1 **Efficient use of harvest data: An integrated population model for exploited**

2 **animal populations**

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18 Running headline: Efficient use of harvest data

19   **Abstract**

20

21   1. Many populations are affected by hunting or fishing. Models designed to assess the

22   sustainability of harvest management require accurate estimates of demographic parameters

23   (e.g. survival, reproduction) hardly estimable with limited data collected on exploited

24   populations. The joint analysis of different data sources with integrated population models

25   (IPM) is an optimal framework to obtain reliable estimates for parameters usually difficult to

26   estimate, while accounting for imperfect detection and observation error. The IPM built so far

27   for exploited populations have integrated count-based surveys and catch-at-age data into age-

28   class structured population models. But the age of harvested individuals is difficult to assess

29   and often not recorded, and population counts are often not performed on a regular basis,

30   limiting their use for the monitoring of exploited populations.

31   2. Here, we propose an IPM that makes efficient use of data commonly collected in exploited

32   marine and terrestrial populations of vertebrates. As individual measures of body mass at both

33   capture and death are often collected in fish and terrestrial game species, our model integrates

34   capture-mark-recapture-recovery data and data collected at death into a body mass-structured

35   population model. It allows the observed number of individuals harvested to be compared

36   with the expected number and provides accurate estimates of demographic parameters.

37   3. We illustrate the usefulness of this IPM using an emblematic game species distributed

38   worldwide, the wild boar *Sus scrofa*, as a case study. For this species that has increased in

39   distribution and abundance over the last decades, the model provides accurate and precise

40   annual estimates of key demographic parameters (survival, reproduction, growth) and of

41   population size while accounting for imperfect detection and observation error.

42   4. To avoid an overexploitation of declining populations or an under-exploitation of

43   increasing populations, it is crucial to gain a good understanding of the dynamics of exploited

44   populations. When managers or conservationists have limited demographic data, the IPM

45   offers a powerful framework to assess population dynamics. Being highly flexible, the

46   approach is broadly applicable to both terrestrial and marine exploited populations for which

47   measures of body mass are commonly recorded and more generally, to all populations

48   suffering from anthropogenic mortality causes.

49

50   **KEYWORDS**

51   body mass-structured population model, exploited populations, harvest, hunting, integrated

52   population model, *Sus scrofa*

1 | INTRODUCTION

Many animal populations are affected by commercial, recreational or subsistence

harvest (Lebreton 2005b; Peres 2010; Ripple *et al.* 2016), i.e. by the removal of individuals

through hunting or fishing. Managing such populations to keep the harvest at sustainable

levels has long been a central purpose (Williams, Nichols & Conroy 2002). It is especially

true in the current context of global change, as both experimental and observational evidence

that harvest may act in synergy with other negative influences such as habitat destruction or

disease outcome is accumulating (Camilo *et al.* 2007; Koons *et al.* 2015; Chen *et al.* 2015).

Likewise, in the so-called harvest-interaction hypothesis, harvest might interact with

population-level effects of climate change in both marine and terrestrial ecosystems. This

interplay between harvest and climate effects may amplify environmentally induced

fluctuations in population size and increases extinction risk, or, alternatively, dampen

fluctuations and increase population growth rates (Gamelon, Sandercock & Sæther 2019).

Models designed to assess the sustainability of harvest management typically require

accurate estimates of demographic parameters (e.g. survival, reproduction) and population

size, which cannot be reliably estimated with limited data. Hence, in particular when

demographic information is limited, the challenge is to make efficient use of available data to

gain a good understanding of the dynamics of exploited populations and be able, in turn, to

provide appropriate management recommendations. When several data types are available,

even if each data type by itself provides limited information on demographic parameters, a

combined analysis within an integrated population model (IPM) approach offers several

advantages (see Schaub & Abadi 2011; Zipkin & Saunders 2018 for reviews). First, a

combined analysis of different data sources always increases the precision of demographic

estimates (for a proof, see Barker & Kavalieris 2001, and for an example, see table 1 in Péron

et al. 2010 who compare parameter estimates and standard errors from a capture-mark-

78   recapture only and an integrated-modeling approach). Second, imperfect detection and

79   observation error inherently associated with data sampled in the field (e.g. population counts)

80   are accounted for. Third, the use of IPM allows some parameters that are difficult or

81   impossible to estimate based on separate analyses to be satisfactorily estimated (for an

82   example, see Péron *et al.* 2010).

83   From the eighties, the simultaneous analysis of different data sources with IPM has

84   received growing interest in fisheries (see Maunder & Punt 2013 for a review). Later, IPM

85   have been proposed as powerful tools to assess the dynamics of terrestrial vertebrate

86   populations (e.g. Besbeas *et al.* 2002 for a study on northern lapwing *Vanellus venellus* and

87   grey heron *Ardea cinerea*) and more recently, they have been applied to exploited populations

88   in terrestrial ecosystems (Gauthier *et al.* 2007; Arnold *et al.* 2018). Strikingly, IPM built on

89   exploited populations usually integrate population surveys (of alive individuals), catch-at-age

90   data and capture-mark-recapture-recovery (CMRR) data into age-structured population

91   models (Methot Jr & Wetzel 2013; Arnold *et al.* 2018; Scheuerell *et al.* 2019). This state-of-

92   the-art limited up-to-now the applicability of IPM for two reasons: i) the age of harvested

93   individuals is often not available because its determination is challenging and generally

94   involves expensive and time-demanding analyses. Instead, body mass at capture and/or death

95   are commonly recorded; ii) information on numbers is rarely based on surveys of alive

96   individuals. Instead, the number of individuals removed through exploitation is commonly

97   recorded in many exploited species.

98   Here, we develop a widely applicable IPM relying on data commonly collected in

99   exploited populations. We illustrate the usefulness of this approach based on the study of a

100   population of an emblematic game species distributed worldwide, the wild boar *Sus scrofa*.

101   This species has tremendously increased in abundance and distribution over the last decades

102   (Massei *et al.* 2015), leading to important damage to crops and high risk of disease

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103   transmission in Europe (see e.g. Schulz *et al.* 2019). Hunting is commonly assumed to help

104   controlling wild boar expansion. Our model differs from previous IPMs applied to vertebrate

105   populations in two respects: i) typical IPMs integrate data into an age-class structured

106   population model. Instead, we build an IPM that integrates CMRR data and individual

107   measures recorded at death into a body mass-structured population model; ii) both alive and

108   dead individuals are considered in the model allowing us to compare the observed number of

109   individuals shot by hunters in each body mass class to the numbers expected from the IPM.

