



HAL
open science

Hunting, Predation and Senescence in Boars

Marlène Gamelon

► **To cite this version:**

Marlène Gamelon. Hunting, Predation and Senescence in Boars. Suresh I.S. Rattan. Encyclopedia of Biomedical Gerontology, Elsevier, 2020, 978-0-12-816076-3. <10.1016/b978-0-12-801238-3.11330-3>. <hal-03282123>

HAL Id: hal-03282123

<https://hal.science/hal-03282123v1>

Submitted on 9 Aug 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

Hunting, predation and senescence in boars

Author Contact Information

Marlène Gamelon

Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway

marlene.gamelon@ntnu.no

+47 73596051

Keywords

age-specific mortality, cause-specific mortality, competing risks, harvest, individual monitoring, life history strategy, sex-specific mortality, survival, *Sus scrofa*, ungulate

Abstract

Identifying the factors causing mortality over life is of great importance in gerontology, ecology and evolution. I first present some general methods to properly estimate age-related causes of mortality. Second, I report some of the studies that have quantified the main causes of mortality affecting wild boar over life, an emblematic game species that has dramatically increased in abundance and distribution across Europe. Hunting is the major cause of mortality, followed by natural mortality (e.g. starvation, senescence) and predation, all these factors of mortality being age- and/or sex-specific. Third, I discuss why it is important to examine how some sources of mortality can interact. Finally, I show how hunting can select for accelerated life history that allows wild boar to compensate high mortality probabilities with high reproductive output.

Glossary

Adults: Individuals older than 2 years of age.

Hunting mortality probability: the annual probability for an individual to die killed by hunting.

Juveniles: Individuals between 0 and 1 year of age, also called piglets.

Mortality due to predation: the annual probability for an individual to die killed by a non-human predator. Main predators for the wild boar are red foxes and wolves.

Natural mortality probability: the annual probability for an individual to die but not from human and non-human predation.

Natural survival probability: the probability for an individual to survive from one year to the next one, in absence of human and non-human predation.

Overall survival probability: the probability for an individual to survive from one year to the next one and thus not to die from hunting, predation or natural causes.

Subadults: Individuals between 1 and 2 years of age, also called yearlings.

48 **Introduction**

49 Identifying the factors causing mortality over life is of great importance in gerontology. This
50 is indeed the first required step to understand the underlying mechanisms shaping mortality,
51 such as genetic mechanisms and environmental factors. The work from Horiuchi and
52 Wilmoth (1) is a nice illustrative study showing the major causes of death over life for
53 females in Japan between 1951 and 1990. The same approach used on males and females in
54 France between 1979 and 1994 indicates that malignant neoplasms, hypertensive disease or
55 liver cirrhosis are some of the main causes of mortality between ages 30 and 54. At older
56 ages, death rates increase drastically caused by infection diseases and heart failure (see Figure
57 2 in Horiuchi et al. (2) showing the age pattern of the cause-of-death structure).

58 A better understanding of the sources of mortality affecting individuals from birth to
59 old ages is also crucial in ecology and evolution. For instance, Forrester and Wittmer (3)
60 reviewed 48 studies to identify the major causes of mortality affecting mule deer and black-
61 tailed deer *Odocoileus hemionus* at different ages. They found that predation is the main
62 cause of mortality for all ages. Also, malnutrition as well as diseases can severely affect
63 survival and more generally the growth of the populations. In addition of affecting population
64 dynamics, the multiples sources of mortality act as selective pressures shaping life history
65 traits. Studies led on harvested animal populations have provided valuable insight on the key
66 role of age-specific mortality on life history evolution. For instance, there is growing
67 evidence that high hunting mortality on the adult class can induce evolutionary changes such
68 as earlier age at maturity and reduced body size (4). On the contrary, a removal of non-
69 mature juvenile individuals may mimic natural mortality and predation pattern and thus limit
70 undesirable evolutionary responses due to harvesting (5). Ultimately, a better knowledge of

71 the causes of mortality affecting wild vertebrates over life might help elaborating appropriate
72 management actions to control populations in a sustainable way.

73 As most ungulate populations in temperate areas, wild boar (*Sus scrofa*) abundance
74 and distribution have increased over the last decades across Europe (6,7). Changes in
75 agricultural practices, reduced hunting pressure, global change and land abandonment have
76 favoured the expansion of this emblematic game species (8). When they overturn soil to feed,
77 wild boars lead to important damages to crops and influence plant, animal, fungi and aquatic
78 communities (see (9) for a review). They are also reservoirs of several diseases with some of
79 them being possibly transmitted to humans, such as brucellosis or leptospirosis (10).
80 Controlling wild boar populations has thus become an important goal for wildlife managers
81 and hunting has long been proposed as a tool to achieve it.

