Oak species are widely distributed across the world (Gea-Izquierdo et al. 2006) and provide an emblematic example of the striking among-year fluctuations in seed production (Koenig et al. 1994, Liebhold et al. 2004). Recent studies of the effect of weather conditions on oak tree reproduction have shown that spring weather conditions play a key role in both pollination success and acorn production in temperate oak forests (Caignard et al. 2017, Bogdziewicz et al. 2018, Schermer et al. 2019). Indeed, while warm and dry spring weathers

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provide favorable conditions to pollination (Schermer et al. 2019), intense late spring frost might inversely act as an environmental veto by impeding flower or seed set over extended geographic areas (Garca-Mozo et al. 2001, Augspurger 2009, Bogdziewicz et al. 2018). In the ongoing context of rapid climate change, climate projection models predict that temperatures will keep rising over the next century (IPCC 2013), which could increase the frequency of weather conditions that favor both oak pollination and fruiting. However, net impact of increased frequency in mast seeding events (defined as years of dramatically high acorn production) on the population dynamics of seed consumers remains to be investigated.

While most studies exploring population consequences of climate change have been conducted on declining and/or endangered populations (e.g., emperor penguin [*Aptenodytes forsteri*], Jenouvrier et al. 2009, 2012, 2014; polar bear [*Ursus maritimus*], Hunter et al. 2011), little is known regarding the response of abundant species to global warming (but see Gaillard et al. 2013, Vetter et al. 2015, and Gauthier et al. 2016 for examples on roe deer [*Capreolus capreolus*], wild boar [*Sus scrofa*], and Greater Snow Goose [*Chen caeruslescens atlantica*], respectively). Thus, we focused on wild boar, a widespread and abundant species across Europe that mainly feeds on acorns when available (Massei et al. 1996, Schley and Roper 2003, Servanty et al. 2009). Due to its strong life-history flexibility (Focardi et al. 2008) and its high reproductive output (Servanty et al. 2007, Gamelon et al. 2017*a*), we expect wild boar to benefit from an increase in frequency of mast seeding events. While previous studies have tested how fluctuating food resources affect wild boar population dynamics, no study has yet been able to investigate the effects of such fluctuations of resource availability on the whole life cycle (i.e., survival, growth, and reproduction) within a single population of this species. However, the need for considering the effects of environmental conditions on the entire life cycle has been previously highlighted, and it is especially true if we aim to predict future populations changes, as stage- and age-specific demographic parameters may respond differently to the same conditions (Ådahl et al. 2006, Jenouvrier 2013, Gauthier et al. 2016). To the best of our knowledge, only two studies provided to date some preliminary information about the potential effects of changing resources on wild boar population dynamics. Bieber and Ruf (2005) brought together demographic parameters of several populations to explore a potential effect of resources on wild boar population growth rate. Gamelon et al. (2017*a*) identified context-dependent demographic responses when investigating the effects of mast seeding on the female reproductive allocation strategy.

Taking advantage of a detailed 34-yr monitoring of a wild boar population in the wild, we aim to investigate how warmer spring conditions induced by climate change could impact the frequency of mast seeding events and thereby affect wild boar population dynamics. To do so, we adopted a three-step approach. First, we assessed the impacts of acorn production on the entire life cycle of wild boar (i.e., on demographic parameters at all stages and ages). Second, we integrated these effects into a stage-structured demographic population model (Gamelon et al. 2012) to measure the effect of acorn production on the population growth rate. Last, we used a set of 10 climate projection models defined at the spatial scale of our study area and a mechanistic model that links weather data to oak forest reproduction to assess the expected frequency of mast seeding events in coming decades. This model accounted for the negative temporal autocorrelation reported in most mast seeding species (Kelly and Sork 2002, Schermer et al. 2019) by preventing two consecutive mast seeding years to occur. In turn, we estimated the expected future dynamics of the population under various climate scenarios.

MATERIALS AND METHODS

Study area and data collection

The study was conducted in the 11,000 ha forest of Châteauvillain-Arc-en-Barrois (northeastern France; 48°02′ N, 4°56′ E). This homogenous broad-leaved deciduous forest is mainly composed of oak (*Quercus petraea*) and beechnut (*Fagus sylvatica*) trees, respectively covering 41% and 30% of the area. The climate is intermediate between continental and oceanic types. Average monthly temperatures ranged from 2.03° ± 0.26°C [mean ± SD] in January to 18.37° ± 0.41°C in August and the mean April temperature increased by 0.062° ± 0.026°C/yr over the course of the study (Appendix S1: Fig. S1).

From 1983 to 2016, wild boars have been annually monitored using a capture–mark–recapture (CMR) program. In this study, a given year corresponded to the period between 1 October and 30 September based on the period of acorn production (Gamelon et al. 2017*a*; Fig. 1). Wild boars were trapped from March to September and individually marked before being released (1,474 females over the course of the study). During each capture or recapture event, body mass was recorded (Fig. 1). Additionally, hunting bags were analyzed each year throughout the hunting season (i.e., from October to February; Fig. 1). Dressed body mass (i.e., body mass once the digestive system, heart, lungs, liver, reproductive tract and blood have all been removed) was recorded along with the date of death for all females shot.

