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1 **Mechanistic modelling of African swine fever: A systematic review**

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16 any organization or entity with any financial interest or non-financial interest in the subject matter or
17 materials discussed in this manuscript.

18

19 Short title/running head: ASF Mechanistic Modelling — Systematic Review

20

21 **Abstract**

22 The spread of African swine fever (ASF) poses a grave threat to the global swine industry.
23 Without an available vaccine, understanding transmission dynamics is essential for designing effective
24 prevention, surveillance, and intervention strategies. These dynamics can often be unraveled through
25 mechanistic modelling. To examine the assumptions on transmission and objectives of the mechanistic
26 models of ASF, a systematic review of the scientific literature was conducted. Articles were examined
27 across multiple epidemiological and model characteristics, with filiation between models determined
28 through the creation of a neighbor-joined tree using phylogenetic software.

29 Thirty-four articles qualified for inclusion, with four main modelling objectives identified:
30 estimating transmission parameters (11 studies), assessing determinants of transmission (7), examining
31 consequences of hypothetical outbreaks (5), assessing alternative control strategies (11). Population-
32 based (17), metapopulation (5), and individual-based (12) model frameworks were represented, with
33 population-based and metapopulation models predominantly used among domestic pigs, and
34 individual-based models predominantly represented among wild boar. The majority of models (25) were
35 parameterized to the genotype II isolates currently circulating in Europe and Asia.

36 Estimated transmission parameters varied widely among ASFV strains, locations, and
37 transmission scale. Similarly, parameter assumptions between models varied extensively. Uncertainties
38 on epidemiological and ecological parameters were usually accounted for to assess the impact of
39 parameter values on the modelled infection trajectory. To date, almost all models are host specific,
40 being developed for either domestic pigs or wild boar despite the fact that spillover events between
41 domestic pigs and wild boar are evidenced to play an important role in ASF outbreaks. Consequently,
42 the development of more models incorporating such transmission routes is crucial. A variety of codified
43 and hypothetical control strategies were compared however they were all *a priori* defined interventions.
44 Future models, built to identify the optimal contributions across many control methods for achieving
45 specific outcomes should provide more useful information for policy-makers. Further, control strategies
46 were examined in competition with each other, which is opposed to how they would actually be
47 synergistically implemented. While comparing strategies is beneficial for identifying a rank-order
48 efficacy of control methods, this structure does not necessarily determine the most effective
49 combination of all available strategies. In order for ASFV models to effectively support decision-making
50 in controlling ASFV globally, these modelling limitations need to be addressed.

51 **Keywords**

52 African swine fever, modelling, systematic review, phylogenetic tree

53

54 **Abbreviation List**

- 55 1. African swine fever (ASF)
- 56 2. African swine fever virus (ASFV)
- 57 3. European Union (EU)
- 58 4. Foot and mouth disease (FMD)
- 59 5. Classical swine fever (CSF)
- 60 6. Population-based model (PBM)
- 61 7. Individual-based model (IBM)
- 62 8. Susceptible, exposed, infectious, removed (SEIR)
- 63 9. Susceptible, exposed, infectious (SEI)
- 64 10. Denmark Technical University, Davis Animal Disease Simulation, African Swine Fever model
- 65 (DTU-DADS-ASF)
- 66 11. Between Farm Animal Spatial Transmission model (Be-FAST)
- 67 12. North American Animal Disease Spread Model (NAADSM)
- 68 13. Susceptible, infectious (SI)
- 69 14. Confidence interval (CI)
- 70 15. Highest posterior density interval (HPDI)
- 71 16. Credible interval (CrI)

72 Introduction

73 African swine fever (ASF) is one of the highest consequence diseases of domestic pigs, listed as a
74 notifiable disease by the World Organization for Animal Health (OIE, 2019). With a case-fatality rate
75 approaching 100% for highly-virulent strains and severe trade restrictions wherever its emergence is
76 recognized, this hemorrhagic fever is socioeconomically devastating to both individual farms and
77 affected countries (FAO, 2009; Blome et al., 2013; Dixon et al., 2020).

78 African swine fever is caused by the ASF virus (ASFV), a double-stranded DNA virus belonging to
79 the sole genus *Asfivirus* within the *Asfarviridae* family, and is the only known DNA arbovirus (Alonso et
80 al., 2018; Dixon et al., 2020). The virus is genetically and antigenically highly variable, and with twenty-
81 four genotypes identified ASFV can infect all members of the *Suidae* family, though only *Sus scrofa*
82 (including domestic and feral pigs, and Eurasian wild boar) exhibit clinical disease (Sánchez-Vizcaíno et
83 al., 2012; Dixon et al., 2020).

84 Endemic to most sub-Saharan countries, ASF was discovered following the introduction of
85 European domestic pigs into Kenya in 1921 (Barongo et al., 2015; Portugal et al., 2015). The first
86 incursion outside Africa occurred in Portugal in 1957, and throughout the latter-half of the 20th century
87 outbreaks had been reported in multiple European countries, the Caribbean, and Brazil (Costard et al.,
88 2009). By 1995 the European outbreaks were controlled all but for the island of Sardinia, where ASF
89 genotype I is now endemic since its introduction in 1978 (Costard et al., 2009; Cwynar et al., 2019).

90 In 2007, ASF was again introduced to Europe through the Georgian Republic (Gulenkin et al.,
91 2011). Highly virulent among both domestic pigs and wild boar, the Georgia 2007/1 isolate — identified
92 as belonging to ASFV genotype II — rapidly spread across the Caucasus region (Rowlands et al., 2008;
93 Gulenkin et al., 2011). Ukraine and later Belarus reported cases in 2012 and 2013, respectively, and in
94 2014 ASF was identified in the European Union (EU) following incursion into Lithuania, Latvia, Poland,
95 and Estonia (Bosch et al., 2017). In addition to spreading through the EU, ASFV was detected in China —
96 the world's largest pork producer — in 2018 and subsequently reported in many south-east Asian
97 countries (FAO, 2020; Vergne et al., 2020b). Transmission pathways across affected regions have been
98 variable, with some countries experiencing dissemination exclusively within wild boars and others
99 seeing a spread pattern predominantly among domestic pigs with likely intermittent spillover from wild
100 boars (Chenais et al., 2019).

101 No treatment or vaccine exists for ASF, and established control measures reflect the necessity of
102 aggressive action to achieve outbreak control. The lack of available vaccination or treatment is due to
103 many factors including knowledge gaps on ASFV infection and immunity, variation among strains and
104 protective antigens, experimental testing being limited to only pigs and boar kept in high biosecurity
105 facilities, and adverse reactions seen during historical vaccination attempts (Rock, 2017; Gavier-Widén
106 et al., 2020). Should an outbreak be identified, EU legislation mandates depopulation of affected farms,
107 contact tracing of animals and animal products, and the establishment of protection and surveillance
108 zones around the affected premise within which disinfection, movement restriction, and active
109 surveillance measures must occur (Council of the European Union, 2002). Similarly, recommendations
110 by the European Commission on wildlife management includes the definition of core infected and
111 surrounding surveillance zones, active carcass search and removal, installation of fences, and intensive
112 wild boar depopulation (FAO, 2019). Designing effective prevention, surveillance, and intervention
113 strategies requires the understanding of transmission dynamics, and these dynamics can often be
114 unraveled through the use of mechanistic modelling (Keeling and Rohani, 2008).

115 Mechanistic models have been successfully applied to many epizootic incursions including foot-
116 and-mouth disease (FMD) (Pomeroy et al., 2017), classical swine fever (CSF) (Backer et al., 2009), and

117 bluetongue (Courtejoie et al., 2018), to assess vaccination strategies, design and evaluate targeted and
118 alternative control strategies, and elucidate epidemiological parameters, respectively. Mechanistic
119 models can be constructed through a variety of frameworks (e.g. population- or individual-based models
120 (PBM or IBM)) with differences among multiple model characteristics including the approaches to space
121 (i.e. spatially or non-spatially explicit), time (i.e. discrete or continuous), and uncertainty (deterministic
122 or stochastic) (Bradhurst et al., 2015). The objective of a model will inform the selection of such design
123 parameters, which will also play a role in informing the underlying model assumptions (Marion and
124 Lawson, 2015). Only following the incursion of ASF into the Eurasian continent did mechanistic models
125 of ASF begin to be explored, as identified in a literature review of modelling viral swine diseases
126 (Andraud and Rose, 2020). In order to identify gaps in specific ASF modelling strategies with regard to its
127 present epidemiology, through examining the assumptions on transmission and objectives of the
128 mechanistic models of ASF, a systematic review of the scientific literature was conducted.

129

130 **Material and methods**

131 *Literature search*

132 The systematic review was performed in accordance with PRISMA guidelines (Liberati et al.,
133 2009). The search query was constructed to identify all publications on ASF in any species that
134 incorporated the use of mechanistic models. No restrictions were imposed on publication language
135 (other than through the use of English search terminology), study location, or publication date. Eight
136 target publications on mathematical modelling of ASF, selected through author familiarity of the subject
137 and diverse among animal host and literature type (black and white literature and grey literature), were
138 identified to calibrate the literature search. The literature search was conducted initially on January 31,
139 2020 through terms agreed upon by all researchers in the following Boolean query: “*African swine*
140 *fever*” AND *model** AND (*math** OR *mechani** OR *determin** OR *stochast** OR *dynam** OR *spat** OR
141 *distrib** OR *simulat** OR *comput** OR *compart** OR *tempor**). Terms were searched in the fields title and
142 abstract, title abstract and subject, or title and topic, for Medline, CAB Abstracts, and Web of Science,
143 respectively. The search was repeated prior to publication (January 18, 2021) to capture all relevant
144 articles through December 31, 2020.