82 Interestingly, this species exhibits an unusual life history strategy among ungulates
83 rendering its regulation challenging. Firstly, females are particularly fecund, being able to
84 produce up to 14 piglets in a single litter (11), at young ages (from their first year of life, 12)
85 after having reached only 33–41% of their asymptotic adult body mass (13). Secondly, the
86 generation time, i.e. the mean age of mothers at childbirth, is close to 2 years in some heavily
87 hunted populations whereas it is around 6 years for similar-sized ungulates (14). This short
88 generation time characterizing wild boar life history is typically observed in passerine birds
89 or rodents. This indicates an especially fast turnover, with compensation for reduced survival
90 in heavily hunted environment by reallocation of resources to reproduction (12,14).

91 The purpose of this chapter is to identify the sources of mortality affecting wild boar
92 over life, discuss how they can interact and shape life history traits. First, I present some
93 general methods to properly estimate age-related causes of mortality. Second, I report some
94 of the studies that have quantified the main causes of mortality affecting wild boars from

95 young to older ages. Based on this literature survey, I discuss the type of mortality an
96 individual is likely to experience according to its age and sex. Third, I argue why it is
97 important to examine how some sources of mortality can interact. Fourth, I discuss how wild
98 boar population growth rates can increase despite a somewhat low survival.

99

100 **Estimating cause-specific mortality**

101 The multiple sources of mortality that affect human and non-human individuals
102 compete and their probability of winning depends on the strength of the different causes of
103 mortality (15). Statisticians have thus long been interested in properly decomposing mortality
104 into its different sources, the so-called “competing risks”.

105 Sometimes, the fate of an individual (i.e. alive or dead) and the cause of death are
106 precisely known. This is the case in medicine, human demography, in plants and captive
107 animal populations. Also, in free-ranging animals, the recent advances in GPS and
108 radiotelemetry technology may allow to identify the cause of death (16). Estimating age- and
109 cause-specific mortality probability is thus straightforward with classical competing risk
110 statistical models (see (17) for a review of methods to estimate cause-specific mortality in
111 presence of competing risks; see also the books from (18,19)).

112 However, in non-captive animal populations, knowing the fate of an individual is
113 challenging. For instance, an individual alive is not necessarily detected by the observer. On
114 top of that, when the individual dies, identifying the cause of death is difficult because death
115 is never observed in a wild population. Thanks to the development of multi-state capture-
116 recapture (CR) models, estimating cause-specific mortality probability when detection is
117 imperfect and the cause of death is unobservable is now possible (20). Briefly, these methods

118 are applicable to the study of marked animals that are recaptured several times during their
119 life and recovered from at least one known cause of mortality (hunting for instance, see
120 (12,21) for case studies on wild boar). For example, Koons et al. (22) estimated age- and
121 cause-specific mortality probability, namely the mortality probability due to hunting vs. the
122 mortality probability due to human-unrelated causes, on lesser snow geese *Chen caerulescens*
123 *caerulescens* and roe deer *Capreolus capreolus* by fitting multi-state CR models. Noticeably,
124 mortality probability, defined as the probability for an individual to die during a given time
125 interval, is commonly used in the fields of statistical modelling of CR data. On the contrary,
126 mortality hazard rate, corresponding to the latent intensity of deadly events that an individual
127 is exposed to, is classically used in medicine and human demography (see (15) for a
128 discussion on the use of mortality hazard rates instead of mortality probabilities).

129

130 **Hunting**

131 From a literature survey, I report some of the studies that have quantified the main
132 causes of mortality affecting wild boars from young to older ages using individual monitoring
133 (table).

134 <Table near here>

135 Hunting is one of the major causes of mortality for the wild boar in Europe (7,23).
136 The annual probability for an individual to be killed by hunting ranges from 11 to almost
137 50% in the reviewed studies (table). It is noteworthy that this probability is often age-
138 dependent. For instance, thanks to a long-term individual monitoring and the use of CR
139 models, it has been shown that this source of mortality increases with increasing ages in
140 males at Châteauvillain in France (24). In the Nature Reserve of Somiedo in Spain, adults are
141 also those that are preferentially removed by hunting (25). This age-specific pattern of

142 human-induced mortality may be explained by the reluctance to shoot juveniles, a general
143 feature observed among hunters (26). Moreover, in wild boar, the probability to be killed by
144 hunting depends on the sex of the individual, subadult and adult males being more likely to
145 die from hunting than females.

