

Research

Efficient use of harvest data: a size-class-structured integrated population model for exploited populations

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Many animal populations are subject to hunting or fishing in the wild. Detailed knowledge of demographic parameters (e.g. survival, reproduction) and temporal dynamics of such populations is crucial for sustainable management. Despite their relevance for management decisions, structure and size of exploited populations are often not known, and data limited. Recently, joint analysis of different types of demographic data, such as population counts, reproductive data and capture–mark–recapture data, within integrated population models (IPMs) has gained much popularity as it may allow estimating population size and structure, as well as key demographic rates, while fully accounting for uncertainty. IPMs built so far for exploited populations have typically been built as age-structured population models. However, the age of harvested individuals is usually difficult and/or costly to assess and therefore often not available. Here, we introduce an IPM structured by body size classes, which allows making efficient use of data commonly available in exploited populations for which accurate information on age is often missing. The model jointly analyzes size-at-harvest data, capture–mark–recapture–recovery data and reproduction data from necropsies, and we illustrate its applicability in a case study involving heavily hunted wild boar. This species has increased in abundance over the last decades despite intense harvest, and the IPM analysis provides insights into the roles of natural mortality, body growth, maturation schedules and reproductive output in compensating for the loss of individuals to hunting. Early maturation and high reproductive output contributed to wild boar population persistence despite a strong hunting pressure. We thus demonstrate the potential of size-class-structured IPMs as tools to investigate the dynamics of exploited populations with limited information on age, and highlight both the applicability of this framework to other species and its potential for follow-up analyses highly relevant to management.

Keywords: exploited populations, harvest, hunting, integrated population model, monitoring, size-class-structured population model, *Sus scrofa*



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Introduction

Many animal populations are affected by commercial, recreational or subsistence harvest (Lebreton 2005, Peres 2010, Ripple et al. 2016), i.e. by the removal of individuals through hunting or fishing. Managing harvested populations in a sustainable way has long been a central topic in applied ecology (Williams et al. 2002). It is especially true in the current context of global change, as harvest may act in synergy with other detrimental effects such as habitat destruction or fragmentation (Camilo et al. 2007, Chen et al. 2015, Koons et al. 2015, Regehr et al. 2017). Likewise, harvest might interact with population-level effects of climate change in both marine and terrestrial ecosystems (the so-called 'harvest-interaction' hypothesis, Gamelon et al. 2019a). This interplay between harvest and climate may amplify environmentally induced fluctuations in population size and increase extinction risk, or, alternatively, dampen fluctuations and increase population growth rates (Gamelon et al. 2019a).

Models designed to assess interactive effects of harvest and other stressors on population dynamics and to predict sustainability of harvest management typically require detailed information on demographic parameters (e.g. survival, reproduction) and population size. Nonetheless, these quantities are challenging to estimate in absence of detailed long-term data (Clutton-Brock and Sheldon 2010). When demographic information is limited, the challenge lies in making efficient use of available data to gain an understanding of the dynamics of exploited populations that is sufficient to provide appropriate management recommendations. Available demographic data can be of different types, including population counts, data on reproduction and capture–mark–recapture (CMR) data. When several data types are available, a combined analysis within an integrated population model (IPM) approach may offer several advantages (reviewed by Schaub and Abadi 2011, Zipkin and Saunders 2018), even if each data type by itself provides only limited information on demographic parameters. First, combined analysis of different data sources usually increases the precision of demographic estimates (Barker and Kavalieris 2001, Péron et al. 2010). Second, imperfect detection and observation error inherently associated with data sampled in the field (e.g. population counts) can be accounted for and associated uncertainty is encapsulated in model predictions, providing a more realistic picture. Third, the use of IPMs may allow estimating additional parameters that are difficult or impossible to quantify using separate analyses of available data. For instance, Péron et al. (2010) estimated dispersal rate in a black-headed gull *Chroicocephalus ridibundus* population at the regional scale, a parameter notoriously difficult to assess. Another striking example of demographic parameter difficult to estimate is immigration, which can be quantified through the use of IPMs (Abadi et al. 2010b).

Integrated analysis of different data sources as a tool to model the dynamics of exploited populations has been used for decades in fisheries research (reviewed by Maunder and Punt 2013). More recently, IPMs have been

applied to harvested populations in terrestrial ecosystems (Gauthier et al. 2007, Conn et al. 2009, Fieberg et al. 2010, Péron et al. 2012, Lee et al. 2015, Staton et al. 2017, Arnold et al. 2018). Importantly, IPMs built on exploited populations often integrate age-at-harvest data and capture–mark–recapture–recovery (CMRR) data into age-structured population models (Methot Jr and Wetzel 2013, Arnold et al. 2018, Scheuerell et al. 2019). However, it is noteworthy that the applicability of this type of IPMs for exploited populations is limited because age-at-harvest data is often not available. Indeed, ageing individuals in the wild is challenging and generally involves expensive and time-demanding analyses (see Morrongiello et al. 2012 for a straightforward analysis of growth rings on fish scales and turtle carapace scutes for age determination). Most established techniques for age assessment, such as analyses of tooth wear for mammals (Hamlin et al. 2000) or otoliths for fish (Black et al. 2008), are hardly applicable routinely in exploited populations.

To overcome these limitations, we here develop an IPM relying on data commonly collected in exploited populations. Our model differs from traditional IPMs applied to vertebrate populations in two ways. First, it integrates CMRR data and an individual trait recorded at death (body size) into a size class-structured population model. Body size measurements are often easier and less costly to obtain from field studies of wild populations than age estimates, particularly when harvesting is part of the data collection process. Second, the model makes inference on population size using size-specific counts of individuals that have died due to harvesting. For each size class, the model allows us to get annual estimates of demographic parameters and of the number of alive individuals, a parameter often difficult to estimate and highly important for population management.

We illustrate the usefulness of this IPM for assessing population dynamics based on the case study of an economically important game species, the wild boar *Sus scrofa*. Wild boars have increased in abundance and have extended their range over the last decades in Europe (Massei et al. 2015) and North America (Lewis et al. 2019), leading to important damage to crops and high risk of disease transmission (see Schulz et al. 2019 for an example with the African swine fever). Hunting is nowadays the only way to control wild boar expansion worldwide. Demographic parameters – and consequently population dynamics – of ungulates such as wild boar are strongly influenced by body size (reviewed by Gaillard et al. 2000), and, contrary to large herbivores, age is not a structuring factor of survival in wild boar (Focardi et al. 2008). Therefore, body size is the most appropriate structuring factor to model exploited wild boar populations (Gamelon et al. 2012). Moreover, contrary to age, size information is routinely collected by hunters, making size-structured model relevant for modeling many game species. Although we focused on wild boar as a case study, the approach we propose can be reliably used for assessing population dynamics of a large range of vertebrate populations subjected to human exploitation.

Material and methods

Demographic data collection

We studied a wild boar population located in the 11 000 ha forest of Châteauvillain-Arc-en-Barrois in north-eastern France (48°02'N, 4°55'E). Between 1991 and 2016, as part of an intensive capture–mark–recapture program, 1152 wild boar females were captured between March and September using live-trapping techniques (e.g. corral traps). At each capture event, we recorded the date of capture, marked/identified and subsequently weighed all females before releasing them again. No information was available for marked individuals that died from natural causes (e.g. disease): these females were never recovered. Between October and February, wild boars are heavily harvested. Hunters are instructed to avoid shooting the largest females with a dressed body mass of ≥ 50 kg (otherwise they must pay a financial penalty proportional to the female's mass) and obliged to report any kill. All females shot by hunters (previously marked or not) were weighed and their date of death was recorded by the staff of the Office Français de la Biodiversité. As wild boar rut usually begins in mid-December, females can be in oestrus, ovulating, pregnant or reproductively inactive when shot during the hunting season. Analysis of carcasses of shot females therefore

allowed determining whether a female was reproductively active (i.e. in oestrus, ovulating or pregnant) or not. Among pregnant females, the number of fetuses present in the uteri was recorded.

Three types of demographic data were thus available (Fig. 1): CMRR data (with live recaptures between March and September, and harvest recoveries between October and February), size-at-harvest data (from October to February) and reproduction data (from October to February). CMRR data consisted of individual capture histories of 1152 marked females, which contained additional information on individual body mass (in kg) at each capture (alive) and when shot (dead). Size-at-harvest data were represented by the number of females of a given body mass shot by hunters during the hunting season of each study year ($n = 7350$ over the entire study period). Yearly reproduction data included the number of reproductively active females ($n = 1679$) among all shot females whose reproductive status had been assessed ($n = 3648$) and the number of fetuses counted in utero ($n = 4344$) of pregnant females ($n = 811$).