145

146 *Study Selection*

147 Inclusion criteria for the articles were the topic of African swine fever and reference to a
148 mechanistic model either directly or indirectly (e.g. through mention of a specific type of model).
149 Exclusion criteria were more exhaustive and consisted of the following: non-population models (e.g.
150 within-host), virological and genomic models, non-suid models (e.g. models exclusively of the arthropod
151 vector), and non-mechanistic models (e.g. statistical or purely economic models).

152 Primary screening of title and abstract was performed by two authors. Kappa scores (κ) were
153 calculated to determine interrater reliability. Discussion among authors occurred until a consensus on
154 qualifying studies was reached. Full-text articles were subsequently assessed for eligibility with all the
155 above criteria plus the additional inclusion criteria of containing an explicit process of infection and not
156 being a duplication of published results, and cross-validated by other authors. Snowball sampling was
157 used to identify any remaining mechanistic modelling articles. Specific screening questions are available
158 online as supplementary material.

159

160 *Data collection process*

161 Table shells were created to capture study design and model properties. Publication information
162 (authors, year), ASF outbreak data (host, ASFV strain (genotype and isolate), location of study), research
163 methodology (data collection method, study direction (ex-post or ex-ante)), model components
164 (framework, temporality, spatiality, infection states), model descriptors (transmission scale, basic
165 epidemiological unit, model objective), and model parameter assumptions were all recorded.

166

167 *Filiation tree construction*

168 To assess model filiation, a distance-based phylogenetic tree of the selected studies was
169 constructed. This was performed via the neighbor-joining method of tree construction using Molecular
170 Evolutionary Genetics Analysis (MEGA) software (Kumar et al., 2018). This methodology was chosen as it
171 produces a parsimonious tree based on minimum-evolution criterion (Saitou and Nei, 1987; Pardi and
172 Gascuel, 2016). Full characteristics of all models were assessed (Supplementary Material, Table A), and
173 cross-correlation between those characteristics resulted in the selection of four main variables: host
174 (domestic pig, wild boar, or both), data collection methodology (experimental, observational, or
175 simulation), model framework (PBM, IBM, or metapopulation), and model objective (estimating
176 parameters, assessing alternative control strategies, assessing determinants of transmission, or
177 examining consequences of hypothetical outbreaks). Vectors of each model were constructed by
178 dummifying selected model components by their subcategory and then calculating pairwise differences
179 between all model pairings. The corresponding values formed a distance matrix that was then used for
180 analysis.

181

182 **(Results) Included publications and epidemiological characteristics**

183 *Publications*

184 A total of 351 articles were identified across all databases (Figure 1). Following removal of
185 duplicate references, 171 records remained for primary screening. Out of these, 36 full-text articles
186 were determined to qualify for secondary screening. With $\kappa = 0.65$, the reviewers were determined to
187 be in substantial agreement (Landis and Koch, 1977). Four articles were excluded in secondary
188 screening. Two additional studies were identified through snowball sampling resulting in 34 articles for
189 review. A marked increase in the number of mechanistic modelling publications occurred in the most
190 recent year of review (Figure 2). Closely split between models among domestic pigs and wild boar
191 (referred to as “pigs” and “boar” in tables and figures), 2020 saw a doubling in the number of publications
192 (10) compared to previous most-published years.

193

194 *Epidemiological characteristics*

195 Out of 34 mechanistic modelling studies on ASF, 20 modelled disease dynamics specifically in
196 domestic pigs, 12 modelled disease dynamics specifically in wild boar, and two included transmission
197 between wild and domestic hosts (Table 1). The majority of studies (25) were parameterized to the
198 genotype II strains currently circulating in Europe (i.e. Georgia 2007/1, Armenia 2008), including the first
199 mechanistic model of ASF (Gulenkin et al., 2011) and all but one of the wild boar models.

200 Different strains were considered depending on their geographical spread. Genotype I dynamics
201 were modelled both in Sardinia where it is endemic (Mur et al., 2018; Loi et al., 2020), and in an

202 experimental study with the Malta 1978 and Netherlands 1986 isolates (Ferreira et al., 2013). Genotype
203 IX was modelled in its home range of Eastern Africa both ex-post to a historical outbreak (Barongo et al.,
204 2015) as well as via a simulation for assessing control measures (Barongo et al., 2016). Genotype II
205 strains were examined ex-post among domestic pigs to historical outbreaks in the Russian Federation
206 (Gulenkin et al., 2011; Guinat et al., 2018), via transmission experiments in domestic pigs (Guinat et al.,
207 2016b; Hu et al., 2017; Nielsen et al., 2017) or between both domestic pigs and wild boar (Pietschmann
208 et al., 2015), and through a multitude of in-silico simulations of both domestic pigs (Halasa et al., 2016a,
209 2016b, 2016c, 2018; Andraud et al., 2019; Faverjon et al., 2020; Lee et al., 2020; Vergne et al., 2020a)
210 and wild boar herds (Lange, 2015; Lange and Thulke, 2015; Thulke and Lange, 2017; Lange et al., 2018;
211 Gervasi et al., 2019; Halasa et al., 2019; Croft et al., 2020; O'Neill et al., 2020; Pepin et al., 2020; Taylor
212 et al., 2020). One model of ASF spread, which was focused on spread due to wild boar dispersion,
213 considered the influence of transmission from outdoor free-range domestic pigs (Taylor et al., 2020).

214 The term “herd” was chosen to refer to an animal collective and will be used for the remainder
215 of this article, with it being interchangeable with the terms farm (Gulenkin et al., 2011; Nigsch et al.,
216 2013; Mur et al., 2018), production unit (Halasa et al., 2016a), and parish (Barongo et al., 2016). Further,
217 for the purpose of standardization of terms for model comparison, sub-population groups of wild boar
218 (known as sounders) are herein referred to as herds as well.

219

220 **(Results) Model objectives and filiation**

221 *Model objectives*

222 Four main modelling objectives were identified: Estimating parameters (11), assessing
223 determinants of transmission (7), examining consequences of hypothetical outbreaks (5), and assessing
224 alternative control strategies (11) (Table 2).

225 The majority of domestic pig models — including the first two ASF models (Gulenkin et al., 2011;
226 Ferreira et al., 2013) — and three of the wild boar models (Pietschmann et al., 2015; Lange and Thulke,
227 2017; Loi et al., 2020) focused on estimating various transmission parameters using either experiment-
228 based or field-observation data. The predominant parameters calculated were the transmission
229 coefficient β (which determines the rate of new infections per unit time, via the product of the contact
230 rate and transmission probability) and the basic reproduction ratio R_0 (the average number of secondary
231 cases produced by one infectious individual in a fully susceptible population) (Table 3) (Anderson and
232 May, 1992; Keeling and Rohani, 2008). β s ranged from 0.0059 herds per infected herd per month for
233 between herd transmission of genotype IX (Barongo et al., 2015) to 2.79 (95% CI 1.57, 4.95) pigs per day
234 for within-pen transmission of the Malta 1978 isolate (Ferreira et al., 2013). R_0 values ranged from 0.5
235 (95% CI 0.1, 1.3) for indirect transmission of the Armenia 2008 isolate between boar and pigs
236 (Pietschmann et al., 2015) to 18.0 (95% CI 6.90, 46.9) for transmission of the Malta 1978 isolate
237 between domestic pigs (Ferreira et al., 2013). Among the wild boar models, Pietschmann et al. (2015)
238 used the Armenia 2008 isolate to calculate R_0 among wild boar and between boars and pigs in a
239 laboratory setting, Lange and Thulke (2017) trained an artificial neural network on spatiotemporally-
240 explicit case notification data to determine the probability of carcass-mediated and direct transmission
241 between boar herds, and Loi et al. (2020) estimated both the basic and effective reproduction numbers
242 (R_0 and R_e , respectively) in Sardinia through historical hunting data coupled with virological and
243 serological testing data. Lastly, via estimating R_0 and the disease-free equilibrium for varying parameter
244 sets, one recent model examined the mathematical theorems behind the differential equations used in
245 many ASF models to determine if integer or fractional order systems better describe ASF epidemic
246 dynamics (Shi et al., 2020).

247 Seven simulation models were used to disentangle determinants of transmission of ASF. Of the
248 four models in domestic pigs, the first model by Nigsch et al. (2013) simulated international trade
249 patterns to determine the EU member nations most susceptible to importation and exportation of ASF.
250 Halasa et al. (2016a) simulated ASFV transmission within a pig herd to examine the influences of dead
251 animal residues and herd size, and Mur et al. (2018) simulated ASFV transmission between pig herds in
252 Sardinia to determine the influence of farm and contact type. Lastly among pigs, Vergne et al. (2020a)
253 looked at the influence of the feeding behavior of *Stomoxys* flies on ASFV transmission in a simulated
254 outdoor farm. Halasa et al. (2019) examined the transmission pathway of ASFV in wild boar among
255 varying population densities. This past year Pepin et al. (2020) modelled the contribution of carcass-
256 based transmission to the on-going outbreak in boar in Eastern Europe, while O'Neill et al. (2020) looked
257 at the influence of host and environmental factors on ASFV persistence in scenarios of contrasting
258 environmental conditions.