146 This sex-specific pattern of human-induced mortality may result from contrasting
147 abilities to escape from hunters. Indeed, wild boar live in matrilineal social groups with one
148 large female leading a group (27) composed of juveniles with limited movement abilities
149 (28). Contrary to solitary subadult and adult males, family groups tend to favour coppice
150 habitats rather than bushlands during the hunting season (29). This can explain why subadult
151 and adult males are more likely to be hunted than females. Sex-specific patterns of human-
152 induced mortality may also simply result from hunting rules that orientate hunting pressure
153 on individuals with specific phenotypic characteristics. At Châteauvillain in France for
154 instance, hunters have to pay a financial penalty if they shoot females larger than 50 kg (30).
155 As a consequence, they prefer shooting a solitary male instead of shooting in a group, thus
156 increasing mortality on subadult and adult males and relaxing the hunting pressure on adult
157 females.

158

159 **Predation**

160 In some of the studied areas, human is not the only predator. In one Italian study site
161 where both red foxes (*Vulpes vulpes*) and wolves (*Canis lupus*) are present, the monitoring of
162 164 wild boars tagged with radio-collars or transmitters equipped with a mortality sensor has
163 shown that 2 of them died from predation (table, 28). In Poland, the analysis of wolf fecal
164 samples has confirmed that wild boar is part of the wolf diet (31). In a recent review, Mori et
165 al. (32) highlights that wild boar even constitutes the largest frequency of ungulate prey in

166 wolf diet across Italy, before roe deer, red deer (*Cervus elaphus*) and livestock (32).
167 However, for the wild boar, mortality due to predation does not exceed 0.06 and thus remains
168 small compared with human-induced mortality (table). Remarkably, this cause of mortality
169 mainly affects wild boar at young ages. In Italy, they represent 77% of the wolf diet and this
170 proportion even reaches 94% in Poland. Once again, such an age-specific pattern of predator-
171 induced mortality may be explained by the low abilities of juveniles to escap when facing a
172 predator.

173

174 **Other sources of mortality**

175 Wild boar can die from natural causes (i.e. not from human or non-human predation).
176 Natural mortality remains low, especially at adult stages (see table), translating to high
177 natural survival. This is expected among ungulates, where the average natural adult survival
178 probability was estimated to be 0.88 in males (see (36) for an analysis among 18 species) and
179 may exceed 0.95 in females (34). The reported studies (table) provide estimates of natural
180 survival at adulthood but age-specific survival patterns are ignored. However, a decline of
181 natural survival with increasing ages (hereafter actuarial senescence) may occur as a result of
182 the decline of the forces of natural selection with age (35), the selection of genes with a
183 beneficial effect early in life that are deleterious later on (36) as well as high fertility
184 translating to high rate of senescence (37).

185 Senescence is pervasive in the wild (see (38) for a review) and wild boar is not an
186 exception (39). Indeed, during an 18-year period at Castelporziano in Italy, 1783 juveniles
187 and subadults were marked with ear-tags, released after handling and recaptured later on. The
188 three oldest monitored individuals were 13 years of age. Thanks to this long-term individual
189 monitoring, we estimated natural survival probabilities for each age and sex (39). We found a

190 decrease of survival with age from age 3 onwards, with males exhibiting lower natural
191 survival than females. Sex-specific reproductive tactics that increase mortality risks for males
192 (40) can explain this between-sex difference. Also, harsh environmental conditions such as
193 droughts may affect male survival stronger than female survival (33). However, it is
194 noteworthy that this between-sex difference in adult survival remains quite weak (about 10%,
195 as in humans). Compared to other ungulates, wild boar females have earlier actuarial
196 senescence for their body size. The high and early fertility of wild boar females may advance
197 the age from which the decline of the forces of natural selection occurs (39).

