Tools and opportunities for African swine fever control in wild boar and feral pigs: a review

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Abstract

The native Eurasian wild boar (*Sus scrofa*) is a relevant wildlife host for African swine fever (ASF) virus, contributing to infection maintenance and spread and representing a challenge for disease control. Combining published scientific evidence with expert opinion, we provide an updated global overview of ASF control in wild boar and feral pigs in different epidemiological scenarios. We synthesize current knowledge on key background aspects of wild boar ecology and management and on ASF epidemiology in wild boar and their relative, the feral pig. We propose that establishing a proper surveillance and monitoring scheme is a requisite for disease control in wildlife and that ASF and wild boar should be monitored in an integrated way, considering the changes in the host population as well as the spatial spread and temporal distribution of disease indicators, to make possible a critical assessment of the impact of interventions. The main body of the manuscript reviews the intervention options and ASF control attempts and their outcomes in different epidemiological situations from peacetime to endemicity. Current ASF control in wild boar relies on three essential tools: carcass destruction, wild boar culling, and fencing. The experience gained since the onset of the ongoing ASF pandemic shows that certain combinations of interventions can slow down ASF spread and eventually succeed in ASF eradication in wild boar, at least after point introductions. Several strengths and weaknesses of these strategies are identified.

Key words: Epidemiology; Intervention options; Pest species; *Sus scrofa*; Virus; Wildlife disease

Introduction

The ongoing African swine fever (ASF) pandemic is unprecedented in its geographical spread and impact on the global pork industry (Sánchez-Cordón et al., 2018; Sauter-Louis et al., 2021a) and wild suid populations (Morelle et al., 2020). In ASF-affected countries of Eurasia, the native Eurasian wild boar (*Sus scrofa*) is a relevant wildlife host for ASF virus (ASFV), contributing to infection maintenance and spread and representing a challenge for disease control (Iacolina et al., 2021). Since 2007, ca. 50,000 wild boar cases and domestic pig outbreaks of ASF have been reported in Europe, the vast majority (86%) in wild boar (Bergmann et al., 2021). There is a plethora of articles in the scientific literature dealing with ASF in wild boar (or their relative, the feral pig), including about 100 reviews published from 1983 to April 2022. These reviews include 45 extensive scientific opinions and reports and opinions from the European Food Safety Authority (EFSA), where literature review is often combined with outbreak data analyses, expert assessments, and modelling (https://efsa.onlinelibrary.wiley.com/doi/toc/10.2903/1831-4732.african-swine-fever), as well as 19 non-institutional reviews which specifically address ASF control in wild boar in some detail (e.g., Blome et al., 2020; Sauter-Louis et al., 2021a; Woźniakowski et al., 2021). However, none of the existing reviews provides a full image of the global literature on ASF control in wild boar along with expert insights.

The epidemiological links between ASF in domestic pigs and in wild boar are strongly supported by field evidence and modelling (EFSA et al., 2022), and challenge the heterogeneous national wildlife health surveillance schemes in Europe (Lawson et al., 2021) and elsewhere. In view of a need for disease control in wildlife or at the wildlife-livestock interface, the first action is setting up an appropriate integrated monitoring program (Cardoso et al., 2022), and immediately deciding whether to intervene or not, eventually applying all available tools (Gortázar et al., 2015). Disease control interventions change from preventive ones during peacetime to more active ones during the epidemic and eventual endemic phases (Sauter-Louis et al., 2021a). Interventions and intervention-capacities will also vary between point introductions such as those in Czechia and Belgium (Cukor et al., 2021; Linden et al., 2019) and front-like situations like in several other European countries or in South Korea (Jo & Gortázar, 2021; Lim et al., 2023; Sauter-Louis et al., 2021a).

Views on the relative importance of wild boar in ASF maintenance and spread, the tools available for wild boar and ASF control, and their expected success, vary among epidemiological situations and geographical settings (Dixon et al., 2020). We aim to identify the types of available evidence to clarify key concepts, and to identify knowledge gaps and potential weaknesses in ASF control in wild boar (Armstrong et al., 2011; Munn et al., 2018). We first synthesize current knowledge on key background aspects of ASF and wild boar, namely wild boar (and feral pig) ecology and management, and ASF epidemiology in wild boar. The main body of the manuscript reviews integrated monitoring and intervention options and addresses ASF control in wild boar in different epidemiological situations: from peacetime to endemicity. We use two main sources of information. First, a review of the existing literature and second, insights from selected experts with hands-on experience in a broad range of epidemiological situations.

Methods

We choose the form of a traditional review and opinion paper as opposed to systematic reviews and scoping reviews, although specific sections such as the ones on control options and outcome of interventions would fit into the shape of a scoping review (Arksey & O'Malley, 2005). We intended to be systematic, transparent, and reproducible and to include steps to reduce error by the inclusion of multiple reviewers (Peters et al., 2015).

Literature search

We screened Scopus in April 2022 for "African swine fever" and refined the search by including "wild boar" OR "feral pig". The next step consisted of checking the titles and, if necessary, abstracts for their relationship with ASF control and wild boar or feral pig, excluding all references dealing only with molecular biology and host-pathogen interactions, diagnostic tools, disinfection, pig farming, as well as primary research and reviews not specifically focusing on ASF or wild boar/feral pigs. In this selection, we recorded the publication type (opinion, review, primary research (PR) field, PR lab, PR model) and subject. Regarding the subject, we were mainly targeting ASF detection, monitoring, and control in wild boar or at the wild boar-pig interface, but also recording relevant references on molecular epidemiology; pathogenesis; wild boar ASF epidemiology; wild boar – pig interface and farm biosecurity; vectors; vaccines; wild boar ecology, population dynamics and management; outbreak reports and geographical situation assessments; risk assessments; and others. One reference can belong to more than one category. Finally, in those studies which explored the utility of intervention options, we explored their stated or perceived efficacy (success or failure).

Expert insights

Twelve experts (see list of authors) from countries or regions representing recent introductions (continental Italy), successfully controlled point introductions (Belgium and Czech Republic), front-like situations (Germany, South Korea), endemic situations (Estonia - Baltic States and Sub-Saharan Africa), and ASF-free at-risk countries (Canada, Spain) were invited to provide their knowledge on ASF epidemiology and control, and to rank the main intervention options both in effectiveness and practicability.

Narrative sections

We included narrative sections on key aspects of wild boar and ASF, namely on wild boar and feral pig ecology and management, ASF epidemiology in wild boar, integrated monitoring, intervention options, and disease management in different epidemiological scenarios.

Literature search and expert opinion results

The initial list of 3,003 after searching “African swine fever”, 528 when including “wild boar” or “feral pig”, and it was finally trimmed to 468 references after applying the filtering criteria mentioned above (See Appendix S1 for the complete list of references). Regarding the type of the study, the observational ones (n= 192 -published studies-) were the most frequent, followed by reviews (n= 102) (Fig. 1). Regarding the topic, those focused on wild boar and ASF epidemiology (n= 148) were the most common, followed by wild boar and domestic pig interface (n= 105), and ASF detection, monitoring and control (n= 99). We also observed an exponential growth in the number of wild boar ASF-papers published after ca. 2010 (Fig. 1). The majority of the studies were focused on ASF emergence in Europe.

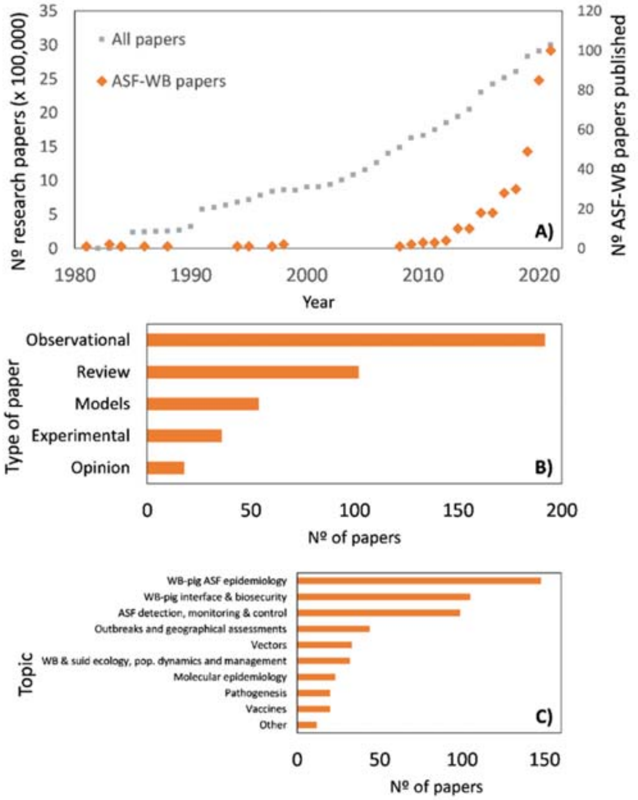

Figure 1. Summary of published studies about African swine fever (ASF) and wild boar (WB). Panel-A shows the temporal trend of publications (1980-2021) of those focused on ASF in wild boar (orange diamonds) and research papers on any topic (grey squares). Panel-B shows the number of ASF papers classified into five categories according to the type of study: i) observational (field-data-based studies), ii) reviews, iii) models, iv) experimental (laboratory experiments-data-based studies), and v) opinion. Panel-C shows the number of ASF papers classified into 10 theme categories according to the topic of the study.

