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Epidemiology of African swine fever virus

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ABSTRACT

African swine fever virus used to occur primarily in Africa. There had been occasional incursions into Europe or America which apart from the endemic situation on the island of Sardinia always had been successfully controlled. But following an introduction of the virus in 2007, it now has expanded its geographical distribution into Caucasus and Eastern Europe where it has not been controlled, to date. African swine fever affects domestic and wild pig species, and can involve tick vectors. The ability of the virus to survive within a particular ecosystem is defined by the ecology of its wild host populations and the characteristics of livestock production systems, which influence host and vector species densities and interrelationships. African swine fever has high morbidity in naïve pig populations and can result in very high mortality. There is no vaccine or treatment available. Apart from stamping out and movement control, there are no control measures, thereby potentially resulting in extreme losses for producers. Prevention and control of the infection requires good understanding of its epidemiology, so that targeted measures can be instigated.

1. Introduction

African swine fever (ASF) is caused by the African swine fever virus (ASFV) which is a member of the *Asfarviridae* family. It is the only DNA virus transmitted by arthropods. It is highly contagious, resulting in up 100% morbidity in previously unexposed pig herds with mortality varying between 0 and 100% depending on the virus, the host, the dose and route of the exposure of the virus. There is no treatment or vaccine. The disease was confined to Africa until spreading to Europe in the middle of the last century, and later on also to South America and the Caribbean. In Europe (apart from Sardinia) and in South America/Caribbean the infection was eradicated via drastic control and eradication programmes. But in 2007, it was introduced into Caucasus and then Eastern Europe where it has become endemic. ASFV can infect a range of wild and domestic suids, resulting either in clinical disease in domestic and feral pigs and wild boar or an asymptomatic carrier state, especially in the case of African wild suids. Soft tick vectors have also been identified: *Ornithodoros erraticus* in Spain and Portugal and members of the *Ornithodoros moubata* complex in Africa. The epidemiology of the disease and the ability of the virus to survive within a particular ecological system is defined by its wild animal habitat and livestock production system characteristics that influence host and vector species densities and interrelationships. There is now widespread concern that ASFV may spread further across Europe and into Asia, in context of increased trade activity and given that domestic pig populations are increasing, particularly in Eastern Asia.

2. African swine fever hosts

2.1. Domestic pigs

When introduced into a region or domestic pig population, ASF is typically associated with high morbidity and mortality rates and the rapid spread of outbreaks. However, the literature suggests that in endemic regions, mortality rates have decreased and subclinical or chronic ASFV infections have become more frequent (Allaway et al., 1995; Fasina et al., 2010; Owolodun et al., 2010b; Thomson, 1985). The chronic forms observed in the Iberian Peninsula (1960–1995) were due to infections with ASFV low virulence viruses and may have been the consequence of the use of live attenuated vaccines during the 1960s (Sanchez-Vizcaino et al., 2012). In Africa, different hypotheses have been proposed to explain the observed resistance to ASFV infection, including acquired immunity from previous exposure to lower doses of virus or to related viruses of reduced virulence (Penrith et al., 2004a) – which may have emerged from circulation in domestic pig populations. It has also been suggested that local pig breeds are genetically less

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susceptible to ASFV infection, however it has been demonstrated experimentally that increased resistance was not an inheritable characteristic (Penrith et al., 2004a).

Subclinically infected, chronically infected or recovered pigs are likely to play an important role in the epidemiology of the disease, for disease persistence in endemic areas as well as for causing sporadic outbreaks or introduction into disease-free zones (Allaway et al., 1995; Boinas et al., 2004; Leitao et al., 2001; Sánchez-Vizcaíno and Arias, 2012; Wilkinson and Pensaert, 1989). Although no long-term carrier state has been demonstrated, such pigs were shown to remain infected for up to several weeks (Wilkinson, 1984), and can transmit the disease to other susceptible pigs either via direct contacts or indirectly via tick bites or following the ingestion of contaminated meat and products.

2.2. Wild suids

Warthogs (*Phacochoerus africanus*) are considered the original vertebrate host of ASF and are involved in a sylvatic cycle with ticks of the *O. moubata* complex (Plowright et al., 1969b; Thomson, 1985). They are also considered the most important vertebrate reservoir for ASFV in Africa, due to their wide distribution and ecology which provides opportunities for contact with both *Ornithodoros* ticks living in burrows and domestic pigs (Jori and Bastos, 2009; Plowright, 1981; Plowright et al., 1994). Warthogs are asymptomatic carriers of the disease: viraemia and virus replication occur in young infected warthogs bitten in their burrows by infected soft ticks (Thomson, 1985; Thomson et al., 1980), and ASFV then persists in lymph nodes (Plowright, 1981; Plowright et al., 1994; Wilkinson and Pensaert, 1989).