198 In the first year of life, natural mortality can be higher than at adulthood (table). At
199 Castelporziano for instance, juvenile survival probability was only 0.68 [0.64; 0.72] (39). The
200 major cause of natural mortality that has been identified is caused by severe winters (see
201 (41,42) for large-scale studies). Snow cover and low temperatures make food resources in the
202 soil hardly accessible and increase juvenile mortality through disease and/or starvation. For
203 some authors, milder winters and thus enhanced juvenile survival might explain the recent
204 expansion of the species observed in the last decades (42). At Castelporziano, characterized
205 with a typical Mediterranean climate, severe droughts might explain such a low piglet
206 survival (43). In the second year of life, we found that natural survival reaches up to 0.85
207 [0.77; 0.91] for females and drops to 0.57 [0.50; 0.64] for males. Such a high natural
208 mortality for subadult males has already been reported in another site, at Châteauvillain in
209 France (12). At this period of their life, males often disperse from their natal area to become
210 solitary (44) and face with particularly increased mortality risks (e.g. starvation, collision
211 with vehicles).

212

213 **Interaction between causes of mortality**

214 It is clear from the three previous sections that different sources of mortality affect
215 wild boars from birth to older ages (see Figure for a schematic summary). These causes of
216 mortality are age-specific. For instance, while predators preferentially remove piglets, hunters
217 remove relatively more subadults and adults. They are also sex-specific, with higher mortality
218 risks due to starvation and collision with vehicles for males than for females. Finally, they
219 depend on the location of the studied population. For instance, the probability of dying from
220 starvation because of winter harshness or from predation by wolves obviously depends on the
221 study area.

222 <Figure near here>

223 Importantly, these sources of mortality can be additive. Basically, it means that they
224 are independent on each other and the overall mortality probability corresponds to the sum of
225 all causes of mortality. In other words, an individual that dies from hunting would have
226 survived in absence of hunting. But sources of mortality can be dependent on each other and
227 interact. They might be compensatory, i.e. negatively correlated such as the overall mortality
228 probability is lower than the sum of all causes of mortality. For instance, in a harvested duck
229 population, Hepp et al. (45) showed that the individuals with the lowest body condition and
230 thus with the lowest natural survival were more likely to be killed by hunting. In that case, an
231 increase of hunting mortality leads to a reduction in natural mortality because the “strongest”
232 individuals remain in the population. In that respect, predation by non-human predators is
233 directly comparable, because it mainly affects vulnerable individuals in a population such as
234 juveniles and senescents that often exhibit the highest natural mortality probability. Also, an
235 increase of hunting mortality or mortality due to predation might reduce population density
236 and thus disease transmission or competition among individuals. This ultimately leads to a
237 decrease of natural mortality (46). Sources of mortality may be dependant, i.e. positively
238 correlated such as the overall mortality probability is higher than the sum of all causes of

239 mortality. In that case, hunting can increase the mortality due to other causes. For instance,
240 trophy hunting that aims at removing individuals with the largest horns/antlers potentially
241 removes the individuals that perform the best in the population (47), leading to an increase of
242 natural survival. Hunting might also influence the way individuals use their habitat. In willow
243 ptarmigan *Lagopus lagopus* for instance, individuals spend more time in dense forests where
244 foraging opportunities and availability of food resources are limited, thus leading to a
245 decrease of body condition (48) and potentially high natural mortality. This change of habitat
246 also increases the risk of predation (48). As a consequence, understanding how hunting
247 interacts with other causes of mortality has become a central goal in animal ecology ((49), see
248 e.g. (50) for a case study on willow ptarmigan).

249 In wild boar, whether mortalities are additive, compensatory or depensatory is a
250 question that has been addressed in the population of Châteauvillain, in France. In that area,
251 hunting constitutes the main source of mortality, followed by natural mortality (see table).
252 Servanty et al. (21) found that these two sources of mortality are depensatory, natural
253 mortality increasing with hunting mortality. Several factors can explain this result. First,
254 selective hunting with the removal of the “best” individuals in the population may lead to
255 increased natural mortality probability. However, hunters are posted around a given area and
256 wait for animals startled by beaters and dogs. It is thus unlikely that they actually assess the
257 phenotypic quality of the individuals when they are flushed out of the vegetation. Second,
258 increased emigration in response to hunting can wrongly be interpreted as higher natural
259 mortality. However, wild boar is sedentary (44) and it is unlikely that increasing hunting
260 pressure is associated with increasing emigration rates. The only plausible explanation for an
261 increased natural mortality with high hunting mortality is crippling loss. Individuals wounded
262 or killed by hunting but never retrieved and recovered by hunters are considered as dead from
263 natural causes. This can explain higher mortality probabilities when the probability to be

264 killed by hunting is high (21). Whether compensatory mortalities are a common feature among
265 wild boar populations or are specific to the studied population remains to be investigated.