Regarding the perceived utility of intervention options, professional culling (n=16), and carcass search and destruction (n=15) were the most tested interventions (Appendix S1). While contradictory results were found in the depopulation measures, more agreement was observed about the utility of carcass search and destruction, fencing, wild boar-related biosafety, and habitat management (Fig. 2).

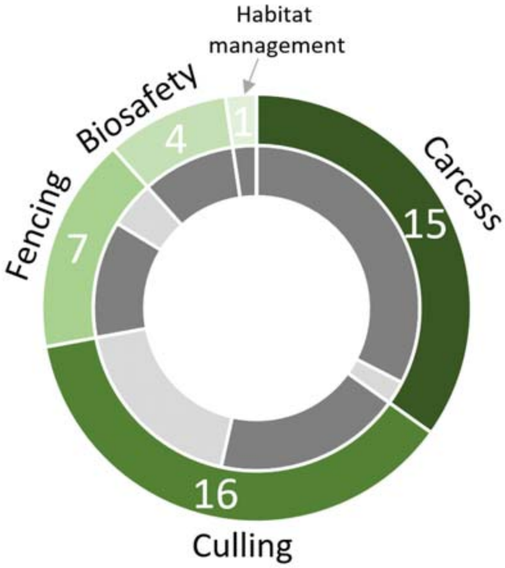

Figure 2.- Intervention actions tested in published studies to control the spread of the African swine fever virus in wild boar populations. The external ring length is proportional to the frequency of each type of intervention, and labels indicate the number of studies; while the internal ring represents perceived success (dark grey) or failure (light grey). Intervention options included in the plot represent: carcass (carcass search and destruction), culling (depopulation measures), fencing (fencing and barriers), biosafety (wild boar hunting and manipulation biosafety) and habitat management (wild boar habitat management).

Expert rankings of the intervention options were highly variable (Fig. 3). Carcass search and destruction was ranked as the most effective intervention both in point and front-like settings (Fig. 3); recreational hunting and farm biosecurity were also top-ranked in endemic scenarios. Translocation control measures were ranked to be the practical action to prevent point introductions. More divergence was found in the practicality of interventions in front-like and endemic scenarios.

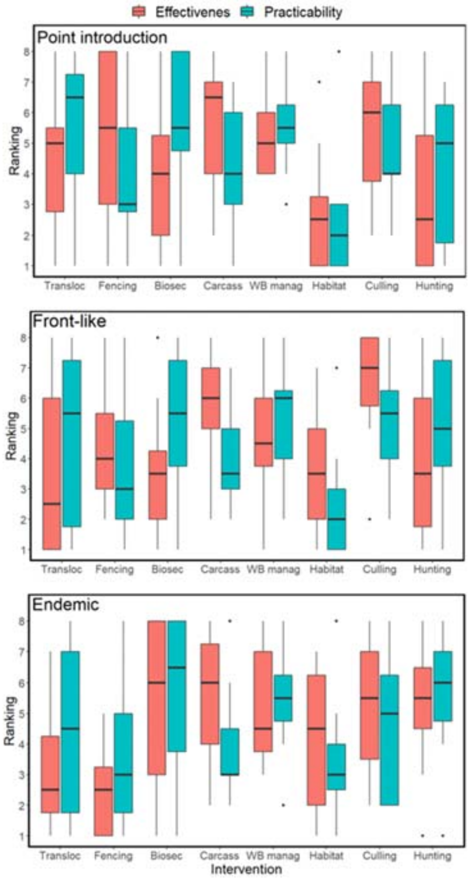

Figure 3.- Main intervention options ranked from 1 (worst) to 8 (best) according to the expert's experience both in effectiveness (orange) and practicality (blue). Box plots (horizontal line = median; box = first quartile (bottom limit) to third quartile (upper limit); lines = lower and upper limit; points = outliers) are used to plot the data. Intervention options were ranked for each of the three main African swine fever scenarios: point introductions (upper panel), front-like settings (central), and endemic (bottom). Abbreviations: transloc (wild boar translocation control), fencing (barriers and fencing), biosec (farm biosecurity), carcass (carcass removal and destruction), WB management (wild boar management biosafety), habitat (habitat management), culling (professional culling), and hunting (recreational hunting).

Wild boar and feral pig ecology and management

Successfully preventing and eventually controlling and/or eradicating ASF in wild boar or at the wild boar-pig interface requires understanding the species' ecology, behaviour, and management. A summary of key ecological parameters is provided in Table 1. The wild boar is a widespread native palearctic ungulate whose population has sharply increased in the last decades (Massei et al., 2015). Its historical range extends through Europe and most of Asia up to Japan, and northern Africa. It is the ancestor of the domestic pig, and a variety of wild boar/pig crossbreeds also occur both inside and outside its historical range. Outside the historical range of wild boar, these suids are generally known as feral pigs (wild pigs) and regarded as invasive (Lowe et al. 2004).

Table 1: Summary of basic ecological and management variables of wild boar (*Sus scrofa*) and feral pig. Abbreviations: ASF African swine fever.

Variable	Key aspects	References
Habitat	Adapted to a broad range of environmental conditions occupying a variety of habitats from deserts and marshlands or high mountains to woodlands, agricultural lands, and even urban areas.	Risch et al., 2021
Diet	Generalist. Acorns and other forest fruits, roots, as well as invertebrates such as earthworms. Cereals, cultivated fruits, and other crops are significant resources in agricultural landscapes. Vertebrates are also consumed, both as prey and as carrion. This includes cannibalism and thus the possibility of carrion-mediated ASF transmission	Cukor et al., 2019 Ježek et al., 2016 Pepin et al., 2021 Probst et al., 2017
Movement ecology	Home ranges: from 30 to 5000 ha, locally even larger. Daily distances: from 2 to 20 km·day^{-1}. Large movements of > 100 km have been reported. Dispersal usually occurs at the end of the first year of life, and average distances are ca. 15 and 5 km for males and females,	Garza et al., 2018 Jerina et al., 2014 Johann et al., 2020 Keuling et al., 2010 Laguna et al., 2021 Palencia et al., 2021a Podgórski et al., 2018 Russo et al., 1997 Truvé & Lemel, 2003

	respectively. Dispersing individuals may play a relevant role in ASF spread in populations with low inter-group connections.	
Social organization	Matrilineal groups of adult and subadult sows and their piglets, while males are more independent. There is little overlap between group home ranges.	Pepin et al., 2021 Podgórski et al., 2014
Reproduction	Seasonality: Reproduction is slightly seasonal. Pregnancy rates in Europe range from 8% in July to 52% in February. The peak of farrows occurs during spring. Sexual maturity is linked to body weight rather than age, and a minimum of 15-35kg are needed to achieve maturity. This can already take place at seven months for females. Litter size: average of 4.4 piglets/female (ranging from 1.2 to 9.0)	Fonseca et al., 2011 ENETWILD-consortium et al., 2022a Sáez-Royuela & Tellería, 1986
Mortality	Hunt: Hunting is the main cause of adult wild boar mortality in central Europe. Disease: Regionally, diseases such as tuberculosis or ASF can also cause significant mortality. Predation: The wolf (*Canis lupus*) is the only predator with a locally significant impact on wild boar population dynamics, with consequent impacts on disease dynamics	Barasona et al., 2016 EFSA et al., 2022 Keuling et al., 2013 Tanner et al., 2019
Farming	Wild boar farms exist in many countries. These constitute a risk for wild boar introduction into new areas and are linked with wild boar translocations and subsequent disease risks. Fenced game parks or fenced hunting areas also occur worldwide but are especially common in southwestern Europe, parts of central Europe and the Americas.	Aschim, 2022 Gortázar et al., 2006 Michel et al., 2017 Vicente et al., 2007
Abundance	Population density estimates reported in central and southern Europe are often between 5-10 ind·km^2 but densities of 20-30 ind·km^2 or even higher are sometimes reported (for instance, in peri-urban areas and in fenced game estates where year-round artificial feeding is provided). In North America, feral pig densities can reach ca. 30 ind·km^2	Baber & Coblentz, 1986 Castillo-Contreras et al., 2018 ENETWILD-consortium et al., 2022b González-Crespo et al., 2018