110   For each mass class, the model allows us to get accurate and precise annual estimates of

111   demographic parameters (i.e. survival, reproduction) and of the number of alive individuals,

112   while accounting for imperfect detection and observation error. Although we targeted wild

113   boar as a case study in this work, the approach we propose can be reliably used for assessing

114   population dynamics of any exploited size-structured population of vertebrates.

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116   **2 | MATERIALS AND METHODS**

117   **2.1 | Demographic data collection**

118   We studied a wild boar population located in the 11,000 ha forest of Châteauvillain-

119   Arc-en-Barrois in North-Eastern France (48°02'N, 4°55'E). Between 1991 and 2016, thanks

120   to an intensive capture-mark-recapture program, 1,152 females were captured from March to

121   September using traps, marked and released in their environment. For each capture event, we

122   recorded the date of capture and body mass. Between October and February, wild boars were

123   harvested. All females shot by hunters (previously marked or not) were weighed and their

124   date of death was accurately recorded. No information was available for individuals that died

125   from natural causes. As wild boar rut generally begins in mid-December, females are often

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126   pregnant when shot during the hunting season. For pregnant females, the number of fetuses

127   present in the uteri was recorded.

128   Three types of demographic data were thus available: CMRR data, hunting data and

129   reproduction data.

130   i) CMRR data provided individual histories of 1,152 marked females together with the

131   body mass at each capture (alive) and when shot (dead).

132   ii) Hunting data were the number of females shot by hunters in year t, y_t together with

133   their body mass at death (n=7,350 over the study period).

134   iii) Reproduction data were the number of pregnant females shot in year t, R_t (n = 811

135   over the study period) together with their body mass as well as the number of fetuses at t, J_t (n

136   = 4,344 over the study period).

137   The Integrated Population Model (see Fig. 1 for a schematic representation of the IPM

138   we built) was made of two types of components (Schaub & Abadi 2011; Zipkin & Saunders

139   2018): i) a population model iterating a population vector, which links demographic rates (e.g.

140   survival, reproduction) to the population vector; ii) probabilistic models and their likelihood

141   functions for each of the three data sets (CMRR data, hunting data, reproductive data)

142   separately. In turn, we obtained a joint likelihood combining these components.

143

144   **2.2 | Population model**

145   The population vector was considered each year at the end of the hunting season and

146   before reproduction (pre-breeding census). From life history of wild boar and available data

147   (data on body mass, not on age and data on numbers of individuals killed, not on numbers of

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148   alive individuals), the population vector considered three classes of body mass (<30 kg

149   (small), between 30 and 50 kg (medium) and >50 kg (large) (see Gamelon *et al.* 2012)) and

150   two states (alive and shot by hunters) for each body mass-class. The population vector had

151   thus 6 components: 3 body mass-classes × 2 states.

152   The stage-structured matrix population model allows stage-specific population sizes at

153   year *t+1* to be estimated from stage-specific population sizes at year *t* and demographic rates

154   (Caswell 2001). We built a female body mass-structured matrix model by considering the

155   three classes of body mass previously defined and the two states: alive and shot by hunters.

156   The output of this body mass-structured matrix model structured according to body mass can

157   be directly compared with the observed distribution of hunted individuals among body mass-

158   classes. Females can reproduce in all the three classes. Females may remain in the same body

159   mass-class from one year to the next, with a probability *pSS* for small females and *pMM* for

160   medium females. All large females remained in the large body mass class. Alternatively,

161   small females can move to the medium body mass class with a probability *pSM* or move

162   directly to the largest class with a probability *pSL* (such as *pSL=1-pSS-pSM*). Medium

163   females can move to the next class with a probability *pML* (such as *1-pMM*). There was no

164   backward transition towards a lighter body mass class. As wild boar females are sedentary

165   (Truvé & Lemel 2003; Keuling *et al.* 2010), we assumed no immigration and emigration.

166   We defined $N_{S,t}$ as the number of small females, $N_{M,t}$ the number of medium females

167   and $N_{L,t}$ the number of large females alive in year *t*. To account for demographic stochasticity

168   in survival processes, we used binomial processes to describe the number of females in each

169   body mass class.

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170   i.   The number of small females alive in year t $N_{S,t}$ is the number of small females in

171   year t-1 that remained small plus the number of small females produced by mature

172   females in year t-1 ($NewBorn_{t-1}$) that survived, such as:

173    $N_{S,t} \sim Bin\ (N_{S,t-1},\ pSS_{t-1} \times Sn_{S,t-1} \times (1-h_{S,t-1})) + Bin\ (NewBorn_{t-1},\ Sn_{S,t-1} \times (1-h_{,S,t-1}) \times Spn_{t-1} \times piOs_{t-1})$

174   (2)

175   where Sn_j is the survival probability during the first part of the year without hunting, and 1-h_j

176   the proportion of females that survived from hunting in the body mass class j. Survival

177   probability is defined as 1-NM_j, with NM_j the natural mortality bringing together all causes of

178   death except hunting (e.g. diseases). The proportion of females shot by hunters in the class j h_j

179   is defined as $\frac{MH_j}{1-NM_j}$, with MH_j the hunting mortality. Assuming that natural mortality was

180   negligible during the hunting period (which is not a very stringent assumption as the

181   multiplicative relationship between natural survival and survival to hunting holds even with

182   some overlap in time between the two sources of mortality), at the end of the year, survival

183   probability for females in the body mass class j equals $Sn_j \times (1-h_j) = (1-NM_j) \times (1-\frac{MH_j}{1-NM_j}) = 1-$

184   NM_j-MH_j (Lebreton 2005a). Spn is the post-natal survival probability (from birth to weaning)

185   and $piOs$ the probability for newborn to remain in the small body mass class.

