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REVIEW ARTICLE

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Epidemiology of African swine fever in Africa today: Sylvatic cycle versus socio-economic imperatives

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Abstract

African swine fever (ASF) is believed to have evolved in eastern and southern Africa in a sylvatic cycle between common warthogs (*Phacochoerus africanus*) and argasid ticks of the *Ornithodoros moubata* complex that live in their burrows. The involvement of warthogs and possibly other wild suids in the maintenance of ASF virus means that the infection cannot be eradicated from Africa, but only prevented and controlled in domestic pig populations. Historically, outbreaks of ASF in domestic pigs in Africa were almost invariably linked to the presence of warthogs, but subsequent investigations of the disease in pigs revealed the presence of another cycle involving domestic pigs and ticks, with a third cycle becoming apparent when the disease expanded into West Africa where the sylvatic cycle is not present. The increase in ASF outbreaks that has accompanied the exponential growth of the African pig population over the last three decades has heralded a shift in the epidemiology of ASF in Africa, and the growing importance of the pig husbandry and trade in the maintenance and spread of ASF. This review, which focuses on the ASF situation between 1989 and 2017, suggests a minor role for wild suids compared with the domestic cycle, driven by socio-economic factors that determine the ability of producers to implement the control measures needed for better management of ASF in Africa.

KEYWORDS
African swine fever, bushpigs, control, domestic pigs, socio-economic factors, sub-Saharan Africa, sylvatic cycle, warthogs, wild suids

1 | INTRODUCTION

African swine fever (ASF), a viral haemorrhagic fever of pigs caused by a unique DNA virus, the only member of its family and genus (*Asfarviridae: Asfivirus*), is considered to be one of the most serious diseases of pigs and a major threat to pig industries worldwide (Costard, Wieland, et al., 2009). ASF is believed to have evolved in a sylvatic cycle that occurs in eastern and southern Africa between common warthogs (*Phacochoerus africanus*) and argasid ticks of the *Ornithodoros moubata* complex that share their burrows (Plowright, Thomson, & Neser, 1994). Since the middle of the last century, introduction of the disease into new areas (West Africa, Europe, the Caucasus, the Caribbean and Brazil) has demonstrated that, unless drastic measures are implemented to eradicate ASF, it can be maintained and efficiently spread by domestic pigs and can become endemic in the absence of African wild suids or ticks (Arias & Sánchez-Vizcaíno, 2002; Brown, Penrith, Fasina, & Beltrán-Alcrudo, 2018; Gogin, Gerasimov, Malogolovkin, & Kolbasov, 2013; Moura, McManus, Bernal, & de Melo, 2010; Mur et al., 2016). Nevertheless, the well-documented sylvatic cycle between warthogs and soft ticks, which is often incorrectly extrapolated to include other wild suid species, has resulted in an indelible impression that wild suids are still the major player in ASF transmission in Africa. The experience of Africa over the last decades suggests that domestic pigs and the way they are managed now occupy centre stage and pose the greatest challenges for control of ASF. Transmission in domestic pigs occurs predominantly by direct contact and through the feeding of infected meat products, either through swill feeding or scavenging practices, although the involvement of *O. moubata* complex ticks has also been described (Haresnape, Lungu, & Mamu, 1985, 1987; Haresnape & Mamu, 1986).

This review examined published accounts as well as the available official reports of ASF outbreaks in sub-Saharan Africa to international and regional organizations between 1989 and 2017 to try to determine the main drivers of ASF on the continent. The origin of reported outbreaks is frequently unknown but there is sufficient information to build a certain level of understanding of the drivers of ASF maintenance and spread in Africa and the relative importance of African wild suids and domestic pigs in the epidemiology of ASF in Africa today. Studies in resource-poor pig-keeping communities in African countries, in particular, have demonstrated that socio-economic factors are major constraints for control of ASF (Chenais, Boqvist, Emanuelson, et al., 2017; Chenais, Boqvist, Sternberg-Lewerin, et al., 2017). The aim of the study is to provide information useful for future research planning and ASF management strategies.

2 | THE CURRENT ASF SITUATION IN AFRICA

Although Africa's pig population only constitutes around 5% of the global pig population, it has more than doubled in the last three decades according to the Food and Agriculture Organization of United Nations (FAO, 2017). Much of this growth has occurred in response to an increase in demand for meat by rapidly expanding urban middle class populations throughout sub-Saharan Africa, including in countries that had relatively small pig populations (FAO, 2012b; Ikeya, 2015; Mopate Logtene, Vounparet, Issa, & Kabore-Zoungrana, 2014; Muhanguzi, Lutwama, & Mwiine, 2012; Okello, Amonya, Okwee-Acai, Erume, & De Greve, 2015). The increase in the pig population has been accompanied by an increase in the number of countries affected by ASF, as well as an apparent increase in the number of outbreaks experienced in countries with a long history of infection (Penrith, Vosloo, Jori, & Bastos, 2013).

By the end of 2017, 33 African countries were known to have experienced outbreaks of ASF between 1989 and 2017 according to information from the World Organisation for Animal Health (OIE) and published literature. Comparison of the reports to OIE and the African Union Interafrican Bureau for Animal Resources (AU-IBAR) revealed important discrepancies, with four countries having reported outbreaks to AU-IBAR that were not reported to OIE. Only one of these, an outbreak in Ethiopia in 2011, was confirmed and reliably reported, with genetic characterization of the viruses from the initial outbreak and subsequent outbreaks in 2013–2014 (Achenbach et al., 2017). The Gambia also reported an outbreak to AU-IBAR in 2011, which is credible, as although until 2017 this country had not reported ASF to OIE, outbreaks were confirmed in 1997, 1999, 2000 (Brown et al., 2018; FAO; http://www.fao.org/docrep/003/y0482e/y0482e05.html) and again in 2007 on the basis of media reports (http://allafrica.com/stories/200710221245.html, http://www.africanagriculture.co.zw/2007/08/swine-fever-hits-gambia.html). Consequently, it should be regarded as part of the ASF-endemic area comprised of the Casamance province of Senegal and Guinea Bissau (Etter et al., 2011; Lefèvre, 1998). Two further countries that have not reported ASF before or since, Liberia (2010 and 2011) and Niger (2009) reported outbreaks to AU-IBAR (AU-IBAR, 2009, 2010, 2011). It is not known whether these outbreaks were laboratory confirmed. If ASF outbreaks did occur in those two countries, the probable number of African countries that have experienced ASF would be 35 (Figure 1). However, outbreaks in Lesotho and Mauritius reflected in the AU-IBAR yearbooks for 2006 and 2010, respectively, were discounted on the basis of the authors' experience and knowledge. Lesotho is surrounded by the zone in South Africa in which the warthog/tick sylvatic cycle is absent and has never reported ASF outbreaks in its small pig population, while Mauritius experienced its last outbreak of ASF in 2008 following the first and only introduction of the disease in 2007, and eradication was confirmed through laboratory investigations (Lubisi, Dwarka, Meenowa, & Jaumally, 2009). Mauritius officially confirmed in its self-declaration to OIE of regaining its freedom from ASF, that the event was solved on the 12 July 2008 and that no outbreaks occurred in the following 3 years (http://www.oie.int/fileadmin/Home/eng/Publications_%26_Documentation/docs/pdf/bulletin/Bull_2012-3-ENG.pdf).