259 Assessing alternative control strategies via simulations was the most frequent objective among
260 wild boar studies (Lange, 2015; Lange and Thulke, 2015; Thulke and Lange, 2017; Lange et al., 2018;
261 Gervasi et al., 2019). The strategies examined consisted of combinations of mobile barriers,
262 depopulation, feeding bans, intensified and targeted hunting, carcass removal, and variations in active
263 and passive surveillance. Taylor et al. (2020) focused on varying intensities of carcass removal, hunting,
264 and fencing for interrupting ASF spread due only to wild boar movements. In domestic pigs, control
265 strategies that were assessed consisted of improving the sensitivity of detection of ASF by farmers
266 (Costard et al., 2015), enhancing biosecurity (Barongo et al., 2016), theoretical vaccination (Barongo et
267 al., 2016), and instituting EU-legislated and nationally-legislated (Danish) control measures in
268 combination with alternative methods (Halasa et al., 2016c). These codified measures simulated by
269 Halasa et al. (2016c) encompassed a nationwide shutdown of swine movements, culling of infected
270 herds, implementation of both movement restriction and enhanced surveillance zones, contact tracing,
271 and pre-emptive depopulation of neighboring herds. Most recently, Faverjon et al. (2020) quantified the
272 mortality thresholds that permit the best balance between rapid detection of ASF while minimizing false
273 alarms within domestic pig herds, and Lee et al. (2020) modelled ASF in Vietnam to determine the
274 efficacy of movement restrictions of varying intensities.

275 Five models assessed the consequences of hypothetical outbreaks, with four focusing on the
276 Georgia 2007/1 strain. Three models examined ASF within industrialized swine populations, with
277 transmission through both Danish (Halasa et al., 2016b, 2018) and French (Andraud et al., 2019) swine
278 systems simulated. Croft et al. (2020) examined the outcome of natural circulation of ASF in an isolated
279 boar population in an English forest, and Yang et al. (2020) applied ASF parameters to their network
280 model of wild boar to determine its spread in the United States.

281

282 *Filiation tree and model characteristics*

283 The generation of the neighbor-joined filiation tree allowed for the identification of three
284 clusters of models: models used for parameter estimations, simulation models in domestic pigs, and
285 individual-based models (Figure 3). The individual-based simulation models (with the exceptions of
286 Gervasi et al. (2019) and Yang et al. (2020)) grouped at the bottom of the tree, the domestic pig
287 simulation models clustered in the middle (with the exception of O'Neill et al. (2020) focused on wild
288 boar), and the parameter estimation models clustered in the top-most group.

289 The parameter estimation cluster, internally parsed by data collection methodology, consisted
290 mostly of stochastic, non-spatial population-based models that derived parameters for within-herd
291 (including within and between pen) transmission between pigs (Ferreira et al., 2013; Guinat et al.,

292 2016b; Hu et al., 2017; Nielsen et al., 2017; Guinat et al., 2018) (Table 2). Gulenkin et al. (2011) and
293 Barongo et al. (2015) calculated ASF parameters for transmission between herds, and Loi et al. (2020)
294 estimated transmission parameters between wild boar. Seven of the nine models focused on the
295 currently-circulating genotype II strain. Though the Shi et al. (2020) model also estimated parameters,
296 due to its simulation methodology it was clustered with the rest of the domestic pig simulations.

297 Five population-based models were used to simulate within-herd transmission in domestic pigs
298 (Barongo et al., 2016; Halasa et al., 2016a; Faverjon et al., 2020; Shi et al., 2020; Vergne et al., 2020a),
299 and one did so for wild boar (O'Neill et al., 2020), though capturing between-herd transmission
300 dynamics saw the use of stochastic, temporally discrete, spatially-explicit metapopulation models
301 (Halasa et al., 2016b, 2016c, 2018; Mur et al., 2018; Andraud et al., 2019). Two named metapopulation
302 models were represented: the Denmark Technical University - Davis Animal Disease Simulation - African
303 Swine Fever (DTU-DADS-ASF) model (Halasa et al., 2016b, 2016c, 2018; Andraud et al., 2019) and the
304 Between Farm Animal Spatial Transmission (Be-FAST) model (Mur et al., 2018). Both the Be-FAST and
305 DTU-DADS-ASF models were updates of previously published models. The Be-FAST model, originally
306 designed to simulate CSF spread within and between farms, was adapted for the ASF situation in
307 Sardinia. The DTU-DADS-ASF model, an extension of the existing DTU-DADS model originally designed
308 for the spread of foot-and-mouth disease in pigs, was constructed through inserting the within-herd
309 model sensitive to unit size (from Halasa et al. (2016a)) into the existing DTU-DADS model. This new
310 model, reflecting an industrialized swine population, simulated epidemiological and economic outcomes
311 of an outbreak (Halasa et al., 2016b) and was later used to assess alternative control strategies (Halasa
312 et al., 2016c). This model was further refined to exemplify the Danish and French swine populations,
313 where the consequences of hypothetical outbreaks were assessed (Halasa et al., 2018; Andraud et al.,
314 2019).

315 Both the DTU-DADS-ASF and the Be-FAST models relied on simulated live-animal movements
316 and kernel-based distances to model susceptible-infectious contacts between herds. In the DTU-DADS-
317 ASF model, movements (including both animal movements between herds and indirect contacts such as
318 abattoir movements and contact with vehicles and animal health workers) were simulated through
319 series of transmission probabilities parameterized to historical movement frequency data in the
320 represented location (Denmark or France). Distance-based probabilities between herds were used to
321 model local spread. The Be-FAST model also considered direct and indirect contact between herds, using
322 a metapopulation framework to model trade networks and indirect means of spread (Ivorra et al.,
323 2014). Whereas the Be-FAST model used SI infection states within herds, the DTU-DADS-ASF simulation
324 used a modified SEIR model with the infectious state split into sub-clinical and clinical states.

325 Stochastic, discrete, spatially-explicit individual-based models, mostly focused on assessing
326 alternative control strategies, were the predominant approaches to modelling ASF in wild boar, with the
327 exceptions of Croft et al. (2020) who used a deterministic approach and Gervasi et al. (2019) and Yang et
328 al. (2020) who used deterministic non-spatial population-based models. Of the spatially-explicit
329 individual-based models, unlike in the domestic pig metapopulation models, disease spread was
330 simulated exclusively through movement-based algorithms. For the ASF Wild Boar model (Lange, 2015;
331 Lange and Thulke, 2015; Thulke and Lange, 2017; Lange et al., 2018), the model replicated from it
332 (Halasa et al., 2019), and the model by Pepin et al. (2020), this was accomplished using a rasterized
333 spatial habitat grid. In order to avoid raster-associated bias in their model, Croft et al. (2020) elected
334 against a grid-based landscape, instead using a mosaic of irregular polygons scaled to the average wild
335 boar herd range. In all these models, individual animal movements occurred via dispersal and
336 orientation probabilities of each individual animal, followed by upper-bounded number of dispersal
337 steps that could be taken. Unlike domestic pig simulations or the Halasa et al. (2019) and Pepin et al.
338 (2020) wild boar simulations, the ASF Wild Boar individual-based models (Lange, 2015; Lange and

339 Thulke, 2015; Thulke and Lange, 2017; Lange et al., 2018) and Croft et al. (2020) used weekly not daily
340 time steps in their process scheduling.

341 Three domestic pig models used individual-based frameworks as well, to examine routes of ASF
342 transmission between EU Member States (Nigsch et al., 2013), the efficacy of movement-restriction
343 control measures (Lee et al., 2020), and to assess controlling the silent release of ASF from farms
344 (Costard et al., 2015). For evaluating transmission determinants in the EU, Interspread Plus — a
345 proprietary software program that allows for modelling a variety of animal diseases — used movement-
346 based algorithms to simulate disease spread between herds but did not account for distance-based
347 transmission routes. It was used to model the transmission of ASF both within and between countries.
348 Both pig movements between farms as well as indirect contacts within-country were modelled, followed
349 by simulated export movements. A similar stochastic, discrete, spatially-explicit state-transition model
350 was adapted to the swine network in Vietnam by Lee et al. (2020) — the North American Animal Disease
351 Spread Model (NAADSM). Here, farm-type-dependent contact probabilities and rates simulated animal
352 trade movements. To ascertain the risk of ASF spread secondary to an emergency sell-off of pigs,
353 Costard et al. (2015) developed their own individual-based model. Here, ASF transmission was
354 stochastically simulated within a herd and then coupled to data on the behavior of farmers to determine
355 the risk of ASF spread outside the affected herd.