186   ii.   The number of medium females alive in year t $N_{M,t}$ is the number of small females in

187   year t-1 that entered the medium class, plus medium females in year t-1 that remained

188   medium plus the newborn females produced by mature females in year t-1 that

189   became medium (1-$piOs$) and survived, such as:

190    $N_{M,t} \sim Bin\ (N_{S,t-1},\ pSM_{t-1} \times Sn_{M,t-1} \times (1-h_{M,t-1})) + Bin\ (N_{M,t-1},\ pMM_{t-1} \times Sn_{M,t-1} \times (1-h_{M,t-1})) + Bin$

191    $(NewBorn_{t-1},\ Sn_{M\,t-1} \times (1-h_{M,t-1}) \times Spn_{t-1} \times (1-piOs_{t-1}))$ (3).

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192   iii.   The number of large females alive in year t $N_{L,t}$ is the number of small and medium

193   females in year t-1 that entered the large class, plus large females in year t-1 that

194   survived, such as:

195     $N_{L,t} \sim Bin\ (N_{S,t-1},\ pSL_{t-1} \times Sn_{L,t-1} \times (1-h_{L,t-1})) + Bin\ (N_{M,t-1},\ pML_{t-1} \times Sn_{L,t-1} \times (1-h_{L,t-1})) + Bin\ (N_{L,t-1},$

196     $Sn_{L,t-1} \times (1-h_{L,t-1}))$ (4).

197   We used a Poisson distribution for the annual number of newborn females produced by small,

198   medium and large females, such as:

199     $NewBorn_t \sim Poisson\ (N_{S,t} \times BP_{S,t} \times LS_{S,t} \times 0.5 + N_{M,t} \times BP_{M,t} \times LS_{M,t} \times 0.5 + N_{L,t} \times BP_{L,t} \times LS_{L,t} \times 0.5)$

200   (5)

201   with $BP_{j,t}$ the annual proportion of breeding females and $LS_{j,t}$ the annual litter size of each

202   body mass class j. We assumed a balanced sex ratio at birth (Servanty et al. 2007).

203   In addition to the number of females alive in each body mass class, we estimated the

204   annual body mass-specific numbers of females that were shot $NH_{S,t}$, $NH_{M,t}$ and $NH_{L,t}$:

205   i.   The number of small females shot by hunters in year t $NH_{S,t}$ is the number of small

206   females in year t-1 that remained small and survived from natural causes but were

207   shot during the hunting season, plus the number of small females produced by mature

208   females in year t-1 also shot, such as:

209     $NH_{S,t} \sim Bin\ (N_{S,t-1},\ pSS_{t-1} \times Sn_{S,t-1} \times h_{S,t-1}) + Bin\ (NewBorn_{t-1},\ Sn_{S,t-1} \times h_{,S,t-1} \times Spn_{t-1} \times piOs_{t-1})$ (6).

210   ii.   Similarly, the number of medium females shot by hunters in year t $NH_{M,t}$ is:

211     $NH_{M,t} \sim Bin\ (N_{S,t-1},\ pSM_{t-1} \times Sn_{M,t-1} \times h_{M,t-1}) + Bin\ (N_{M,t-1},\ pMM_{t-1} \times Sn_{M,t-1} \times h_{M,t-1}) + Bin$

212     $(NewBorn_{t-1},\ Sn_{M\ t-1} \times h_{M,t-1} \times Spn_{t-1} \times (1-piOs_{t-1}))$ (7);

213   iii.   The number of large females shot by hunters in year t $NH_{L,t}$ is:

214     $NH_{L,t} \sim Bin\ (N_{S,t-1},\ pSL_{t-1} \times Sn_{L,t-1} \times h_{L,t-1}) + Bin\ (N_{M,t-1},\ pML_{t-1} \times Sn_{L,t-1} \times h_{L,t-1}) + Bin\ (N_{L,t-1},\ Sn_{L,t-}$

215     $_1 \times -h_{L,t-1})$ (8).

216

2.3 | Model for hunting data

218   Hunting data consisted of the annual numbers of females shot by hunters by body

219   mass classes (small, medium and large), denoted as $y_{S,t}$, $y_{M,t}$ and $y_{L,t}$, respectively. For these

220   data, we used the likelihood of a state-space model (de Valpine & Hastings 2002), which

221   consists of a process model (i.e. the population model previously described, that is the

222   population size as a function of demographic rates and the population size the preceding year)

223   and an observation model. The observation model describes the link between the hunting data

224     $y_{S,t}$, $y_{M,t}$ and $y_{L,t}$ and the true number of females shot by hunters in the population ($NH_{S,t}$, $NH_{M,t}$

225   and $NH_{L,t}$) (yellow part, Fig. 1). For each body mass class j, we assumed that: $y_{j,t}$

226     $\sim Normal(NH_{j,t},\ \tau_{j,t})$ truncated to positive values, with $\tau_{j,t} = \frac{1}{\sigma_j^2 \times y_{j,t}^2}$, where σ_j^2 is the term we are

227   estimating. $\tau_{j,t}$ is the observation error and incorporates both errors in hunting data and lack of

228   fit of the state equations to the true dynamics of the population (see p. 230 in Schaub & Abadi

229   2011). Note the trick often used in JAGS that consists in defining the distributions by their

230   precision $\tau_{j,t}$ rather than their variance σ_j^2, the precision being the inverse of the variance. The

231   likelihood of the state-space model is then the product of the likelihood of the process and the

232   observation equations. The state-space likelihood for hunting data already includes all

233   parameters we want to estimate but they are hardly estimable based on hunting data alone and

234   require additional information coming from CMRR and reproduction data.

235 **2.4 | Model for capture-mark-recapture-recovery data**

236   CMRR data were analysed using a multistate model (see Lebreton *et al.* 2009 for a

237 review) that allows natural mortality *NM* to be estimated separately from hunting mortality

238 *MH* (Lebreton, Almeras & Pradel 1999; Gamelon *et al.* 2012) for each body mass class (grey

239 part, Fig. 1). We described the fate of an individual using ten states (see Appendix S1). States

240 1, 2 and 3 were for individuals alive in the small, medium and large body mass classes,

241 respectively. States 4, 5 and 6 were for individuals just shot, again in the three body mass

242 classes, respectively. States 7, 8 and 9 were for individuals that recently died from natural

243 causes, again in the three body mass classes, respectively. The state "dead from a natural

244 cause" cannot be observed because no information was available for individuals that did not

245 die from hunting. State 10 corresponded to individuals already dead. The state "already dead"

246 cannot be observed either but brought together all the dead individuals. To account for the

247 dependency between states (i.e. from year t to $t+1$, individuals either survive, die shot by

248 hunters or die from natural causes, see Appendix S1), we used a Dirichlet distribution to

249 model the transitions between states thus ensuring that the sum of these probabilities always

250 equals to 1. The parameters in the multistate model were annual natural mortality $NM_{j,t}$ and

251 hunting mortality $MH_{j,t}$ for each body mass class j. Moreover, yearly transition probabilities

252 from one body mass class to the next (i.e. pSS_t, pSM_t, pSL_t, pMM_t, pML_t) were estimated. To

253 account for the dependency between transition probabilities (i.e. $pSL_t=1-pSS_t-pSM_t$), we used

254 a Dirichlet distribution to model the transitions from the small body mass class to the others.