A total of 5,134 outbreaks were reflected in the sources used. Most of the information was retrieved from OIE Handistatus-II and OIE WAHID, spanning the period 1996–2017. Additional outbreaks between 1989 and 1995 have been included because good information was available from a series of reports to OIE, published literature or personal experience of the authors. The results for 2017 are less complete than for the preceding years, because of the time it takes for 6-month reports to be submitted, processed and published in WAHIS. Seventeen countries (Burkina Faso, Burundi, Côte d'Ivoire, Democratic Republic of Congo [DRC], Ghana, Guinea Bissau, Madagascar, Mozambique, Namibia, Nigeria, Rwanda, Senegal, South Africa, Tanzania, Togo, Uganda, Zambia) reported one to multiple outbreaks via immediate notification or biannual reports, some of which only covered the first 6 months of 2017. A further five countries (Cameroon, Cape Verde, Central African Republic (CAR), The Gambia and Nigeria [annual report]) reported unquantified presence of the disease. Chad, Mali and Mauritius reported absence of the disease for the whole year, and Botswana, Republic of Congo, Ethiopia and Lesotho reported absence of the disease for the first 6 months, with the report for the second half of the year pending. Among the countries that have previously reported ASF, no reports for 2017 were as yet available for Angola, Benin, and Malawi.

The actual number of outbreaks experienced during the review period would undoubtedly have been very much higher than those

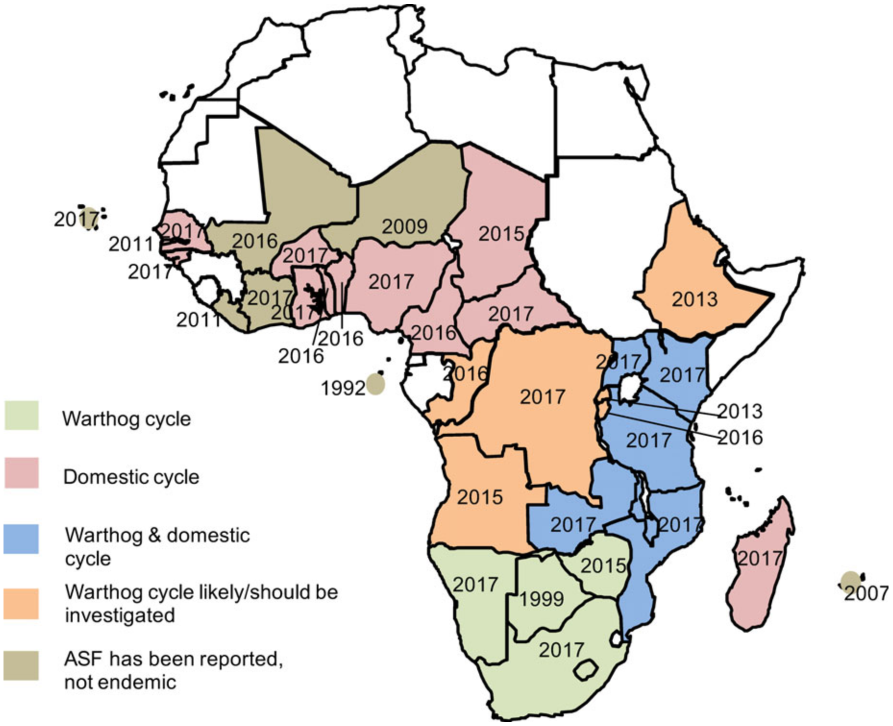

FIGURE 1 Distribution of African swine fever endemic and non-endemic areas and the predominant cycle in endemic areas where known. The date of the last reported outbreak for each country is provided

reflected in reports. Reporting of ASF is at best sporadic and incomplete for many reasons that include poor communication channels, fear of unwanted consequences and apathy on the part of people in endemic areas who experience the disease frequently. To provide an example of the discrepancy between official reporting and information that is locally available, a study in Gulu District of Uganda reported that between April 2010 and November 2011, 1,141 pigs in 211 herds in 43 villages died in ASF outbreaks (Barongo et al., 2015), whereas the OIE reflects the loss of 320 pigs in five outbreaks in the Gulu District during the same period (http://www.oie.int/wahis_2/public/wahid.php/Diseaseinformation/statusdetail). In a study in Rombo District, Kilimanjaro Region of Tanzania, 1,083 pig-keeping households reported losing pigs during outbreaks that swept through the district between March and August 2013 (Swai & Lyimo, 2014), whereas the OIE database reflects the loss of 330 pigs in five outbreaks in the Kilimanjaro Region in April and May 2013 (http://www.oie.int/wahis_2/public/wahid.php/Diseaseinformation/statusdetail). Several countries either sporadically or routinely simply report presence of the disease without attempting to quantify it. The conclusion, however, is that ASF is both rife and widespread in sub-Saharan Africa.

3 | OUTBREAKS RELATED TO WILD AFRICAN SUIDS

Only 602 (11.7%) of the outbreak reports specified the confirmed source of the outbreak. Of these, 533 (88.5%) were reported to have originated from domestic pigs, while 69 (11.5%) specified warthog contact. None of the reports specified contact with bushpigs or wild suids other than warthogs as the confirmed or strongly suspected source of the outbreak.