IPM construction

Integrated population models consist of two components, a population process model and a set of different data

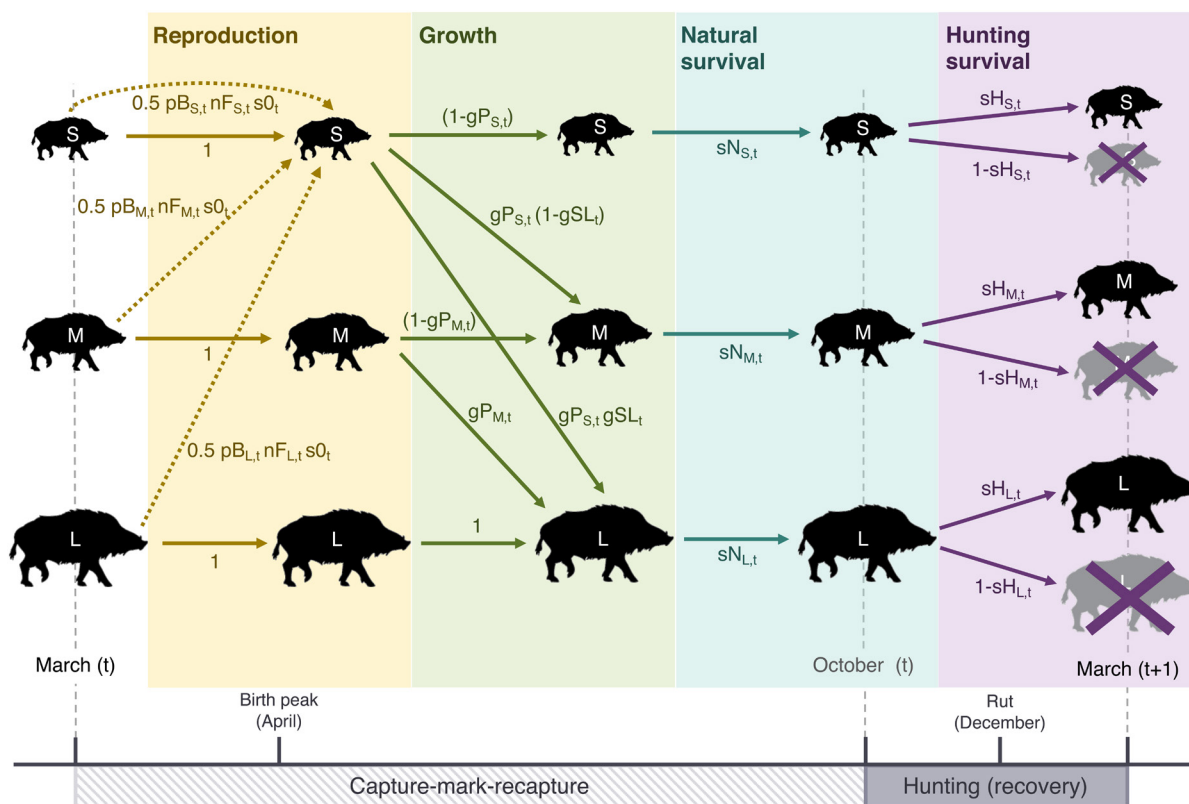


Figure 1. Wild boar life cycle graph. Three body mass classes (small *S*, medium *M* and large *L*) are considered. Starting in March, females of all body mass classes may reproduce (yellow dotted lines). Subsequently, they may grow to a larger body mass class or remain in the same class (green lines). They can then survive over the non-hunting season (turquoise lines) until October. Finally, females can survive or die during the hunting season from October to the end of February (purple lines). See Table 1 for parameter definitions.

likelihoods (Besbeas et al. 2002), both of which are combined and analyzed under a joint likelihood (Schaub and Abadi 2011, Zipkin and Saunders 2018). The population process model describes true changes in both population size and structure over time. It links demographic parameters to population dynamics. Data likelihoods, on the other hand, are probabilistic models that link different types of observed data to demographic rates and population-level quantities contained in the population model. In the following, we first describe the size-structured population model for wild boar, and then provide details on the separate data likelihoods for size-at-harvest, CMRR and reproduction data. A schematic representation of the entire IPM can be found in Fig. 2 and all parameter names are defined in Table 1.

Size-structured population model

We built a population model for wild boar structured by size classes. We assumed that population dynamics were well represented by the female segment of the population as the number of males is not limiting reproductive output in the polygynous wild boar (Gamelon et al. 2012), and therefore built a female-based model. Body mass (in kg) was used to categorize wild boar females into three size classes. Hereafter, the two terms ‘mass’ and ‘size’ are used interchangeably. The three body mass classes were: small (< 30 kg), medium (30–50 kg) and large (> 50 kg). These body mass classes are based on phenotypic characteristics and social structure of wild boar (Gamelon et al. 2012). Large females (> 50 kg)

lead matrilineal social groups (Kaminski et al. 2005), which contain females of all ages (subadults – between 1 and 2 years old – and adults – older than 2 years old) and juveniles of both sexes (younger than 1 year old). Juveniles are lighter than 30 kg and clearly distinguishable by their striped and subsequently wear a reddish coat (subadults).

We used a pre-breeding census, with the start of the population’s annual cycle being placed in March, just prior to the reproductive peak (Fig. 1). From there, the model describes the population’s transitions through seasons of reproduction, growth and natural mortality to October and finally through the hunting season to March of the next year (Fig. 1). All transitions are assumed to be subject to demographic stochasticity and therefore modelled as Poisson or Binomial random variables.

Starting from March of year t , females in any size class z ($marN_{z,t}$, where $z=S$ for small, M for medium and L for large) can reproduce according to a breeding probability $pB_{z,t}$ and produce a litter of $nF_{z,t}$ piglets, half of which are assumed to be daughters (Gamelon et al. 2012). The annual number of offspring produced by mothers in size class z is therefore formulated as:

$$Off_{z,t} \sim \text{Poisson}(marN_{z,t} \times pB_{z,t} \times nF_{z,t} \times 0.5)$$

The newly born piglets are subject to early mortality, and only those surviving the first three months of life will be counted

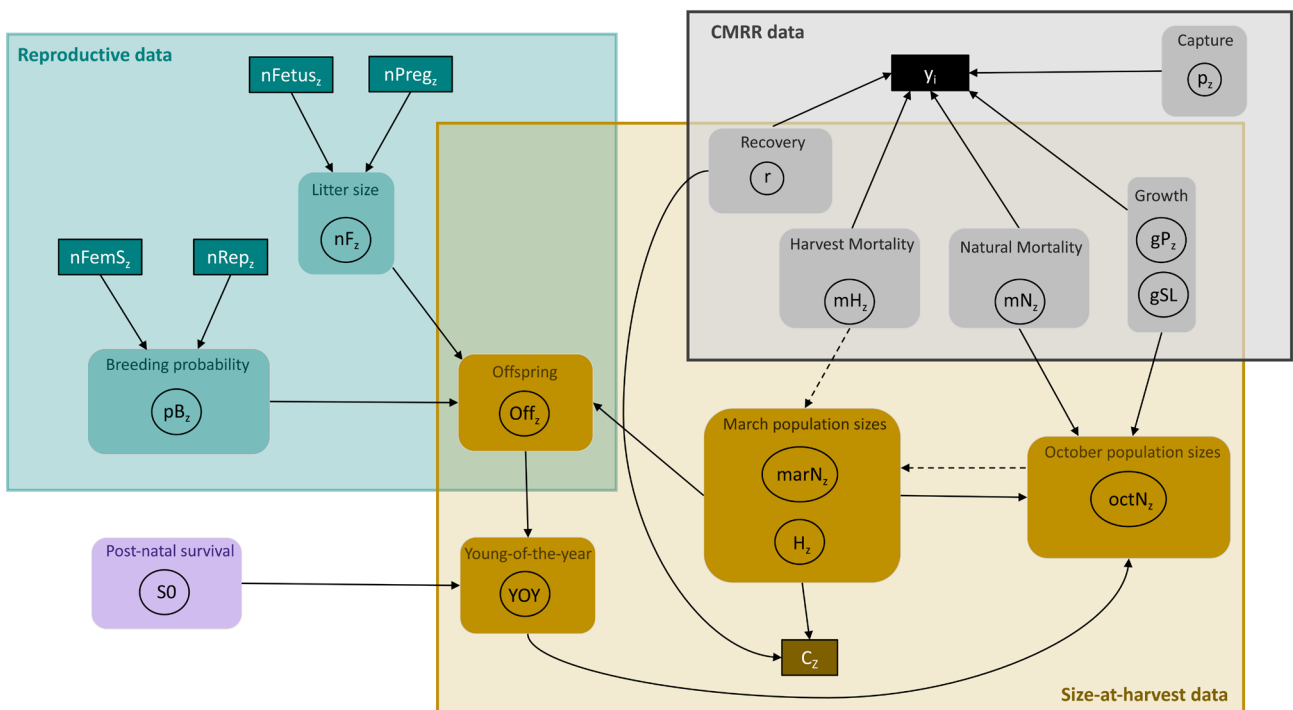


Figure 2. Directed acyclic graph (DAG) of the IPM. Squares represent data nodes, circles represent the parameters to be estimated. The index z takes values of S , M and L for small, medium and large size classes respectively. Time indices are omitted for simplicity. Solid arrows represent dependencies within the same time-step while dashed arrows represent dependencies between time-steps (time t to $t+1$). See Table 1 for parameter and data node definitions.

Table 1. Notation and biological meaning of data, latent states and parameters.