Reproductive tracts were also collected and carefully analyzed to assess the reproductive status of each female shot (i.e., 4,244 females over the course of the study, previously marked or not). The presence of Graafian follicles and/or *corpora lutea* in the ovaries indicates that females were in oestrus or that conception had occurred

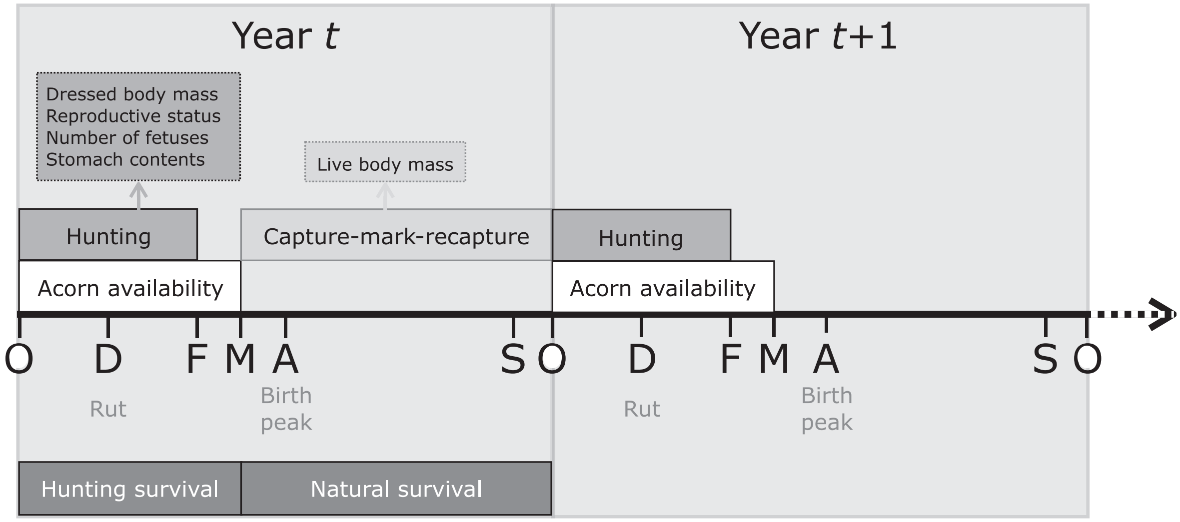

FIG. 1. Timeline of data collection using both capture–mark–recapture (CMR) protocol and hunting bags. A given year goes from 1 October (O) to 30 September (S) to match the period of acorn availability. The hunting period, capture period, seed availability period, and the type of data collected during each of these events are represented over the course of two consecutive years, along with the main rut and birth timings. The capital letters O, D, F, M, and A correspond to October, December, February, March, and April months, respectively.

(Gamelon et al. 2017*a*). These females, as well as pregnant females, were classified as breeders. Otherwise, they were considered as non-breeders. The number of embryos or fetuses was recorded for all pregnant females to measure litter size. Information on individuals that died from natural causes (e.g., diseases, injuries, etc.) was not available.

Finally, acorn production was measured indirectly each year by analyzing stomach contents of shot wild boars whenever it was possible (i.e., 3,090 stomach contents analyzed throughout the study period; Brandt et al. 2006; see also Servanty et al. 2009 and Gamelon et al. 2017*a* for a similar approach). Three categories of acorn production were defined depending on the quantity of seeds found in the stomachs: (A) years of high acorn production, referred to hereafter as mast seeding years, when acorns represented 75–90% of stomach contents; (AA) years of low acorn production, when acorns represented 50–65% of stomach contents; and (N) years of non-acorn production, when acorns represented less than 3% of stomach contents (see Servanty et al. 2009 for further details).

Demographic parameter estimation

To estimate body-mass-specific mortality and transition probabilities between body mass classes in each of the three categories of acorn production, we used the multistate CMR-recovery model previously described in Gamelon et al. (2012) (see also Appendix S2 for detailed information on the multistate model). Briefly, females died from two broad causes of mortality, namely hunting mortality (Mh) and non-hunting mortality we designated as natural mortality (Mn) because very few individuals died from human-related causes other than hunting, such as car collisions. Hunting-related mortality such as crippling loss was not detectable and thus was identified as part of natural mortality (Servanty et al. 2010, Gamelon et al. 2012). Additionally, note that natural survival Sn simply corresponds to 1 − natural mortality (Mn) and that the proportion of individuals removed annually by hunting was defined by $h = \text{Mh}/(1 - \text{Mn})$. Therefore, an individual had a survival probability at the end of each year equal to natural survival (Sn) times the probability of not being shot during the hunting season ($1 - h$) (Fig. 2; Gamelon et al. 2012). Annual hunting mortality Mh, natural mortality Mn and transition probabilities from one body mass class to another one (pSS, pSM, pSL, and pML) were estimated using the multistate model fitted within a Bayesian framework using Markov Chain Monte Carlo (MCMC) simulations. We ran three independent chains of 25,000 MCMC iterations, with a burn-in of 8,000 iterations thinning every fifth observation, resulting in 5,000 posterior samples for each chain. The Brooks and Gelman diagnostic was used to assess convergence ($R < 1.2$; Brooks and Gelman 1998), which was reached for all nodes. The analyses were implemented using JAGS (Plummer 2003) version 4.3.0 with R version 3.5.2 (R Development Core Team 2017) with package rjags (Plummer 2016; see Appendix S2 for further details).