Sixteen countries (Angola, Botswana, Burundi, Republic of Congo, DRC, Ethiopia, Kenya, Malawi, Mozambique, Namibia, South Africa, Rwanda, Tanzania, Uganda, Zambia and Zimbabwe) belong to the eastern and southern African region in which the ancient sylvatic cycle occurs. Although it has not been demonstrated in all the listed countries, all of them fulfil at least some of the criteria for historic endemic infection (Tables 1–3). Two mainland southern African

TABLE 1 Characteristics of areas with and without the sylvatic cycle in warthogs and ticks

Areas with an ancient sylvatic cycle	Areas without an ancient sylvatic cycle
Sylvatic cycle between warthogs and ticks is known to exist (infection demonstrated in warthogs, *Ornithodoros* ticks from warthog burrows, or both)	Sylvatic cycle between warthogs and ticks has not been demonstrated
History of ASF in domestic pigs predates the first introductions into Europe (1957, 1960)	History of ASF outbreaks dates from about 1959 or later
Multiple genotypes of ASFV have been retrieved from domestic pigs and/or the natural hosts of the virus	A single genotype is present
Reports exist of outbreaks in domestic pigs that are reliably linked to wild pig contact	Reports of outbreaks not linked to wild pigs

TABLE 2 Summary of epidemiological characteristics of each of the 35 African countries reporting ASF outbreaks from 1989 to 2017

Country	ASF confirmed in warthog/ ticks	Long history ASF	Genotypes	Outbreaks linked to wild pigs
Angola	No	Yes	I	No
Benin	No	No	I	No
Botswana	Yes	No[a]	III, VII	Yes
Burkina Faso	No	No	I	No
Burundi	?	No	X	No
Cabo Verde	No	No	I	No
Cameroon	No	No	I	No
CAR[b]	No	No	No information	No
Chad	No	No	No information	No
Congo Republic	?	No	I, IX	No
DRC	?	Yes	I, IX, XIV	No
Côte d'Ivoire	No	No	I	No
Ethiopia	?	No	XXIII	(no reasons)
Gambia	No	No	I	No
Ghana	No	No	I	No
Guinea Bissau	No	No	I	No
Kenya	Yes	Yes	I, IX, X	Yes (historic)
Liberia	No	No	No information	No
Madagascar	No	No	II	No
Malawi	Yes	Yes	V, VIII, XII	No
Mali	No	No	I	No
Mauritius	No	No	II	No
Mozambique	Yes	Yes	II, V, VI, VIII, XXIV	Yes (rarely)
Namibia	Yes	Yes	I, XVIII	Yes
Niger	No	No	No information	No
Nigeria	No	No	I	No
Rwanda	?	No	No information	No
S Tomé/ Principe	No	No	I	No
Senegal	No	No	I	No
South Africa	Yes	Yes	III, IV, VII, XIX-XXII	Yes
Tanzania	Yes	Yes	II, IX, X, XV, XVI	Yes
Togo	No	No	I	No
Uganda	Yes	Yes	IX, X	Yes
Zambia	Yes	Yes	I, II, VIII, XI-XIV	Yes
Zimbabwe	Yes	No	I, II, VIII, XVII	Yes

CAR: Central African Republic; DRC: Democratic Republic of Congo.
[a]Botswana has few pigs and has experienced outbreaks of ASF in 1987 and 1999. [b]As the outbreaks in CAR and Chad were related to a contemporaneous outbreak in Cameroon the most probable cause was genotype I.

countries (Lesotho and Swaziland [recently renamed Eswatini]) have never reported ASF. Both have small pig populations. A recent survey reported no infection in *Ornithodoros* ticks from warthog burrows in Swaziland (Boshoff, Bastos, Dube, & Heath, 2014). It is likely that the sylvatic cycle is absent from both countries.

Warthog contact has been demonstrated or suspected to be the cause of outbreaks in Botswana, Kenya, Malawi, Namibia, South Africa, Tanzania, Zambia and Zimbabwe. The two reported outbreaks in Botswana, occasional outbreaks in Zimbabwe (with the exception of the 2015 outbreak), about half of the outbreaks in Namibia, and all of the outbreaks within the ASF Control Area of South Africa have been attributed to warthog contact on good evidence mainly reflected in OIE reports. Historical outbreaks in Kenya were attributed to warthog contact (Montgomery, 1921), but there has been no evidence of warthog involvement in reported outbreaks in domestic pigs since the re-emergence of ASF in 1994 (Okoth et al., 2012; M.L. Penrith, unpublished report, 1996). However, indirect evidence of possible transmission to pigs from a warthog/tick cycle in Central Kenya has been inferred on the basis of molecular data (Gallardo, Okoth, et al., 2011). One report of outbreaks in Malawi reflected in OIE Handistatus II for 1997 was attributed to warthogs, with no details provided. Warthog contact was suspected but not confirmed in outbreaks that occurred in the Livingstone area of Zambia in 2004 and 2006 (Simulundu et al., 2017). Most of a cluster of outbreaks that occurred in Northern Tanzania in 2013 were reported to have resulted from feeding catering swill containing infected pork leftovers and movement of infected pigs, but the fact that the outbreaks started close to conservation areas suggested that the initial outbreak may have resulted from warthog contact (Misinzo et al., 2014). The fact that in several countries wild pigs, in particular warthogs, are largely if not entirely restricted to conservation areas has been cited as a factor that reduces their likely role of the epidemiology of ASF in domestic pigs, which in some cases has been confirmed by molecular studies of viruses (Haresnape & Mamu, 1986; Wambura, Masambu, & Msami, 2006). However, it is probable that free-range pigs farming in close proximity to conservation areas poses a higher risk of infection with African swine fever virus (ASFV; Katale, Fyumagwa, Mdaki, & Hoare, 2012; Kukielka et al., 2016).

4 | OUTBREAKS RELATED TO DOMESTIC PIGS

As noted previously, 88.5% of the ASF outbreaks reported between 1989 and 2017 for which the source was confirmed originated in domestic pig populations, with movement of pigs or their products and swill feeding with material containing leftover pork named most frequently as the cause of the outbreak.