Demographic and observation parameters	
$pB_{z,t}$	Breeding probability of females in size class z in year t
$nF_{z,t}$	Litter size of females in size class z in year t
$S0_t$	Postnatal survival in year t
$gP_{z,t}$	Growth probability of size-class z females in year t
gSL_t	Probability of a small female to grow into the large size class in year t
$sN_{z,t}$	Natural survival probability of size-class z females from March to October of year t ($= e^{-mN_{z,t}}$)
$mN_{z,t}$	Natural mortality hazard rates of size-class z females from March to October of year t
$dN_{z,t}$	Natural mortality probability of size-class z females from March to October of year t ($= 1 - sN_{z,t}$)
$sH_{z,t}$	Hunting survival probability of size-class z females from October of year t to March of year $t+1$ ($= e^{-mH_{z,t}}$)
$mH_{z,t}$	Hunting mortality hazard rates of size-class z females from October of year t to March of year $t+1$
$dH_{z,t}$	Hunting mortality probability of size-class z females from March to October of year t ($= 1 - sH_{z,t}$)
$p_{z,t}$	Recapture probability of size-class z females in year t
r_t	Recovery probability for females of any size during the hunting season from October of year $t-1$ to March of year t
Population-level quantities	
$H_{z,t}$	Number of size-class z females shot between October of year $t-1$ and March of year t
$marN_{z,t}$	Number of size-class z females alive in March of year t
$Off_{z,t}$	Number of offspring produced by size-class z females in year t
YOY_t	Total number of young-of-the-year (i.e. offspring that survived over the first three months)
$octN_{z,t}$	Number of size-class z females alive in October of year t
Observational data	
$C_{z,t}$	Number of size-class z females reported as shot between October of year $t-1$ and March of year t
$nRep_{z,t}$	Number of reproductive size-class z females reported as shot between October of year $t-1$ and March of year t (i.e. females in oestrus, having ovulated or pregnant)
$nFemS_{z,t}$	Number of size-class z females reported as shot between October of year $t-1$ and March of year t for which reproductive status has been assessed
$nFetus_{z,t}$	Number of fetuses counted in pregnant size-class z females reported as shot between October of year $t-1$ and March of year t
$nPreg_{z,t}$	Number of pregnant size-class z females reported as shot between October of year $t-1$ and March of year t
$Y_{i,1:T}$	Multistate capture history of individual i over from the first (1) to the last (T) year of the study period

among the young-of-the-year (YOY) and recruited into the population. This postnatal survival $S0_t$ is described as a binomial process:

$$YOY_t \sim \text{Binomial}(\text{sum}(Off_{z,t}), S0_t)$$

Next, each individual has a chance to either remain in the current size class or grow to any larger size class with a growth probability $gP_{z,t}$. No backward transitions towards lighter size classes was ever observed in the studied population. For small individuals, $gP_{S,t}$ is the probability of growing either into the medium or the large size class. Given a small individual grows to a larger class, the probability of immediately growing to the large class is gSL_t . For medium individuals, $gP_{M,t}$ is the probability of becoming large. Large individuals cannot grow any larger. We denote the numbers of individuals growing from any size class z to any other size class z' as $G_marN_{z,z',t}$. The growth process can be summarized using the following deterministic model:

$$G_marN_{z,z',t} = \begin{bmatrix} 1 - gP_{S,t} & gP_{S,t}(1 - gSL_t) & gP_{S,t}gSL_t \\ 0 & 1 - gP_{M,t} & gP_{M,t} \\ 0 & 0 & 1 \end{bmatrix} \times \begin{bmatrix} marN_{S,t} + YOY_t \\ marN_{M,t} \\ marN_{L,t} \end{bmatrix}$$

In our IPM, we accounted for demographic stochasticity growth outcomes by formulating the above model using (sequential) binomial trials (see model code for details of implementation).

Following growth, the population experiences a non-harvest season lasting roughly from March to the end of September. During this season, individuals in any size class z may die from natural mortality causes (probability $1 - sN_{z,t}$) or survive with probability $sN_{z,t}$ ($= e^{-mN_{z,t}}$, where $mN_{z,t}$ is the natural mortality hazard rate, Ergon et al. 2018) to early October:

$$octN_{z,t} \sim \text{Binomial}(\text{sum}(G_marN_{z,z',t}), sN_{z,t})$$

Note that since growth is assumed to happen prior to the non-harvest season, individual survival probabilities correspond to the newly attained size class (post-growth). The remainder of the year (from October of year t to March of year $t+1$) constitutes the hunting season. Since our study population is heavily hunted, we assumed that natural mortality during the hunting season was negligible, and survival through the hunting season ($sH_{z,t}$) therefore depends entirely on hunting mortality ($sH_{z,t} = e^{-mH_{z,t}}$, where $mH_{z,t}$ is the hunting mortality hazard rate). The population present in March of year $t+1$

is therefore made up of all individuals that were not killed during the hunting season:

$$marN_{z,t+1} \sim \text{Binomial}(octN_{z,t}, sH_{z,t})$$

By estimating the number of survivors during the hunting season and assuming all mortality is due to hunting, we can further quantify the true number of size-class z individuals that died due to hunting in the time interval $t \rightarrow t+1$ as $H_{z,t+1} = octN_{z,t} - marN_{z,t+1}$.

The above stepwise formulation of the population model can also be summarized into and represented by a standard matrix population model (Caswell 2001) and the corresponding projection matrix is given in the Supporting information.

We built this IPM assuming a closed population (no immigration/emigration) as the dispersal probability for female wild boar is generally very low (Truvé and Lemel 2003, Keuling et al. 2010) and the home range of any female much smaller than the studied forest (Saïd et al. 2012).

Size-at-harvest data likelihood

Size-at-harvest data $C_{z,t}$ consisted of the annual numbers of size-class z females shot and reported by hunters, with index t indicating the hunting season from October in year $t-1$ to March in year t . As such, these data indirectly contain information about population size and take on the role population counts fulfill in traditional IPMs. We formulated the likelihood for these data as a state-space model (de Valpine and Hastings 2002, Conn et al. 2008), which links a process model (i.e. the previously described size-class-structured population model) and an observation model. The observation model describes the link between the size-at-harvest data $C_{z,t}$ and the true number of females shot by hunters in the population ($H_{z,t}$) (yellow part, Fig. 2). In order for a shot individual of size z to appear in $C_{z,t}$, it needs to be reported (with probability r_t). $C_{z,t}$ can therefore be described as a binomial random variable:

$$C_{z,t} \sim \text{Binomial}(H_{z,t}, r_t)$$

Note that since reporting of shot wild boars is mandatory in the study area, we expected r_t to be close to 1 (as previously estimated in Gamelon et al. 2011) and assumed it to be independent of body size class.

Capture-mark-recapture-recovery (CMRR) data likelihood

CMRR data were analyzed using a multistate model (reviewed by Lebreton et al. 2009) that allows separating estimation of size-class-specific parameters associated with growth, natural mortality and hunting mortality (Lebreton et al. 1999, Gamelon et al. 2012). We described the fate of a marked individual i using seven states. States 1, 2 and 3 were 'alive' in the small, medium and large body mass classes, respectively. Similarly, states 4, 5 and 6 were individuals 'recently shot' in

the three body mass classes. Finally, state 7 collected all individuals that either 'recently died from natural causes' or had been 'dead' for more than one year. Annual transitions among these states depended on size-class- and year-specific probabilities of growth ($pG_{z,t}$ and pSL_t), survival/mortality during the non-hunting season ($sN_{z,t} = e^{-mN_{z,t}}$) and survival/mortality during the hunting season ($sH_{z,t} = e^{-mH_{z,t}}$) as depicted in Fig. 1 (solid arrow transitions only). Individual capture histories $y_{i,1:T}$ (where $1:T$ is the duration of the study period) were then modelled as the outcome of observing individuals in their respective states with size-class-specific capture probabilities $p_{z,t}$ for states 1–3 and size-class-independent reporting probability r_t for states 4–6 (state 7 was unobservable). We provide the full state transition and observation matrices in the Supporting information and refer to the reader to Chapter 9 in Kéry and Schaub (2012) for the details of the Bayesian implementation of multistate models.

Reproduction data likelihoods

Necropsies of shot wild boar females allowed us to estimate annual size-class-specific breeding probability ($pB_{z,t}$) and litter size ($nF_{z,t}$). Breeding probability corresponds to the proportion of shot size z females that showed signs of reproductive activity between October of year $t-1$ and March of year t ($nRep_{z,t}$) relative to all shot females for which reproductive status could be assessed ($nFemS_{z,t}$) via a binomial likelihood:

$$nRep_{z,t} \sim \text{Binomial}(nFemS_{z,t}, pB_{z,t})$$

The total number of fetuses counted in the uteri of pregnant females with size z shot between October of year $t-1$ and March of year t ($nFetus_{z,t}$), on the other hand, can be modelled as a Poisson random variable with an expected value equal to the product of the number of all shot females with size z that were pregnant ($nFemS_{z,t}$, which is a subset of reproductively active females $nRep_{z,t}$) and the size-specific average litter size:

$$nFetus_{z,t} \sim \text{Poisson}(nFemS_{z,t} \times nF_{z,t})$$

By sharing the parameters $pB_{z,t}$ and $nF_{z,t}$ between the population model and the likelihoods for reproduction data from shot females, we assume that average breeding probability and litter size are identical for females that are shot before and that survive to give birth (i.e. the reproductive status does not affect hunting mortality).