Once annual posterior mean natural mortality within all body mass classes (Mns, Mnm, and Mnl) and transition probabilities (pSS, pSM, pSL, and pML) were estimated, we fitted regressions within a Bayesian framework using MCMC simulations to assess whether

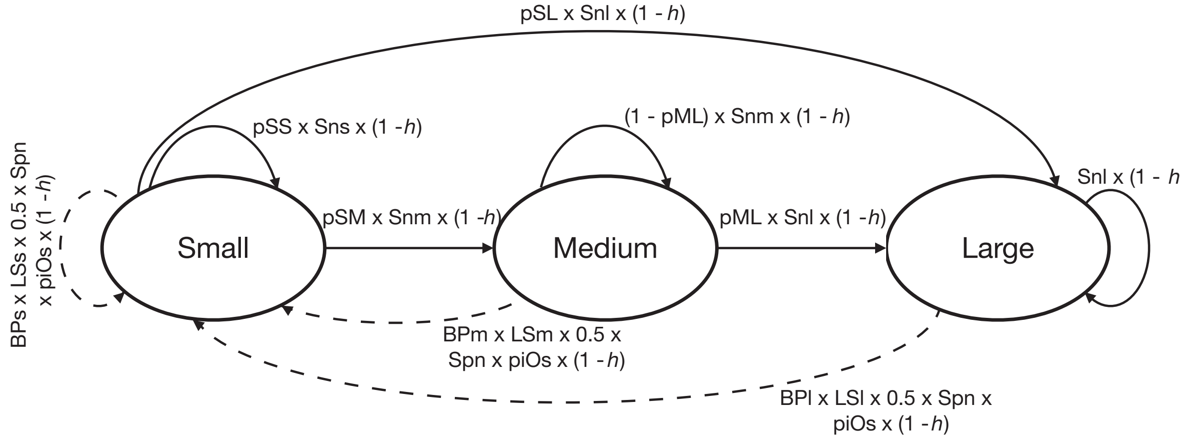

FIG. 2. Wild boar female life cycle. Three body mass classes are considered: small (<30 kg), medium (30 kg < body mass < 50 kg), and large (>50 kg) females. Solid lines represent the probability of surviving estimated as natural survival (Sn) multiplied by the probability of not being shot $(1 - h)$, and either remaining in the same body mass class until the next year (pSS and (1 − pML)) or moving upward the following class (pSM, pSL, and pML). Dashed lines represent the fecundity estimated as the product of breeding proportion (BP), litter size (LS), postnatal survival (Spn), sex ratio (we assumed a balanced sex ratio, which is supported by empirical evidence; Servanty et al. 2007), probability to remain in the small body mass class (piOs) and to survive $(\mathrm{Sn} \times (1 - h))$. Newborn individuals produced by females from all three body mass classes also have a probability to survive and move directly to the medium-sized class within the year equal to $(1 - \mathrm{piOs}) \times \mathrm{Snm} \times (1 - h)$.

these demographic parameters were constant over time or depended on acorn production (discrete factor with three modalities N, AA, and A), i.e., two models were tested for natural mortality and two models were tested for transitions probabilities. Data were logit-transformed and a normal distribution was used to implement the regressions. We also assessed whether reproductive parameters (i.e., proportion of breeding females BP and litter size LS; Fig. 2) were constant over time, depended on acorn production, and/or body mass class (discrete factor with three modalities small (<30 kg), medium (between 30 and 50 kg), and large (>50 kg); see Appendix S2: Fig. S1; Gamelon et al. 2012), including the interaction between body mass class and acorn production. We thus tested 10 models in total for reproductive parameters, five for BP and five for LS. Bernoulli and Poisson distributions were used for modeling female reproductive status (i.e., breeding vs. non-breeding) and litter size variation, respectively. Model selection was based on the Widely Applicable Information Criterion (WAIC) using the loo package (Vehtari et al. 2017). As done for the CMRR model, we ran three independent chains of 25,000 MCMC iterations, with a burn-in of 8,000 iterations thinning every fifth observation, resulting in 5,000 posterior samples for each chain and the Brooks and Gelman diagnostic was used to assess convergence. Mean parameter estimates and their associated standard deviations obtained from the selected models provided the probability of dying from natural causes within each body mass class (i.e., small, medium, and large), the probability of transitioning to another body mass class for all considered transitions, and the proportion of breeding females and the litter size in each body mass class and/or in each category of acorn production (i.e., A, AA, and N).