Nine of the 16 countries where a sylvatic cycle cannot be excluded experienced outbreaks that were demonstrably not directly linked to sylvatic hosts (Angola, Republic of Congo, Kenya, Mozambique, South Africa, Tanzania, Uganda, Zambia, Zimbabwe) (OIE WAHID; Penrith et al., 2007; van Heerden, Malan, Gadaga, &

TABLE 3 Evidence for the ancient sylvatic cycle in 16 southern and East African countries

Country	Evidence/positive characteristics	Source
Countries where ASFV infection has been documented in wild suids and/or *Ornithodoros* ticks		
Botswana	Warthogs positive for antibodies to ASFV; sporadic outbreaks in domestic pigs; two genotypes from two outbreaks	Boshoff, Bastos, Gerber, and Vosloo (2007); Simpson and Drager, (1979)
Congo Republic	Infection detected in a warthog; two genotypes identified to date	Gallardo, Anchuelo, et al. (2011); Plowright et al. (1994)
Kenya	Long history of ASF; high infection rate in warthogs and ticks; early outbreaks in domestic pigs warthog-associated; two genotypes	DeTray (1963); Lubisi, Bastos, Dwarka, and Vosloo (2005); Montgomery (1921); Plowright et al. (1994)
Malawi	Long history of ASF; ASFV isolated from warthogs and ticks[a]; three genotypes	Bastos et al. (2003); Haresnape and Mamu (1986); Haresnape et al., (1987); Lubisi et al. (2005); Matson (1960); Turnbull, (1932, 1933, 1934)
Mozambique	Relatively long history of ASF; high infection rate in warthogs and ticks; five genotypes identified to date	Bastos et al. (2004), De Abreu, Valadão, Limpo Serra, Ornelas Mário, and Sousa Montenegro (1962), Lubisi et al. (2005); Mendes (1971), Penrith et al. (2007), Quembo et al. (2018)
Namibia	Relatively long history of ASF; high infection rate in warthogs and ticks; two genotypes identified to date	Boshoff et al. (2007), Plowright et al. (1994)
South Africa	Long history of ASF; high infection rate in warthogs and ticks; seven genotypes identified to date	Boshoff et al. (2007), De Kock, Robinson, and Keppel (1940), Mansvelt (1963), Plowright et al. (1994), Steyn (1928)
Tanzania	Long history of ASF; high infection rate in warthogs and ticks; five genotypes	Katale et al. (2012), Lubisi et al. (2005), Misinzo et al. (2014), Montgomery (1921), Plowright et al. (1969a)
Uganda	Relatively long history of ASF; fairly high infection rate in warthogs and ticks; two genotypes present	Atuhaire et al. (2013), Kukielka et al. (2016), Plowright et al. (1994), Ståhl et al. (2014)
Zambia	Long history of ASF; ASFV isolated from ticks in warthog burrows at all locations investigated; seven genotypes present	Boshoff et al. (2007), Simulundu et al. (2018), Wilkinson et al. (1988)
Zimbabwe	High infection rate in warthogs and ticks; rare isolated outbreaks in pigs, four genotypes identified to date	Bastos et al. (2003), Boshoff et al. (2007), van Heerden et al. (2017), Plowright et al. (1994)
Countries where a sylvatic cycle needs further investigation		
Angola	Long history of ASF, genotype I	Bastos et al. (2003), Gago da Camara (1933), Mendes (1994)
Burundi	Geographic location, genotype X	Bastos et al. (2003), Lubisi et al. (2005)
DRC	Long history of ASF; three genotypes identified to date	Gallardo, Anchuelo, et al. (2011), Lubisi et al. (2005), Mulumba-Mfumu et al. (2017), Saliki, Thiry, & Pastoret (1985)
Ethiopia	Unique genotype with two subtypes isolated from outbreaks in domestic pigs	Achenbach et al. (2017)
Rwanda	No information about genotypes or infection in sylvatic hosts: geographical location makes sylvatic cycle likely	

DRC: Democratic Republic of Congo.
[a]From domestic pig shelters.

Spargo, 2017). However, it is likely that some outbreaks resulted from amplification in domestic pigs after an initial infection derived from the sylvatic cycle (Geertsma, Mpofu, & Walters, 2012; Misinzo et al., 2014; Swai & Lyimo, 2014). Although the origin of the initial outbreak in Ethiopia in 2011 and subsequent outbreaks were not determined, the fact that molecular studies revealed two variants of a new *p72* genotype raised a suspicion that the outbreaks could be linked to a sylvatic cycle (Achenbach et al., 2017).

In other outbreaks, a sylvatic origin could be ruled out or was highly unlikely (Misinzo et al., 2012; van Heerden et al., 2017). Outbreaks reported from the environs of large cities such as Luanda, Maputo and Dar-es-Salaam are unlikely to have direct links to the sylvatic cycle due to a lack of contact between pigs kept in urban environments and wild hosts. In a study of outbreaks in DRC between 2005 and 2012, it was concluded that a sylvatic origin was only likely to be implicated in outbreaks that involved free-ranging pigs in rural areas where interaction with wild suids was likely, which left the great majority of outbreaks linked to domestic pigs (Mulumba-Mfumu et al., 2017). The only outbreak reported from Congo Republic for which some information about source is available was an outbreak close to the DRC border in 2003, with simultaneous reports of disease from both sides of the border (OIE, 2003). According to Plowright et al. (1994) ASFV infection was reported in warthog from Congo Republic in 1975, but warthogs are now considered to be possibly extinct in that country (De Jong, Cumming, d'Huart, & Butynski, 2016), indicating that all outbreaks are considered to have resulted from domestic pig contact given the rarity/absence of the wild suid host.

Infection with ASF in the remaining countries, which lack a sylvatic cycle, is considered or known to be due to later introductions, with the majority having become endemically infected (Table 4). Outbreaks result from circulation of the virus in domestic pigs and are invariably linked to anthropogenic activities. There have been two major introductions into western Africa. The first occurred during the period from 1957 to the early 1980s, when ASF was also first introduced into Europe and the Americas, and involved Senegal, Cape Verde, Gambia and Guinea Bissau in West Africa, and Cameroon and São Tomé e Principe in western Central Africa (Bastos et al., 2003; Ekue & Wilkinson, 2000; Wesley & Tuthill, 1984). The second wave of introductions into West Africa started with an outbreak in 1996 in Côte d'Ivoire, followed by further epidemics from 1996 to 2003 that involved Benin, Nigeria, Togo, Ghana and Burkina Faso (Brown et al., 2018). This period also saw increased ASF activity in the western focus of already infected Senegal, Gambia and Cape Verde.