356

357 **(Results) Model insights and assumptions**

358 *Model parameters*

359 ASF transmission parameters, estimated from models with both individuals and herds acting as
360 the basic epidemiological unit (depending on the study), were often used to parameterize future models
361 — though a variety of other parameter data sources were identified as well (Table 4). This resulted in a
362 range of values being used for ASFV's infectious period, incubation period (the time between infection
363 and clinical signs), and latent period (classically considered as the time between infection and
364 infectiousness, though in Costard et al. (2015) this was defined as infectious without clinical signs) across
365 all models. When ASF data was unavailable, certain parameters had to be adapted from other disease
366 models. Transmission probabilities for pig movements (Nigsch et al., 2013), indirect contacts (Nigsch et
367 al., 2013; Halasa et al., 2016a, 2016b, 2016c; Mur et al., 2018; Halasa et al., 2018; Andraud et al., 2019),
368 and local spread (Halasa et al., 2016a, 2016b, 2016c, 2018; Mur et al., 2018; Andraud et al., 2019) were
369 adapted from CSF studies, as was the range for R_0 in Costard et al. (2015). When alternative control
370 strategies were evaluated, some parameters that determined the probability of success of a control
371 measure and the time required for its implementation were adapted from CSF or FMD studies as well
372 (Halasa et al., 2016b, 2016c, 2018; Andraud et al., 2019).

373 Limited field data for wild boar resulted in the evolution of many assumptions as new
374 information was discovered. Carcass-based transmission was modelled through direct transmission
375 within and between groups first as sex-dependent (Lange and Thulke, 2015), then neither age nor sex-
376 dependent (Lange, 2015; Lange and Thulke, 2017), and then as age-dependent (Lange et al., 2018).
377 Infection probability per carcass was originally parameterized at 20% according to the best-fit model
378 that explained the observed data (Lange and Thulke, 2015). Camera trapping data (Probst et al., 2017)
379 and the results of Lange and Thulke (2017) resulted in this parameter being refined to 2-5% in the
380 subsequent model (Lange et al., 2018). The assumed live infectious periods in the wild boar models were
381 predominantly 5-7 days (Lange, 2015; Lange and Thulke, 2015, 2017; Thulke and Lange, 2017; Lange et
382 al., 2018; Halasa et al., 2019; Loi et al., 2020; O'Neill et al., 2020; Pepin et al., 2020; Taylor et al., 2020),
383 however greater variation was seen among the assumed carcass infectious periods.

384 In the ASF Wild Boar models, carcass persistence – synonymous with carcass infectivity – was
385 originally statically modelled at 8 weeks (Lange and Thulke, 2015). However, after disease spread was
386 observed and a model was fit, the spread was best explained using a 6-week carcass persistence time
387 (Lange, 2015). Carcass persistence time was further revised to 4 weeks in Lange and Thulke (2017) and
388 Thulke and Lange (2017) (and similarly used in Halasa et al. (2019) in line with field research on
389 vertebrate scavenging behavior from Ray et al. (2014)). The carcass persistence parameter was then
390 further revised to reflect a seasonally-dependent variability in Lange et al. (2018), with persistence times
391 ranging from 4 weeks in the summer to 12 weeks in the winter, in accordance with seasonal differences
392 observed in field research (Ray et al., 2014). This seasonal variability in carcass persistence was also
393 assumed in Pepin et al. (2020). In the later wild boar models, O'Neill et al. (2020) assumed a static
394 carcass infectivity time of 8 weeks, and Taylor et al. (2020) used a PERT distribution of parameters 2, 4,
395 and 18 weeks (specifically: 15, 26, and 124 days), with the latter model also accounting for the
396 probability of carcass removal during the period.

397 The first wild boar individual-based models (Lange, 2015; Lange and Thulke, 2015) used a 4 km²
398 geographical unit, corresponding to the home range of a wild boar herd, in accordance with ecological
399 data from radio-tracking sessions from Spitz and Janeau (1990) and Leaper et al. (1999). At this unit size
400 there may be some interactions between neighboring herds, though as boar prefer to stay within their
401 home range and interact with their groupmates, long distance movements are consequently mostly
402 related to dispersal of juveniles. The geographical raster was later increased to units of 9 km² (Lange
403 and Thulke, 2017; Thulke and Lange, 2017; Lange et al., 2018) to avoid perfect overlap between the
404 study area and voxel size used in the model (Lange and Thulke, 2017), as necessary for the model
405 objective. The wild boar individual-based model by Halasa et al. (2019), replicated from Lange (2015)
406 and Lange and Thulke (2017), again used 4 km² units. The more recent boar models increase the
407 geographical unit size, with Pepin et al. (2020) using 25 km² grid cells, and Taylor et al. (2020) applying
408 100 km² cells over the Polish landscape.

409 Lastly, the timing of viral release varied across the wild boar individual-based models as well. In
410 order to allow population dynamics to become established, virus release was originally set for the first
411 week of the 4th year of simulation run and to 10 hosts in Lange and Thulke (2015). This parameter was
412 adjusted to the beginning of June of the 5th year of simulation (corresponding to the dispersal period for
413 juveniles) and for 25 hosts (Lange, 2015). The next model iterations (Lange and Thulke, 2017; Thulke and
414 Lange, 2017) simulated ASFV release at the end of June of the 4th year of simulation and to 10 hosts, and
415 the following model (Lange et al., 2018) released the infection at the end of June of the 6th year of
416 simulation to 5 hosts. The model described in Halasa et al. (2019) allowed one year for population
417 dynamics to emerge (as evidenced by the dramatic increase in groups in the population graph prior to
418 stabilization), with virus release occurring at the beginning of the second year and to only one random
419 boar. There is no mention of the wild boar population stabilizing before virus introduction. Conversely,
420 Pepin et al. (2020) used a 10-year burn-in period for population dynamics to stabilize prior to ASF
421 release.

422

423 *Transmission determinant assessment*

424 Halasa et al. (2016a) revealed that ASFV's path of transmission through a domestic pig herd is
425 influenced by subclinical animal infectiousness, dead animal residues, and herd size. For spread between
426 pig herds, for the endemic situation in Sardinia where free-roaming unregistered pigs (known as *brado*)
427 complicate eradication efforts, Mur et al. (2018) identified local spread through fomites as the primary
428 transmission route. Brado and wild boar were indicated to play central roles in the occurrence of ASF
429 cases, reinforcing the importance of herd biosecurity in interrupting transmission. On the international

430 scale, it was demonstrated that limited transmission of ASF between EU member nations would occur
431 through swine trade networks prior to disease detection, reinforcing the importance of surveillance
432 measures (Nigsch et al., 2013). Factors influencing the path of transmission of ASFV were also assessed
433 for wild boar in Denmark, where the model showed that the density, size, and location and dispersion of
434 a boar population will affect transmission and circulation of ASF (Halasa et al., 2019). The importance of
435 carcass-based transmission was quantified in Pepin et al. (2020), where it was inferred over half of the
436 transmission events were from infected carcass contact. When observed dynamics of ASF in boar in
437 Europe were modelled – specifically to capture the troughs and peaks of infection and population
438 densities – differences in temperature and scavenger abundance were shown to impact carcass
439 degradation affecting outbreak severity, reinforcing the role of carcasses in epidemic maintenance
440 (O’Neill et al., 2020).

441 One model explored the role of insect vectors in contributing to disease spread (Vergne et al.,
442 2020a), demonstrating that only a small percentage of ASFV transmission events would be due to stable
443 flies, assuming an average abundance of flies (measured once previously as 3-7 flies per pig). However,
444 as vector abundance increased ten- and twenty-fold, the percentage of transmission due to the insects
445 increased dramatically as well. Transmission was also highly sensitive to blood-meal regurgitation
446 quantity and ASFV infectious dose, indicating areas of necessary further study.

447

448 *Alternative control strategy assessment and prediction of consequences of hypothetical outbreaks*

449 When control strategies were compared and the consequences of outbreaks assessed, Costard
450 et al. (2015) showed that increasing farmers’ awareness of and sensitivity of detection to ASF will not
451 reduce the risk of silent release through emergency sales. Barongo et al. (2016) demonstrated that, in a
452 free-range pig population, rapid biosecurity escalation (within 2 weeks of outbreak onset) would
453 significantly decrease the burden of disease. Halasa et al. (2016c) showed that, for industrialized
454 European swine populations, including virological and serological testing of up to five dead animals per
455 herd per week within the perimeter of an outbreak, in addition to established national and EU
456 measures, provided the most effective control strategy. When the consequence of using shorter
457 durations of control zones was assessed, the model predicted such a reduction would greatly reduce
458 economic losses without jeopardizing worsening transmission (Halasa et al., 2018). Conversely,
459 increasing the size of the area under surveillance would offset the increased incurred cost through
460 shortening the epidemic’s duration (Halasa et al., 2018). For arresting ASF spread in Vietnam, movement
461 restrictions were used as the control method and it was shown they would have to interdict at least half
462 of all pig movements to be effective. This was problematic as many traders were identified to specifically
463 avoid quarantine checkpoints and sell pigs through illegal means (Lee et al., 2020).