266

267 **Hunting mortality and life history strategy**

268 Wild boar survival is strongly affected by hunting at all ages. In addition, predation,
269 starvation, disease, collision with vehicles and finally senescence at older ages are additional
270 sources of mortality for the species. All these causes of mortality may result in a particularly
271 low overall survival probability. At Châteauvillain in France, overall survival probability is
272 close to 0.45 for females and drops to 0.23 for adult males (24) leading to a somewhat short
273 lifespan for such a long-lived species. In that context, one can wonder how wild boar
274 numbers can still increase throughout Europe despite such a low overall survival.

275 This is because fecundity has become the focus of all selective pressures and
276 particularly of hunting pressure. At Châteauvillain in France, birth dates have advanced by up
277 to 12 days in a 22-year period, selected by a high hunting pressure. This allows juveniles born
278 early in the season, to grow for longer and thus reach the threshold body mass to reproduce
279 early in life, in their first year of life (12). These findings of earlier age at first breeding are in
280 line with a demographic analysis (see 14) that has compared two wild boar populations in
281 contrasting environments: the French population suffering from a high hunting pressure and
282 the lightly hunted Italian population at Castelporziano in Italy (see table). This analysis shows
283 that the lightly hunted population has a typical demography of long-lived species with a high
284 contribution of adult survival to the population growth rate and a generation time of 3.6
285 years. However, the heavily hunted population has a typical demography of short-lived
286 species such as passerines, with the highest contribution for juvenile survival and exhibits an
287 accelerated life history with a shorter generation time close to 2 years (14). Therefore, in

288 environments characterized with a hunting mortality probability, wild boar females
289 compensate by reallocating resources to reproduction early in life. This explains why an
290 increase of hunting mortality probability does not translate to reduced population growth
291 rates in wild boar, contrary to other ungulate species such as roe deer. In that respect, wild
292 boar exhibits an unusual life history strategy among ungulates.

293

294 **References**

295

296

- 297 1. Horiuchi S, Wilmoth JR. Age patterns of the life table aging rate for major causes of death in
298 Japan, 1951-1990. *J Gerontol A Biol Sci Med Sci.* 1997;52(1):B67-77.
- 299 2. Horiuchi S, Finch CE, Meslé F, Vallin J. Differential Patterns of age-related mortality increase in
300 middle age and old age. *J Gerontol Ser A.* 2003;58(6):B495–507.
- 301 3. Forrester TD, Wittmer HU. A review of the population dynamics of mule deer and black-tailed
302 deer *Odocoileus hemionus* in North America. *Mammal Rev.* 43(4):292–308.
- 303 4. Proaktor G, Coulson T, Milner-Gulland EJ. Evolutionary responses to harvesting in ungulates. *J*
304 *Anim Ecol.* 2007;76(4):669–78.
- 305 5. Milner JM, Bonenfant C, Mysterud A. Hunting Bambi - evaluating the basis for selective
306 harvesting of juveniles. *Eur J Wildl Res.* 2011;57(3):565–74.
- 307 6. Apollonio M, Andersen R, Putman R. European ungulates and their management 21st century.
308 Cambridge University Press. 2010.
- 309 7. Massei G, Kindberg J, Licoppe A, Gačić D, Šprem N, Kamler J, et al. Wild boar populations up,
310 numbers of hunters down? A review of trends and implications for Europe. *Pest Manag Sci.*
311 2015;71(4):492–500.
- 312 8. Massei G, Genov PV. The environmental impact of wild boar. *Galemys Bol Inf Soc Esp Para*
313 *Conserv Estud Los Mamíferos.* 2004;16(1):135–45.
- 314 9. Barrios-Garcia MN, Ballari SA. Impact of wild boar (*Sus scrofa*) in its introduced and native range:
315 a review. *Biol Invasions.* 2012;14(11):2283–300.
- 316 10. Meng XJ, Lindsay DS, Sriranganathan N. Wild boars as sources for infectious diseases in livestock
317 and humans. *Philos Trans R Soc B Biol Sci.* 2009;364(1530):2697–707.
- 318 11. Servanty S, Gaillard J-M, Allainé D, Brandt S, Baubet E. Litter size and fetal sex ratio adjustment
319 in a highly polytocous species: the wild boar. *Behav Ecol.* 2007;18(2):427–32.