Among-year variation in demographic parameters and detection parameters

We accounted for temporal variation in all demographic parameters, as well as recapture and recovery probabilities, by including normally distributed random-year effects on the relevant link scale according to the following equation:

$$\text{link}(X_{z,t}) = \text{link}(\mu_z^X) + \varepsilon_t^X$$

Here, $X_{z,t}$ is the value of demographic parameter X for size z females in year t , μ_z^X is the average size-class-specific X over time (intercept) and ε_t^X is the random effect on X in year t . The link scales were log for early, natural and hunting mortality hazard rates (and, by extension, loglog for the corresponding survival probabilities) and litter size, and logit for growth, recapture, and recovery probabilities. We used the same temporal random effects for modelling among-year variation in a given parameter for all three size classes, assuming that good environmental conditions would be similarly beneficial for females of all size classes and that poor conditions would similarly negatively affect females of all size classes.

Additionally, previous research has shown that the availability of acorns, from October to February, can substantially influence both the overall proportion and size distribution of breeding females (Servanty et al. 2009, Gamelon et al. 2017, 2021, Touzot et al. 2020). In the case of breeding probability, we therefore accounted for this by letting the intercept depend not only on size class, but also on the combination of size class and acorn availability. The latter was defined using a categorical variable with three levels: N = no acorn, A = average availability of acorns, H = high availability of acorns/mast seeding (see Servanty et al. 2009, Gamelon et al. 2017, Touzot et al. 2020 for a detailed description of the three categories of acorn mast years). The breeding probability model thus included a categorical interaction between size class and acorn availability.

Model implementation

Assuming independence among the datasets, the likelihood of the IPM is the product of the likelihoods for the different datasets (Besbeas et al. 2002, Kéry and Schaub 2012): size-at-harvest data, CMRR data and reproduction data. Since some individuals are part of several datasets, the independence assumption is not fully met in our case. However, this is unlikely to cause a substantial bias in results as recent simulation studies have shown that violation of the independence assumption has little impact on IPM estimation and performance (Abadi et al. 2010a, Plard et al. 2019a, Weegman et al. 2021). We fit the IPM in a Bayesian framework using NIMBLE (ver. 0.9.1 of the nimble R package, de Valpine et al. 2017). We used vague priors for all parameters (code), and initial values for all nodes were simulated manually prior to running the model to avoid initialization problems. Parameters were estimated by running four Markov chain Monte Carlo (MCMC) chains of 150 000 iterations (the first 70 000 of which were discarded as burn-in), which were subsequently thinned by a factor 10. We used visual inspection of the MCMC chains and the Brooks and Gelman diagnostic \hat{R} to assess model convergence (Brooks and Gelman 1998). All analyses and plotting were done in R ver. 4.0.2 (<www.r-project.org>).

Model assessment

We used three complementary approaches to assess the ability of our IPM to provide biologically relevant estimates of

demographic parameters and population dynamics. First, we checked evidence for major lack of fit by comparing our IPM's predictions of population size, harvest numbers and reproductive parameters to observed data (Supporting information). Second, we checked posterior overlaps of demographic parameters estimated from the IPM to estimates obtained from separate, independent analysis of CMRR and reproduction data to test for potential major discrepancies among data sources included in the IPM (Supporting information). Third, we determined the IPM's ability to make biologically realistic short- to mid-term population forecasts using two simulation approaches: 1) stochastic matrix projections using posterior samples to determine realism of population size forecasts and; 2) continuation of MCMC predictions for an additional three years (2017–2019) and comparison of predicted versus realized number harvested in those years (Supporting information). In addition to the three types of model assessment, we also tested whether estimates were robust to the model's assumption about the timing of life history events (growth prior to the non-hunting season, Supporting information). Background, implementation details and results for each part of model assessment are provided in Supporting information.

Results

All four MCMC chains reached convergence. In the following, we present estimates of our IPM for parameters associated with demographic rates, population-level properties and detection, as well as conclusions from model assessment. Numerical results are presented as posterior median [95% credible interval]. A visualization of posterior distributions for all parameters can be found in the Supporting information.

Natural mortality, hunting mortality and postnatal survival

Both natural and hunting mortalities varied among size classes (Fig. 3A, D) and across time, the latter more so for hunting than natural mortality (Fig. 3A, C). Natural mortality hazard rate was estimated at a time-average of 0.43 [0.29, 0.59], 0.04 [0.00, 0.22] and 0.15 [0.07, 0.26] for small, medium and large females, respectively. The resulting probabilities of dying from natural causes between March and October ($dN_{z,t} = 1 - sN_{z,t} = 1 - \exp(-mN_{z,t})$) were 0.35 [0.25, 0.44], 0.04 [0.00, 0.20] and 0.14 [0.08, 0.22] for the three size classes, and therefore highest for small individuals, followed by large and finally medium ones (Fig. 3D). Hunting mortality probability ($dH_{z,t} = 1 - sH_{z,t} = 1 - \exp(-mH_{z,t})$), on the other hand, was highest for small females (0.85 [0.80, 0.91]) and lowest for large females (0.24 [0.21, 0.29]), with medium females falling in between (0.47 [0.40, 0.56]) (Fig. 3A). The corresponding hunting mortality hazard rates were 1.93 [1.60, 2.42], 0.63 [0.52, 0.83] and 0.27 [0.23, 0.34]. Hunting mortality was therefore substantially higher than natural mortality for all size classes. Postnatal survival

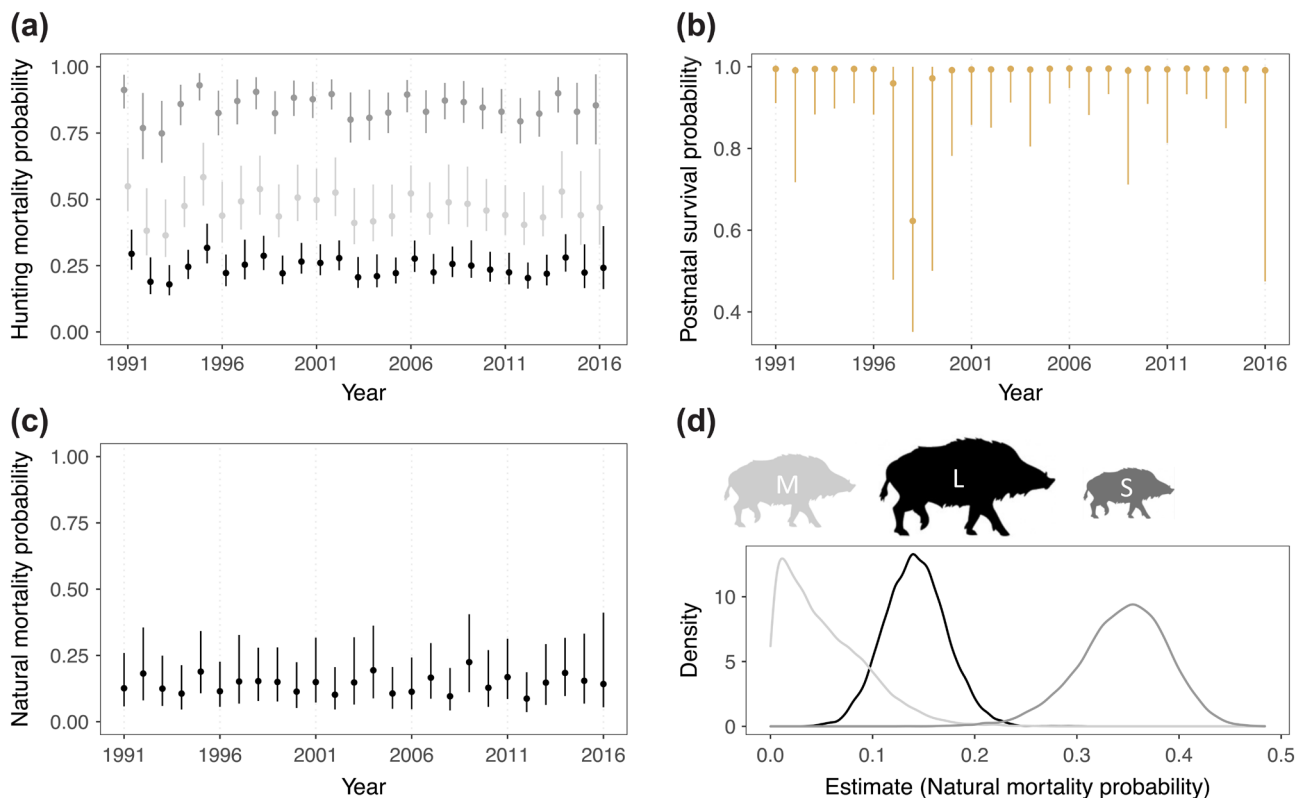


Figure 3. Posterior medians and associated 95% credible intervals of (A) annual hunting mortality probability dH for each body mass class (small = grey, medium = light grey and large = black), (B) postnatal survival probability and (C) annual natural mortality probability dN for the large class. (D) Posterior distribution of time-average natural mortality probability for the three body mass classes.

(i.e. the probability of surviving from birth to weaning (i.e. at about three months of age), S_0) was estimated at a time-average of 0.99 [0.96, 1.00] but uncertainty was high in certain years (Fig. 3D).

Growth transition probabilities among body mass classes

Small females had a time-average probability of 0.30 [0.23, 0.40] to grow into the medium size class ($\mu_S^{gP} \times (1 - \mu_S^{gSL})$) and of 0.07 [0.03, 0.14] to grow into the large size class ($\mu_S^{gP} \times \mu_S^{gSL}$) within a year. They were therefore more likely to remain small than to grow. Medium-sized females were also more likely to stay in their current size class, with a probability of growing large of 0.45 [0.30, 0.63]. All growth probabilities varied considerably across years (Supporting information).