The role of bushpigs (*Potamochoerus larvatus*) and red river hogs (*Potamochoerus porcus*) in the epidemiology of ASF has not yet been elucidated (Haresnape et al., 1985; Jori and Bastos, 2009; Jori et al., 2007; Luther et al., 2007; Roger et al., 2001; Thomson, 1985; Wilkinson, 1984). ASFV replication was demonstrated in bushpigs, and included transmission to pigs and soft ticks in some instances (Anderson et al., 1998; Oura et al., 1998). However, acquisition of infection and mechanisms of transmission to other ASFV hosts have not been determined. Bushpigs can be found in East, central, southern Africa and Madagascar (Jori and Bastos, 2009; Jori et al., 2007; Ravaomanana et al., 2011; Roger et al., 2001) but they are not considered important reservoirs for ASF, maybe because their nocturnal habits, low densities of population and non-use of burrows limit interactions with domestic pigs and soft ticks.

Other wild suids (e.g. giant forest hog – *Hylochoerus meinertzhageni*) have been reported as infected with ASFV occasionally (Heuschele and Coggins, 1965a; Thomson, 1985), but their involvement in the epidemiology of the disease is considered negligible (Jori and Bastos, 2009).

In Europe, wild boar and feral pigs have been shown to have the same susceptibility to ASFV as domestic pigs (Jori and Bastos, 2009; McVicar et al., 1981). Evidence of infection was reported in the Iberian Peninsula (Caiado et al., 1988; Perez et al., 1998; Wilkinson, 1984), Sardinia (Laddomada et al., 1994), Cuba (Simeon-Negrin and Frias-Lepoureau, 2002), Mauritius (Lubisi et al., 2009) and Russia (Beltran Alcrudo et al., 2009). ASF outbreaks in wild boar fade out and contact with infected domestic pigs or other sources of infection is required for maintaining disease circulation in wild boar populations (Laddomada et al., 1994; Mur et al., 2012a; Perez et al., 1998; Ruiz-Fons et al., 2008). However, they could facilitate the spread of the disease in areas with free-range pigs – such as in the Caucasus and Russia – via either direct contact with domestic pigs, fomites or ingestion of infected carcasses.

2.3. Soft ticks

O. erraticus was first identified as a biological vector and reservoir for ASFV in Spain (Sanchez-Botija, 1963), which led to the discovery that ticks from the *O. moubata* complex play a role in the epidemiology of the disease in Africa (Plowright et al., 1969a).

In Africa, *O. moubata* ticks are a source of infection with ASFV for both domestic and wild pigs. Transmission occurs during blood meals (Plowright, 1981; Plowright et al., 1969b) and infected ticks are able to retain the virus for long periods and transmit it to susceptible hosts. In addition, transstadial, transovarial and sexual transmission in *O. moubata* ticks (Hess et al., 1989; Plowright et al., 1970, 1974; Rennie et al., 2001; Wardley et al., 1983) allows for the persistence of ASFV infection in the absence of viraemic hosts. However, ASFV infection can also cause mortality in ticks (Kleiboeker and Scoles, 2001), and the persistence of infection depends on the initial infection titre and thus the level of viraemia in infected pigs (Haresnape et al., 1988; Plowright, 1981). *O moubata* ticks are widely distributed in southern Africa and are also present in Madagascar (Plowright et al., 1994; Roger et al., 2001; Uilenberg, 1963), while there is limited evidence of their distribution in central Africa (De Glanville et al., 2010; Ekue and Wilkinson, 1990; Hoogstraal et al., 1954; L. Mulumba-Mfumu, personal communication). They are considered important for the persistence of ASF.

O. moubata is thought to be absent from West Africa. ASFV has been detected in *Ornithodoros sonrai* ticks from Senegal, but authors suggest they are likely to have a limited role in the epidemiology of the disease, if any (Vial et al., 2007).

Only transstadial transmission of ASFV by ticks was demonstrated on the Iberian Peninsula (Caiado et al., 1988; Sánchez-Vizcaíno and Arias, 2012), however *O. erraticus* were also considered to have a key role in the long-term maintenance of disease (Oleaga-Perez et al., 1990; Perez-Sanchez et al., 1994; Sanchez-Botija, 1963).