- 320 12. Gamelon M, Besnard A, Gaillard J-M, Servanty S, Baubet E, Brandt S, et al. High hunting pressure
321 selects for earlier birth date: wild boar as a case study. *Evolution*. 2011;65(11):3100–12.
- 322 13. Servanty S, Gaillard J-M, Toïgo C, Brandt S, Baubet E. Pulsed resources and climate-induced
323 variation in the reproductive traits of wild boar under high hunting pressure. *J Anim Ecol*.
324 2009;78(6):1278–90.
- 325 14. Servanty S, Gaillard J-M, Ronchi F, Focardi S, Baubet E, Gimenez O. Influence of harvesting
326 pressure on demographic tactics: implications for wildlife management. *J Appl Ecol*.
327 2011;48(4):835–43.
- 328 15. Ergon T, Borgan Ø, Nater CR, Vindenes Y. The utility of mortality hazard rates in population
329 analyses. *Methods Ecol Evol*. 2018;0(ja).
- 330 16. Tomkiewicz SM, Fuller MR, Kie JG, Bates KK. Global positioning system and associated
331 technologies in animal behaviour and ecological research. *Philos Trans R Soc Lond B Biol Sci*.
332 2010;365(1550):2163–76.
- 333 17. Heisey DM, Patterson BR. A review of methods to estimate cause-specific mortality in presence
334 of competing risks. *J Wildl Manag*. 2006;70(6):12.
- 335 18. Crowder MJ. *Classical competing risks*. CRC Press; 2001.
- 336 19. Collett D. *Modelling survival data in medical research*. CRC Press. Vol. Third Edition. 2014.
- 337 20. Pradel R. Multievent: an extension of multistate capture-recapture models to uncertain states.
338 *Biometrics*. 2005;61(2):442–7.
- 339 21. Servanty S, Choquet R, Baubet E, Brandt S, Gaillard J-M, Schaub M, et al. Assessing whether
340 mortality is additive using marked animals: a Bayesian state-space modeling approach. *Ecology*.
341 2010;91(7):1916–23.
- 342 22. Koons DN, Gamelon M, Gaillard J-M, Aubry LM, Rockwell RF, Klein F, et al. Methods for studying
343 cause-specific senescence in the wild. *Methods Ecol Evol*. 2014;5(9):924–933.
- 344 23. Keuling O, Baubet E, Duscher A, Ebert C, Fischer C, Monaco A, et al. Mortality rates of wild boar
345 *Sus scrofa* L. in central Europe. *Eur J Wildl Res*. 2013;59(6):805–14.
- 346 24. Toïgo C, Servanty S, Gaillard J-M, Brandt S, Baubet E. Disentangling natural from hunting
347 mortality in an intensively hunted wild boar population. *J Wildl Manag*. 2008;72(7):1532–9.
- 348 25. Nores C, Llaneza L, Álvarez Á. Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus*
349 predation: an example in northern Spain. *Wildl Biol*. 2008;14(1):44–51.
- 350 26. Sæther B-E, Engen S, Solberg EJ. Effective size of harvested ungulate populations. *Anim Conserv*.
351 2009;12(5):488–95.
- 352 27. Kaminski G, Brandt S, Baubet E, Baudoin C. Life-history patterns in female wild boars (*Sus*
353 *scrofa*): mother–daughter postweaning associations. *Can J Zool*. 2005;83(3):474–80.
- 354 28. Merli E, Grignolio S, Marcon A, Apollonio M. Wild boar under fire: the effect of spatial
355 behaviour, habitat use and social class on hunting mortality. *J Zool*. 2017;303(2):155–64.