Over less than 30 years invasive wild pigs have expanded and have undergone the most extensive and rapid range increases ever recorded (Brook & van Beest, 2014). ASF has been recently detected in America but only in the island nations of Dominican Republic (29 July 2021) and Haiti (19 September 2021), not on the mainland (OIE 2021). However, even a single case in any of the large pork-producer countries would be catastrophic. Large numbers of pig farms and an extensive and rapidly expanding invasive wild pig population create important concerns regarding ASF. Aschim (2022) investigated in Western Canada the distribution of free-ranging wild pigs overlapping with 2,549 domestic pig farms over 331,542.7 km^2, which represented 21% of the entire study area. Wild pigs were significantly closer to small-domestic pig 'backyard' farms than the large-scale commercial domestic pig farms. GPS-collared wild pigs visited frequently domestic pig farms during all the seasons. ASF could enter continental America by two main paths: i) by infection in feral pigs, for instance in peri-urban habitats (e.g., when feeding on garbage) (Castillo-Contreras et al. 2018 and 2021); or ii) by infection in domestic pig holdings (Jo and Gortázar, 2020). Both could finally derive into spread at the wildlife-livestock interface. Risk analysis and mitigation approaches that prevent wild pig-domestic pig livestock contact are fundamental to the prevention of disease transmission at this interface (Miller et al., 2013).

The native Eurasian wild boar is characterized by extreme ecological plasticity and is adapted to a broad range of environmental conditions occupying a variety of habitats (Bieber and Ruf, 2005; ENETWILD-consortium et al., 2022a). Wild boar distribution and abundance depend mainly on the availability of energy-rich food sources. The wild boar is a social species and its behaviour could influence ASFV transmission at fine spatio-temporal scales (Podgórski & Śmietanka, 2018). Waterholes and feeding points increase the contact rates between social groups and have been linked to disease risks (Barasona et al., 2014; Barroso et al., 2020; Podgórski et al., 2018; Yang et al., 2021). No single fence is 100% effective for wild boar, watercourses being the most vulnerable points. Fence crossings are more frequent among males and during food shortage periods (Laguna et al., 2022). This is relevant for disease spread in areas with outdoor pig production (Jiménez-Ruiz et al., 2022).

Due to its distribution, abundance, and impact, the wild boar is regarded as an ecosystem engineer and an important component of native Eurasian vertebrate communities. However, overabundant wild boar (and feral pigs at any density) affect biodiversity conservation, cause road accidents, damage crops and, most importantly, transmit infections to human beings and livestock (Barasona et al., 2021; Barrios-Garcia & Ballari, 2012; Barroso et al., 2020; Fernández-López et al., 2022). To effectively control wild boar in the short term, high harvest rates of over 60% of the population are advised (González-Crespo et al., 2018; Keuling et al., 2013; Sanguinetti & Pastore, 2016; Toïgo et al., 2017), although this is challenging to achieve at large geographical scales (EFSA et al., 2018). Nevertheless, after the collapse of the Soviet Union in 1991, wild boar abundances declined by 50% in just five years (Bragina et al., 2015) evidencing that intense hunting at a large geographical scale can change population trends. By contrast, current harvest rates seem insufficient to control the population trends in Europe (Keuling et al., 2016; Massei et al., 2015). Recreational hunting in the Americas has contributed to feral pig range expansion and is therefore not considered a viable control tool (Beasley et al., 2018). In Europe, today's recreational hunting contributes to mitigate wild boar overabundance but does not impede ongoing population growth (Massei et al., 2015; Quirós-Fernández et al., 2017). In Switzerland, hunting clearly reduced wild boar crop damage, while alternative methods such as crop fencing and diversionary feeding were not effective (Geisser & Reyer, 2004). However, hunter numbers are declining over time (Massei et al., 2015) and there are no suitable alternatives to hunting available (Gortázar & Fernández-de-Simón, 2022).

ASF epidemiology in wild suids and the role of vectors

African swine fever (ASF) has become established in many countries globally. In eastern and southern Africa, where ASF virus evolved in a sylvatic cycle between common warthogs

(*Phacochoerus africanus*) and argasid ticks (soft ticks) of the *Ornithodoros moubata* complex that live in their burrows, ASF has been endemic for millennia, and has been known in domestic pig populations for more than a century (Montgomery, 1921; Mulumba-Mfumu et al., 2019). Recent research that found fragments of ASF-viral DNA incorporated in the genome of *O. moubata* complex ticks suggests that the virus evolved in the ticks approximately 1.42 million years ago (Forth et al., 2020). The warthog-tick sylvatic cycle is unique to eastern and southern Africa. Countries where the cycle occurs are characterized by a long history of ASF outbreaks in domestic pigs and the presence of multiple p72 genotypes of ASF virus (Penrith et al., 2019). Although they are impervious to the pathogenic effects of the virus, bushpigs (*Potamochoerus larvatus*) have no association with *Ornithodoros* ticks and only limited transmission to in-contact pigs from acutely experimentally infected bushpigs occurred (Anderson et al., 1998). A single report of the isolation of ASFV from a giant forest hog (*Hylochoerus meinertzhageni*) exists (Heuschele & Coggins, 1965). Currently giant forest hog – domestic pig interactions are unlikely (Jori & Bastos, 2009), but could become more frequent in the future due to deforestation, population growth and encroachment.

The role of wild boar in ASF differs from the role of African wild suids. While African wild suids do not die of ASF and the virus is rarely found in carcasses and, if present, is generally restricted to lymph nodes and spleen, the consequence of an infection in wild boar is similar to domestic pigs i.e., mortality rates of about 90% within 4 to 15 days post-infection. In most of Eurasia, suitable soft ticks are either absent or not relevant for ASF transmission, while close contacts in social groups or with infected carcasses likely play a relevant role in ASF epidemiology (Pepin et al., 2020). The role of dipterans as mechanical vectors has been suspected in ASF transmission. This possibility was experimentally confirmed under laboratory conditions for *Stomoxys* stable flies (Olesen et al., 2018) and preliminary field evidence starts to emerge, with findings of ASFV DNA in *Stomoxys* and other dipterans captured in pig farms (Turčinavičienė et al., 2021). Sampling at wild boar baiting sites in Estonia failed to detect ASFV DNA in potential vector species, although the sampled species differed from those of the farm study (Herm et al., 2021).

In domestic pigs, this tenacious virus has been shown to persist in the blood (540 days at 4°C), spleen (204 days), bone marrow (180 days), skin/fat (300 days) and frozen meat (1000 days) (EFSA, 2014). It is characterized by low transmissibility, making ASF spread between family groups relatively slow except if social groups congregate at feeding stations or water holes (EFSA et al., 2017; Iacolina et al., 2021). Natural ASF spread, estimated at 0.4 km/week in Belgium, can be further slowed down by barriers and is also slower in open or fragmented habitats (Dellicour et al., 2020; Griciuvienė et al., 2021). ASFV spread is probably more efficient in a pig farm than in free-living wild boar. Larger distances of ASFV spread are usually human-mediated (Iscaro et al., 2022b; Taylor et al., 2020). The most efficient means of transmission is blood contact, for instance by inspecting or feeding on infected carcass remains. However, through time, once a highly pathogenic virus strain enters a natural wild boar population, the mortality can be over 90% (Chenais et al., 2019; Morelle et al., 2020).

The currently ongoing Eurasian ASF epidemic is caused by highly virulent genotype II strains (Iacolina et al., 2021). Even though several strains with lower virulence have been detected in the Baltic States, they seem to be able to spread only in limited areas and time periods (Vilem et al., 2020; Zani et al., 2018). Low-virulence strains represent challenges for ASF diagnosis (Sun et al., 2021a and 2021b), display different shedding patterns and especially a lower positivity in faeces (Kosowska et al., 2021; Sun et al., 2021). The more virulent strains seem to have an advantage, suggesting that infected carcasses play an important role in the transmission and persistence of the virus (Morelle et al., 2019; Pepin et al., 2020). Virulent strains are likely to spread more easily also because they cause bleeding in diseased animals and blood contains the virus in large amounts, allowing more effective transmission.