Five other *Ornithodoros* species have been experimentally infected with ASFV: four are found in North America and the Caribbean (*O. coriaceus*; *O. turicata*; *O. parkeri* and *O. puertoricensis*) and *O. savignyi* from the desert areas of North Africa (EFSA, 2010b; Sanchez-Vizcaino et al., 2009). No other haematophagous invertebrate has been identified as biological vector for ASFV, but mechanical transmission within 48 h of a blood meal on an infected pig has been demonstrated for *Stomoxys calcitrans* (Mellor et al., 1987).

3. Transmission cycles

3.1. Sylvatic cycle

The sylvatic cycle has been well documented in southern and eastern Africa, where it involves warthogs and ticks of the *O. moubata* complex (Plowright et al., 1994, 1969b; Thomson, 1985; Wilkinson and Pensaert, 1989). Young suckling warthogs are infected in burrows infested with soft ticks. A short period of viraemia follows and allows transmission of ASFV to naïve ticks during blood meals (Heuschele and Coggins, 1965b, 1969; Thomson, 1985; Thomson et al., 1980). Warthogs remain asymptomatically infected for life, but due to the absence of horizontal and vertical transmission between warthogs, the maintenance of infection is dependant on *O. moubata* ticks (Jori and Bastos, 2009; Penrith et al., 2004b). Tick colonies can maintain ASFV infection for up to 15 months in the absence of blood meals (Hess et al., 1989; Plowright et al., 1970, 1974), and allow subsequent transmission cycles with warthogs at the next farrowing season.

In areas with both warthogs and soft ticks, infection rates of the wild suids can be very high (Plowright et al., 1994), but the

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infestation rates of warthog burrows and ASF infection rates of ticks can vary considerably (Bastos et al., 2009; Plowright et al., 1969a,b). Also, as indicated in the review by Jori and Bastos (2009), the presence of both warthogs and ticks in a region does not necessarily imply the existence of a sylvatic cycle. For example, it is suspected that a sylvatic cycle does not occur in West Africa, and warthogs or soft ticks have rarely been found infected (Jori and Bastos, 2009; Jori et al., 2007; Penrith et al., 2004b; Taylor et al., 1977; Vial et al., 2007).

3.2. Tick-pig cycle

Ornithodoros spp. ticks have frequently been found infesting pig pens in Africa and the Iberian Peninsula (Caiado et al., 1988; Haresnape and Mamu, 1986; Haresnape and Wilkinson, 1989; Haresnape et al., 1988; Oleaga-Perez et al., 1990; Wilkinson et al., 1988), where they readily feed on pigs and can be involved in the transmission and long-term maintenance of ASF. In some areas of Spain, the occurrence of ASF outbreaks was significantly associated to the presence of *O. erraticus* (Perez-Sanchez et al., 1994).

As described previously, *Ornithodoros* ticks can maintain ASFV infection for several months or even years after feeding on viraemic animals. In Portugal, ASF is thought to have re-emerged in 1999 on a previously infected farm due to the continued presence of *O. erraticus* ticks (Boinas et al., 2011; Sanchez-Vizcaino et al., 2009). In Madagascar, ASFV was isolated from ticks found on a farm where no pig had been introduced for at least four years (Ravaomanana et al., 2010). In such circumstances, the risk of ASF infection only decreases when tick populations become extinct following the absence of hosts over an extended period of time (Oleaga-Perez et al., 1990). Control measures therefore need to include application of acaricide and/or abandonment of infested buildings (Plowright et al., 1994). To support the strategic implementation of such measures, diagnostic tests have been developed to identify pigs that have been parasitised by *Ornithodoros* ticks (Canals et al., 1990; Diaz-Martin et al., 2011; Oleaga-Perez et al., 1994).

3.3. Domestic cycle

Once introduced into domestic pig populations, ASFV is transmitted through direct contacts and by fomites (Arias et al., 2002a; Plowright et al., 1994; Sánchez-Vizcaíno and Arias, 2012) at local, regional and even international levels. Pig trade and/or movement and lack of biosecurity practices highly contribute to the local spread of ASF in endemic areas.

All excretions and secretions of infected pigs can contain virus, and ASFV may remain viable in blood and tissues for long periods. Transmission via direct contact can thus occur for several weeks (Wilkinson and Pensaert, 1989).