255 This ensures that the sum of the probabilities (i.e. $pSS_t + pSM_t + pSL_t$) always equals to 1.

256 Regarding the observation process, if an individual was alive, it could be recaptured with

257 probability p or not recaptured with probability $1-p$; if an individual just died from hunting, its

258 death could be reported "dead recovery" with probability r or not reported with probability $1-$

259   *r*. Recapture and recovery probabilities were also time and body mass-class dependent (see

260   Appendix S2 and S3).

261

262   **2.5 | Model for reproduction data**

263   Reproduction data consisted of the annual numbers of pregnant females shot by body

264   mass classes (small, medium and large), denoted as $R_{S,t}$, $R_{M,t}$ and $R_{L,t}$, respectively and the

265   annual numbers of fetuses counted by body mass classes, denoted as $J_{S,t}$, $J_{M,t}$ and $J_{L,t}$,

266   respectively. We assumed that the number of fetuses per body mass class $J_{j,t}$ is Poisson

267   distributed such as: $J_{j,t} \sim Poisson\ (R_{j,t} \times LS_{j,t})$, where $LS_{j,t}$ is the term we are estimating, that is

268   the litter size for a female belonging to the body mass class *j* (blue part, Fig. 1).

269

270   **2.6 | Model implementation**

271   Assuming independence among the datasets, the likelihood of the IPM was the

272   product of the likelihoods of the three different datasets (Besbeas *et al.* 2002; Kéry & Schaub

273   2012): hunting data, CMRR data and reproduction data. The IPM was fit within the Bayesian

274   framework and we used non-informative priors for all the parameters. We only constrained σ_j

275   in the state-space model to be small using a Uniform distribution between 0 and 0.1, so that

276   the observation errors $\tau_{j,t} = \frac{1}{\sigma_j^2 \times y_{j,t}^2}$ can be large. Markov chain Monte Carlo (MCMC)

277   simulation was used for parameter estimation. All the parameters described in Fig. 1 were

278   estimated within the IPM, even parameters difficult to estimate and often assessed from

279   expert opinion such as *Spn* and *piOs* (see Gamelon *et al.* 2012). The analyses were

280   implemented using JAGS (Plummer 2003) version 4.3.0 called from R version 3.4.3 (R

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281   Development Core Team 2017) with package rjags (Plummer 2016). The JAGS code for

282   fitting the IPM is available in Appendix S3.

283   To assess convergence, we ran three independent chains for 230,000 MCMC

284   iterations, with an adaptation of 180,000 iterations thinning every 100th observation resulting

285   in 1,500 posterior samples. We used the Brooks and Gelman diagnostic $R^{\square}$ to assess the

286   convergence of the simulations and used the rule $R^{\square} < 1.2$ to determine whether convergence

287   has been reached (Brooks & Gelman 1998). Convergence was reached for most of the nodes

288   except for four years (1996-1999) in which not all parameters had converged. To ensure that

289   the priors for initial population sizes do not influence estimates of demographic rates and

290   body mass-specific numbers the first year of the study (i.e., in 1991), only the years between

291   1992 and 2016 were included in the analyses.

292

293   **3 | RESULTS**

294   **3.1 | Recapture, recovery and mortality probabilities**

295   Estimated recapture probabilities fluctuated a lot through years, from 0.04 to 0.74 for

296   small females (mean p_S=0.36), from 0.03 to 0.82 for medium females (mean p_M=0.38) and

297   from 0.002 to 0.62 for large females (mean p_L=0.10). These high fluctuations of the average

298   recapture probabilities over years are consistent with earlier studies (see Appendix C in

299   Servanty *et al.* 2010). In accordance with previous work (Toïgo *et al.* 2008; Servanty *et al.*

300   2010; Gamelon *et al.* 2011), dead recovery reporting probabilities were high for all body mass

301   classes, ranging from 0.75 to 0.97 for small females (mean r_S=0.90), from 0.79 to 0.96 for

302   females in the medium body mass class (mean r_M=0.88) and from 0.74 to 0.93 for large

303   females (mean r_L=0.84). Mortality probability also fluctuated over the study period (Fig. 2

304   A,B). As expected for this heavily hunted population, hunting mortality *MH* was much higher

305 than natural mortality *NM* for small and medium females. Interestingly, the estimate of the

306 mean post-natal survival was 0.60 [min=0.22; max=0.88] over the study period, and thus

307 close to the value generally set by expert opinion (0.75, see e.g. Gamelon *et al.* 2012) .

308

309 3.2 | Transition probabilities among body-mass classes

310 Females in the small body mass class had an estimated probability of 0.48 to remain in

311 this class on the average (*pSS*) (Fig. 2C). Alternatively, they moved to the medium-sized class

312 with an estimated probability *pSM* equal to 0.19 on the average, and to the large-sized class

313 with a probability *pSL* of 0.33. Females in the medium body mass class had an estimated

314 probability of 0.41 to enter the large class on the average (*pML*), other medium females

315 remaining in the medium-sized class (*pMM*). Newborn females had an estimated probability

316 of 0.88 [min=0.56; max=0.98] to remain in the small body mass class (*piOs*) on the average,

317 this probability being usually set to 0.60 by expert opinion (see e.g. Gamelon *et al.* 2012).