Stage-structured population model

Once all the demographic parameters were estimated (i.e., body mass class-specific transition probabilities, natural mortality, proportion of reproductive females, and litter size) in each resource-specific situation, they were used to implement three population models. To do so, we extended the deterministic stage-structured demographic population model proposed by Gamelon et al. (2012) for this wild boar population by building not one but three female-based pre-breeding census models (Fig. 2), one for each resource-specific situation (i.e., A, AA, and N). We estimated the asymptotic population growth rate (λ) based on mean parameter values and their associated standard deviations for each resource-specific situation (i.e., A, AA, and N; popbio package). More specifically, 1,000 values were randomly drawn from a normal distribution for each parameter in each resource-specific situation, thus allowing us to estimate the corresponding asymptotic population growth rate. Note that the proportion of individuals removed by hunting (defined as $h = \mathrm{Mh}/(1 - \mathrm{Mn})$) was set to its average value across all body mass classes and categories of acorn production based on the sequence of acorn production observed in the past (i.e., between 1983 and 2016) and on the mean demographic parameters obtained from the selected models (estimate of 0.424, see Appendix S3: Fig. S1). This ensured that the annual population size obtained when using the past sequence of acorn production was fairly stable (asymptotic population growth rate of 1.048

previously published; Gamelon et al. 2012; Appendix S3: Fig. S1) and that the potential changes observed later in the dynamics of the population actually resulted from a response to resource availability and not from fluctuations in hunting pressure.

Population projections under global warming

We used 10 different climate scenarios of future spring temperatures (De Cáceres et al. 2018; Appendix S4 for a full description). Various scenarios regarding the future evolution of greenhouse gas concentration (used as a proxy of anthropogenic activity and development) are considered in the models. Additionally, a reference scenario assuming no temperature increase over time was generated using the climatic data (i.e., mean April and minimum March temperatures) historically recorded from 1959 to 2012 on our study site (Appendix S5 for further information). These climate scenarios allowed acorn dynamics data to be generated until 2100 (see Appendix S5 for details on the procedure). To do so, we used the Resource Budget Model (RBM) developed by Schermer et al. (2019) to assess the response of fruiting dynamics to climate change over the next century in our study area. This model, based on meteorological inputs impacting acorn production dynamics (i.e., average April temperatures and minimum March temperatures), also accounts for the effects of reserve depletion after a mast seeding event by generating negative temporal autocorrelation within fruiting dynamics (Schermer et al. 2019; Appendix S5 for more details). To account for environmental stochasticity, we split the climatic series into 4-yr time intervals and randomly mixing the values included in each interval (Appendix S5). Thus, 100 scenarios of spring temperatures were generated for each of the 10 climatic models considered. Then, the simulated acorn data were divided into classes according to the three categories of acorn production (i.e., A, AA, and N). Each category of acorn production has been previously calibrated using a 500-yr time series of acorn data obtained when the climatic data historically recorded on the study site were used in the RBM and the observed frequencies of years A, AA, and N (i.e., respectively 0.12, 0.24, and 0.64; Appendix S5: section 10, Fig. S1).

Finally, we projected the response of the wild boar population to the simulated sequences of A, AA, and N years, which allowed us to compare wild boar population dynamics resulting from a scenario assuming no change of spring temperatures during the next century to a scenario of global warming. In particular, we were interested in estimating the mean population size and 95% CI, along with the coefficient of variation (CV) obtained over the next century for each of the simulated population size trajectory. To account for demographic stochasticity, which was found to be the main source of uncertainty surrounding the future dynamics of an abundant species in Gauthier et al. (2016)'s work, all demographic parameters were randomly drawn from a normal distribution based on the means and variances provided by the selected models at each time step of the simulations.

In all simulations, we considered that the population was extinct when ≤1 female remained in the population. The population vector (N_0) corresponding to the body mass class-specific number of females was used to initiate all simulations. N_0 was defined using the stable stage structure of the mean stage-structured population model for which mean demographic parameters were estimated between 1983 and 2016 (Caswell 2001) (Appendix S6 for further details).

Results

Effects of acorn production on wild boar demographic parameters

There was no effect of acorn production on natural mortality of small, medium, and large females (Table 1A–C), growth (i.e., transition probability from one body mass class to another; Table 1D–G), or litter size. Litter size was only affected by female body mass (Table 1H), such that heavier females had larger litter sizes (Table 2). Similarly, the breeding probability was influenced by female body mass (Table 1I) with heavier females having a higher breeding probability than lighter females (Table 2). Noticeably, the breeding probability of each body mass class increased with the amount of acorn available (Table 2). Only 15.5% ± 1.2% (mean ± SD) of small females reproduced during years of no acorn production, whereas 28.1% ± 3.5% did during mast seeding years. Similarly, the breeding proportion of large females increased from 60.2% ± 1.9% to 90.7% ± 2.4% with increasing acorn production.