TABLE 4 ASF in countries without the ancient sylvatic cycle

Country	History	Source
Benin	First report 1997; now endemic; genotype I	Attakpa et al. (2014), Bastos et al. (2003), Brown et al. (2018), Kpodékon et al. (2015)
Burkina Faso	First report 2003; now endemic; genotype I	Brown et al. (2018)
Cape Verde	Believed present from 1959; genotype I	Brown et al. (2018), Gallardo et al. (2009), Penrith et al. (2013)
Cameroon	First report 1982; now endemic; genotype I	Bastos et al. (2003), Ekue and Wilkinson (1990, 2000), Nana-Nukechap and Gibbs (1985)
CAR	First report 2010, ex Cameroon	World Organisation for Animal Health, OIE WAHID interface
Chad	First report 2010, ex Cameroon	Ban-bo, Idriss, and Squarzoni (2012), Bidjeh et al. (2015)
Côte d'Ivoire	First report 1996, eradicated; recurred 2014; genotype I	Bastos et al. (2003), Brown et al. (2018), El Hicheri et al. (1998), Kouakou et al. (2017)
Gambia	Believed to have similar status to Senegal; genotype I	Bastos et al. (2003), Brown et al. (2018)
Ghana	First report 1999, eradicated; recurred in 2002, now endemic; genotype I	Bastos et al. (2003), Brown et al. (2018)
Guinea Bissau	Believed to have similar status to Senegal; genotype I	Brown et al. (2018
Liberia	Reported to AU-IBAR 2010, 2011	AU-IBAR (2010, 2011)
Madagascar	First reported 1998 (first cases 1997); now endemic; genotype II	Roger et al. (2001), Gonzague et al. (2001), Ravaomanana et al. (2011), Gonzague et al. (2001), Ravaomanana et al. (2011), Roger et al. (2001)
Mali	First report 2016, probably ex Burkina Faso	World Organisation for Animal Health, OIE WAHID interface
Mauritius	First reported 2007, eradicated; genotype II	Lubisi et al. (2009)
Niger	Reported to AU-IBAR, 2009	AU-IBAR (2009)
Nigeria	First confirmed outbreak reported 1998; now endemic; genotype I (unconfirmed small outbreak in 1973)	Babalobi et al. (2007), Bastos et al. (2003), Brown et al. (2018), Otesile et al. (2005), Owolodun et al. (2010), Taylor, Best, and Couquhoun (1977)
São Tomé e Principe	First reported in 1979, eradicated; genotype I	Sánchez-Botija (1982), Wesley and Tuthill (1984)
Senegal	First identified in 1959; endemic; genotype I	Bastos et al. (2003), Brown et al. (2018), Etter et al. (2011)
Togo	First reported in 1998; now endemic; genotype I	Bastos et al. (2003), Brown et al. (2018)

CAR: Central African Republic.

An introduction into Chad and the CAR occurred in 2010 and was traced to pork from Cameroon that was sold in Chad (Bidjeh et al., 2015). In spite of its insignificant pig population, a small outbreak occurred in Mali in 2016 close to the border with Burkina Faso in an area where an ASF outbreak had occurred shortly beforehand, all as reported in immediate notifications to the OIE.

The Indian Ocean islands were historically free from ASF, but in recent decades both Madagascar and Mauritius have experienced outbreaks of ASF, which in both countries were thoroughly investigated. Madagascar experienced its first outbreaks in 1997, confirmed as ASF in 1998 and ascribed to an introduction from Mozambique due to a close relationship to Mozambican ASF viruses (Bastos, Penrith, Macome, Pinto, & Thomson, 2004; Gonzague et al., 2001; Roger, Ratovonjato, Vola, & Uilenberg, 2001; Rousset et al., 2001). When ASF became endemically established in Madagascar, the presence of both bushpigs (*Potamochoerus larvatus*) and *O. moubata* complex ticks due to earlier introduction caused concern for the development of potential reservoir hosts (Roger et al., 2001). However, to date investigations provided no evidence of any interaction between bushpigs and ASFV or tampans (Ravaomanana et al., 2011). Investigation of *Ornithodoros* from pigsties resulted in a single finding of ASFV infection in tampans from one pig sty that had been unoccupied for some time, but the authors considered it unlikely that the ticks were playing a major role in the persistence of ASF in Madagascar (Ravaomanana et al., 2010). The introduction of ASF that occurred in Mauritius in 2007 probably came from Madagascar, as the virus was identical although 10 years had elapsed since its introduction into Madagascar (Lubisi et al., 2009). Eradication was rapidly achieved because the small pig population was decimated, there were no free-ranging domestic pigs and there are no African wild suid species or *Ornithodoros* ticks, the only "wild" pigs being feral domestic pigs descended from the original pigs introduced to the island by sailors several centuries previously (Jori et al., 2013; Lubisi et al., 2009).

The marked increase in ASF activity noted mainly from the 1990s but starting with the introduction into Cameroon in 1982 (Nana-Nukechap & Gibbs, 1985) was correlated with a rapid increase in the number of pigs produced in a number of African countries (Penrith et al., 2013).

5 | TRANSMISSION ROUTES OF ASFV IN SYLVATIC CYCLES

Transmission of ASFV from African wild suids to domestic pigs is far less efficient than transmission among domestic pigs. Although the involvement of warthogs in ASF was suspected from the earliest discovery of the disease (Montgomery, 1921), the mechanism of transmission to domestic pigs proved difficult to explain. Direct transmission of the virus from acutely infected warthogs to other warthogs or to domestic pigs by contact did not occur under experimental conditions (Montgomery, 1921; Thomson, Gainaru, & van Dellen, 1980) and was only achieved with difficulty by feeding minced tissues from the warthogs to domestic pigs (Thomson et al., 1980). Infection of domestic pigs by feeding them with offal from hunted warthogs is therefore not considered to constitute an important source of outbreaks in domestic pigs (Plowright et al., 1994).