464 Models that assessed the consequences of hypothetical outbreaks did so for specific
465 industrialized (Danish and French) swine populations and two independent populations of wild boar.
466 The simulations of ASFV spread in the domestic pig compartment only predicted short and small
467 epidemics (mean duration less than one month) in both Denmark and France, with disease spread
468 primarily driven by animal movements and often contained upon implementation of the codified
469 national and EU control strategies (Halasa et al., 2016b; Andraud et al., 2019). As the epidemic could
470 fade out in the inciting herd, some (14.4% of epidemics originating in nucleus herds, 12.1% from sow
471 herds) were predicted to never be detected. Further, the initial outbreak was predicted to have the
472 highest economic cost — more-so than any subsequent outbreaks — due primarily to the ensuing trade
473 restrictions that dwarf the direct costs (Halasa et al., 2016b). In France, due to the pyramidal structure
474 of the swine production system, variation was seen dependent upon the index herd’s location in the
475 production pyramid (Andraud et al., 2019). Geographic dispersal of ASF cases was highly dependent on

476 the density of herds where the outbreak initialized, with cases spreading up to 800km from herds in low-
477 density areas. If ASF spread originated from free-range pig herds, as opposed to the top of the
478 production pyramid, it was predicted to potentially affect up to 15 herds. Similar to the results of the
479 assessment of transmission determinants by Mur et al. (2018), local transmission appeared to be the
480 driving route. Among wild boar models, the consequences of concern were the outcome of natural
481 circulation of ASFV in a closed population, where any outbreak was determined to be self-limiting (Croft
482 et al., 2020), and the impact of baiting on disease establishment, where through modelling changes in R_0
483 it was seen that such practice would relatively increase the risk of an ASF epidemic taking hold (Yang et
484 al., 2020).

485 Wild boar simulations demonstrated the importance of long-term sustained control efforts (i.e.
486 over many generations of wild boar), as the scale of depopulation required for a more rapid solution
487 would likely be untenable (Lange, 2015). As the simulation model parameters were refined with
488 updated evidence, delayed carcass removal (two or more weeks postmortem) was shown to have no
489 effect on curtailing ASF spread; only carcass removal within 1 week (an impractical assumption, given
490 current reported carcass removal rates) was shown to have a positive effect (Thulke and Lange, 2017).
491 This conclusion was expanded in Lange et al. (2018), where successful carcass removal within a core
492 area was shown to reduce the required hunting intensity. A distinction between control methods
493 required for scenarios of focal introduction as opposed to spread from adjacent endemic areas was
494 identified as well: in the case of focal introduction, due to the small size of the affected area, it's
495 possible that a high carcass removal rate could achieve control without the need for intensive hunting
496 (Lange et al., 2018). When surveillance methods were compared, passive surveillance —assuming a 50%
497 carcass detection rate — was shown to be more effective than active surveillance at detecting ASF cases
498 in a small population, however active surveillance was better when both disease prevalence and
499 population density were low (<1.5% prevalence, < 0.1 boar/km²) and the hunting rate was over 60%
500 (Gervasi et al., 2019). When transmission from free-range, outdoor pigs was factored into the spread of
501 ASF from wild boar dispersion, hunting was shown to reduce the number of new cases but not the size
502 of the area at risk, and conversely fencing reduced the size of the region at risk of ASF but not the
503 number of cases (Taylor et al., 2020).

504

505 Discussion

506 Mechanistic modelling has been a valuable tool for deriving infection parameters, unraveling
507 routes of transmission, assessing alternative control strategies, and determining the consequences of
508 hypothetical outbreaks of ASF. However, despite all that has been elucidated, there is still much
509 research to be done. Existing ASF models are limited in the contexts of their application, their means of
510 evaluating control strategies, and the lack of a bridge between domestic and wild compartments, and
511 attention should be given to resolving these shortcomings.

512 ASF simulation models, either in domestic pigs or wild boar, have been applied only to a limited
513 number of contexts, despite the epidemic risk faced by all European countries and the insights one could
514 get from mechanistic models to anticipate virus emergence. Simulations of ASF outbreaks in domestic
515 pigs, for the current epidemic of the circulating Georgia 2007/1 isolate, have been published only for
516 two European (Denmark and France) and one Asian (Vietnam) nation. Many differences exist between
517 countries in terms of the type of production system, the distribution of farm types, and the source-
518 nation of imported pigs, preventing the extrapolation of results from one nation to another. Similarly,
519 the presence and distribution of, and control mandates against, wild boar are not uniform between
520 areas, precluding extrapolation of model results outside the area of study. Though the general utility of
521 different control strategies has been indicated, real-world data on wild boar abundance, as difficult as it

522 may be to assess, is needed to facilitate parameterization of these models to real-world scenarios. When
523 the wild boar individual-based models were applied to real-world locations, they were run only at low-
524 population scales: in Denmark where there exists a legal mandate for their elimination, in the Baltic
525 nations but only in the area of the international border, a forest in England, and part of Poland. Of the
526 five-year period in which wild boar models were published, almost half of such publications occurred in
527 the most recent year, 2020. Whereas earlier wild boar models were constructed by only one group, the
528 diversity among the 2020 models is a promising trend in the direction of ASF ecological modelling.
529 However, as the number of individuals being modelled grows the required computing time grows
530 cubically (Keeling and Rohani, 2008), so insightful as these individual-based models may be, presently
531 they may be too computationally expensive to adapt to larger populations in other scenarios or scales.

532 All models that assessed control strategies did so through comparing a finite set of *a priori*
533 defined interventions. Many control strategies were examined in competition with each other, which is
534 opposed to how they would be actually implemented. For instance, the efficacy of active and passive
535 surveillance for wild boar was considered independently and without the influence of the other in
536 Gervasi et al. (2019), when in reality such methods would be implemented synergistically. While
537 comparing strategies is beneficial for identifying a rank-order efficacy of control methods, this structure
538 does not necessarily determine the most effective combination of all available strategies. Future models
539 should be built to identify the optimal contributions of each control method for achieving specific
540 outcomes (e.g. elimination of ASF cases, or minimizing overall economic impact). This can be achieved
541 by using an objective function where the function inputs are the parameters defining the control
542 strategies (e.g. size and duration of the surveillance and protection zone) and the function output is a
543 measure of the epidemic impact (e.g. total cost of the epidemic) (Rushton et al., 1999; Moore et al.,
544 2010). Optimization algorithms can then be used to examine the space of the input parameter values to
545 find which ones minimize the function output (Hauser and McCarthy, 2009; Moore et al., 2010). It is
546 expected that such modelling output will generate more precise information to policy-makers for
547 designing cost-benefit control strategies.

548 All models that assess control strategies assume the employed strategies will remain constant
549 over the period of implementation. Due to the evolving nature of epidemics, this is unlikely to reflect
550 real-world conditions. Future models may consider including temporal components to the control
551 strategies, both through parsing by specific pre-defined time points (e.g. optimal control strategies to be
552 used before and after R_0 becomes less than 1), as well as via objective functions to identify when is the
553 best time to implement certain strategies (especially with regards to types of surveillance).

554 Accounting for limitations in the surveillance data used to fit mechanistic models (such as
555 imperfect case detection and delays in reporting) is an important consideration in model development.
556 For instance, many models rely on pig mortality thresholds for detecting ASF, though ASFV could
557 circulate in a herd for almost a month prior to it being detected through such criteria (Guinat et al.,
558 2018). The DTU-DADS-ASF simulation factored in a parameter to account for delays during contact
559 tracing, though detection delays due to imperfect herd-level surveillance (such as from small changes in
560 mortality) was not simulated. Among wild boar, passive carcass detection and under-reporting was a
561 common limitation, as such detection was both seasonally variable and irregular. Taylor et al. (2020)
562 accounted for this through including an “under-reporting factor” in their parameters, while Pepin et al.
563 (2020) fit parameters for this uncertainty using approximate Bayesian computation, though the
564 influence of a lack of negative surveillance data was identified in their analysis. Similarly, when
565 parameters were estimated among wild boar in Sardinia, both non-uniform sampling and a lack of
566 passive surveillance samples were identified as limitations. Though no adjustments were made to
567 address them, the large quantity of data potentially offset the bias, as suggested by the authors.

568 Refining this uncertainty through field studies of wild boar could benefit future models and is worthy of
569 investigation.

570 Resolving structural uncertainty is another on-going gap in ASF modelling that requires
571 improvement. This uncertainty is demonstrated in multiple ways, such as through the range of values
572 among parameter assumptions and the various routes of transmission (and corresponding scale) that
573 are modelled: where specific routes of indirect transmission may be parameterized in one model
574 another will group all such routes under a single local transmission parameter. Quantifying the
575 contribution of individual indirect routes of transmission to ASF spread is one of many areas for
576 refinement through further research. Whereas uncertainty is a quality inherent to all models, studies
577 have shown that this can be minimized through ensemble modelling, where the results of multiple
578 models are aggregated to generate a common final output. Combinations of models providing the best
579 predictions was demonstrated through the results of the *RAPIDD Ebola forecasting challenge*
580 competition: among a variety of individual- and population-based, stochastic and deterministic,
581 mechanistic and semi-mechanistic models, ensemble predictions routinely performed better than any
582 individual model (Viboud et al., 2018). A similar modelling challenge on ASF was launched in 2020,
583 involving several modelling teams. Though still a work-in-progress, it is anticipated that this exercise will
584 be able to provide similar assessments among ASF models, potentially reinforcing the importance of
585 utilizing synthesized results (INRAE, 2020).

586 Prior to 2020, there was a noticeable lack of diversity among the existing models. Though the
587 proliferation of models last year helped to offset this imbalance, still over one-third (5/14) of the
588 domestic pig simulations are derived from the DTU-DADS-ASF (and component precursor Halasa et al.
589 (2016a)) model. Similarly, prior to 2020 all but one of the wild boar models were derived from Lange and
590 Thulke's ASF Wild Boar model, and Croft et al. (2020) used epidemiological parameters from Lange and
591 Thulke's model as well. The influx of recent wild boar models by Croft et al. (2020), O'Neill et al. (2020),
592 and Pepin et al. (2020) provided contrasting simulations of wild boar and carcass-based transmission in
593 different outbreak scenarios, helping to diversify the field. This diversity aids in reinforcing the shared
594 conclusions among the different models, such as the importance of combining targeted hunts or culls
595 with active carcass removal to achieve outbreak control while avoiding eradication of the wild boar
596 population (Lange, 2015; O'Neill et al., 2020).