Case clusters may occur as family groups (Frant et al., 2021b) or within distances of up to two km and within one week (Allepuz et al., 2022) and seasonality is reported in some settings, although this could also be driven by changes in carcass detectability (e.g., more cases in winter in Poland, Frant et al., 2021a). In Estonia and Latvia there are two distinct peaks in the prevalence curve of ASF virus-positive wild boar found dead – the winter and summer peaks, whereas in Lithuania only the winter peak can be observed (EFSA, 2020a and 2021a). The peaks in prevalence coincide with the period of more rapid spatial spread in Estonia (EFSA et al., 2018). The biological explanation for this phenomenon has yet to be elucidated.

Since mortality rate is high, in wild boars ASF is mostly detected in carcasses through passive (general) surveillance, while only a small proportion of serum samples derived from active (targeted) surveillance have specific antibodies while being PCR negative, suggesting recovery from infection (Oļševskis et al., 2020). In the Baltic countries, where wild boar populations had been increasing for 30 years as in other parts of Europe (Massei et al., 2015), ASF entry in 2014 triggered a pronounced five year-long decline in hunting harvest results (an indicator of relative wild boar abundance), which fell back to values similar to year 2000 (EFSA et al., 2022). From 2014 to 2017 the disease spread as an epidemic wave through the wild boar population of most of the territory of Estonia and Latvia, while the speed of spatial spread in Lithuania has been considerably slower (EFSA et al., 2017). Since 2020, hunting harvests are rising again in all three countries despite ASF (EFSA et al., 2022; Schulz et al., 2021; Schulz et al., 2022).

In the Baltic States, the epidemic wave passing through the wild boar population caused almost complete demographic depletion. However, limited circulation of the virus could be observed in pockets behind the wave in the following years. In Estonia the wild boar density was estimated to be less than 0.1 adults per km^2 after the epidemic wave (EFSA 2021a), and less than 0.3 adults per km^2 in mainland Italy six months after the first positive case reported (Palencia et al., 2023). It is not fully understood how ASFV is able to survive at such extremely low (<1 ind$\cdot km^{-2}$) wild boar densities. Modelling suggests that, in addition to local, mostly intra-group, frequency-dependent direct transmission, two complementary mechanisms might contribute to

ASF maintenance, namely a certain proportion of infected wild boar not succumbing immediately to the infection and a prominent role of infected carcasses in virus maintenance in the environment (Gervasi & Guberti, 2021; O'Neill et al., 2020; Yang et al., 2021). In certain regions, re-entry of infected wild boar from neighbouring infected countries must also be considered (Schulz et al., 2021).

The approximate time scheme of an ASFV introduction into a natural wild boar population is represented in Figure 4. ASF typically leads to a population reduction of 85–95% in the initial epidemic phase. The disease does not exhibit a typical epidemic pattern for highly virulent and transmissible, acute infections with self-limiting localized epidemics, and instead can persist for several years at low (1–3%) prevalence in low-density populations (EFSA et al. 2017). Table 2 presents information on wild boar harvest in Belgium before and after the ASF outbreak, comparing the infected area with the surrounding white zone with intense wild boar cull.

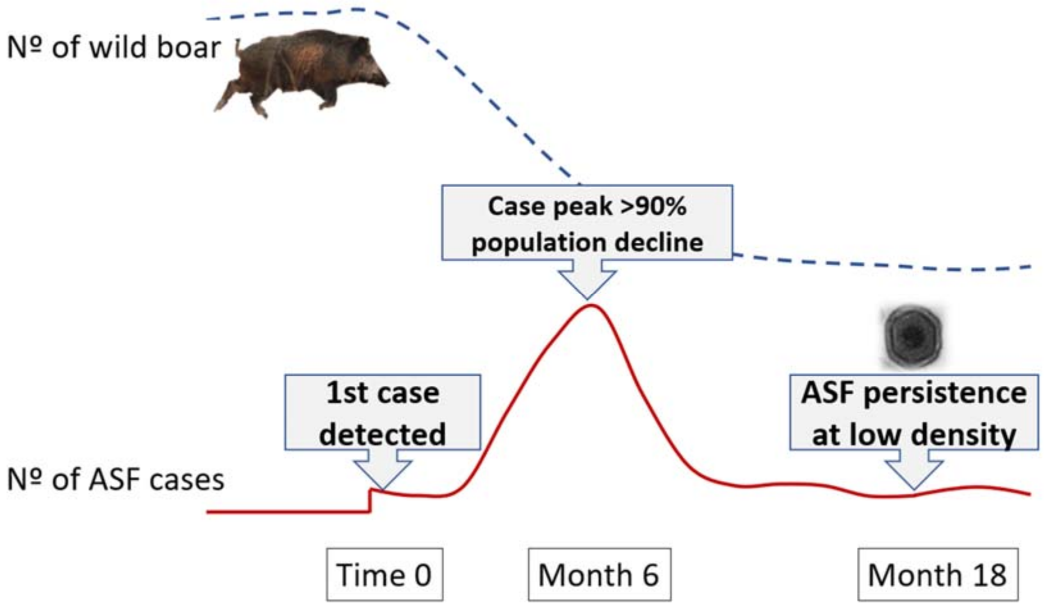

Figure 4.- The impact of an African swine fever (ASF) epidemic (virulent strain) on wild boar population dynamics. The solid line represents the number of ASF cases and the dashed line the

wild boar population size. The number of cases peaks about six months after epidemic onset, stabilizing thereafter with soft fluctuations. The wild boar population drops by about 90% during the epidemic peak and stabilizes thereafter. Field evidence from the Baltic States shows that ASF virus can persist through time despite the huge drop in wild boar populations. This is a simple representation of the authors' expert opinion.

Table 2.- Wild boar mortality data recorded during the hunting season before the Belgian African swine fever (ASF) outbreak (2017-2018) and during the three seasons following the outbreak (% compared to 2017-2018, considering both hunting- and ASF-mediated mortality). Personal communication: A. Licoppe.

ZONE	2017-2018	2018-2019	2019-2020	2020-2021
Infected zone (598 km²)	*754*	1505 ***(+100%)***	607 ***(-19%)***	120 ***(-84%)***
White zone (508 km²)	*1042*	1803 ***(+73%)***	2516 ***(+141%)***	526 ***(-50%)***

Modelling also suggests that a faster degradation of carcasses due to elevated temperatures or abundant obligate scavengers may reduce the severity of the outbreak, while the higher underlying host density and longer breeding season associated with supplementary feeding of wild boar leads to a more pronounced epidemic outbreak and longer disease persistence (O'Neill et al., 2020). As there is no vaccine available, early detection and quick response are key for successful ASF control (EFSA et al., 2020; O'Neill et al., 2020). See Appendix S2 for a table with EFSA documents and their contents as relevant to this review.

Integrated monitoring and surveillance

Establishing a proper monitoring scheme is the key requisite for disease control in wildlife (Lawson et al., 2021; Mazzamuto et al., 2022). Infections shared with wildlife, such as ASF, should preferably be monitored in an integrated way, i.e., considering the changes in host population as well as in infection distribution and prevalence (Barroso et al., 2023). Integrated monitoring will allow changes in abundance (e.g., due to unnoticed disease outbreaks) and disease occurrence to be identified early and enable the critical assessment of the impact of eventual interventions (Cardoso et al., 2022; Gortázar et al., 2015).

Diagnostic testing

Spleen and whole blood are target tissues for ASFV detection by qPCR (de Carvalho Ferreira et al., 2014; Petrov et al., 2014). Easy-to-handle swabs (of whole blood, Petrov et al., 2014) and pre-hydrated sponges can sample, inactivate and store ASFV DNA for qPCR from environment and surfaces (Kosowska et al., 2021). Swabs and filter paper samples can also be used for serum antibody detection (Blome et al., 2014). The probability of finding positive antibody or PCR test results is higher in juveniles than in adults, and far higher in found-dead animals than in hunter-harvested ones (Schulz et al., 2019). However, at low wild boar densities, accurate ASF surveillance is challenging and depends on carcass search effort (Gervasi & Guberti, 2021, Schulz et al., 2021).