Due to this increase in female breeding proportions with increasing acorn availability, the asymptotic population growth rate (λ; including a proportion of individuals removed by hunting of 0.424 for all body mass classes) strongly differed among the three population models. The parameter λ ranged from 1.001 [0.980–1.022] (mean [95% CI]) under a scenario of non-acorn production (acorn category N) to 1.197 [1.167–1.229] under a scenario of high acorn production (acorn category A), with an intermediate value of 1.096 [1.068–1.122] under a scenario of low acorn production (acorn category AA). These results demonstrate that, despite an annual removal of more than 40% of the individuals by hunting, the population could still increase by almost 20% if facing frequent mast seeding years.

Population projections under global warming

Future conditions of acorn production.—Using the RBM, we simulated scenarios of acorn production over the next century in relation to the temperatures predicted by 10 different climate models in our study area. As expected, we found that the frequency of mast seeding

Table 1. Model selection for the effect of acorn production and/or body mass on natural mortality of small (A), medium (B), and large (C) females, transition probabilities between body mass classes (D, E, F, and G), (H) litter size, and (I) proportion of reproductive females.

Model	Np	ΔWAIC	ω
(A) Natural mortality of small females			
Constant	**1**	**0.00**	**0.84**
Acorn production at time *t*	3	3.30	0.16
(B) Natural mortality of medium females			
Constant	**1**	**0.00**	**0.84**
Acorn production at time *t*	3	3.30	0.16
(C) Natural mortality of large females			
Constant	**1**	**0.00**	**0.99**
Acorn production at time *t*	3	17.70	0.01
(D) Probability of remaining in the small class			
Constant	**1**	**0.00**	**0.85**
Acorn production at time *t*	3	3.50	0.15
(E) Probability of transitioning from the small to the medium class			
Constant	**1**	**0.00**	**0.81**
Acorn production at time *t*	3	2.90	0.19
(F) Probability of transitioning from the small to the large class			
Constant	**1**	**0.00**	**0.68**
Acorn production at time *t*	3	1.50	0.32
(G) Probability of transitioning from the medium to the large class			
Constant	**1**	**0.00**	**0.61**
Acorn production at time *t*	3	0.90	0.39
(H) Litter size			
Body mass	**3**	**0.00**	**0.81**
Body mass + acorn production at time *t*	6	3.40	0.15
Body mass × acorn production at time *t*	9	6.20	0.04
Constant	1	99.80	0.00
Acorn production at time *t*	3	101.10	0.00
(I) Proportion of reproductive females			
Body mass × acorn production at time *t*	**9**	**0.00**	**0.99**
Body mass + acorn production at time *t*	6	25.80	0.01
Acorn production at time *t*	3	150.40	0.00
Body mass	3	878.00	0.00
Constant	1	1049.50	0.00

Notes: Displayed are the number of parameters (Np), Widely Applicable Information Criterion (WAIC), difference between a given model and the model with the lowest WAIC (ΔWAIC), and WAIC weight measuring the likelihood that a given model is the best among the candidate models (ω). The selected models are in boldface type.

years should potentially increase with the rise of spring temperatures predicted by all the climate scenarios (Appendix S7: Fig. S1 for examples of temperature trajectories). For the reference scenario, which assumed no temperature increase over the next century (i.e., based on the distributions of spring temperatures observed between 1959 and 2012 in our study area), the probability of having mast seeding years in the next century was set to 0.070 ± 0.003 (mean ± SE; Fig. 3a). On the other hand, the probability of having mast seeding years in the next century increased regardless of the temperature forecasted by the different climate models used in the RBM, ranging from 0.172 ± 0.002 for Model 5 to 0.311 ± 0.003 for Model 4. This probability increased even more over the last 20 yr of the simulations (i.e., from 2080 to 2100; Fig. 3b) and peaked for instance at 0.409 ± 0.004 for Model 4 (see Appendix S8: Table S1 for detailed frequency values).

Wild boar population projections.—In response to the expectation of marked increases of frequency in mast seeding events in the future, all 1,000 simulations indicated an increase of the wild boar population size. Indeed, between 2013 and 2100, the wild boar population size would reach over 220,000 individuals in the reference scenario (Fig. 3c), with a mean population size of 224,779 [80,852–442,542] individuals in 2100. It would increase from 9,204 [6,239–13,076] to 3,095,332 [920,783–8,104,213] individuals in the scenarios generated from the different climate models (Fig. 3d). Thus, the predicted population size at the end of the century would be on average 13.77 times higher in the scenarios expected under climate change than in the reference scenario. Furthermore, we observed a strong increase of the fluctuations in population size over time in response to future climate change (mean CV = 2.016 [1.716–2.329]) compared to the reference scenario (mean CV = 1.167 [0.951–1.389]) (Fig. 4). Thus, over the next century, we expect temporal variation in wild boar population size to be on average 1.73 times higher in the context of global warming than in the reference scenario (Fig. 4). Note that our projections pertained to the assumption of density independence, which might be violated in the future.