597 Only one simulation model considered transmission between domestic pigs and wild boar
598 despite differences in the observed transmission pathways between countries. While the individual-
599 based wild boar models not accounting for transmission with domestic pigs may be sufficient for areas
600 with ASF dissemination exclusively in the wildlife compartment, areas where spillover — however
601 intermittently — likely occurs will require models that address this aspect. The one simulation that did
602 consider this inter-compartment transmission relied on contact parameters derived for a free-range
603 savannah-like outdoor farm not typically representative of European swine operations (though the
604 authors accounted for this by assuming such contact as an upper-limit). While this model by Taylor et al.
605 (2020) is a critical step towards a unified ASF model of both domestic pig and wild boar transmission, it
606 also indicates the need to better define the parameters informing wild boar and domestic pig contact
607 risks and rates through further research. Simulation models of hypothetical outbreaks and alternative
608 control strategies that link the domestic and wildlife compartments are critical for informing decision-
609 making. Just as this has been done for multiple other animal diseases such as Aujeszky's disease and
610 hepatitis E (Charrier et al., 2018), foot-and-mouth disease (Ward et al., 2015), and bovine tuberculosis
611 (Brooks-Pollock and Wood, 2015), this should be a priority for all nations at risk of ASF importation.

612 While mathematical models can provide many insights into disease control, they are far from
613 the only tool available. Recent ASF outbreaks have been successfully controlled without the use of

614 mathematical models, such as in the Czech Republic and Belgium. Multisectoral collaboration between
615 epidemiologists, veterinarians, virologists, ecologists, field-work studies, and expert opinion plays an
616 integral role in ASF control. From model building to outcome validation and decision analysis, experts from
617 these fields should be included to maintain an inclusive multi-faceted approach to ASF modelling.

618

619 7. Conclusions

620 With outbreaks across 18 European and 12 Asian nations, ASF has become established as an
621 urgent threat to the global swine industry (ProMED-mail, 2020; Taylor et al., 2020). Mechanistic models
622 have shown much potential for helping to confront this epidemic, however, more modelling studies
623 using empirical data derived from real epidemics are needed, especially for generating better estimates
624 of transmission parameters. As these parameters are integral to designing calibrated intervention plans
625 (such as identifying optimal protection and surveillance zones, or (when available) the fraction of
626 necessary vaccination coverage), and since these parameters have been seen to vary between individual
627 ASF outbreaks, extrapolation of parameters between independent outbreak scenarios is precarious at
628 best. Deriving parameters from Georgia 2007/1 genotype II historical outbreaks beyond the two
629 examinations of the past Russian Federation epidemic (Gulenkin et al., 2011; Guinat et al., 2018) is
630 critical for further refining models to combat the on-going ASF pandemic. Limitations of surveillance
631 systems in obtaining accurate data are an active impediment. Though this is being overcome through
632 more complex modelling and inference techniques (e.g. approximate Bayesian computation), existing
633 labour and workforce limitations hinder field data collection.

634 Prior to this past year, there was a need to diversify modelling approaches through developing
635 additional frameworks (as almost half of the studies at the time stemmed from one of either two
636 models: DTU-DADS-ASF (Halasa et al., 2016b) and ASF Wild Boar (Lange and Thulke, 2015)), however the
637 large influx of modelling teams in 2020 seeking to address ASF unknowns is a promising direction for the
638 field that will probably be reinforced due to the ASF modelling challenge. In addition, current evidence
639 indicates that spillover events between domestic pigs and wild boar play an important role in ASF
640 outbreaks, and this transmission should be a component of models going forward. Finally, to date, only
641 codified, hypothetical and *a priori* defined interventions were compared. Therefore, moving from
642 intervention comparison to identifying optimized control strategies is critical. Doing so will enable
643 policy-makers to identify the ideal course of action rather than a relatively better option among pre-
644 determined routes.

645 From a decision point of view, while we promote models to support policy, policy-makers should
646 consider several models together. As ensemble modelling studies have not been performed yet, we
647 recommend using existing models as decision guides only for the specific scenarios modelled. Due to the
648 uncertainty of even basic parameters, and as evidenced in the sensitivity analyses of different models,
649 we do not encourage extrapolating results to non-modelled scenarios (e.g. across national borders). The
650 current modelling body provides excellent insight for addressing ASF transmission at a multitude of
651 scales, and these studies should be referenced as such when forming policy decisions on that level by
652 considering all associated models (i.e. for addressing ASF in Sardinia considering the results of both Mur
653 et al. (2018) and Loi et al. (2019), or when deciding on intra-herd strategy considering the results of
654 Costard et al. (2015), Halasa et al. (2016a), Faverjon et al. (2020), and Vergne et al. (2020a)). For ASF
655 modelers, until uncertain parameters are further refined, we hope our consolidation of parameter
656 assumptions and results will facilitate parameter selection for future models. Addressing all these
657 modelling hurdles is expected to generate more appropriate information, for policy-makers and
658 modellers to contribute to the control of ASF both locally and globally.

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941 Figure 1. PRISMA flow diagram for article selection

942 (See attached jpg)

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944 Figure 2. Publications by year

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947 Figure 3. Filiation tree of articles

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950 Table 1. Epidemiological characteristics of articles

Reference	Host	ASFV isolate	ASFV genotype	Location	Data collection method
Gulenkin et al., 2011	Pig	Georgia 2007/1	Genotype II	Russian Federation	Observational
Ferreira et al., 2013	Pig	Malta 1978 Netherlands 1986	Genotype I	Laboratory	Experimental
Nigsch et al., 2013	Pig	-	-	European Union	Simulation
Barongo et al., 2015	Pig	-	Genotype IX	Uganda	Observational
Costard et al., 2015	Pig	-	-	Non-specific	Simulation
Barongo et al., 2016	Pig	-	-	Eastern Africa	Simulation
Guinat et al., 2016b	Pig	Georgia 2007/1	Genotype II	Laboratory	Experimental
Halasa et al., 2016a	Pig	Georgia 2007/1	Genotype II	Non-specific	Simulation
Halasa et al., 2016b	Pig	Georgia 2007/1	Genotype II	Denmark	Simulation
Halasa et al., 2016c	Pig	Georgia 2007/1	Genotype II	Denmark	Simulation
Hu et al., 2017	Pig	Georgia 2007/1	Genotype II	Laboratory	Experimental
Nielsen et al., 2017	Pig	Georgia 2007/1	Genotype II	Laboratory Russian Federation	Experimental
Guinat et al., 2018	Pig	Georgia 2007/1	Genotype II	Russian Federation	Observational
Halasa et al., 2018	Pig	Georgia 2007/1	Genotype II	Denmark	Simulation
Mur et al., 2018	Pig	-	Genotype I	Sardinia	Simulation
Andraud et al., 2019	Pig	Georgia 2007/1	Genotype II	France	Simulation
Faverjon et al., 2020	Pig	Georgia 2007/1	Genotype II	Laboratory	Simulation
Lee et al., 2020	Pig	Georgia 2007/1	Genotype II	Vietnam	Simulation
Shi et al., 2020	Pig	-	-	Laboratory	Simulation
Vergne et al., 2020a	Pig	Georgia 2007/1	Genotype II	Non-specific	Simulation
Pietschmann et al., 2015	Pig, Boar	Armenia 2008	Genotype II	Laboratory	Experimental
Taylor et al., 2020	Pig, Boar	Georgia 2007/1	Genotype II	Europe	Simulation
Lange, 2015	Boar	Georgia 2007/1	Genotype II	Non-specific	Simulation
Lange and Thulke, 2015	Boar	Georgia 2007/1	Genotype II	Non-specific	Simulation
Lange and Thulke, 2017	Boar	Georgia 2007/1	Genotype II	Baltic region	Observational
Thulke and Lange, 2017	Boar	Georgia 2007/1	Genotype II	Baltic region	Simulation
Lange et al., 2018	Boar	Georgia 2007/1	Genotype II	Baltic region	Simulation
Gervasi et al., 2019	Boar	Georgia 2007/1	Genotype II	Non-specific	Simulation
Halasa et al., 2019	Boar	Georgia 2007/1	Genotype II	Denmark	Simulation
Croft et al., 2020	Boar	Georgia 2007/1	Genotype II	England	Simulation
Loi et al., 2020	Boar	-	Genotype I	Sardinia	Observational
O'Neill et al., 2020	Boar	Georgia 2007/1	Genotype II	Spain, Estonia	Simulation
Pepin et al., 2020	Boar	Georgia 2007/1	Genotype II	Poland United States of America	Simulation
Yang et al., 2020	Boar	-	-	United States of America	Simulation