318

319 3.3 | Reproduction

320 For reproduction parameters, litter sizes *LS* were strongly body mass-specific, being the

321 largest for large females (mean LS_L=6.08 young) and the smallest for females of the small-

322 sized class (mean LS_S=4.21 young) (Fig. 3). These results are in accordance with previous

323 studies (Gamelon *et al.* 2013). As for mortality probabilities, litter sizes fluctuated a lot over

324 the study period, from 1.79 to 7.69 young produced for small females (LS_S), from 3.91 to 7.50

325 young for females in the medium weight class (LS_M) and from 4.97 to 7 young for large

326 females (LS_L). Breeding proportions, i.e. the proportion of breeding females among those in

327 each body mass class, fluctuated over years, especially for females in the small body mass

328   class. These probabilities ranged from 0.36 to 0.84 (mean BP_S=0.58) for small females, from

329   0.43 to 0.65 (mean BP_M=0.53) for medium females, and from 0.48 to 0.61 (mean BP_L=0.53)

330   for large females.

331

3.4 | Population sizes

333   High annual fluctuations in mortality, transition between body mass classes and

334   reproductive rates translated to high variation in population size over years (Fig. 4). Each

335   year, with a mean of NH_S=143 females, most of the females removed from hunting belonged

336   to the small-sized class (Fig. 4A). The mean number of females shot by hunters in the

337   medium class NH_M was estimated to be 81, whereas they were very few large females in the

338   hunting bags (mean NH_L=35). Noticeably, the numbers of females shot in each body mass

339   class expected from the IPM was very close to the observed numbers y_j (dots in Fig. 4A).

340   Observation errors σ were estimated at 0.096 for small and medium females and 0.099 for

341   large females. In terms of numbers of females alive in the population, small females

342   constituted the largest part of the population (mean number of small females N_S=290),

343   followed by medium (mean N_M=77) and then large females (mean N_L=36) (Fig. 4B).

344

4 | DISCUSSION

346   We develop here an IPM that makes efficient use of data commonly collected in

347   exploited populations, i.e. body mass at captures/death as well as number of individuals

348   removed by harvesting. Our model makes it possible to directly compare the observed and the

349   expected number of individuals shot. It also provides accurate and precise estimates of key

350   demographic parameters, including some that cannot be estimated from separate analyses.

16

351   Using a wild boar population as a case study, we demonstrate that this framework is a

352   powerful tool to gain a good understanding of the dynamics of exploited populations.

353

354   **4.1 | A comprehensive picture of population dynamics**

355   In accordance with previous work (Toïgo *et al.* 2008; Gamelon *et al.* 2011), we

356   showed that hunting mortality probabilities *MH* are high for all body mass classes.

357   Conversely, natural mortality *NM* was low (Fig. 2 A,B). This is expected among ungulates

358   where the average natural adult survival probability *Sn* often exceed 0.95 in females (Gaillard

359   *et al.* 2000). These hunting and natural mortality patterns are in accordance with other hunted

360   wild boar populations (see Gamelon 2019 for a review). Our IPM thus confirms that hunting

361   is an important driver of wild boar population dynamics. Regarding to reproduction

362   parameters, wild boar is a highly fecund species, being able to produce large litters (Fig. 3) as

363   early as their first year of life (Servanty *et al.* 2009) at a body mass lower than 30 kg (small

364   mass-class). Together with reduced survival due to hunting, this leads to a short generation

365   time, i.e. a low mean age of mothers at childbirth (Gaillard *et al.* 2005, 2016) close to two

366   years, whereas it is close to six years for similar-sized ungulates (Servanty et al. 2011). This

367   unusual life history among ungulates (Focardi *et al.* 2008), characterized with a fast turnover

368   of individuals in the population, explains why the number of individuals in the population did

369   not collapse (Fig. 4B) during the study period despite such a high hunting pressure, and why

370   younger/lighter females constitute more than 50% of the individuals alive. By analyzing

371   simultaneously CMRR data, reproductive data and hunting data, and by estimating jointly all

372   the demographic parameters, our IPM offers a comprehensive picture of the underlying

373   demographic mechanisms allowing this population not to collapse over the last 25 years

374   despite a high hunting pressure.

4.2 | Estimates for demographic parameters hardly measurable in the field

The size of exploited populations is generally poorly known, and the IPM allows us to get accurate and precise estimates even in the absence of surveys of the number of individuals alive, which are usually needed to make relevant management recommendations. Interestingly, the model also allows us to estimate some growth parameters that are difficult to measure in the field, because they would require multiple captures of the same individuals over their lifespan. We found marked year-to-year variation in the probability for a female to remain in the same body mass class or enter a heavier body mass class (Fig. 2C). A large body of empirical evidence shows that increasing density is generally associated with reduced body mass in large herbivores (Bonenfant *et al.* 2009). Fluctuations in the strength of density dependence in body growth could explain such among-year variation in transition probabilities. Factors affecting transitions between body mass classes remain to be carefully explored, offering exciting avenues of research. Likewise, the IPM allowed us to get annual estimates of post-natal survival, a parameter often tricky to estimate empirically. For instance, Baubet et al. (2009) aimed to tag piglets inside their birth nest to assess post-natal survival from birth to weaning. They failed in this task not only because of expected difficulties to locate the birth nests, but also because it induced abandonment of the piglets after tagging. By jointly analysing different data sources, the IPM is a powerful tool to achieve such a goal.

4.3 | A framework based on data commonly collected in exploited populations

To make harvest sustainable, i.e. avoid overharvest of declining populations or avoid applying too low harvest rate to increasing populations, the dynamics of exploited populations should be fully understood. In frequent situations where data are limited, it might be a tricky task. Our IPM is not solely a powerful tool to understand the dynamics of increasing wild

399 boar populations, but it is clearly applicable to many other populations in both terrestrial and

400 marine environments. For instance, a lot of commercially important marine fish species are

401 subject to strong harvesting (Pauly *et al.* 2002; Hutchings & Reynolds 2004). The IPM can be

402 a suitable tool to anticipate the collapse of some of them (Hutchings & Myers 1994; Myers,

403 Hutchings & Barrowman 1997) by making efficient use of the limited data available (see

404 Maunder 2004; Saunders, Cuthbert & Zipkin 2018 for the use of IPM in prospective

405 analyses).