Passive (general) surveillance and early detection

Passive (general) surveillance, i.e., the search for dead or visibly sick wild boars to test them for ASFV by qPCR, is the main tool for early ASF detection. In low-density wild boar populations, in remote regions where wildlife disease surveillance is not a priority, or if low-pathogenic ASFV strains circulate, ASF in wild boar may run undetected over prolonged time periods (Vergne et al., 2020). Passive (general) surveillance, although expensive, is the main means of ASF monitoring in wild boar (Frant et al., 2021a; Gervasi & Guberti, 2021; Jo & Gortázar, 2020). Valuable information can be obtained by estimating the post-mortem interval of ASFV-positive wild boar carcasses (Probst et al., 2020). Wild boar carcasses from road traffic accidents should also be investigated as part of passive surveillance (Frant et al., 2021a; Schulz et al., 2020).

Indirect evidence might point to ASF outbreaks and can serve as a disease signal. For instance, big data on ASF-related news and ASF information-seeking behaviour can be used for

ASF surveillance at large geographical scales (Arsevska et al., 2018; Tizzani et al., 2021). Changes in predator diet including increased predation on livestock can also be another potential indicative of ASF (or other disease) causing demographic impact on the prey population (wild boar in this case) (Klich et al., 2021).

Active (targeted) ASF surveillance

Active (targeted) ASF surveillance is based on sampling hunter-harvested wild boars, and wild boars culled for reasons other than visible disease. Both qPCR and serology are used for diagnosis. The likelihood of finding test-positive cases by active (targeted) surveillance is low as compared to passive (general) surveillance, especially during the onset of an epidemic (Gervasi & Guberti, 2021), while the proportion of seropositive qPCR negative wild boar tends to increase through time (Martínez-Avilés et al., 2020). The random sampling nature of active (targeted) surveillance provides valuable epidemiological information despite the low prevalence, but requires large sample sizes.

While ASF surveillance of farmed pigs is relatively straightforward, it can be challenging in free ranging wild boar. Based on the stability of ASFV DNA in faeces and the proportion of ASFV-positive faecal samples from known-infected wild boar, faeces have been proposed as a suitable sample for non-invasive active ASFV surveillance (de Carvalho Ferreira et al., 2014). This could eventually be combined with using wild boar faeces as an indicator of abundance and spatial aggregation (Acevedo et al., 2007).

Wild boar and feral pig population monitoring

In addition to indirect abundance indicators, efforts have focused on developing and harmonizing methods to estimate wild boar density (ENETWILD-consortium et al., 2019; Palencia et al., 2023). Particularly, the use of motion-activated cameras (camera traps) is nowadays the reference method to estimate wild boar density (ENETWILD-consortium et al., 2022; Palencia et al., 2021b), generating values for wild boar densities at European scale (ENETWILD-consortium et al., 2022) and measuring population trends after an ASF outbreak

(Bollen et al., 2021; Morelle et al., 2020). The sampling design applied to estimate density is compatible with the monitoring of other relevant variables in the context of ASF management, such as average daily distance travelled (Palencia et al., 2021a), direct and indirect interaction rates (Triguero-Ocaña et al., 2020), recruitment, and compliance of human restriction rules (Palencia et al., 2023). Other approaches, such as hunting bags accounting not only for hunted animals but corrected by the hunted area or the number of hunters among other factors (ENETWILD-consortium et al., 2019), or approaches based on individual recognition of feral pigs, have been described as reliable (Jiménez et al., 2017).

The ENETWILD consortium (www.enetwild.com) developed a citizen science project named Mammalnet (https://mammalnet.com/) and the European Wildlife Observatory (https://wildlifeobservatory.org/). Among the tools developed there is an App, iMammalia (https://mammalnet.com/imammalia/), that allows public sharing of geographically localized photos of a living animal or a carcass in an open repository. This tool has been used for wild boar carcass signalling in Serbia (Graham Smith pers. comm.).

Intervention options

In wildlife diseases, intervention options beyond not acting have been divided into preventive actions, vector control, population control, and vaccination (Gortázar et al., 2015; Wobeser, 2002). However, vectors have limited relevance for ASFV maintenance in the current pandemic and approved vaccines are still not available (Dixon et al., 2020). Hence, in addition to the options of zoning and no action, the tools currently at hand are restricted to preventive actions and wild boar population control. ASF control measures applied in wild boar populations are harmonized among the EU countries and defined in legislation and guidance documents (http://data.europa.eu/eli/reg_impl/2021/605/oj; https://ec.europa.eu/food/system/files/2020-04/ad_control-measures_asf_wrk-doc-sante-2015-7113.pdf). In brief, they are aimed to restrict the virus spread in front of the epidemic wave and to keep the density low behind the wave. Both objectives are to be achieved by reducing wild boar numbers with intensified and targeted hunting efforts and removal of infected carcasses. This section briefly lists the main ASF intervention tools in wild boar and at the wild boar-pig interface, along with key references.

Preventive and biosafety-related actions

Translocation control

Translocation control is meant to prevent the introduction or re-introduction of pathogens via the release of infected free-living or captive wildlife. This is currently in place in the EU regarding international wild boar transport. However, wild boar can still be legally translocated within country boundaries under national regulations. Illegal translocations may occur, but international movements are unlikely to be frequent.

Barriers and fencing

Wild boars are not contained by natural barriers such as large rivers or high mountains (EFSA 2014, 2015). The pros and cons of fencing have been reviewed (Gortázar et al., 2015; Mysterud & Rolandsen, 2019). Indirect effects on other species should be accounted, and conflicts have already emerged in the context of ASF fencing in Germany. Regarding ASF control, fences are used in four different ways, namely (1) as large geographical barriers, for instance along country boundaries (Jo & Gortázar, 2021; Mysterud & Rolandsen, 2019; Sauter-Louis et al., 2021a); (2) as local hotspot fencing to reduce disease spread, for instance after point introductions of ASF (Dellicour et al., 2020; EFSA et al., 2018a, 2019); (3) as a means for facilitating depopulation measures in infected zones (Belgium) and the periphery of the infected zones (white zones); and (4) as a component of pig farm biosecurity (EFSA et al., 2021b; Jiménez-Ruiz et al., 2022).

Fences, roads, and rivers delay but do not impede ASF spread in infected regions (Han et al., 2021; Sauter-Louis et al., 2021a). Large-scale fencing failed to control ASF entry in Bulgaria (Mysterud & Rolandsen, 2019), Germany (Sauter-Louis et al., 2021a), and South Korea (Jo & Gortázar, 2021) (Fig 2., Appendix S1), but it is been considered in north Italy.. In South Korea, ASF expansion gained speed after a sudden switch from small-scale fencing and silent culling to non-silent culling possibly due to biosafety failures (Jo & Gortázar, 2021).

Construction and maintenance costs need to be considered in all fencing options and are proportional to fence length and durability (Jori et al., 2020). Fence-crossing success depends on fence construction and habitat (streams), wild boar gender (males are more likely to succeed), and season, with more successful crossings taking place during periods of food scarcity season than during the hunting season (Laguna et al., 2022).

Farm biosecurity

Pig farm biosecurity is marginal to the scope of this review. However, it is listed here since it constitutes an integral part of ASF control, especially regarding the wild boar-pig interface. Available biosecurity measures (BSMs) will depend on the type of farm (backyard holdings vs. commercial ones; farm size; open-air vs. indoor farming) and have been reviewed recently evidencing the scarcity of available scientific information. It is expected that the regular implementation of independent and objective on-farm biosecurity assessments using comprehensive standard protocols will reduce the higher risk of ASF introduction and spread related to outdoor pig farms (EFSA et al. 2021b). Specific BSM assessments are available for outdoor production systems such as Iberian pigs (Jiménez-Ruiz et al., 2022).

Carcass removal and destruction

Carcass removal is one of the interventions applied in the successful eradication of the ASF point introduction in Belgium (EFSA et al. 2018a, 2019). In the Czech outbreak, however, this measure was delayed by the veterinary services and a systematic search for carcasses started only nine months after the first case detection. The reason was concerns that a systematic search would cause longer wild boar movements. Czech hunters responsible for carcass searching were paid compensations of €600/km^2, plus €190 for each carcass.