Although an association between warthogs and *O. moubata* in the Luangwa Valley of Zambia was reported as early as 1915 (Lloyd, 1915; Wilkinson, Pegram, Perry, Lemche, & Schels, 1988), the involvement of *O. moubata* complex in the transmission of ASF in Africa was only investigated and confirmed much later (Plowright, Parker, & Peirce, 1969a), after a related species, *Ornithodoros erraticus*, was found to inhabit pig shelters and harbour ASF virus after its introduction into the Iberian Peninsula (Sánchez-Botija, 1963). ASF infection in *O. moubata* complex ticks inhabiting warthog burrows was subsequently confirmed in South Africa, Namibia, Zambia and Zimbabwe (Thomson et al., 1983; Wilkinson et al., 1988). However, transmission of the virus from warthogs to pigs remained a conundrum, because viraemia in adult warthogs was typically too low to enable infection of ticks. An explanation began to emerge when levels of viraemia capable of infecting ticks that fed on them were found in young warthogs that spent most of their time the burrows where they were born (Thomson, 1985; Thomson et al., 1983). Transmission of ASFV to domestic pigs by ticks travelling on warthogs or warthog carcasses had been suggested by Plowright, Parker, and Peirce (1969b), but as adult *Ornithodoros* ticks feed rapidly and drop off their hosts, they are rarely if ever found on warthogs. However, surveys of ectoparasites on warthogs in Namibia and the ASF endemic area in South Africa confirmed large numbers of *Ornithodoros* nymphs travelling on warthogs (Boomker, Horak, Booyse, & Meyer, 1991; Horak, Biggs, Hanssen, & Hanssen, 1983; Horak, Boomker, De Vos, & Potgieter, 1988), supporting the conclusion that transmission of ASFV from warthogs to domestic pigs by ticks was a plausible source of outbreaks.

Direct contact between domestic pigs and warthogs in most African countries is limited by the fact that warthogs tend to be restricted to wildlife conservation areas (Haresnape, Wilkinson, & Mellor, 1988; Kukielka et al., 2016; Misinzo et al., 2014; Vercammen & Mason, 1993). South Africa and Namibia are exceptions, as warthogs are more widespread and historically outbreaks usually occurred on farms where warthogs were present and pigs were allowed to roam or were kept in poorly fenced premises that permitted warthogs to move in to benefit from feed and water made available to the pigs (Penrith et al., 2013). In Kenya and in South Africa, confining pigs in double-fenced premises that precluded proximity of warthogs proved effective in preventing the pigs from becoming infected (Penrith et al., 2013).

The role of other wild African suids, if any, is likely to be incidental because their habits differ from those of warthogs and are unfavourable for an association with *Ornithodoros* ticks (Jori & Bastos, 2009; Jori et al., 2013). A recent model based assessment of risk factors for ASF outbreaks in Africa suggested that the giant forest hog, *Hylochoerus meinertzhageni*, is an important threat at regional level for ASF in East Africa (Huang, Langevelde, Honer, Naguib, & Boer, 2017). However, this hypothesis can most likely be discounted as only one historical record of ASF infection in a true giant forest hog (*H. m. meinertzhageni*) has ever been reported (Heuschele & Coggins, 1965) and this subspecies is declining, having likely disappeared from Burundi and Rwanda, and occurring in fragmented populations in other East African countries (d'Huart & Reyna, 2016). Furthermore, in East African regions reporting ASF outbreaks, this wild suid subspecies either occurs in forested mountain areas at altitudes of 1,000–3,800 m or is confined to game reserves (d'Huart & Reyna, 2016), where direct contact with domestic pigs is unlikely. The authors of the model admitted that the role for giant forest hogs in East Africa would likely be an indirect one, requiring that the forest hogs would infect other wild suid species and/or *O. moubata* complex ticks, both of which are improbable. Assumptions that ASF infection is the norm in African wild suids and *Ornithodoros* ticks in endemic areas and that there is an association between all the African wild suid species and the tick vectors may have led to an erroneous outcome of the model for East Africa, which correctly indicated that, in West Africa, ASF is associated with increasing domestic pig and human populations (Huang et al., 2017).

In reality, levels of infection in ticks from warthog burrows in endemic areas in eastern and southern Africa have mostly been found to be low, in the range of 0.17%–3.8% (Plowright et al., 1969b; Thomson, 1985), and similar overall infection rates were reported from ticks from pig shelters in the endemic area in Malawi (Haresnape et al., 1988). A higher infection rate was recently reported for ticks from warthog burrows in the Gorongosa National Park in Mozambique, where 19% of the sample was positive for ASFV genome by nested PCR, although virus was isolated from only a little under half of the PCR positive samples (Quembo, Jori, Vosloo, & Heath, 2018). Interestingly, 75% of the warthogs sampled in the same study were positive for antibodies to ASFV, but this may be attributable to the small sample size (*n* = 12) (Quembo, Jori, Heath, Pérez-Sánchez, & Vosloo, 2016). Warthog infection rates in areas where the sylvatic cycle is present are usually close to 100%, although lower rates (50%–90% in Uganda and 75% in Gorongosa National Park, Mozambique) have been reported (Plowright et al., 1994; Quembo et al., 2016). Only 2.5% of warthogs sampled in the Mkuze National Park in Northern Kwazulu-Natal, South Africa, were reported positive for antibodies to ASFV, accompanied by a very low infection rate (0.06%) in *Ornithodoros* sampled from warthog burrows in the same area (Thomson, 1985; Thomson et al., 1983). A molecular reassessment of the ASF status of *Ornithodoros* from that area detected no ASFV and concluded that the infection may no longer be present there (Arnot, du Toit, & Bastos, 2009).

Unlike warthogs, eastern bushpigs (*P. larvatus*) have been shown to be capable of transmitting the virus to domestic pigs by contact under experimental conditions, but transmission did not appear to be highly efficient (Anderson, Hutchings, Mukarati, & Wilkinson, 1998). Limited field surveys undertaken on bushpigs in Zimbabwe, Malawi and Madagascar had negative results (Anderson et al., 1998; Haresnape et al., 1988; Ravaomanana et al., 2011). Studies in Uganda and South Africa suggested low natural infection rates. One out of 11 bushpigs tested positive for ASFV DNA and two out of seven tested positive for antibodies to ASFV in a survey in Uganda (Ståhl et al., 2014), and 10 times fewer bushpigs than warthogs tested positive for ASF virus in the endemic area in South Africa (Mansvelt, 1963). Tissue samples from one out of eight bushpigs examined in a National Park in Kenya that bordered on an area where ASFV positive pigs were found positive for ASFV (Okoth et al., 2012).