Discussion

Our study shows that wild boar females positively respond to mast seeding events through higher breeding proportions. The expected increase of spring temperatures under global warming might translate into higher frequencies of mast seeding events, which, in turn, could positively influence wild boar population dynamics.

From demographic parameters to population growth rate: effects of pulsed resources on wild boar population dynamics

The proportion of breeding females was positively associated with the amount of available resources (Servanty et al. 2009, Gamelon et al. 2017*a*; Table 1I). On the other hand, and in accordance with previous studies (Gamelon et al. 2017*a*), we found no effect of food resources on litter size (Table 1H). The number of offspring produced only depends on female body mass, with heavier females producing larger litters (see also Gamelon et al. 2013, Frauendorf et al. 2016, Malmsten

Table 2. Parameters (mean ± SD) estimated from the selected models (see Table 1).

Parameter	Biological meaning	N	AA	A
Mns	natural mortality of small females	0.022 ± 0.002	0.022 ± 0.002	0.022 ± 0.002
Mnm	natural mortality of medium-sized females	0.080 ± 0.007	0.080 ± 0.007	0.080 ± 0.007
Mnl	natural mortality of large females	0.083 ± 0.006	0.083 ± 0.006	0.083 ± 0.006
h	proportion of individuals killed by hunting for each sex and body mass class	0.429	0.429	0.429
BPs*	proportion of small reproductive females	0.155 ± 0.012	0.139 ± 0.017	0.281 ± 0.035
BPm*	proportion of reproductive medium-sized females	0.510 ± 0.016	0.639 ± 0.022	0.774 ± 0.030
BPl*	proportion of large reproductive females	0.602 ± 0.019	0.801 ± 0.025	0.907 ± 0.024
LSs	mean number of juveniles produced by small females	3.918 ± 0.250	3.918 ± 0.250	3.918 ± 0.250
LSm	mean number of juveniles produced by medium-sized females	4.707 ± 0.104	4.707 ± 0.104	4.707 ± 0.104
LSl	mean number of juveniles produced by large females	6.096 ± 0.121	6.096 ± 0.121	6.096 ± 0.121
pSS	probability of small females remaining in the same class during the year	0.137 ± 0.014	0.137 ± 0.014	0.137 ± 0.014
pSM	probability of small females entering the medium-sized class during the year	0.234 ± 0.025	0.234 ± 0.025	0.234 ± 0.025
pSL	probability of small females entering the large class during the year	0.556 ± 0.028	0.556 ± 0.028	0.556 ± 0.028
pML	probability of medium-sized females entering the large class during the year	0.490 ± 0.036	0.490 ± 0.036	0.490 ± 0.036
Spn	postnatal survival	0.750	0.750	0.750
piOs	probability of juvenile females entering the small class during the year	0.600	0.600	0.600

Notes: These estimates were then used to build the three population matrices corresponding to three categories of acorn production (i.e., years of A, high production; AA, low production; and N, no production). Parameters for which an asterisk* was added correspond to parameters that varied both among body mass classes (small [*s*], medium [*m*], and large [*l*]) and among acorn production categories. Note that piOs (i.e., the probability of juvenile females to enter the small body mass class within the year) and Spn (postnatal survival) were not estimated but come from expert opinion, and were set to values previously reported in Gamelon et al. (2012).

et al. 2017, Bergqvist et al. 2018). For instance, litter size increased in response to the increase of both occurrence of mast seeding events and temperatures in Germany (Frauendorf et al. 2016), whereas no effect of climate (either summer or winter temperatures and precipitations) on litter size occurred in Scandinavia (Bergqvist et al. 2018).

Likewise, no effect of mast conditions occurred on growth and natural mortality (Table 1A–G). Most studies conducted on wild boar have focused on the effects of winter conditions (i.e., temperatures and snow cover) on survival. Wild boars, especially juveniles, are highly susceptible to cold winter conditions (Melis et al. 2006, Cutini et al. 2013, Vetter et al. 2015) and early onset of winter (Geisser and Reyer 2005). However, these studies also highlighted that this decrease in survival was not caused by a negative energy balance, but by a mismatch between the occurrence of these severe winter conditions and the presence of highly available food resources (Vetter et al. 2015). Thus, a mast seeding event can allow juveniles to reach the minimal body mass required to survive harsh winter conditions (Geisser and Reyer 2005, Vetter et al. 2015). Furthermore, the presence of another mast seeding tree species might compensate for years of low oak production (Groot Bruinderink et al. 2009, Cutini et al. 2013). Therefore, a buffering effect of beech trees (*Fagus sylvatica*), which occupy 30% of our study area, along with the omnivorous diet of wild boar (Massei et al. 1996, Servanty et al. 2009), might explain why years of non-acorn production did not depress survival or growth of wild boar females.