Modelling often supports a key role of carcasses in ASF maintenance, even at low wild boar densities, and hence emphasizes the importance of carcass destruction (EFSA et al. 2018b;

Gervasi & Guberti, 2021; O'Neill et al., 2020; Pepin et al., 2020; but see Taylor et al., 2020). It has been one of the most applied interventions, and frequently with successful results (Fig. 2; Appendix S1). However, models also suggest that only high carcass removal rates (>40%) in a relatively short time (<1 month) are likely to significantly impact on ASF maintenance (Croft et al., 2020; EFSA et al., 2018b). Paying incentives helps to increase the number of retrieved carcasses but had no clear effect on disease indicators in some countries and might imply biosecurity risks depending on participant compliance with hygiene regulations (Jo & Gortázar, 2021; Schulz et al., 2019).

Moreover, finding wild boar carcasses (and older carcass remains) in dense vegetation is no easy task, and performing systematic carcass search, removal, and destruction operations represents a significant logistic challenge (Desvaux et al., 2021). Methodologies to optimize carcass search efforts have been suggested, mostly based on knowledge on the expected distribution of infected carcasses, e.g., in dense vegetation or close to water (Allepuz et al., 2022; Lim et al., 2021).

In regions with significant populations of obligate scavengers such as griffon vultures (*Gyps fulvus*), these might contribute to carcass cleaning in relatively open landscapes, potentially contributing to ASF control (O'Neill et al., 2020). Wolves (*Canis lupus*) and jackals (*Canis aureus*) have also been suggested to contribute to ASF control (Kemenszky et al., 2022; Szewczyk et al., 2021). Drones (in open areas, as used on the Oder River islands between Poland and Germany) and hunting dogs may have the potential to contribute to carcass search efforts (Desvaux et al., 2021; Havránek et al., 2020).

Wild boar management biosafety

Infected wild boar, pigs, and pork meat or other blood-containing materials represent a risk for human-mediated ASF spread. In South Korea, significant biosafety risks arose from the movements of people handling or in contact with wild boar such as hunters, military, and volunteers, as well as from swill feeding of wild boar and by environment contamination during pig cull operations (Jo & Gortázar, 2021). By contrast, the success of ASF eradication in the Czech Republic and Belgium was associated in part with compliance with biosecurity rules (Fig. 2, EFSA et al. 2018a).

Hunting waste management is an often-neglected aspect of hygiene. In Spain, proper waste management contributed to reducing wild boar tuberculosis prevalence by 25% (Cano-Terriza et al., 2018). In the case of ASF entry, hygiene aspects need to be well established and accepted by the hunters (Lizana et al., 2022).

Population control

Habitat management

It has been suggested that the effectiveness of habitat management for wild boar control depends on the surface to be managed and the available timeframe (Jori et al., 2020). At the small scale of a point introduction, ensuring food availability inside the delimited infected zone might be wise to prevent wild boar movements (EFSA et al. 2018a). However, feeding bans were imposed in the successfully controlled Belgian outbreak (see Appendix S3).

At large scales and with long-term schemes, funding and social sustainability issues might arise (Jori et al., 2020). The regulation of wild boar baiting and feeding as an ASF control tool remains highly controversial (Schulz et al., 2019). Modelling suggests that inter-group contacts resulting from baiting increase the risk of ASF maintenance (Yang et al., 2021), and that the higher host density and longer breeding season associated with supplementary feeding leads to ASF persistence (O'Neill et al., 2020). Winter feeding bans implemented in Latvia since 2014 -while baiting for hunting is still allowed- had no effect on disease indicators (Schulz et al., 2019).

Professional culling

Professional culling as opposed to recreational hunting can be performed using firearms or traps. The use of poison is possible in Oceania and North America, where feral pigs are invasive (Beasley et al., 2021), but not in Europe. The advantages of professional culling include the strict recording of effort and results, presumably better adherence to hygiene regulations, and the generally silent culling procedures.

Trapping is perceived as resource-intensive but has good acceptability (Jori et al., 2020) and can be efficient in removing whole sounders, achieving a 90% population decline in 12 months (Lewis et al., 2022). In South Korea, up to 7.5 wild boar per km^2 were trapped during the ongoing ASF pandemic, without a clear effect on disease indicators although ASF spread was slower during silence hunting, included trapping (Jo & Gortázar, 2021). The practicality and effectiveness of professional culling inside and outside infected zones would benefit from additional research. By now, discrepancies have been found in the studies that assessed its utility in experimental settings (Fig. 2, Appendix S1).

Recreational hunting

In peacetime, recreational hunting is regarded as one tool in the box for wild boar management if the option is available. Even if hunting is often not sufficient to stabilize wild boar populations, it will contribute and make additional efforts cheaper (Gortázar & Fernandez-de-Simon, 2022). Modelling suggests that preventive low-intensity (6%) feral pig population reduction might reduce future ASF maintenance likelihood (Yang et al., 2021).

Regulated and supervised recreational hunting took place in the white zones (around the infected ones) in Belgium and Czechia. In ASF-endemic Romanian hunting grounds, intense hunting was a protective factor for ASF in wild boar (EFSA et al. 2022). However, group hunting may carry biosafety risks (Jo & Gortázar, 2021) and cause longer wild boar movements (Laguna et al., 2021). Thus, the pros and cons of using recreational hunting in ASF control, both outside and inside infected zones, need to be considered for each specific setting (Guberti et al. 2019).

Disease management in different epidemiological scenarios

Management of ASF outbreak is challenging, different tools may be used in different epidemiological settings, and both the intervention options and the success probabilities are highly context-dependent (Sauter-Louis et al., 2022). Figure 5 summarizes the management actions tested in the European continent for preventing or controlling ASF in wild boar, while a more in-detail list regarding ASF control and monitoring is provided in Appendix S2.

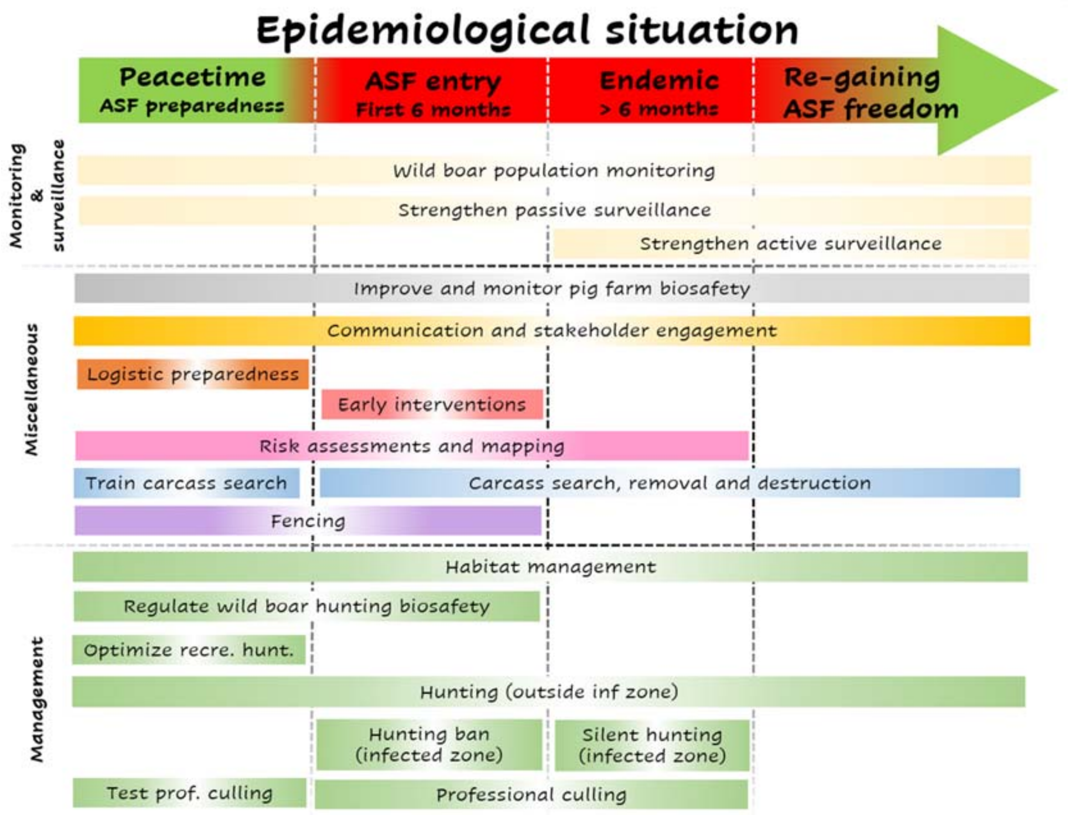

Figure 5. Summary of management actions tested in the European continent for preventing or controlling African swine fever (ASF) in wild boar. Abbreviations: hunt.: hunting; prof.: professional; recre.: recreational.