A recent study that investigated contact between wild suids and domestic pigs at a wildlife/farming interface in Uganda suggested that direct contacts occurred rarely if at all, but indirect contacts through shared grazing and water sources could potentially occur at the interface and could result in transmission of ASF virus (Kukielka et al., 2016). However, the study concluded that management practices, including some that resulted in exposure to potential infection from wild suids, were a major driver of ASF in northern Uganda.

6 | TRANSMISSION ROUTES OF ASFV IN DOMESTIC CYCLES

Since domestic pigs transmit ASF virus far more efficiently than African wild suids and are much more numerous, their role as a major driver of ASF is not surprising. Domestic pigs in the acute stage of infection develop high viraemia and shed large amounts of virus in various secretions and excretions. The virus can tolerate a wide range of temperature and pH and can survive long periods in fresh and frozen pork. Pigs can become infected through direct contact with infected pigs or materials contaminated by infected pigs and eating uncooked meat products derived from infected pigs, as well as when infected *Ornithodoros* ticks feed on them (Penrith, Thomson, & Bastos, 2004). Stable flies (*Stomoxys calcitrans*) have been shown to be able to transmit the virus between pigs for 24–48 hr (Mellor, Kitching, & Wilkinson, 1987). Aerosol transmission of the virus over short distances within buildings has been demonstrated (de Carvalho Ferreira, Weesendorp, Quak, Stegeman, & Loeffen, 2013; Wilkinson, Donaldson, Greig, & Bruce, 1977). The virus is most efficiently spread through movement of pigs and pork.

The systems in which pigs are produced determine the level of risk for ASF. The introduction of ASF into a number of previously uninfected countries in West Africa from 1996 to 2003 resulted in endemic establishment of the disease in most of them; among them, Nigeria has the largest population of pigs in Africa (Brown et al., 2018). While supplying urban populations with cheap sources of protein has encouraged the growth of commercial pig farming, the commercial sector in most African countries is small and the majority of the pigs are kept by smallholders in backyards or in traditional free-ranging systems (FAO, 2012a, 2012b, 2012c; Lekule & Kyvsgaard, 2003; Penrith et al., 2013; Wilson & Swai, 2014). Low or no biosecurity in these systems is favourable for the maintenance and spread of ASF (Penrith et al., 2013). Perusal of literature on pig production in sub-Saharan Africa confirms that the main reason for keeping pigs is income generation (Penrith et al., 2013), but prices tend to be low due to unfavourable marketing conditions that include a lack of organization of the market (Antwi & Seahlodi, 2011; FAO, 2012a, 2012b, 2012c; Mbuthia, Rewe, & Kahi, 2014; Mutambara, 2013a, 2013b; Wilson & Swai, 2014). As a result, producers are reluctant or unable to invest in improving management by confining their pigs, feeding them on commercial rations and providing basic health care (Lekule & Kyvsgaard, 2003; Penrith et al., 2013; Verhulst, 1993). The risks posed by feeding pigs garbage, either as swill or by releasing them to scavenge, and by selling pigs through agents who move from farm to farm, are compounded by panic selling of pigs and infected pork during outbreaks of ASF, which serves to spread the disease (Brown et al., 2018; Chenais, Boqvist, Sternbgerg-Lewerin, et al., 2017; Dione, Ouma, Opio, Kawuma, & Pezo, 2016; Dione et al., 2017; Lichoti et al., 2016; Muwonge et al., 2012; Nantima et al., 2015). A survey of pig sales patterns on the border between Kenya and Uganda revealed that producers selling sick pigs tend to seek markets in communities further away from their usual outlets (Lichoti et al., 2016). The behaviour of pig farmers has therefore become the major driver of ASF in sub-Saharan Africa (Chenais, Boqvist, Sternbgerg-Lewerin, et al., 2017; Penrith et al., 2013).

The first historical record of apparent maintenance of ASF virus circulation in a population of domestic pigs in Africa without wild suid involvement was an outbreak that was later confirmed as ASF in Angola in 1932 (Gago da Camara, 1933; Mendes, 1994). The source of disease was believed to be local breed pigs kept by the indigenous population in a traditional free-ranging husbandry system (Mendes, 1994). To our knowledge, although various studies on the disease in Angola have been published, warthog involvement has never been investigated. Archaeological evidence suggests that domestic pigs have a long history in Angola (Amills, Ramírez, Galman-Omitogun, & Clop, 2013). It can be speculated that these early pigs may have been exposed to ASF through the sylvatic cycle and may have developed some resistance to the disease before the advent of European settlers who introduced Iberian pigs (Amills et al., 2013). The possibility that the warthog/tick sylvatic cycle still exists in Angola cannot be excluded, but it is probable that it now plays a minor role, if any, in the epidemiology of ASF in that country. During the 1950s, considerable research effort that included attempts to produce an ASF vaccine was invested in Angola by the Portuguese government, who had plans for large-scale pig production in the fertile highlands to feed the army (Mendes, 1994). It is probable that warthog involvement was absent at least in the areas covered by the research, which did reveal local breed pigs with higher resistance to virulent ASF viruses (Nsalambi, 1987).

The discovery of a cycle of maintenance and transmission of ASFV between domestic pigs and *O. moubata* complex ticks in the Mchinji district in Malawi revealed a pig population with improved resistance to the pathogenic effects of ASFV and the ability of the disease to persist without involvement of wild suids (Haresnape & Mamu, 1986; Haresnape et al., 1985, 1987). Similarly resistant populations of domestic pigs have been reported in Kenya (Okoth et al., 2012), along the Kenya/Uganda border on both sides (Abworo et al., 2017; Thomas et al., 2016); Mozambique (Penrith et al., 2007; Penrith, Thomson, Bastos, Phiri, et al., 2004) and the Eastern Province of Zambia (Simulundu et al., 2017). The involvement of ticks in these populations has not been documented and requires further investigation. Such populations undoubtedly provide an advantage in endemic ASF areas, as mortality due to the disease is lower, but another advantage is that they could provide models for studying the mechanism for their resistance to the pathogenic effects of multiple strains of virulent ASF viruses (Penrith, Thomson, Bastos, Phiri, et al., 2004). An effective vaccine that protects against multiple strains of ASFV would immeasurably aid efforts to manage the disease, and the immune system of such pigs may hold the key to such a vaccine.