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Reference	Host	Framework	Time	Space	Model Objective
Gulenkin et al., 2011	Pig	PBM	Continuous	No	Estimate parameters
Ferreira et al., 2013	Pig	PBM	Discrete	No	Estimate parameters
Nigsch et al., 2013	Pig	IBM	Discrete	Movement	Assess transmission determinants
Barongo et al., 2015	Pig	PBM	Continuous	No	Estimate parameters
Costard et al., 2015	Pig	IBM	Discrete	No	Assess alt. control strategies
Barongo et al., 2016	Pig	PBM	Continuous	No	Assess alt. control strategies
Guinat et al., 2016b	Pig	PBM	Discrete	No	Estimate parameters
Halasa et al., 2016a	Pig	PBM	Discrete	No	Assess transmission determinants
Halasa et al., 2016b	Pig	Meta-population	Discrete	Movement and distance	Assess consequences of outbreak
Halasa et al., 2016c	Pig	Meta-population	Discrete	Movement and distance	Assess alt. control strategies
Hu et al., 2017	Pig	PBM	Continuous	No	Estimate parameters
Nielsen et al., 2017	Pig	PBM	Discrete	No	Estimate parameters
Guinat et al., 2018	Pig	PBM	Continuous	No	Estimate parameters
Halasa et al., 2018	Pig	Meta-population	Discrete	Movement and distance	Assess consequences of outbreak
Mur et al., 2018	Pig	Meta-population	Discrete	Movement and distance	Assess transmission determinants
Andraud et al., 2019	Pig	Meta-population	Discrete	Movement and distance	Assess consequences of outbreak
Faverjon et al., 2020	Pig	PBM	Discrete	Distance	Assess alt. control strategies
Lee et al., 2020	Pig	IBM	Discrete	Movement	Assess alt. control strategies
Shi et al., 2020	Pig	PBM	Continuous	No	Estimate parameters
Vergne et al., 2020a	Pig	PBM	Continuous	No	Assess transmission determinants
Pietschmann et al., 2015	Pig, Boar	PBM	Discrete	No	Estimate parameters
Taylor et al., 2020	Pig, Boar	IBM	Discrete	Movement	Assess alt. control strategies
Lange, 2015	Boar	IBM	Discrete	Movement	Assess alt. control strategies
Lange and Thulke, 2015	Boar	IBM	Discrete	Movement	Assess alt. control strategies
Lange and Thulke, 2017	Boar	IBM	Discrete	Movement	Estimate parameters
Thulke and Lange, 2017	Boar	IBM	Discrete	Movement	Assess alt. control strategies
Lange et al., 2018	Boar	IBM	Discrete	Movement	Assess alt. control strategies
Gervasi et al., 2019	Boar	PBM	Discrete	No	Assess alt. control strategies
Halasa et al., 2019	Boar	IBM	Discrete	Movement	Assess transmission determinants
Croft et al., 2020	Boar	IBM	Discrete	Movement	Assess consequences of outbreak
Loi et al., 2020	Boar	PBM	Continuous	No	Estimate parameters
O'Neill et al., 2020	Boar	PBM	Continuous	No	Assess transmission determinants
Pepin et al., 2020	Boar	IBM	Continuous	Movement	Assess transmission determinants
Yang et al., 2020	Boar	PBM	Continuous	No	Assess consequences of outbreak

Table 3. Parameter results

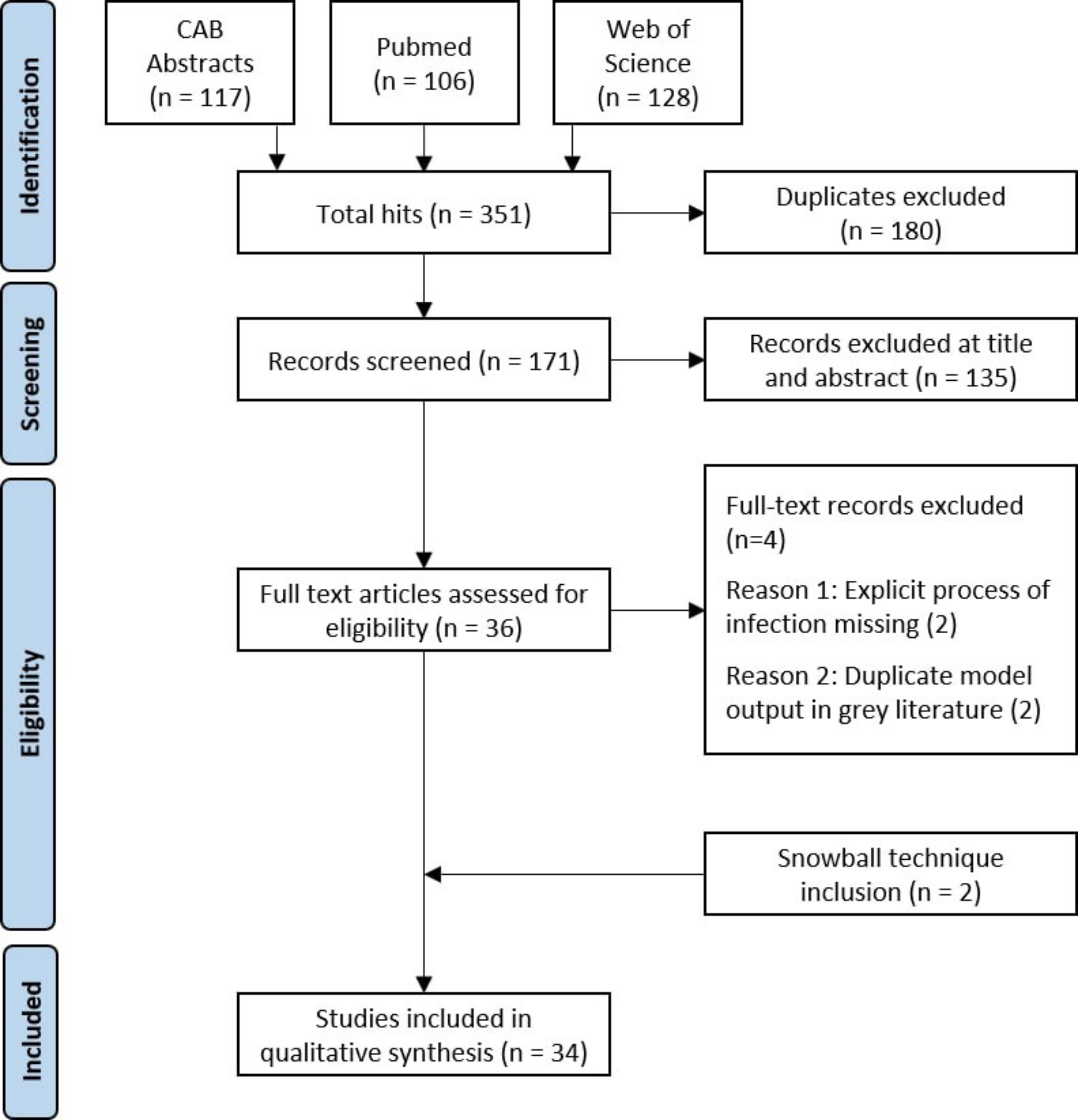
ASFV Strain	Host	Basic epidemiological unit	Scale of transmission	Assumed latent period (days)	Assumed infectious period (days)	β	R_0	Reference
Genotype I	Boar	Individual	Within population	3.57 days	5 - 7	0.5	1.124 (95% CI 1.103–1.145) - 1.170 (1.009–1.332)	Loi et al., 2020
Malta 1978	Pig	Individual	Within pen	4 ± 0.8 (low dose) 5 ± 1.4 (high dose)	Min: 7.0 ± 2.9 Max: 33.6 ± 22.5	2.79 (95% CI 1.57, 4.95)	Min infectious period: 18.0 (95% CI 6.90, 46.9) Max infectious period: 62.3 (95% CI 6.91, 562)	Ferreira et al., 2013
Netherlands 1986	Pig	Individual	Within pen	5 ± 0.5	Min: 5.9 ± 2.6 Max: 19.9 ± 20.2	0.92 (95% CI 0.44, 1.92)	Min infectious period: 4.92 (95% CI 1.45, 16.6) Max infectious period: 9.75 (95% CI 0.76, 125)	Ferreira et al., 2013
Georgia 2007/1	Pig	Individual	Within pen	4	Min: 4.5 ± 0.75 days Max: 8.5 ± 2.75 days	0.62 (95% CI 0.32, 0.91)	Min infectious period: 2.71 (95% CI 1.32, 4.56) Max infectious period: 4.99 (95% CI 1.36, 10.13)	Guinat et al., 2016b
	Pig	Individual	Within pen	Gamma(mean, shape) mean ~ Gamma(4.5, 10) shape ~ Gamma(10, 2)	Gamma(mean, shape) mean ~ Gamma(10,6.0) shape ~ Gamma(19.3, 2)	2.62 (95% HPDI 0.96, 5.61)	24.1 (95% HPDI 7.34, 54.2)	Hu et al., 2017
	Pig	Individual	Within pen	3 - 5	4.5 ± 0.75	1.00 (95% CI 0.56, 1.69)	(not reported)	Nielsen et al., 2017
	Pig	Individual	Between pen	4	Min: 4.5 ± 0.75 days Max: 8.5 ± 2.75 days	0.38 (95% CI 0.06, 0.70)	Min infectious period: 1.66 (95% CI 0.28, 3.31) Max infectious period: 3.07 (95% CI 0.37, 6.97)	Guinat et al., 2016b
	Pig	Individual	Between pen	Gamma(mean, shape) mean ~ Gamma(4.5, 10) shape ~ Gamma(10, 2)	Gamma(mean, shape) mean ~ Gamma(10,6.0) shape ~ Gamma(19.3, 2)	0.99 (95% HPDI 0.31, 1.98)	9.17 (95% HPDI 2.67, 19.2)	Hu et al., 2017
	Pig	Individual	Between pen	3 - 5	4.5 ± 0.75	0.46 (95% CI 0.16, 1.06)	(not reported)	Nielsen et al., 2017
	Pig	Individual	Within herd	-	1 - 5	(not reported)	8-11	Gulenkin et al., 2011
	Pig	Individual	Within herd	Gamma(mean, shape) mean ~ Gamma(6.25, 10) shape ~ Gamma(19.39, 5)	Gamma(mean, shape) mean ~ Gamma(9.12, 10) shape ~ Gamma(22.20, 5)	0.7 (95% HPDI 0.3, 1.6) - 2.2 (95% HPDI 0.5, 5.3)	4.4 (95% CrI 2.0, 13.4) - 17.3 (3.5, 45.5)	Guinat et al., 2018
	Pig	Herd	Between herd	-	1 - 5	(not reported)	2-3	Gulenkin et al., 2011
Armenia 2008	Boar	Individual	Within pen	4	2 - 9	(not reported)	6.1 (95% CI 0.6, 14.5)	Pietschmann et al., 2015
	Pig, Boar	Individual	Within pen	4	2 - 9	(not reported)	5.0 (95% CI 1.4, 10.7)	Pietschmann et al., 2015
	Pig, Boar	Individual	Between pen	4	2 - 9	(not reported)	0.5 (95% CI 0.1, 1.3)	Pietschmann et al., 2015
Genotype IX	Pig	Herd	Between herd	-	1 month	1,77	1.77 (95% CI 1.74, 1.81)	Barongo et al., 2015
	Pig	Herd	Between herd	-	1 month	0,0059	1.58 (range not reported)	Barongo et al., 2015
	Pig	Herd	Between herd	-	1 month	1,90	1.90 (95% CI 1.87, 1.94)	Barongo et al., 2015
Not specified	Pig	Herd	Within population	2.86 - 8.33 days	1.25 – 100	0.001 – 0.3	0.8043 – 3.7695	Shi et al., 2020