<u>Peacetime: prevention and preparedness</u>

Communication and stakeholder engagement

Communication to relevant stakeholders and the public, stakeholder involvement, and training are important components of outbreak preparedness. Stakeholder engagement and public awareness are needed from early on, before ASF reaches a country. Jori et al. (2020) produced a comprehensive list of potentially relevant stakeholders to consider in the event of an ASF outbreak in wild boar, who should be contacted to collaborate beforehand.

Hunter attitudes and beliefs regarding ASF surveillance, case reporting, and implication in disease control efforts (hunting, biosafety, carcass search and destruction) have been addressed in different regions and contexts (Emond et al., 2021; Stončiūtė et al., 2021; Urner et al., 2020; Urner, Sauter-Louis, et al., 2021; Urner, Seržants, et al., 2021; Vergne et al., 2016). Latvian hunters perceived passive (general) ASF surveillance as a topic of duty and ethics rather than an issue-driven by incentives – they get involved because of being responsible, not because of money (Urner, Sauter-Louis, et al., 2021). However, incentives for carcass reporting were deemed favourable by Estonian and Lithuanian hunters (Stončiūtė et al., 2021; Urner et al., 2020). Reducing the infection pressure in the forests was regarded as motivating by Latvian hunters (Urner, Sauter-Louis, et al., 2021), while reduction of workload, improved feedback and relationships with government officials were deemed favourable by Lithuanian hunters (Stončiūtė et al., 2021). These insights are important to set up successful nation and social specific collaboration schemes with hunters and hunter organizations. Conversely, information on the attitudes of other stakeholders regarding ASF is scarce (Vergne et al., 2016).

Training for outbreak management

Specific training for animal disease emergencies, often with a focus on ASF, is provided to official veterinary services in most industrialized countries. However, information and specific training are not always extended to other relevant components of the administration, such as environment authorities, police, and others, and often exclude important actors outside administration such as field veterinarians and hunters. Joint field training events, including practical exercises of wild boar carcass search, sampling, retrieval, and destruction, might help to understand the huge logistic demands arising in case of an ASF outbreak. A video illustrating such field training can be found here: https://www.irec.es/divulgacion-cientifica/video-actuacion-ante-emergencias-sanitarias-jabali/. Night shooting and trapping also require special training.

Wild boar management and integrated monitoring

The relevance and characteristics of integrated monitoring are addressed above. Monitoring wildlife populations over large areas is challenging, but outputs are already available such as the 2x2 km wild boar density model developed from hunting data (ENETWILD consortium et al. 2021). In addition to monitoring, exploring the feasibility and efficacy of different wild boar hunting methods and their effect on wild boar disturbance should be assessed in peacetime (Jori et al., 2020). Also in peacetime, it is worth testing other population control tools such as trapping and night shooting.

ASF risk assessments

In 2014, the risk of ASF entry was estimated low for Belgium, where ASF entered in 2018. However, international experts ranked this risk two times higher than national ones (Roelandt et al., 2017). Risk mapping during peacetime, considering habitat characteristics and wild and domestic suid distribution patterns, might help to focus preventive actions and optimize future outbreak management (Bosch et al., 2017; Fekede et al., 2021; Wormington et al., 2019). Detailed spatial information on wild boar population genetics can assist in defining corridors and natural or artificial barriers (Griciuvienė et al., 2021; Reiner et al., 2021).

Material and logistic preparedness

Animal disease emergencies are demanding and require capacities that go beyond the common capacities of most veterinary services, different stakeholders' structures and categories, and range from real-time coordination to safe carcass destruction. See Appendix S2 for an incomplete checklist.

<u>Recent ASF entry</u>

Point introductions

Point introductions of ASFV into wild boar populations have been recorded in three European countries during the current ASF epidemic: Czech Republic, Belgium, and Italy (see

Appendix S3). While the origin of these outbreaks is unknown, the main hypothesis suggested that all are were linked to human activities.

After confirmation of the first case, opportunistic carcass search helps to define the infected area, and then zoning can take place. Immediate control measures intend to reduce wild boar movements and to avoid disturbance (e.g., banning hunting and forestry and recreational activities, fencing) while maximizing carcass destruction (EFSA et al. 2019). Later in time, feeding bans and population control are eventually implemented, including trapping (e.g., 1 trap·1 km^{-2} in Czech Republic, 3 traps·10 km^{-2} in Belgium), night shooting, single hunting at baiting points, and even driven hunts with/without dogs (Appendix S3).

The prospects of ASF control are better for outbreaks which are detected early and thus affect small areas where interventions start soon. This was the case in the Czech outbreak, and disease eradication was achieved in one year. However, on December 2022 (five years after the last case), the ASFV infection in a dead wild boar piglet found near the border with Poland was reported. In Belgium, the affected area was larger and disease eradication took two years. In Italy the spatial and temporal pattern of the first focus suggests an even older and more widespread situation when ASF was first detected, which will prove more challenging to control. In Italy, habitat structure, routine hunting practices, as well as the spread of ASF in wild boar in additional foci in central Italy and domestic pigs, will pose additional challenges. During the first year after the outbreak in northern mainland Italy, two new outbreaks were reported in central Italy (>500 km from the first report) and spill-over to domestic pig farms occurred (Iscaro et al., 2022; Palencia et al., 2023). In northern Greece, a positive wild boar was detected (Brellou et al., 2021). A detailed overview of the point introductions recorded in Europe can be found in Appendix S3.

Front-like settings

Logistics, resources, and expectations will differ between point introductions and front-like ones (Sauter-Louis et al., 2022). In front-like ASF introductions there is continuous infection pressure along a large border. Thus, resources become split between several incursion events (Sauter-Louis et al., 2021a). Such a scenario is evident in Germany, where several federal states are affected by ASF in wild boar (Sauter-Louis et al., 2021b). Combinations of initial hunting bans, targeted fencing (fragmentation of the area and use of natural borders), intensive carcass search (with the help of drones and dogs) and removal, implementation of white zones (using traps and single hunt), and general reduction of the wild boar population were implemented with variable success. Strict implementation of the above-mentioned measures has led to the possibility to lift the first two core zones in the federal state of Brandenburg. However, case numbers are still increasing, and new outbreaks were reported in domestic pigs, two of which were into previously unaffected federal states (Sauter-Louis et al., 2021b, 2022). In another front ASF setting, the South Korean government adopted European strategies to control ASF in wild boar (EFSA et al. 2018a). The South Korean Ministry of Environment (MOE) installed three-layered fences (electric fences for a core area of one wild boar home range, steel wired fences for three to five home ranges, and national-wide steel wired fences for dividing infected zones from safe zones) and hired carcass searching teams in the ASF infected zone. Also, the MOE hired and encouraged hunters with bounty money to reduce wild boar throughout the country (Jo & Gortázar, 2020). Due to political pressure, the strategy against ASF changed from undisturbed control (silent hunting, trapping, and fencing) to aggressive removal in 2020. The ongoing ASF spread demonstrates the risks of non-silent hunting combined with a lack of biosecurity (Jo & Gortázar, 2021). Seven cases of ASF spill-back from wild boar to farmed pigs were reported from October 2020 to October 2021 in South Korea.

Preventive wild boar depopulation in areas at risk close to infected zones (the so-called “white zones”) has successfully been applied around point introductions in Europe (Dellicour et al., 2020; EFSA et al., 2018a, 2019). Modelling suggests that white zones might also work in front-like ASF expansion settings, provided they are applied to leave a reasonable distance to known-infected zones, are wide enough, target an ambitious wild boar density reduction, and there is enough time to reach the target (EFSA et al. 2022). As mentioned above, white zones were successfully implemented in some of the affected regions in Germany and France (Desvaux et al., 2021). The success was only possible with tremendous efforts and may still be at stake due to constant pressure from the surrounding areas.

Stakeholder involvement after ASF entry

Stakeholders vary among and even within countries (Jo and Gortázar 2021) and might include different government agencies as well as police and military, academic, and research institutions, hunters, pig farmers, and general public. Their cooperation is essential for ASF control. In addition, conflicts of interest among stakeholder groups may arise, e.g., between veterinary authorities and nature conservation parties. Here, transparent communication is crucial.