- 356 29. Saïd S, Tolon V, Brandt S, Baubet E. Sex effect on habitat selection in response to hunting
357 disturbance: the study of wild boar. *Eur J Wildl Res.* 2012;58(1):107–15.
- 358 30. Gamelon M, Gaillard J-M, Servanty S, Gimenez O, Toïgo C, Baubet E, et al. Making use of harvest
359 information to examine alternative management scenarios: a body weight-structured model for
360 wild boar. *J Appl Ecol.* 2012;49(4):833–41.
- 361 31. Jędrzejewski Wł, Jędrzejewska B, Okarma H, Schmidt K, Zub K, Musiani M. Prey selection and
362 predation by wolves in Białowieża Primeval Forest, Poland. *J Mammal.* 2000;81(1):197–212.
- 363 32. Mori E, Benatti L, Lovari S, Ferretti F. What does the wild boar mean to the wolf? *Eur J Wildl Res.*
364 2017;63(1):9.
- 365 33. Toïgo C, Gaillard J-M. Causes of sex-biased adult survival in ungulates: sexual size dimorphism,
366 mating tactic or environment harshness? *Oikos.* 2003;101(2):376–84.
- 367 34. Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C. Temporal variation in fitness
368 components and population dynamics of large herbivores. *Annu Rev Ecol Syst.* 2000;31(1):367–
369 93.
- 370 35. Medawar PB. *An unsolved problem of biology.* Lewis, London; 1952.
- 371 36. Williams GC. Pleiotropy, natural selection, and the evolution of senescence. *Evolution.*
372 1957;11(4):398–411.
- 373 37. Hamilton WD. The moulding of senescence by natural selection. *J Theor Biol.* 1966;12(1):12–45.
- 374 38. Nussey DH, Froy H, Lemaître J-F, Gaillard J-M, Austad SN. Senescence in natural populations of
375 animals: widespread evidence and its implications for bio-gerontology. *Ageing Res Rev.*
376 2013;12(1):214–25.
- 377 39. Gamelon M, Focardi S, Gaillard J-M, Gimenez O, Bonenfant C, Franzetti B, et al. Do age-specific
378 survival patterns of wild boar fit current evolutionary theories of senescence? *Evolution.*
379 2014;68(12):3636–3643.
- 380 40. Bonduriansky R, Maklakov A, Zajitschek F, Brooks R. Sexual selection, sexual conflict and the
381 evolution of ageing and life span. *Funct Ecol.* 2008;22(3):443–53.
- 382 41. Melis C, Szafrńska PA, Jędrzejewska B, Bartoń K. Biogeographical variation in the population
383 density of wild boar (*Sus scrofa*) in western Eurasia. *J Biogeogr.* 33(5):803–11.
- 384 42. Vetter SG, Ruf T, Bieber C, Arnold W. What is a mild winter? regional differences in within-
385 species responses to climate change. *PLOS ONE.* 2015;10(7):e0132178.
- 386 43. Focardi S, Gaillard J-M, Ronchi F, Rossi S. Survival of wild boars in a variable environment:
387 unexpected life-history variation in an unusual ungulate. *J Mammal.* 2008;89(5):1113–23.
- 388 44. Truvé J, Lemel J. Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. *Wildl*
389 *Biol.* 2003;9(1):51–7.
- 390 45. Hepp GR, Blohm RJ, Reynolds RE, Hines JE, Nichols JD. Physiological condition of autumn-banded
391 mallards and its relationship to hunting vulnerability. *J Wildl Manag.* 1986;50(2):177–83.

- 392 46. Boyce MS, Sinclair ARE, White GC. Seasonal compensation of predation and harvesting. *Oikos*.
393 1999;87(3):419–26.
- 394 47. Mysterud A, Bischof R. Can compensatory culling offset undesirable evolutionary consequences
395 of trophy hunting? *J Anim Ecol*. 2010;79(1):148–60.
- 396 48. Brøseth H, Pedersen HC. Disturbance effects of hunting activity in a willow ptarmigan *Lagopus*
397 *lagopus* population. *Wildl Biol*. 2010;16(3):241–8.
- 398 49. Péron G. Compensation and additivity of anthropogenic mortality: life-history effects and review
399 of methods. *J Anim Ecol*. 2013;82(2):408–17.
- 400 50. Sandercock BK, Nilsen EB, Brøseth H, Pedersen HC. Is hunting mortality additive or
401 compensatory to natural mortality? Effects of experimental harvest on the survival and cause-
402 specific mortality of willow ptarmigan. *J Anim Ecol*. 2011;80(1):244–58.
- 403

404 Table - Summary of some studies reporting causes of mortality that affect wild boar over life. Location of the studied population, annual
405 mortality probabilities due to hunting, predation or other causes (e.g. disease, starvation) and the reference of the study are provided. Potential
406 age- and sex-related variations in mortality probabilities are also reported with the associated sentences extracted from the papers.
407