At the population level, with increasing amount of acorn production, the increase in the proportion of breeding females translated to a higher asymptotic population growth rate. These findings thereby support the expectation that, despite an annual removal of more than 40% of females within all body mass classes (i.e., hunting rate of 0.424), wild boars positively respond to an increase in resource availability and exhibit the highest population growth rate (1.197) under a succession of abundant acorn production over time. However, in the same hunting conditions, the wild boar population growth rate was close to 1 (1.001) when wild boar faced non-acorn years, which indicates a stationary population size.

Pulsed resources and seed consumer population dynamics under global warming

As expected, we found that mast seeding events could potentially increase in frequency as a response to the warmer spring conditions predicted under various climate models applied to our study site (Appendix S7: Fig. S1 and Appendix S8: Table S1). Higher frequencies of mast

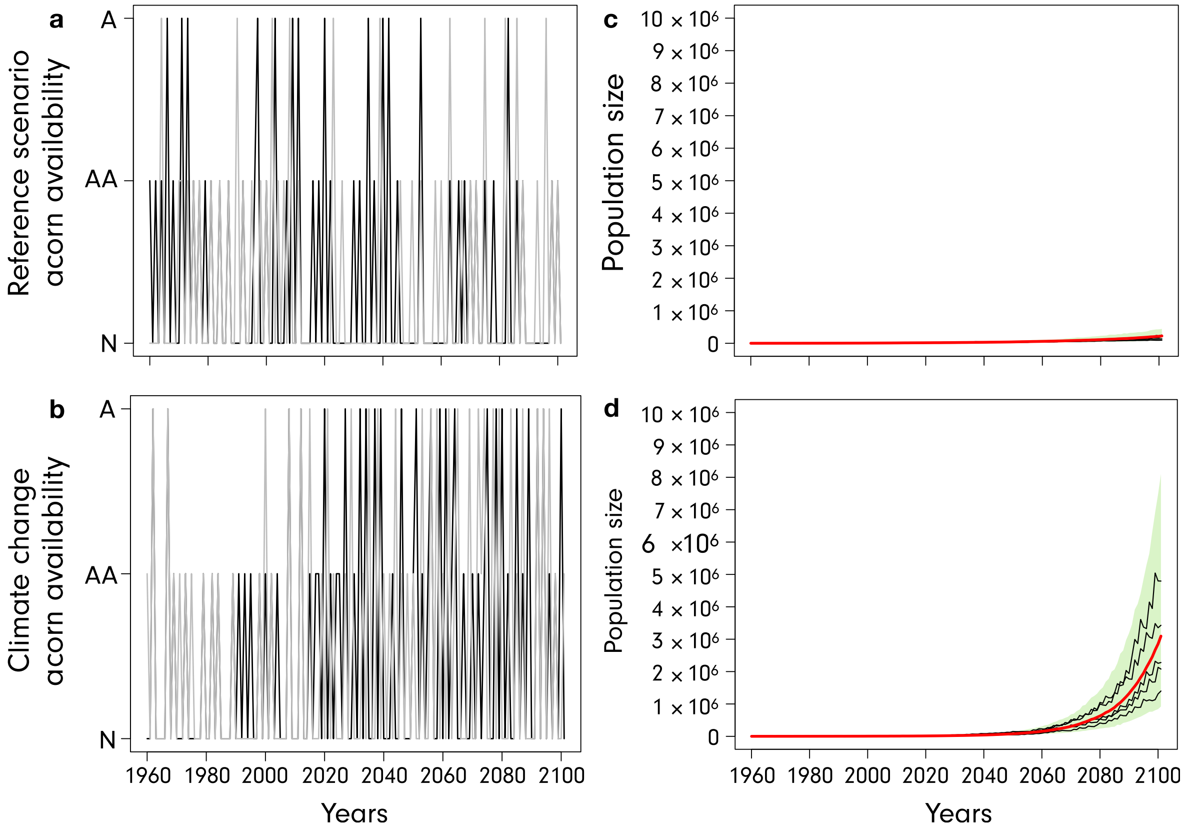

FIG. 3. Predicted wild boar population size according to different scenarios of mast seeding years under climate changes over the next century. Two scenarios of acorn production sequences were considered: the reference scenario without any change in temperatures (first row) and the global warming scenario accounting for the temperature increase expected under most scenarios of climate change (second row). The left column (a, b) shows, for each scenario, two examples of the change (second row). The left column (a, b) shows, for each scenario, two examples of the change in acorn production predicted over 142 yr (from 1959 to 2100), where A stands for years of high acorn production, AA stands for years of low acorn production, and N stands for years of non-acorn production. The right column (c, d) shows, for each scenario, population size trajectories. Five trajectories (out of 100 for the first scenario and out of 1,000 for the second scenario), which were randomly selected, are represented with solid black lines, while the mean trajectories are represented with solid red lines. The 95% confidence intervals associated to the mean trajectories are shown using the light green polygons.