Reproductive parameters

Breeding probabilities varied substantially across years (Fig. 4A) and increased with body size, with a time-average of 11 [5, 26] % of small, 55 [39, 80] % of medium and 70 [53, 86] % of large females reproducing in a year with average acorn production (Fig. 4B). Breeding probabilities were lower in years with low acorn abundance and higher in acorn mast years (high acorn abundance), and the effect of acorn

abundance was more pronounced for small- and medium-sized females than large ones (Fig. 4B). Litter size, on the other hand, varied very little over time (Fig. 4C) but also increased with body size: small, medium and large females produced litters of on average 3.85 [3.36, 4.57], 4.84 [4.62, 7.15] and 6.42 [6.15, 6.79] piglets, respectively.

Detection probabilities

Recapture probabilities depended strongly on body size and were highest for small females at 0.68 [0.45, 0.91] and lowest for large females at 0.04 [0.02, 0.10], with medium females falling in between at 0.23 [0.15, 0.40] (Supporting information). Size-independent hunting reporting probability (recovery) was consistently high and estimated at a time-average of 0.98 [0.89, 1.0] (Supporting information).

Population size and structure

Total population size increased over the first five years of the study period, then stabilized around an average of 280 [228, 378] females in March and 587 [521, 734] in October (Fig. 5). Population size was highest between years 2007 and 2008, with 797 [728, 954] females present in October 2007 and 361 [300, 477] in the subsequent March. In general, the population contained a high proportion of large females in

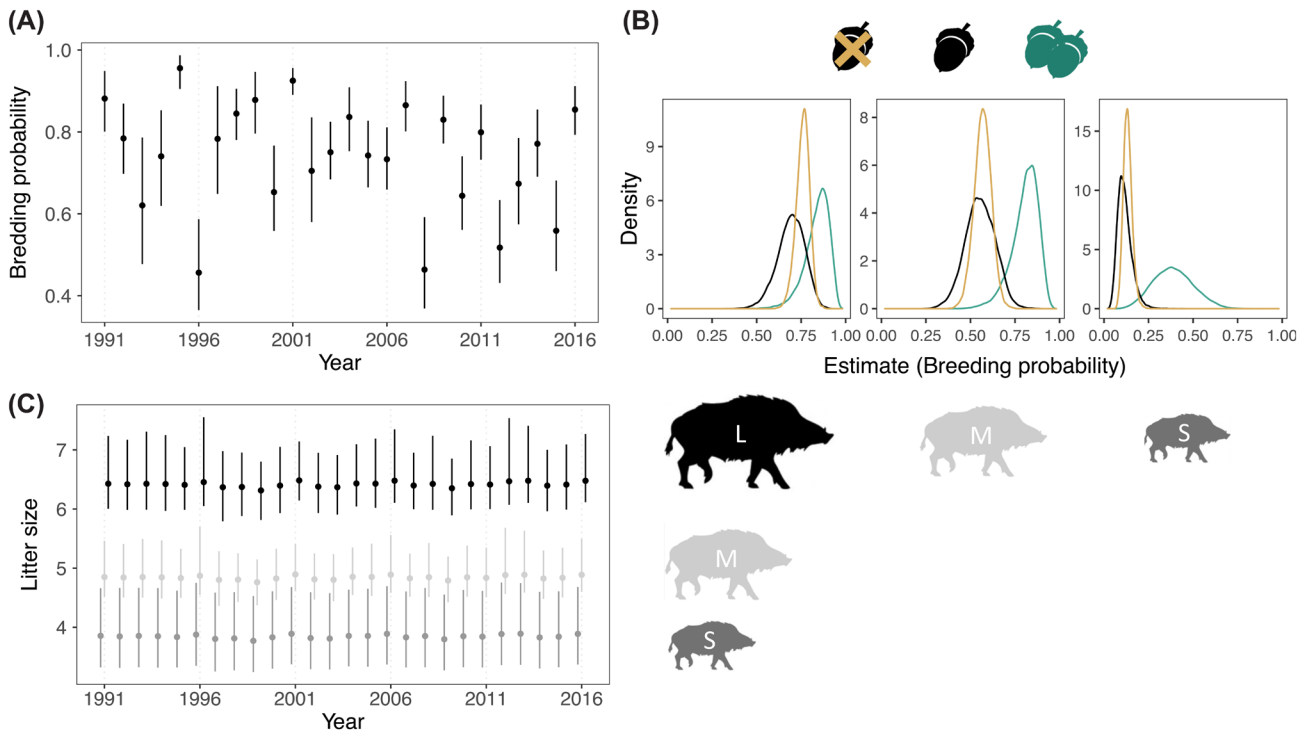


Figure 4. Reproductive parameters estimated from the IPM. (A) Posterior medians and associated 95% credible intervals of annual breeding probabilities for the large size-class. (B) Posterior distributions of average breeding probabilities for the three body mass classes in years with low (yellow), average (black) and high (turquoise) acorn abundance. (C) Posterior medians and associated 95% credible intervals of annual litter size for the three body mass classes.

March, while in October, the size distribution was more balanced (Supporting information). The harvest, on the other hand, was dominated by small individuals (Supporting information). The estimated numbers of harvested individuals

varied across years from a minimum of 98 [95, 202] in the hunting season 1992–1993 to a maximum of 429 [421, 581] in 2007–2008, corresponding to years with relatively low/high harvest mortality (Fig. 3A) and population size (Fig. 5).

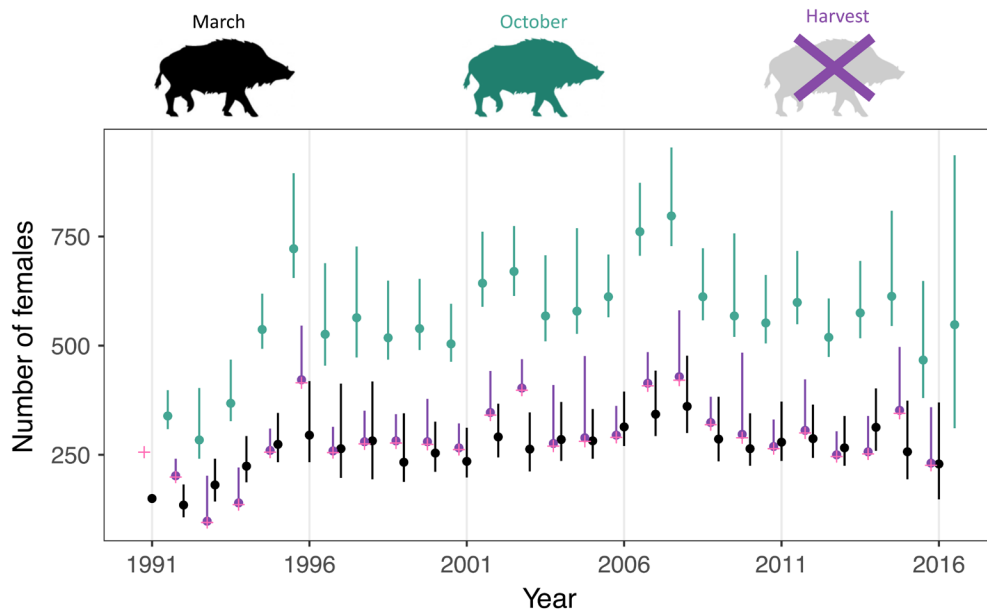


Figure 5. Estimated numbers of female wild boar in March (black), in October (turquoise) and in the harvest (purple). Estimates are plotted as posterior medians (dots) and corresponding 95% credible intervals (vertical lines). Pink crosses represent raw data on counts of harvested females.

Model assessment

Predictions of population size and the number of harvested individuals were closely associated with observed data (Fig. 5), and the same was the case for model estimates of reproductive parameters (breeding probability and litter size in the Supporting information). Posterior distributions of the majority of demographic parameters from the IPM largely overlapped with posteriors obtained from separate analyses of CMRR and reproduction data (Supporting information), providing no evidence for severe lack of fit. Smaller posterior overlap still occurred for a subset of parameters associated with the largest size class, namely the probability of a small female to grow large and subsequent natural and hunting mortality of large individuals. Stochastic projections using matrices parameterized with posterior means of demographic parameters estimated by the IPM produced biologically realistic short- to mid-term population trajectories (Supporting information). None of the simulated populations decreased substantially within a 10-year period, but notably, a few simulations predicted substantial population increase to over 750 females. Furthermore, the IPM produced predictions that matched observed numbers of harvested females for the 2017–2018, 2018–2019 and 2019–2020 hunting seasons (size-at-harvest data that were not part of parameter estimation can be found in the Supporting information). Finally, whether growth was modelled to happen prior to or after the non-hunting season did not substantially affect estimates or conclusions (Supporting information). The results of model assessment and tests are detailed further in the respective sections in Supporting information.

Discussion

We here developed an IPM that makes efficient use of data commonly collected for exploited populations, i.e. counts, body size/mass and assessment of reproductive status of females shot by hunters. Through integrated analysis of such data with CMRR data, this model provides estimates of key demographic parameters – including some that cannot be estimated using independent analyses – while fully accounting for uncertainty. Using a wild boar population as a case study, we demonstrate that this framework is a relevant tool to obtain a comprehensive picture of the dynamics of exploited populations, particularly those with missing data on age.