Population	Hunting	Predation	Others	Age-related variation	Sex-related variation	Reference
Castelporziano, Italy	11%	0%	32%	<p>Hunting: “Harvest rates were highest for juveniles and subadults, albeit for juveniles the proportion harvested alternated between very low (>2%) to moderately high (10-15%) in different years.”</p> <p>Others: “for females, [natural] survival was constant among age classes, [natural] survival of males differed among age classes”.</p>	<p>Hunting: “The proportion of males harvested was always larger than the proportion of females, indicating a higher harvest probability for males”.</p> <p>Others: “[natural] survival of males and females differed only for yearlings”.</p>	(43)
Nature Reserve of Somiedo, Spain	12%	4.5%	NA	<p>Hunting: “the mortality caused by hunting drives tends to affect the adult age groups more”.</p> <p>Predation: “Wolf exerts a higher pressure on juveniles rather than on adults”.</p>	NA	(25)
Tuscan Apennines, Italy	45.6% ¹	2 individuals out of 105 during a 9-year period	1 individual out of 105 during a 9-year period	<p>Hunting: “subadult wild boars, no matter their sex, had a slightly significantly higher probability to be killed than adults and piglets.”</p>		(28)
Bialowieza Forest,	16%	6%	NA	Predation:	NA	(31)

Poland				“Wolves hunted young individuals”.		
Châteauvillain, France	49.8%	0%	15%	<p>Hunting: “Probability of being harvested was high and increased with age [for males], from 0.41 for piglets to 0.70 for adults”/ “Probability of being harvested did not differ between piglets and adults and averaged 0.38 [for females]”.</p> <p>Others: “We estimated natural mortality² of wild boar males at 0.14 [...] regardless of age-class.”/ “piglet females had a higher natural mortality rate (0.18) than adults (0.12).”</p>	<p>Hunting: “harvest focused on adult males, [...] with limited hunting pressure on adult females and piglets”.</p> <p>Others: “Natural mortality of adults was similar for males and females”.</p>	(24)

408 ¹ This value corresponds to the sum of legal hunting (32%) and poaching (13.6%) rates.

409 ² Natural mortality corresponds to mortality excluding hunting mortality.

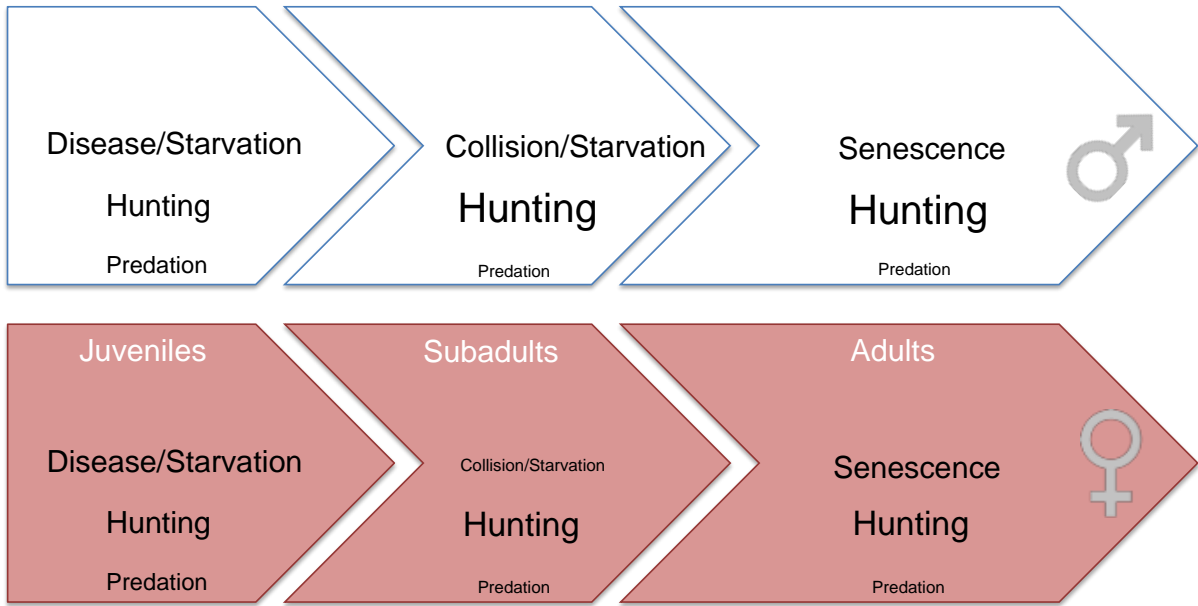
410

411

412

413 Figure – Wild boar life cycle showing the causes of mortality affecting wild boar over life
414 (from left to right) in males (upper plot) and females (lower plot). The font size indicates the
415 relative importance of each cause of mortality (small font size corresponds to low importance
416 and large font size to high importance).

417



418

419

420

421

422

423

424

425

426

427