406   The use of IPM as a management tool is not novel in fisheries (see Maunder & Punt

407 2013 for a review) but they are to date based on age-structured population models. However,

408 fish are indeterminate growers for which demographic parameters are usually strongly mass-

409 dependent. Moreover, while taking reliable mass measurements of animals killed by humans

410 is straightforward, information on age is more cumbersome and often inaccurate and thus

411 recorded in very few populations only. Even in determinate growers such as birds and

412 mammals, evidence is accumulating that body mass is a crucial structuring factor of

413 population dynamics (Gaillard *et al.* 2000 for a review on large herbivores; see Coulson,

414 Tuljapurkar & Childs 2010 for a case study on Soay sheep *Ovis aries*), making biologically

415 relevant the use of body mass-structured models in IPM for a large range of exploited

416 populations of vertebrates. More generally, our framework based on a body mass-structured

417 model adds to the spate of studies that have recently flourished in the literature showing that

418 trait-based approaches (such as body mass) and demographic approaches are intertwined

419 (Salguero-Gómez *et al.* 2018; Smallegange & Berg 2019). Another clear advantage of our

420 IPM is the inclusion of the number of dead individuals in the body mass-structured population

421 model, whereas all the IPMs built so far only included the number of individuals alive in a

422 population model (Caswell 2001). In exploited populations, getting information on the

423 number of individuals alive is challenging whereas information on the number of individuals

19

424   killed (by hunting or fishing) is often available. This number is even almost perfectly known

425   in our population. With the inclusion of information related to hunting bags, our IPM renders

426   possible a direct comparison between observed and predicted numbers of individuals shot in

427   each body-mass class, a crucial demographic information in exploited populations.

428

429   **4.4 | Possible extensions**

430   The use of the number of individuals harvested in our IPM could be modified to the

431   use of proportions. A classical case is that of duck hunting, in which programs for collecting

432   samples of wings of individuals shot make it possible to estimate the proportion of first-year

433   and after first-year (i.e. adult) individuals of both sexes in the harvest (Raftovich, Chandler &

434   Fleming 2018). Such estimates of age-and sex structures among dead individuals have been

435   used up to now in an ad hoc fashion to match model predictions (Holopainen *et al.* 2018). The

436   analysis of such data based on an IPM would certainly greatly improve our knowledge and

437   understanding of the differences in vulnerability to hunting between young and adults and

438   between sexes in duck populations.

439   Another possible straightforward extension of our IPM could be the modification of

440   the number and size of the body mass classes. Beyond body mass, the IPM is generalizable to

441   all kinds of states, such as breeder/non breeder which is a commonly reported state in CMR

442   studies on birds (see e.g. Pardo, Barbraud & Weimerskirch 2014 for a multistate model on

443   wandering albatross *Diomedea exulans*). Beyond mortality due to hunting and fishing, the

444   IPM can also be expanded to all forms of anthropogenic mortalities (see e.g. Chevallier *et al.*

445   2015 for mortality induced by electrocution in Bonelli´s eagle *Aquila fasciata*). Finally, while

446   we used non-informative priors and allowed all the parameters to be estimated within the

447   IPM, it is straightforward to integrate a priori biological knowledge by setting some

448   parameters to known values or by using informative priors.

449

450   **Conclusions**

451   The recent methodological advances, such as the introduction of MCMC that have

452   highly contributed to the expansion of IPM, allowed us to propose an IPM that makes

453   efficient use of (limited) harvest data for the monitoring of exploited populations. The model

454   is flexible and can be adapted to the life history and the data available for the population of

455   interest. This model that integrates commonly collected data in marine and terrestrial

456   exploited populations is therefore widely applicable.

457

465

466   AUTHOR´S CONTRIBUTIONS

467   EB contributed to data collection. MG, EB, AB, JMG, JDL and OG conceived the study. MG

468   conducted the analyses with insights from OG, wrote the first draft and all authors contributed

469   to revisions of the initial manuscript.

470

471   DATA AVAILABILITY

472   The data supporting the results will be archived in an appropriate public repository in Dryad,

473   should the manuscript be accepted.

474

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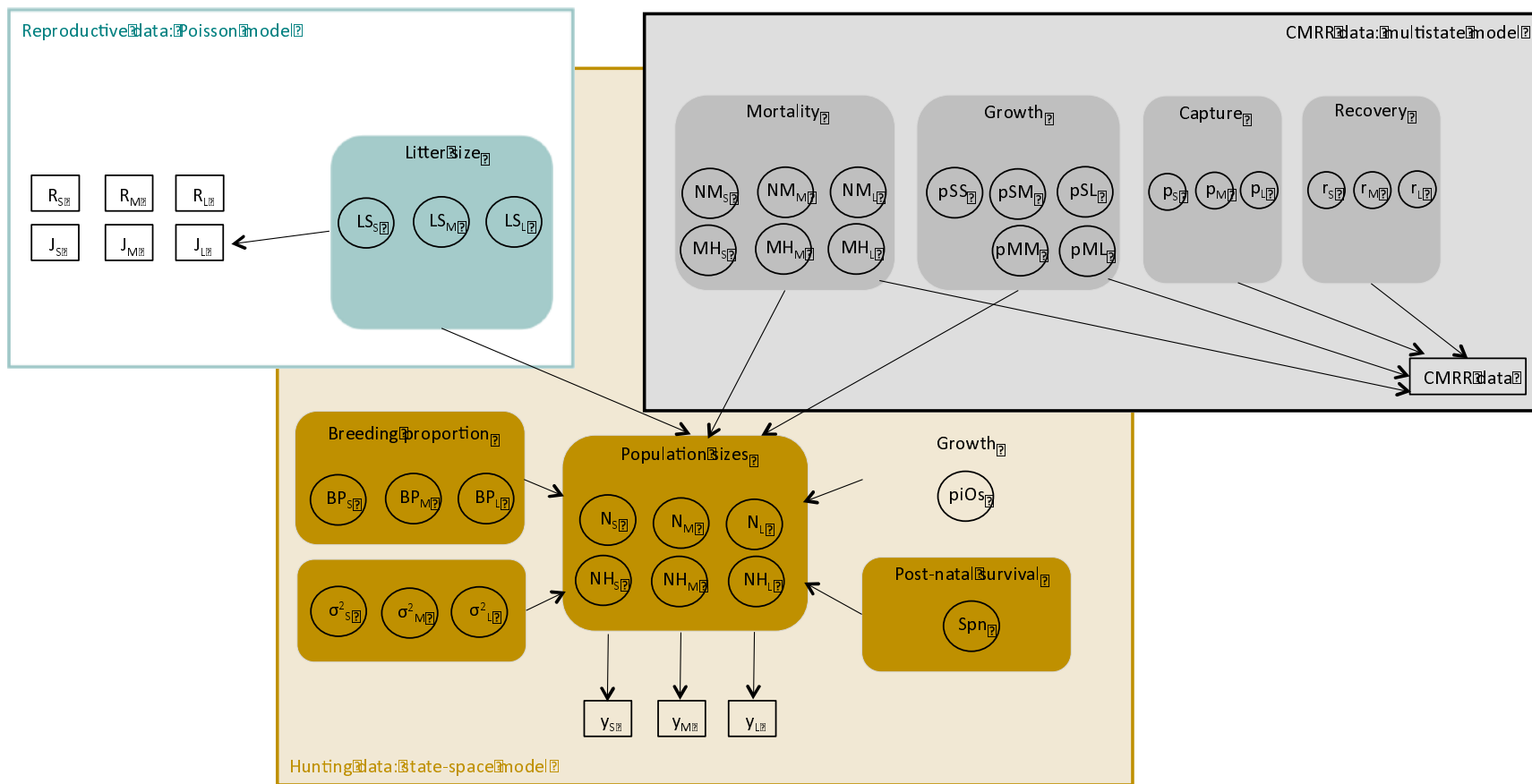
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637