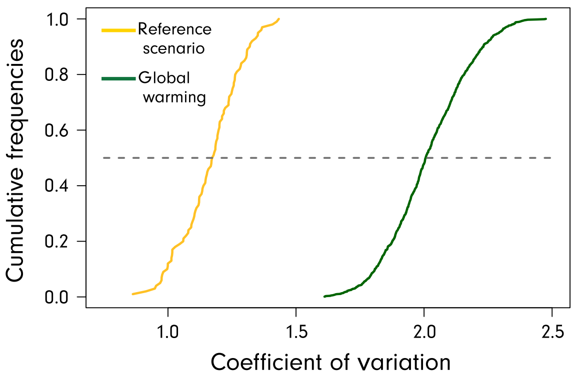

FIG. 4. Cumulative frequency distribution of the coefficients of variation in population size obtained over the next century from the 100 reference scenarios assuming no temperature increase (yellow) and from the 1,000 scenarios predicting increasing frequencies of mast seeding events in response to rising spring temperatures (dark green). The horizontal grey dotted line represents the mean CV of each scenario.

seeding events might increase the average population size (Fig. 3d) and the annual variation in population size of wild boar (Fig. 4), which could become a concern to manage such populations in a sustainable way. Although it is obvious that wild boar densities will also be regulated by density dependence preventing them to reach the unrealistically high numbers we reported in our simulations, our results provide a robust theoretical framework, and thus insights about the possible future of populations relying on mast seeding, an emblematic example of both highly fluctuating and structured (i.e., negative temporal autocorrelation) environmental conditions over time, in the ongoing context of rapid climate changes.

The RBM we used to predict fruiting dynamics accounted for the effects of spring weather conditions during pollen aerial diffusion and environmental veto due to late intense frosts on oak tree reproduction (Garca-Mozo et al. 2001, Augspurger 2009, Bogdziewicz et al. 2018, Schermer et al. 2020). However, it is noteworthy that other mechanisms might also influence mast seeding frequency in oaks and/or other tree species (Pearse et al. 2016). For instance, our projections might not be valid in Mediterranean regions where the dynamics of holm oak (*Quercus ilex*) fruiting is particularly sensitive to water deficits during summer droughts that frequently cause fruit abortion (Bogdziewicz et al. 2017). In addition, our model did not account for plant phenology, which may be highly sensitive to weather conditions and is likely to be impacted by climate change (Duputié et al. 2015, Chuine et al. 2016). While an earlier onset of the growing season of the trees in temperate Europe in response to spring warming has been well documented in the literature (Parmesan and Yohe 2003, Root et al. 2003), predicting the effects of winter temperature increase on plant phenology remains challenging (Chuine et al. 2016). To date, despite these uncertainties, the RBM we used in this study remains one of the most relevant mechanistic models for predicting temperate oak tree reproduction in response to weather variables (Schermer et al. 2019), and thus the dynamics of the associated populations and communities in the context of climate change.

From a more general perspective, our simulations of acorn dynamics accounted for the negative temporal autocorrelation that characterizes mast seeding (i.e., a year of high acorn production is followed by a non-acorn year). In turn, negative temporal autocorrelation in the environment leads to autocorrelated temporal variation in the demographic parameters (i.e., participation of females to reproduction). Temporal autocorrelation plays a key role in population dynamics (Tuljapurkar and Haridas 2006, Engen et al. 2013) and strongly influences the extent to which population growth responds to environmental variation (Metcalf and Koons 2007, Paniw et al. 2018). The effects of temporal autocorrelation on the demographic outputs are expected to be stronger in species with a fast pace of life (such as wild boar) than in species with a slow pace of life (Paniw et al. 2018). Environmental patterning is for instance especially important for the dynamics of fast species such as the edible mice (*Glis glis*), a seed consumer species that relies on beech mast seeding. Indeed, in this species, reproduction is low during years of non-beechnut production while mast seeding years increase reproductive output and decrease adult survival the following year (Ruf et al. 2006).

While predictions of marked population declines and increased extinction risks caused by rising temperatures are growing in the literature (Jenouvrier et al. 2012, Peery et al. 2012; but see Gamelon et al. 2017*b*, Hansen et al. 2019), our study shows that some populations might actually benefit from higher frequencies of mast seeding events (Fig. 3d), particularly those relying on oak mast in temperate areas. Furthermore, we expect consumer species with less opportunistic foraging patterns and marked responses to mast failures to respond more strongly to increasing frequencies of mast seeding events than wild boar. For instance, the eastern chipmunk that does not reproduce both prior and after years of complete mast failures (Bergeron et al. 2011) could be especially responsive to changes in frequencies of mast seeding events. Previous demographic analyses of population responses to climate change have focused on overall demographic output such as population growth rate or key demographic parameters but have not included any mechanistic link between food resources and demography. Our resource-dependent demographic model accounts for the effects of the amount of food resource and its variation over time on all demographic parameters (i.e., survival, growth, and reproduction). It is a powerful tool to make predictions about the expected future of seed consumers under global warming. A promising avenue of research is to develop similar resource-dependent population demographic models for a diversity of population–environment systems, to better anticipate the effects of climate change on populations in the wild and elaborate reliable management strategies.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2134/full

Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0gb5mkkxr