7 | DISCUSSION

The maintenance and circulation of ASFV in domestic pigs largely or entirely in the absence of wild suid involvement is now known to occur in more than half of the countries where ASF is endemic (Penrith et al., 2013). A number of studies in different countries have identified a variety of risks ranging from failure to confine pigs to agents who travel from farm to farm to collect pigs, sometimes selling infected pigs and meat, all of which could be mitigated by the implementation of relatively simple biosecurity measures (Brown et al., 2018; Costard, Porphyre, et al., 2009; Dione et al., 2016, 2017; Fasina, Agbaje, et al., 2012; Fasina, Lazarus, Spencer, Makinde, & Bastos, 2012; Kabuuka et al., 2014; Lichoti et al., 2017; Nantima et al., 2015; Penrith et al., 2007, 2013). In rural areas where there is often extreme poverty swill feeding has a low risk, as there is usually little leftover food, with all parts of slaughtered or hunted animals being consumed by the people (E. Chenais, personal communication, 2017; M.L. Penrith, personal observations), so the greatest challenge is confinement of pigs (Chenais, Boqvist, Sternbgerg-Lewerin, et al., 2017; Penrith, Thomson, Bastos, Phiri, et al., 2004). In settings where pigs are permanently confined, in particular in peri-urban and urban settings, swill feeding often becomes an important risk (Costard, Porphyre, et al., 2009; Penrith et al., 2013).

A process of ASF risk mitigation throughout pig value chains that includes improving pig husbandry practices to achieve an adequate level of biosecurity and eliminating risky trading practices could result in significant reduction, if not elimination, of ASF in domestic pigs. Awareness creation has been identified as important if better management of ASF is to be achieved (Brown et al., 2018; Dione et al., 2016; Nantima et al., 2016; Penrith et al., 2013). However, traditional and smallholder pig farmers most often cannot afford to confine their pigs and feed them, because the operation then becomes unprofitable (Chenais, Boqvist, Sternbgerg-Lewerin, et al., 2017; Costard, Porphyre, et al., 2009; Lekule & Kyvsgaard, 2003; Verhulst, 1993). It is clear that if pig farmers do not directly benefit financially from improving biosecurity, they will not invest in it (Chenais, Boqvist, Sternbgerg-Lewerin, et al., 2017; Costard, Porphyre, et al., 2009).

Currently, reports indicate that the majority of pig producers, particularly in rural areas, depend on local sales, with low prices determined by the buyer rather than the seller and unlikely to increase if the quality of the pigs is improved by investment (FAO, 2012a, 2012b, 2012c; Penrith et al., 2013). Furthermore, recent studies have shown that in the resource-poor settings in which pigs are most often produced in Africa, economic forces are the strongest determinants of responses to outbreaks of ASF, in spite of a good knowledge of ASF (Chenais, Boqvist, Emanuelson, et al., 2017; Chenais, Boqvist, Sternberg-Lewerin, et al., 2017; Lichoti et al., 2017; Nantima et al., 2016; Randrianantoandro, Kono, & Kubota, 2015). Coping strategies to limit economic losses due to ASF include selling potentially infected pigs as quickly as possible before they develop clinical signs and selling infected meat (Chenais, Boqvist, Emanuelson, et al., 2017; Chenais, Boqvist, Sternberg-Lewerin, et al., 2017; van Heerden et al., 2017), reportedly to buyers in more distant destinations (Lichoti et al., 2016; Nantima et al., 2016). Low biosecurity production and risky practices during outbreaks will continue to dominate the epidemiology of ASF in sub-Saharan Africa unless countries invest in creating an enabling environment for smallholder pig farming to move from subsistence level to higher profitability, possibly through a process of vertical integration through partnerships between the commercial sector and smallholder pig farmers as has happened in Kenya (Perry & Grace, 2009), or through the establishment of pig farmer associations that allow individual farmers better access to markets and control over the pork prices.

A study in Kenya showed a marked decline in the warthog population in the rangeland counties between 1977 and 2013, which was correlated with a marked increase in livestock, particularly small ruminants, camels and donkeys (Ogutu et al., 2016). It may be that in some countries the sylvatic cycle might decline to the point of disappearance, but extinction of a species is never positive, and in the case of warthogs, it is fortunately unlikely. Although the contribution of the sylvatic cycle to the ASF situation in Africa is small in comparison to that of the domestic pig industry, its existence is epidemiologically important because it means that unless a conservation disaster occurs, ASF infection can never be eradicated from eastern and southern Africa.

With improved pig husbandry and marketing systems it should be possible to eradicate ASF from those countries where the sylvatic cycle is not present, provided there are sufficient benefits to be attained through improved profitability. This should be particularly feasible in most of the affected countries in West Africa, where investigations have reliably demonstrated absence of *O. moubata* complex ticks south of 13°N (Trape et al., 2013), although it might be necessary to bear the possibility of range expansion due to climate change in mind.

It should also be possible to eradicate ASF from domestic pig populations in countries that do have the sylvatic cycle, but extra vigilance will always be necessary because the sylvatic reservoir must be factored into control strategies in areas where it is relevant and should determine how pigs are farmed in areas where it is present. For this reason, further studies in affected countries like Burundi and Rwanda, where there is very little information available apart from reports of large numbers of ASF outbreaks in recent years to OIE, are clearly necessary to establish the role, if any, of wild suids. Further studies to determine the existence of domestic pig/tick cycles are also necessary, as the presence of infected *Ornithodoros* can seriously hamper control efforts due to the lengthy persistence of the virus in the ticks (Boinas, Wilson, Hutchings, Martins, & Dixon, 2011). Moreover, more systematic and thorough outbreak investigations would further contribute to a better understanding of specific biosecurity and management gaps.

The principal challenge is how to minimize maintenance of ASF in the domestic cycle in ways that do not threaten the survival of poor pig producers, but enable their enterprises to become more sustainable and more profitable. Attempting to eliminate low biosecurity pig production by stringent regulation is doomed to failure, while having a negative impact on the livelihoods of farmers. Such systems will only be reduced or eliminated if biosecurity measures that are simple, effective and affordable are developed and marketing opportunities are created that provide an incentive for investment and modernization of the pig industry.

CONFLICT OF INTEREST

The authors declare that they have no actual or potential financial or personal conflict of interest regarding this publication.

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