638 **Figure 1.** Directed acyclic graph of the IPM. Squares represent the data, circles represent the parameters to be estimated. Arrows represent

639 dependencies. Three types of data are collected: CMRR data, hunting data (y_j) and reproductive data (number of pregnant females (R) and

640 number of fetuses (J) in each body mass class j). Estimated parameters are the body mass-specific recapture probability p_j, recovery

641 probability r_j, natural mortality NM_j, hunting mortality MH_j, litter size LS_j, numbers of females alive N_i, numbers of females shot by hunters

642 NH_j, breeding proportions BP_j, post-natal survival Spn (from birth to weaning), observation error σ_j^2 and transitions between body mass

643 classes (growth) with $piOs$ the probability for newborn remaining in the small body mass class, pSS the probability of small females

644 remaining in this class during the year, pSM the probability of small females entering the medium class, pSL the probability of small females

645 entering the large class, pMM the probability of medium females remaining in this class during the year and pML the probability of medium

646 females entering the large class.

Reproductive data: Poisson model

Litter size

LS_S LS_M LS_L

R_S R_M R_L
J_S J_M J_L

CMRR data: multistate model

Mortality
NM_S NM_M NM_L
MH_S MH_M MH_L

Growth
pSS pSM pSL
pMM pML

Capture
p_S p_M p_L

Recovery
r_S r_M r_L

CMRR data

Breeding proportion
BP_S BP_M BP_L

σ^2_S σ^2_M σ^2_L

Population Sizes
N_S N_M N_L
NH_S NH_M NH_L

Growth
$piOs$

Post-natal survival
Spn

y_S y_M y_L

Hunting data: state-space model

647

648

649   **Figure 2.** Mortality and growth parameters estimated with the IPM (grey part in Fig. 1). Posterior means of A) annual hunting mortality *MH*

650   and B) annual natural mortality *NM* for each body mass class (small S, medium M and large L). Posterior means of C) transition probability

651   between body mass classes (*pSS*: probability of small females remaining in this class; *pSM*: probability of small females entering the medium

652   class; *pSL*: probability of small females entering the large class; *pML*: probability of medium females entering the large class during the year)