Table 4. Parameter assumptions

Reference	Host	Value	Source	Reference	Host	Value	Source
Average ASFV infectious period duration				Beta			
Gulenkin et al., 2011	Pigs	1-5 days	(FAO, 2009)	Barongo et al., 2016	Pigs	PERT(0.2, 0.3, 0.5)	Ferreira et al., 2013
Barongo et al., 2015	Pigs	1 month	(Ferreira et al., 2013)	Halasa et al., 2016a	Pigs	0.30 or 0.60	Guinat et al., 2016b
Guinat et al., 2016b	Pigs	Min: 3 - 6 days Max: 3 - 14 days	(Gabriel et al., 2011; Blome et al., 2012, 2013)	Hu et al., 2017	Pigs	Gamma(2,2)	Gulenkin et al., 2011
Hu et al., 2017	Pigs	Gamma(mean (days), shape) mean ~ Gamma(10,6.0) shape ~ Gamma(19.3, 2)	(Ferreira et al., 2013)	Guinat et al., 2018	Pigs	Gamma(2, 2)	Gulenkin et al., 2011; Guinat et al., 2016b; Hu et al., 2017
Nielsen et al., 2017	Pigs	4.5 ± 0.75 days	(Guinat et al., 2014)	Halasa et al., 2016b, 2016c, 2018	Pigs	Nuclear, production: PERT(0.14, 0.38, 0.8); Boar, backyard, quarantine, hobby: PERT(0.36, 0.60, 0.93)	Guinat et al., 2016b
Guinat et al., 2018	Pigs	Gamma(mean (days), shape) mean ~ Gamma(9.12, 10) shape ~ Gamma(22.20, 5)	(Gulenkin et al., 2011; Guinat et al., 2016b; Hu et al., 2017)	Mur et al., 2018	Pigs	Industrial, closed, semi-free: 1.42, Family: 1.85	Gulenkin et al., 2011
Lange, 2015; Lange and Thulke, 2015, 2017; Thulke and Lange, 2017; Lange et al., 2018	Boar	1 week	(Blome et al., 2012)	Andraud et al., 2019	Pigs	Within herd: PERT(0.6, 1, 1.5)	Halasa et al., 2016b
Halasa et al., 2019	Boar	PERT(1, 5, 7) days	(Olesen et al., 2017)	Faverjon et al., 2020	Pig	Within pen: Truncated normal(min, mean, max, sd)(0, 0.6, 14.3, 0.4) Between pen: Truncated normal(0, 0.3, 14.3, 0.2) Between room: Truncated normal(0, 0.01, 0.1, 0.05)	Ferreira et al., 2013; Guinat et al., 2016a, 2016b
Faverjon et al., 2020	Pig	Uniform (3, 5.5)	(Guinat et al., 2016a, 2016b)	Lee et al., 2020	Pig	Direct contact, indirect contact between small and medium farms: 0.6 Indirect contact to large farms: 0.006	Assumed
Lee et al., 2020	Pig	4-52 weeks	(assumed)	Shi et al., 2020	Pig	0.001 - 0.3	Ferreira et al., 2013
Loi et al., 2020	Boar	5-7 days	(Gabriel et al., 2011; Blome et al., 2012; Guinat et al., 2016b)	Taylor et al., 2020	Boar	Wild boar to pig: Uniform(0, 0.167) Wild boar to wild boar: PERT(0, 0.167, 0.3) Dead wild boar to wild boar: Uniform(0, 0.167)	Pietschmann et al., 2015 and assumed
O'Neill et al., 2020	Boar	Live boar: 5 days Carcasses: 8 weeks	(Gallardo et al., 2015) (Carrasco García, 2016; Probst et al., 2017)	Vergne et al., 2020a	Pig	PERT(0.2, 0.4, 0.6)	Guinat et al., 2016b
Pepin et al., 2020	Pig, Boar	Poisson(5 days)	(Blome et al., 2012; Gallardo et al., 2017)				
Taylor et al., 2020	Boar	Live boar: PERT(3, 6, 10) days Carcasses: PERT(15, 26, 124) days	(Gabriel et al., 2011; Guinat et al., 2014) (Morley, 1993; Olesen et al., 2018; Probst et al., 2017; Chenais et al., 2019) (Guinat et al., 2016b)				
Vergne et al., 2020a	Pig	PERT(3, 7, 14) days	(Guinat et al., 2016b)				
Yang et al., 2020	Boar	5 days	(Davies et al., 2017)				

Table 4. Parameter assumptions (continued)

Reference	Host	Value	Source
Average ASFV incubation period duration			
Gulenkin et al., 2011	Pigs	15 days	OIE, 2008
Nigsch et al., 2013	Pigs	PERT(3, 5, 13) days	FAO, 2009, Depner personal communication
Barongo et al., 2015	Pigs	5-15 days	Sanchez-Vizcaino et al., 2015
Costard et al., 2015	Pigs	Weibull(shape, scale) 2+ (Weibull (1.092, 4.197 (median 5, range 2-19) days	Plowright et al., 1994; Arias and Sanchez-Vizcaino, 2002; Penrith et al., 2004; Sanchez-Vizcaino, 2012
Mur et al., 2018	Pigs	Poisson(8)	Ferreira et al., 2013; OIE, 2014
Faverjon et al., 2020	Pig	Gamma(shape, scale) (13.299, 0.3384482)	Ferreira et al., 2012, 2013; Guinat et al., 2016a, 2016b
Pepin et al., 2020	Boar	Poisson(4) days	Blome et al., 2012; Gallardo et al., 2017
Average ASFV latent period duration			
Nigsch et al., 2013	Pigs	1-2 days	FAO, 2009
Costard et al., 2015	Pigs	Uniform(1,2) days	Arias and Sanchez-Vizcaino, 2002; Plowright et al., 1994
Pietschmann et al., 2015	Both	4 days	Assumed
Guinat et al., 2016b	Pigs	2-5 days	Assumed
Barongo et al., 2016	Pigs	PERT(2.86, 4, 8.3) days	OIE, 2008; FAO, 2008, 2009
Hu et al., 2017	Pigs	Gamma(mean (days), shape) mean ~ Gamma(4.5, 10) shape ~ Gamma(10, 2)	Ferreira et al., 2013
Nielsen et al., 2017	Pigs	3-5 days	Guinat et al., 2014
Guinat et al., 2018	Pigs	Gamma(mean (days), shape) mean ~ Gamma(6.25, 10) shape ~ Gamma(19.39, 5)	Gulenkin et al., 2011; Guinat et al., 2016b; Hu et al., 2017
Mur et al., 2018	Pigs	Poisson(2)	Ferreira et al., 2013; OIE, 2014
Halasa et al., 2019	Boar	PERT(1, 5, 9) days	Olesen et al., 2017
Loi et al., 2020	Boar	3.57 days	Gabriel et al., 2011; Blome et al., 2012; Guinat et al., 2016b
Shi et al., 2020	Pig	2.86 - 8.33 days	Barongo et al., 2016
Vergne et al., 2020a	Pig	PERT(3,4,5) days	Guinat et al., 2016b
Yang et al., 2020	Boar	4 days	Barongo et al., 2016



Publications by year