A comprehensive picture of population dynamics

Through integrated analysis of CMRR data, reproductive data and size-at-harvest data, our IPM offers a comprehensive picture of the demographic mechanisms that prevented collapse of the Châteauvillain-Arc-en-Barrois wild boar population despite an unusually high hunting pressure over the last 25 years (Toïgo et al. 2008). We showed that hunting mortality was size-specific, and highest for small females. Across size

classes, hunting was the primary cause of death and hunting mortality clearly outweighed natural mortality (Fig. 3). Low natural mortality is common among ungulate species, for which average natural adult survival probability often exceeds 0.90 for females (Gaillard et al. 2000). Our finding regarding the relative importance of hunting and natural mortalities are in accordance with both other hunted wild boar populations and previous conclusions for this particular population (reviewed by Toïgo et al. 2008, Gamelon et al. 2011, Gamelon 2020).

Wild boar females in the focal population are highly fecund, being able to produce large litters (Fig. 4C) as early as their first year of life (Servanty et al. 2009) and at a body mass below 30 kg (i.e. small mass-class). Together with reduced survival due to hunting, this leads to a short generation time, i.e. a low mean age of mothers at first reproduction (Gaillard et al. 2005, 2016). Generation time is around two years for hunted wild boar, whereas it is close to six years for other, similar-sized ungulates (Servanty et al. 2011, Gamelon et al. 2021). This unusual life history (Focardi et al. 2008) is reflected in our estimates of a substantial portion of small and medium-sized individuals breeding (particularly under favorable environmental conditions, Fig. 4B). The resulting population dynamics are characterized by a fast turnover of individuals (Supporting information), and this explains why the number of individuals in the population did not decrease drastically during the study period despite the high hunting pressure (Fig. 5).

Demographic parameters of many seed consumer species, such as wild boar, depend on mast seeding (reviewed by Yang et al. 2008, Bogdziewicz et al. 2016, Gamelon et al. 2021). Mast seeding events result in pulsed resource availability, characterized by intermittent production of large seed crops synchronized at the tree population level (Ostfeld and Keesing 2000). Acorn mast events vary in intensity and frequency over years and are major determinants of breeding proportions in wild boar (Servanty et al. 2009, Gamelon et al. 2017, Touzot et al. 2020). Accordingly, we found a marked year-to-year variation in the proportion of breeding females (Fig. 4A) and a positive effect of acorn availability on the breeding probability for all size classes (Fig. 4B).

Substantial among-year variation was also evident for growth parameters, i.e. the probabilities for a female to grow into a heavier body mass class (Supporting information). While previous studies did not find any effect of acorn availability on growth patterns in this population (Touzot et al. 2020, Gamelon et al. 2021), a large body of empirical evidence shows that increasing population density is generally associated with reduced body mass in large herbivores (Bonenfant et al. 2009). Fluctuations in the strength of density dependence could explain such among-year variation in transition probabilities among body mass classes. Weather conditions (e.g. temperature) can also influence the probability for a female to reach a heavier body mass class during the year, especially for small females (Veylit et al. 2020). Since mortality (from both hunting and natural causes) and reproductive output vary substantially according to body mass

(Fig. 3, 4), factors affecting transitions between body mass classes may be crucial for population dynamics and remain to be carefully explored.

Estimates for demographic parameters hard to measure in the field

Despite being useful for making relevant management decisions, the total size of exploited populations is often unknown. The presented IPM allowed us to estimate the annual numbers and size-class-distributions of alive females, both before and after the hunting season, even in absence of detailed count surveys of the population (Fig. 5, Supporting information). Importantly, the Bayesian approach further provided not only single population size estimates, but full quantification of uncertainty around these estimates, which can be crucial when determining population status and harvest strategies (Williams et al. 2002).

Integrated analysis of multiple data sources also allowed us to get annual estimates of postnatal survival, a parameter often tricky to measure empirically. For instance, Baubet et al. (2009) aimed to tag piglets inside their birth nest to assess survival from birth to weaning (i.e. at about three months of age), but failed in this task not only because of difficulties to locate birth nests, but also because piglets were often abandoned after tagging. While IPMs can be relevant tools for estimating parameters hard to measure in the field, it is important to keep in mind that such parameters, which are not (or only weakly) identifiable in independent analyses of components datasets, should be interpreted with caution (Riecke et al. 2019). Violation of model assumptions, unaccounted-for variation and lack-of-fit of an IPM may propagate bias into such 'free' parameters, potentially resulting in misleading conclusions. This was likely the case for the high estimated value of postnatal survival. Our IPM estimated this parameter close to one, which is substantially higher than previously assumed based on expert opinion (0.75, Gamelon et al. 2012, Touzot et al. 2020). Since three complementary model assessment methods did not provide evidence for severe lack of fit of the IPM (Supporting information), this discrepancy does not invalidate the overall results of our analysis. On the contrary, the upward bias of our estimate of postnatal survival is informative on its own, indicating that there likely are parts of the model that do not account sufficiently for variation and/or additional processes. Potential causes for overestimation of postnatal survival could involve unaccounted-for immigration, underestimation of reproductive output or bias in some growth estimates. While the first option seems unlikely given the high degree of female philopatry in wild boar (Truvé and Lemel 2003, Keuling et al. 2010) and the large size of our study area, female reproductive output is likely underestimated in our model due to individual heterogeneity in reproductive timing. Indeed, some females assigned with a non-reproductive status might have been harvested before becoming reproductively active (Servanty et al. 2009). Moreover, the fact that the model assumed equal growth rates for young-of-the year and

> 1 year-old small individuals may have led to bias growth parameter estimate. Perceived bias in estimates of a 'free' parameter in an IPM, here postnatal survival, can therefore provide valuable insights into what processes and parts of the life cycle warrant further study – and, potentially, data collection – to improve biological understanding in future studies.

A framework based on data commonly collected in exploited populations

Models designed to assess interactive effects of harvest and other stressors on population dynamics and predict sustainability of harvest management require detailed information on demographic parameters. More often than not, demographic data are costly and sometimes logistically challenging to come by, and therefore limited. The IPM we propose here uses data integration to overcome data limitations, and is therefore not solely useful to understand the dynamics of this particular wild boar population, but potentially applicable to many other exploited populations in both terrestrial and marine environments. Many commercially important marine fish species, for instance, are subject to strong harvesting pressure (Pauly et al. 2002, Hutchings and Reynolds 2004). Hence, IPM approaches can be suitable tools for both modelling their dynamics (Hutchings and Myers 1994, Myers et al. 1997) and predicting population collapses (Maunder 2004, Saunders et al. 2018). Such IPMs used in fisheries research are usually based on age-structured population models (reviewed by Maunder and Punt 2013). However, fish are indeterminate growers, and their demographic parameters are often strongly dependent on body size. Size or body mass distributions may therefore be more relevant for population dynamics than age distributions (Sauer and Slade 1987). IPMs structured by body mass instead of age may also be more practical to implement as collecting data on body mass of harvested animals is less challenging and more affordable than collecting data on age.

More generally, our framework adds to the spate of studies that have recently flourished in the literature and highlight that trait-based approaches (such as those based on body mass) and demographic approaches are intertwined (Salguero-Gómez et al. 2018, Plard et al. 2019a, Smallegange and Berg 2019). Trait-based demographic approaches usually treat body mass as a continuous variable, and population models coupled with them – for example integral projection models – are therefore structured by continuous traits (Ellner and Rees 2006, Coulson 2012). Recently, continuous trait structure has also been incorporated into integrated approaches using IPMs (Plard et al. 2019b), providing unique insights into how individual differences shape population dynamics. Here, we provide an integrated model for exploited populations structured by discrete body mass classes, which is practical in a management context in many cases for at least three reasons. First, body size classes may be relevant and suitable in practice. Specifically, harvest regulations that require hunters to target or avoid killing individuals of a certain body mass are only feasible if hunters can assess the size of the

target individual prior to the kill, when it is likely moving. While measuring body mass at sight is impossible, assessing which body mass class an animal falls into is doable, particularly when this assessment is aided by knowledge of the social structure and/or phenotypic characteristics. Management recommendations based on body mass classes – instead of exact body mass itself – may thus be more realistic to implement in the field. Second, pooling individuals into size classes may alleviate some challenges associated with heterogeneous measurement error in harvest data collected by citizens (i.e. hunters, Bonney et al. 2014). While body mass of harvested boars in the present study was collected by trained scientists following a specific weighing protocol, information on harvested individuals is collected by the hunters themselves in many other systems. A large number of observers employing different measurement methods can result in heterogeneous measurement error that can be challenging to account for when modeling body size as a continuum, making the use of discrete body size classes more practical in some cases. Third, and as mentioned above, demographic parameters of a variety of exploited species are strongly dependent on body size and it is thus particularly relevant to use size-class-structured models. This is the case for wild boar but also for alligators (Dunham et al. 2014), turtles (Crouse et al. 1987), and many fish species, to name just a few examples. For species in which body size is not a major structuring factor of population dynamics (e.g. in adult birds), our framework can be extended to other traits that are more closely associated with variation in demographic rates (e.g. parasite load, social status). We therefore argue that size-class-structured IPMs, like the one proposed in this study, may be widely applicable for modelling the dynamics of exploited populations for which exact trait measures are not available and for which age is either challenging to estimate and/or weakly associated with demographic variation.