653   for the wild boar population at Châteauvillain-Arc-en-Barrois between 1992 and 2015. CRI are not shown to improve the readability.
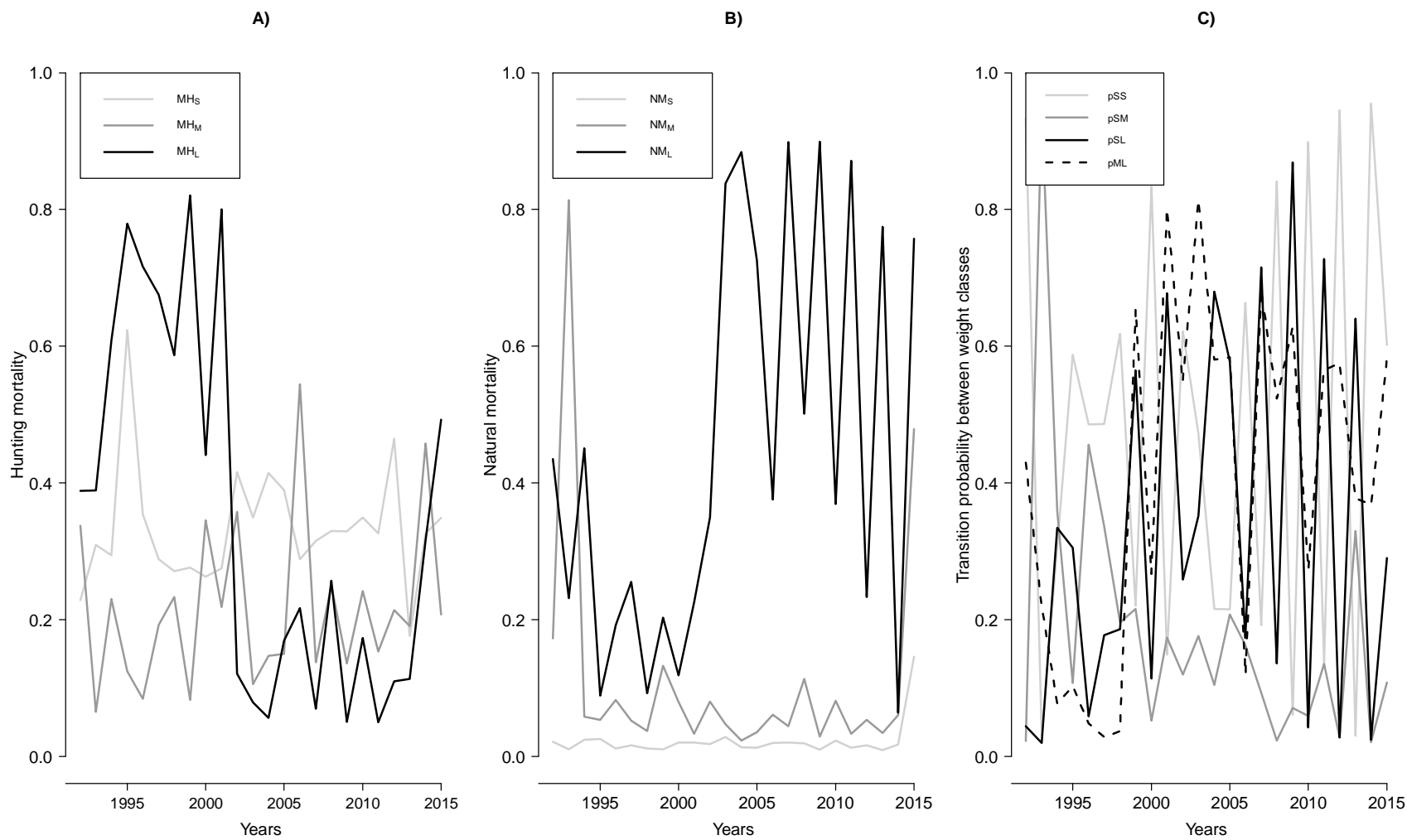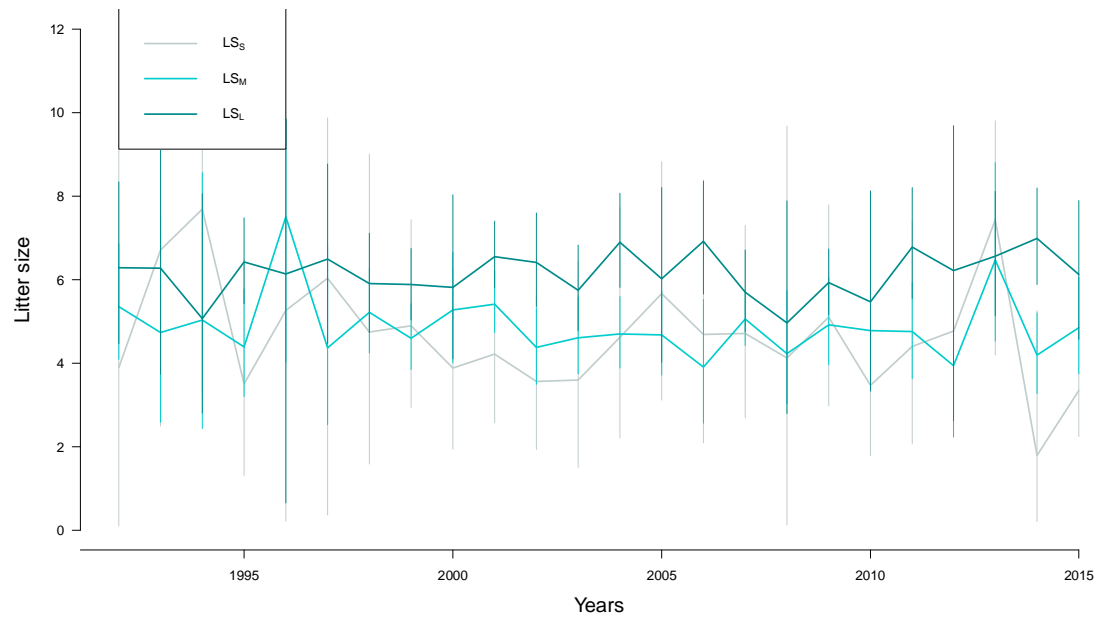
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655

656   **Figure 3.** Reproductive parameters estimated with the IPM (blue part in Fig. 1). Posterior

657   means of annual litter size *LS* for each body mass class (small S, medium M and large L)

658   (together with their 95% CRI) for the wild boar population at Châteauvillain-Arc-en-
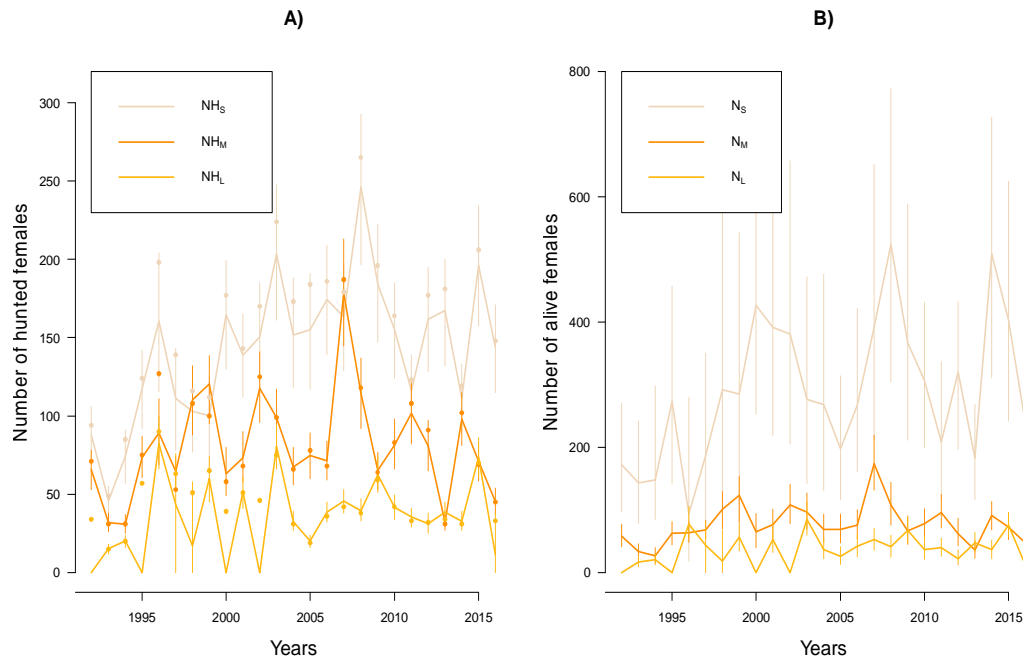
659   Barrois between 1992 and 2015.

660

661

662 **Figure 4.** Population sizes estimated with the IPM (yellow part in Fig. 1). Posterior means (together with their 95% CRI) of A) annual

663 numbers of females shot by hunters NH and B) annual numbers of females alive N in each body mass class (small S, medium M and large L)

664 for the wild boar population at Châteauvillain-Arc-en-Barrois between 1992 and 2016. Dots correspond to observed numbers of females shot

665 by hunters in the three body mass classes (y_S, y_M and y_L).

666

667