In Belgium, a strategic committee was created including veterinarians, epidemiologists, wildlife biologists, academic experts, and administrative staff from regional and federal authorities (Licoppe et al., 2023). The committee met every week (or more frequently if urgent) to provide real-time instructions (for example, the construction of new fences or targeted night shootings) according to the detection of new positive cases. This committee was regularly advised by the EuVet experts. The chain of command reached achievements in the field from instructions by the strategic committee through a technical committee. Active search for carcasses and systematic removal with respect to biosecurity procedures were essential for controlling the epidemic, and this was possible through optimal stakeholder commitment (Licoppe et al., 2023).

In Italy, there was poor communication to inform stakeholders about the severity of the problem and the rationale for interventions, and it was criticised by hunter and farmer associations. A camera trapping study carried out in the infected zone showed that human presence was frequent in the field despite human movement was restricted (Palencia et al., 2023), likely due to the absence of appropriate stakeholders communication (e.g. posters with basic details were deployed more than one year later of ASF emergence). Thus, new foci have emerged in central and south Italy, and spill-over to pig farms occurred. The fact that after five months from the start, no culling had been implemented in the infected or the neighbouring areas, nor had the 270km long fence that had been proposed to circumscribe the infected area been started, left stakeholders disoriented. Stakeholders also perceived frequently a top-down approach, purely official, government-drivenwithout the involvement of scientists and thus losing relevant competencies and data (Vicente et al., 2019). A side effect of an official approach is that poor involvement and cooperation of stakeholders when managing a pathogen that can be spread by human activities could allow further ASF spread.

In summary, front-like ASF settings, as well as those evolving from late-detected point introductions, are unlikely to be controlled with the currently available tools and capacities.

Living with endemic ASF

Endemic ASF in Africa

In Africa, a domestic pig-tick pig cycle was discovered in Malawi (Haresnape et al., 1988) and may be more widespread, but the chief importance of the warthog-tick cycle specifically is that the infection can never be eradicated (Penrith et al., 2019). In almost all African countries today, including those where *Ornithodoros* ticks are not present (Trape et al., 2013), ASF is endemically established in domestic pigs. Subsistence pig keeping increased exponentially since the 1980s due to urbanization and increased demand for pork, while in rural areas pigs are often kept in free-range husbandry systems. The growth in pig-keeping has been accompanied by an exponential increase in ASF associated with low biosecurity in both production systems and value chains, posing a high risk for transmission and spread of ASF (Penrith et al., 2019). Involvement of the sylvatic cycle in ASF epidemiology is infrequent compared with pig-related outbreaks, and therefore currently African challenges in managing ASF are related to socio-economic drivers such as poverty (Penrith et al., 2019).

The wild boar-domestic pig interface

In Europe, the oldest long-time infected region is the Italian island Sardinia. The backyard and free-range domestic pig production and a wild boar-domestic pig cycle suggest similarities to the African situation, which also might occur in parts of south-eastern Europe (EFSA et al. 2019). In more recently ASF-infected regions in Europe, ASF management is still evolving, and applicable interventions remain debated.

For instance, modelling insights point in opposite directions regarding hunting, with some studies advising against it (Gervasi & Guberti, 2021; Taylor et al., 2020) and others in favour (Gervasi & Guberti, 2021; O'Neill et al., 2020). After ASF entry in Bialowieza, Poland, hunting reduced wild boar densities by an additional 11-22% (Morelle et al., 2020). Intense hunting had a positive effect on reducing the probability of recording positive PCR results in wild boar in Romania (EFSA et al. 2022). In the Baltic States, despite all efforts, sustainable reduction of the population density as well as maintaining the low density after the epidemic wave by hunting was not successful. It has not been possible to maintain the motivation of hobby hunters to keep up the hunting pressure. Wild boar is an important game species for hunters in all three countries and they are interested in maintaining the population on their hunting grounds (EFSA et al., 2022). Permission for using sound moderators (silencers) and night vision devices had no impact on disease indicators in Latvia (Schulz et al., 2019). Paying incentives for hunting females and juveniles did not significantly contribute to ASF control in Latvia (Schulz et al., 2019) and South Korea (Jo & Gortázar, 2021). Restrictions on driven hunts had no effect on disease indicators in Latvia (Schulz et al., 2019).

Risk assessment studies and focusing on past case clusters, as well as focusing on high-density wild boar populations might help to concentrate resources in infected areas as observed in Sardinia (Cappai et al., 2020; Loi et al., 2019). In Poland, the probability of detecting a wild boar ASF case increased six times at higher wild boar density and five times in woodlands as compared to other habitats, while indicators of human activity were not relevant (Podgórski et al., 2020).

Regaining ASF freedom

After the initial ASF outbreaks (Genotype I) in Portugal in 1957 and 1960, continental Europe re-gained ASF freedom in 1995. Notably, this was achieved without specific interventions on wild boar (Mur et al., 2012). By contrast, it has been questioned whether an endemic situation of ASF in wild boar is reversible in the current context (Schulz et al., 2019). Moreover, confirming ASF absence in infected regions or in nearby negative regions at a standard design prevalence of 1% is challenging, especially at very low wild boar densities. This can be overcome by considering consecutive time periods or a higher design prevalence (2% instead of 1%). Software such as Epitools allows calculating surveillance sensitivity and other variables (Schulz et al., 2021). EFSA et al. (2021c) proposed an success strategy in two phases, screening and confirmation, based on serological and virological prevalence profiles, where accuracy increased with increasing carcass-based surveillance. In French regions close to the Belgian outbreak, strengthened passive (general) surveillance combining patrols by volunteer hunters, professional systematic combing, and dog detection was set up to support the disease-free status (Desvaux et al., 2021).

Concluding remarks

We synthesized current knowledge on key background aspects of wild boar ecology and management and on ASF epidemiology in wild boar and other suids, and provided an overview of ASF control options in wild boar in different epidemiological scenarios. In the scientific literature, an exponential growth in the number of wild boar ASF-related papers has taken place, especially since 2010 (Fig. 1). However, there are still gaps in ASF research which can eventually be addressed by targeted experimental studies and more precise systematic reviews and meta-analyses. While most primary research was observational ASF epidemiology in wild boar and domestic pigs (Fig. 1), we suggest that future research should fill the observed gap in experimental studies. For instance, on management of wild boar populations or strategies for vaccine deployment in wild populations.

No assessment of bias is conducted in this review, and thus the implications for policymaking are limited (Munn et al., 2018). Five years ago, 20 intervention strategies for ASF control in pig farms and in wild boar were ranked by experts and none of the seven aimed at wild boar was prioritized (Guinat et al., 2017). This was probably because the practicality of interventions on wildlife is often perceived as low. However, the experience gained since the onset of the ongoing ASF pandemic shows that certain interventions or combinations of interventions can slow down ASF spread and eventually succeed in ASF eradication, at least after point introductions. Specifically, carcass search and destruction, and professional culling have been the most tested interventions (Fig. 2), but more experimental studies to assess the reliability of other interventions are still needed. Indeed, the consulted experts ranked fencing interventions higher in point introductions (mean effectiveness 5.33; mean practicality 4.08) than in front-like ones (mean effectiveness 4.50; mean practicability 3.83) or endemic situations (mean effectiveness 2.50, mean practicability 3.42). Carcass removal and destruction was ranked as the most effective intervention in all the ASF scenarios, and it has been already applied in experimental settings (Fig. 2, Appendix S1). Unfortunately, ASF spread in wild boar has never been halted in front-like epidemics. While vaccines are a much-expected but never arriving game-changer, current ASF control in wild boar relies on three essential tools, namely carcass destruction, wild boar culling, and fencing (see a list of strengths and weaknesses identified in Appendix S2). The ongoing ASF pandemic will keep on providing new relevant information, which will help to fill the observed knowledge gaps.

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Supplementary materials

Appendix S1: complete list of references from literature review.

Appendix S2: additional tables providing further details about EFSA reports, primary research in African swine fever (ASF), checklist for preparedness in the event of ASF (strengths and weakness).

Appendix S3: detailed information on the point introduction is Czech Republic, Belgium and Italy.

Conflict of interest

Authors declare no conflict of interest.

Ethics Statement

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. No ethical approval was required as this is a review article with no original research data.

Author contributions

CG conceived the study. PP and CG conducted the review process and managed the writing of the manuscript. SB, RKB, EZ, YSJ, AL, VM, MLP, RP, JV and AV provide a detailed overview of ASF status in their respective countries. All authors contributed critically to the drafts and gave final approval for publication.

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