Limitations and outlook

When assessing the performance of our model, we found that, relative to an independent analysis, the IPM predicted a higher probability of small individuals to grow into the large size class, and large individuals to be more likely to die from natural causes and less likely to die due to hunting (Supporting information). One explanation is that individual differences in body size also affect parameters that are modelled as size-independent, in this case reporting (recovery) rate. In this population, hunters are discouraged from shooting large females (> 50 kg). If this shooting rule leads to a decrease in their likelihood to report an (accidental) kill of such a female, particularly if the female was not marked (i.e. not part of the mark–recapture–recovery study), this would result in the observed downward bias in hunting mortality and upward bias in natural mortality (and possibly also growth) for the largest females. Preliminary analyses allowing for size-dependence in reporting rates indicate that this may indeed be the case, and potential sources of heterogeneity in reporting rates therefore warrant attention in future studies

(Supporting information). Analogously, our framework could be extended to assess the importance of other sources of individual heterogeneity to population dynamics. For example, the collection of wings of shot ducks makes it possible to differentiate both between sexes and between juvenile and adult individuals in the harvest (Péron et al. 2012, Koons et al. 2017, Raftovich et al. 2018). Thus, including age-class and sex-structure into IPMs may shed more light on the dynamics of exploited populations. Stage-structured IPMs, such as the one presented here, are indeed highly versatile and allow modelling populations structured by a variety of individual traits, making them attractive not only for the study of animals with a wide range of life-history strategies, but potentially also for plants which often have complex life cycles with many different stages (Caswell 2001, Salguero-Gómez et al. 2016). Depending on study species and focal individual trait, extensions to account for mortality causes other than harvest and natural may become relevant (e.g. mortality due to poisoning, Tenan et al. 2012).

Just as there is variety in which individual traits are crucial to population dynamics, there is variety in the types of data that may be available for a study species or population. In the IPM we built here for wild boar, a large amount of data on both recaptures and harvests of marked individuals (CMRR data) was central. However, we acknowledge that in the majority of exploited populations, such data may not be available. Nonetheless, the integrated approach may still be very relevant in studies of such populations, even in – and maybe especially because of – absence of long-term CMRR data. Nater et al. (in press), for example, have shown that IPMs can be used to gain detailed insights into the drivers of population dynamics even when data on marked individuals is available only for a handful of individuals and for part of a study period. Furthermore, the Bayesian implementation of IPMs allows including biological knowledge from alternative sources via informative priors to compensate for the lack of mark–recapture data. Natural mortality, in particular, often requires assumptions and/or informative priors, and these can be obtained from published studies on similar (non-exploited) populations, expert knowledge (Servanty et al. 2010), or using promising new approaches involving phylogenetic meta-analyses (Abadi et al. 2014, Porteus et al. 2018).

Finally, building an IPM with a relevant structure and fitting it to suitable data, as done here, is only a first step. It constitutes, for example, an ideal framework to quantify density dependence in both population dynamics and all underlying demographic rates (Gamelon et al. 2016, 2019b). This may be particularly relevant for exploited systems in which harvest itself is density-dependent and may further interact with other density-dependent factors (Boyce et al. 1999). Furthermore, once fitted, the IPM may lend itself to a variety of follow-up analyses with high relevance to population management. Retrospective perturbation analyses, such as transient life table response experiments, can be run on IPM outputs to determine the relative importance of different drivers of past population dynamics at the levels of demographic rates, population structure, trait dynamics and

environmental influences (Koons et al. 2016, 2017, Layton-Matthews et al. 2021). Future population dynamics, on the other hand, can be explored using prospective perturbation analyses, such as sensitivity analyses and scenario simulations, and with the IPM as the starting point of such analyses, forecasts can be made that fully reflect uncertainty, thus facilitating risk analysis by management authorities (Williams et al. 2002, Peeters et al. 2021).

Conclusions

Recent advances in methods for fitting statistical models have led to both an increase in and a diversification of population analyses combining different sources of demographic data. Here, we present an IPM that uses data commonly collected in exploited populations (i.e. harvest counts, CMRR data, reproductive data from necropsies, individual size measurements) but does not require information on individual age. Applied to a case study of a heavily hunted population of wild boar, this integrated analysis provides a comprehensive picture of the demographic mechanisms that have prevented its decline despite an exceptionally high hunting rate. We thus showcase the usefulness of stage-structured IPMs for estimating demographic parameters and population sizes, including uncertainty therein, and highlight their potential for guiding management decisions for exploited species.

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Author contributions

Marlène Gamelon and **Chloé R. Nater** contributed equally to this work. **Marlène Gamelon**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Project administration (lead); Writing – original draft (equal); Writing – review and editing (equal). **Chloé R. Nater**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Eric Baubet**: Data curation (equal); Resources (lead); Writing – review and editing (equal). **Aurélien Besnard**: Conceptualization (equal); Methodology (supporting); Writing – review and editing (equal). **Laura Touzot**: Data curation (equal); Writing – review and editing (equal). **Jean-Michel Gaillard**:

Conceptualization (equal); Writing – review and editing (equal). **Jean-Dominique Lebreton**: Conceptualization (equal); Methodology (supporting); Writing – review and editing (equal). **Olivier Gimenez**: Conceptualization (equal); Methodology (supporting); Writing – review and editing (equal).

Data and code availability

Code for fitting the IPM and producing the plots are available on GitHub: <<https://github.com/ChloeRN/WildBoarIPM>>. The file containing the processed data necessary to fit the model is available upon request from the corresponding author.

References

- Abadi, F. et al. 2010a. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. – *Ecology* 91: 7–14.
- Abadi, F. et al. 2010b. Estimation of immigration rate using integrated population models. – *J. Appl. Ecol.* 47: 393–400.
- Abadi, F. et al. 2014. Importance of accounting for phylogenetic dependence in multi-species mark–recapture studies. – *Ecol. Model.* 273: 236–241.
- Arnold, T. W. et al. 2018. Integrated population models facilitate ecological understanding and improved management decisions. – *J. Wildl. Manage.* 82: 266–274.
- Barker, R. J. and Kavalieris, L. 2001. Efficiency gain from auxiliary data requiring additional nuisance parameters. – *Biometrics* 57: 563–566.
- Baubet, E. et al. 2009. Tagging piglets at the farrowing nest in the wild: some preliminary guidelines. – *Acta Silv. Lign. Hung.* 5: 159–166.
- Besbeas, P. et al. 2002. Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. – *Biometrics* 58: 540–547.
- Black, B. A. B. A. et al. 2008. Establishing highly accurate production-age data using the tree-ring technique of crossdating: a case study for Pacific geoduck *Panopea abrupta*. – *Can. J. Fish. Aquat. Sci.* 65: 2572–2578.
- Bogdziewicz, M. et al. 2016. How do vertebrates respond to mast seeding? – *Oikos* 125: 300–307.
- Bonenfant, C. et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. – In: Caswell, H. (ed.), *Advances in ecological research*. Academic Press, pp. 313–357.
- Bonney, R. et al. 2014. Next steps for citizen science. – *Science* 343: 1436–1437.
- Boyce, M. S. et al. 1999. Seasonal compensation of predation and harvesting. – *Oikos* 87: 419–426.
- Brooks, S. P. and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. – *J. Comput. Graph. Stat.* 7: 434–455.
- Camilo, C. et al. 2007. Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing environmental warming. – *Proc. R. Soc. B* 274: 1023–1028.

- Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. – Sinauer Associates.
- Chen, S. et al. 2015. Human harvest, climate change and their synergistic effects drove the Chinese crested tern to the brink of extinction. – *Global Ecol. Conserv.* 4: 137–145.
- Clutton-Brock, T. and Sheldon, B. C. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. – *Trends Ecol. Evol.* 25: 562–573.
- Conn, P. B. et al. 2008. Bayesian analysis of wildlife age-at-harvest data. – *Biometrics* 64: 1170–1177.
- Conn, P. B. et al. 2009. Simulation performance of Bayesian estimators of abundance employing age-at-harvest and mark-recovery data. – In: Thomson, D. L. et al. (eds), *Modeling demographic processes in marked populations*. Springer, pp. 965–986.
- Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in ecology. – *Oikos* 121: 1337–1350.
- Crouse, D. T. et al. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. – *Ecology* 68: 1412–1423.
- de Valpine, P. and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. – *Ecol. Monogr.* 72: 57–76.
- de Valpine, P. et al. 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. – *J. Comput. Graph. Stat.* 26: 403–413.
- Dunham, K. et al. 2014. A stage-based population model for American alligators in northern latitudes. – *J. Wildl. Manage.* 78: 440–447.
- Ellner, S. P. and Rees, M. 2006. Integral projection models for species with complex demography. – *Am. Nat.* 167: 410–428.
- Ergon, T. et al. 2018. The utility of mortality hazard rates in population analyses. – *Methods Ecol. Evol.* 9: 2046–2056.
- Fieberg, J. R. et al. 2010. Integrated population modeling of black bears in Minnesota: implications for monitoring and management. – *PLoS One* 5: e12114.
- Focardi, S. et al. 2008. Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. – *J. Mammal.* 89: 1113–1123.
- Gaillard, J.-M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – *Annu. Rev. Ecol. Syst.* 31: 367–393.
- Gaillard, J.-M. et al. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. – *Am. Nat.* 166: 119–123.
- Gaillard, J.-M. et al. 2016. Axes of variation in life histories. – In: Kliman, R. M. (ed.), *Encyclopedia of evolutionary biology*. Elsevier, pp. 312–323.
- Gamelon, M. 2020. Hunting, predation and senescence in boars. – In: Rattan, S. I. S. (ed.), *Encyclopedia of biomedical gerontology*. Elsevier Academic Press, pp. 251–257.
- Gamelon, M. et al. 2011. High hunting pressure selects for earlier birth date: wild boar as a case study. – *Evolution* 65: 3100–3112.
- Gamelon, M. et al. 2012. Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar. – *J. Appl. Ecol.* 49: 833–841.
- Gamelon, M. et al. 2016. Density dependence in an age-structured population of great tits: identifying the critical age classes. – *Ecology* 97: 2479–2490.
- Gamelon, M. et al. 2017. Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. – *Oecologia* 183: 1065–1076.
- Gamelon, M. et al. 2019a. Does harvesting amplify environmentally induced population fluctuations over time in marine and terrestrial species? – *J. Appl. Ecol.* 56: 2186–2194.
- Gamelon, M. et al. 2019b. Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size. – *Ecol. Lett.* 22: 797–806.
- Gamelon, M. et al. 2021. Effects of pulsed resources on the dynamics of seed consumer populations: a comparative demographic study in wild boar. – *Ecosphere* 12(5): e03395.
- Gauthier, G. et al. 2007. Population growth in snow geese: a modeling approach integrating demographic and survey information. – *Ecology* 88: 1420–1429.
- Hamlin, K. L. et al. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. – *J. Wildl. Manage.* 64: 441–449.
- Hutchings, J. A. and Myers, R. A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. – *Can. J. Fish. Aquat. Sci.* 51: 2126–2146.
- Hutchings, J. A. and Reynolds, J. D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. – *BioScience* 54: 297–309.
- Kaminski, G. et al. 2005. Life-history patterns in female wild boars *Sus scrofa*: mother–daughter postweaning associations. – *Can. J. Zool.* 83: 474–480.
- Kéry, M. and Schaub, M. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. – Academic Press.
- Keuling, O. et al. 2010. Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. – *Eur. J. Wildl. Res.* 56: 159–167.
- Koons, D. N. et al. 2015. Disentangling the effects of climate, density dependence, and harvest on an iconic large herbivore's population dynamics. – *Ecol. Appl.* 25: 956–967.
- Koons, D. N. et al. 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. – *Ecol. Lett.* 19: 1023–1031.
- Koons, D. N. et al. 2017. Understanding the demographic drivers of realized population growth rates. – *Ecol. Appl.* 27: 2102–2115.
- Layton-Matthews, K. et al. 2021. Environmental change reduces body condition, but not population growth, in a high-arctic herbivore. – *Ecol. Lett.* 24: 227–238.
- Lebreton, J. et al. 2009. Modeling individual animal histories with multistate capture–recapture models. – *Adv. Ecol. Res.* 41: 87–173.
- Lebreton, J.-D. 2005. Dynamical and statistical models for exploited populations. – *Aust. N. Z. J. Stat.* 47: 49–63.
- Lebreton, J.-D. et al. 1999. Competing events, mixtures of information and multistratum recapture models. – *Bird Study* 46: S39–46.
- Lee, A. M. et al. 2015. An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. – *Oikos* 124: 806–816.
- Lewis, J. S. et al. 2019. Historical, current and potential population size estimates of invasive wild pigs *Sus scrofa* in the United States. – *Biol. Invas.* 21: 2373–2384.
- Massei, G. et al. 2015. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. – *Pest Manage. Sci.* 71: 492–500.

- Maunder, M. N. 2004. Population viability analysis based on combining Bayesian, integrated, and hierarchical analyses. – *Acta Oecol.* 26: 85–94.
- Maunder, M. N. and Punt, A. E. 2013. A review of integrated analysis in fisheries stock assessment. – *Fish. Res.* 142: 61–74.
- Methot Jr., R. D. and Wetzel, C. R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. – *Fish. Res.* 142: 86–99.
- Morrongiello, J. R. et al. 2012. Aquatic biochronologies and climate change. – *Nat. Clim. Change* 2: 849–857.
- Myers, R. A. et al. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. – *Ecol. Appl.* 7: 91–106.
- Nater, C. R. et al. in press. Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate. – *Ecosphere*.
- Ostfeld, R. S. and Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. – *Trends Ecol. Evol.* 15: 232–237.
- Pauly, D. et al. 2002. Towards sustainability in world fisheries. – *Nature* 418: 689.
- Peeters, B. et al. 2021. Harvesting can stabilize population fluctuations and buffer the impacts of climate change.
- Peres, C. A. 2010. Overexploitation. – In: *Conservation biology for all*. Oxford Univ. Press, pp. 107–130.
- Péron, G. et al. 2010. Studying dispersal at the landscape scale: efficient combination of population surveys and capture–recapture data. – *Ecology* 91: 3365–3375.
- Péron, G. et al. 2012. Demographic response to perturbations: the role of compensatory density dependence in a North American duck under variable harvest regulations and changing habitat. – *J. Anim. Ecol.* 81: 960–969.
- Plard, F. et al. 2019a. Integrated population models: powerful methods to embed individual processes in population dynamics models. – *Ecology* 100: e02715.
- Plard, F. et al. 2019b. IPM2: toward better understanding and forecasting of population dynamics. – *Ecol. Monogr.* 89(3): e01364.
- Porteus, T. A. et al. 2018. Establishing Bayesian priors for natural mortality rate in carnivore populations. – *J. Wildl. Manage.* 82: 1645–1657.
- Raftovich, R. V. et al. 2018. Migratory bird hunting activity and harvest during the 2016–2017 and 2017–2018 hunting seasons. – U.S. Fish and Wildlife Service, Laurel, Maryland.
- Regehr, E. V. et al. 2017. Harvesting wildlife affected by climate change: a modelling and management approach for polar bears. – *J. Appl. Ecol.* 54: 1534–1543.
- Riecke, T. V. et al. 2019. Integrated population models: model assumptions and inference. – *Methods Ecol. Evol.* 10: 1072–1082.
- Ripple, W. J. et al. 2016. Bushmeat hunting and extinction risk to the world's mammals. – *R. Soc. Open Sci.* 3: 160498.
- Saïd, S. et al. 2012. Sex effect on habitat selection in response to hunting disturbance: the study of wild boar. – *Eur. J. Wildl. Res.* 58: 107–115.
- Salguero-Gómez, R. et al. 2016. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. – *Proc. Natl Acad. Sci. USA* 113: 230–235.
- Salguero-Gómez, R. et al. 2018. Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. – *Funct. Ecol.* 32: 1424–1435.
- Sauer, J. R. and Slade, N. A. 1987. Size-based demography of vertebrates. – *Annu. Rev. Ecol. Evol. Syst.* 18: 71–90.
- Saunders, S. P. et al. 2018. Evaluating population viability and efficacy of conservation management using integrated population models. – *J. Appl. Ecol.* 55: 1380–1392.
- Schaub, M. and Abadi, F. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. – *J. Ornithol.* 152: 227–237.
- Scheuerell, M. D. et al. 2019. An integrated population model for estimating the relative effects of natural and anthropogenic factors on a threatened population of Pacific trout. – *bioRxiv*: 734996.
- Schulz, K. et al. 2019. Epidemiological evaluation of Latvian control measures for African swine fever in wild boar on the basis of surveillance data. – *Sci. Rep.* 9: 4189.
- Servanty, S. et al. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. – *J. Anim. Ecol.* 78: 1278–1290.
- Servanty, S. et al. 2010. Assessing whether mortality is additive using marked animals: a Bayesian state–space modeling approach. – *Ecology* 91: 1916–1923.
- Servanty, S. et al. 2011. Influence of harvesting pressure on demographic tactics: implications for wildlife management. – *J. Appl. Ecol.* 48: 835–843.
- Smallegange, I. M. and Berg, M. P. 2019. A functional trait approach to identifying life history patterns in stochastic environments. – *Ecol. Evol.* 9: 9350–9361.
- Staton, B. A. et al. 2017. From sequential to integrated Bayesian analyses: exploring the continuum with a Pacific salmon spawner–recruit model. – *Fish. Res.* 186: 237–247.
- Tenan, S. et al. 2012. Demographic consequences of poison-related mortality in a threatened bird of prey. – *PLoS One* 7: e49187.
- Toïgo, C. et al. 2008. Disentangling natural from hunting mortality in an intensively hunted wild boar population. – *J. Wildl. Manage.* 72: 1532–1539.
- Touzot, L. et al. 2020. How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. – *Ecol. Appl.* 30: e02134.
- Truvé, J. and Lemel, J. 2003. Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. – *Wildl. Biol.* 9: 51–57.
- Veylit, L. et al. 2020. How do conditions at birth influence early-life growth rates in wild boar? – *Ecosphere* 11: e03167.
- Weegman, M. D. et al. 2021. Partial and complete dependency among data sets has minimal consequence on estimates from integrated population models. – *Ecol. Appl.* 31: e2258.
- Williams, B. K. et al. 2002. Analysis and management of animal populations. – Academic Press.
- Yang, L. H. et al. 2008. What can we learn from resource pulses? – *Ecology* 89: 621–634.
- Zipkin, E. F. and Saunders, S. P. 2018. Synthesizing multiple data types for biological conservation using integrated population models. – *Biol. Conserv.* 217: 240–250.