ASFV is very resistant to inactivation: it remains stable at pH 4–10 and is thus not affected by meat maturation, and requires heating at 60 °C for 20 min to be inactivated. Smoked sausages and air-dried hams require smoking at 32–49 °C for up to 12 h and 25–30 days of drying to be free of ASFV (Plowright et al., 1994). Due to the lengthy persistence of ASFV in tissues such as muscles, fat and bone marrow, pork products such as cured ham can remain infectious for several months (Farez and Morley, 1997; McKercher et al., 1987; Mebus et al., 1993, 1997). The access of pigs to poorly disposed-of carcasses, frozen, insufficiently cooked or cured pork products thus presents a risk of infection.

ASFV can also persist in the environment for several days (Plowright et al., 1994; Sanchez-Vizcaino et al., 2009) and transmission is possible via fomites such as contaminated clothing and shoes, equipment and vehicles (Mur et al., 2012d).

Few analytical studies have identified risk factors for ASF at the farm level. Factors found to increase the risk of outbreaks include: free-ranging (Allaway et al., 1995; Edelsten and Chinombo, 1995; Mannelli et al., 1997), the previous occurrence of the disease on the farm (Randriamparany et al., 2005), the presence of an infected pig farm in the neighbourhood or of an abattoir in the community, and visits by (para)veterinarians in Nigeria (Fasina et al., 2012). A spatial regression analysis found density of the road network, of water bodies and of the domestic swine population to be associated with outbreaks in Russia (Gulenkin et al., 2011), and a spatial spread model by Olugasa and Ijagbone (2007) found the movement of infected animals to be the most important factor for ASF spread. A stochastic model investigating the effect of emergency sale of pigs without detected signs in case of a suspected outbreak [a practice reported by small scale farmers in affected areas (Babalobi et al., 2007; Costard et al., 2009b; Fasina et al., 2010; Randriamparany et al., 2005)] contributes to the spread of the disease in domestic pig populations (Costard et al., 2012b). In all cases, the information described shows that many opportunities exist for the transmission of ASF between pigs.

3.4. Transmission from sylvatic to domestic cycles

The mechanisms of transmission from wildlife to pigs are not fully understood, and different hypotheses have been discussed (Jori and Bastos, 2009).

Transmission from African wild suids to pigs through direct contact seems unlikely (Heuschele and Coggins, 1969; Plowright, 1981; Plowright et al., 1994, 1969b; Thomson, 1985) and has only been reported once for bushpigs, under experimental conditions (Anderson et al., 1998). Interbreeding between bushpigs and domestic pigs has been suspected and could constitute an opportunity for ASF transmission (Jori and Bastos, 2009; Roger et al., 2001).

Opinions on the possibility of transmission through ingestion of infected meat differ. While some authors (Plowright et al., 1969b; Thomson, 1985; Thomson et al., 1980) argued that virus titres in wild suid carcasses are too low to induce infection, others stated that wild suid tissues may contain sufficient virus particles to infect pigs following ingestion (Anderson et al., 1998; Wilkinson, 1984). Furthermore, poorly disposed of pig carcasses can potentially infect bushpigs or warthogs which may scavenge on these.

However, soft tick vectors constitute the most likely mechanism of transmission from African wild suids to domestic pigs (Thomson, 1985; Wilkinson and Pensaert, 1989). This could happen when pigs and warthogs share spaces such as grazing or drinking areas, or when ticks are brought back to human settlements with bush meat (Jori and Bastos, 2009; Thomson, 1985).

4. Molecular epidemiology

Molecular epidemiology has proved useful in investigating epidemiological patterns of ASF as well as the likely origin of the disease when introduced into new regions. However, the outputs need to be considered in parallel with those from other epidemiological studies, in particular because of the issue of representativeness of the samples analysed and viruses isolated. Identification of ASFV genome length variation (Blasco et al., 1989a,b; Chapman et al., 2008) allowed the characterisation of virus isolates, initially by enzyme site mapping (e.g. Dixon and Wilkinson, 1988; Sumption et al., 1990) and then by sequencing of different genome regions. The current approach is to first partially sequence the gene B646L encoding the major protein p72 (Bastos et al., 2003), and then to sequence the Central Variable Region or several other gene regions (e.g. E183L encoding p54 protein, CP204L encoding p30 protein) of closely related isolates to distinguish sub-groups (Boshoff et al., 2007; de Villiers et al., 2010; Gallardo et al., 2009; Lubisi et al., 2005,

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2007, 2009; Nix et al., 2006; Owolodun et al., 2010a; Rowlands et al., 2008).

So far, 22 main ASFV genotypes have been identified by partial sequencing of the gene B646L, 20 of which are restricted to East (13 genotypes) and southern (14 genotypes) Africa (Bastos et al., 2003; Boshoff et al., 2007; Gallardo et al., 2009; Lubisi et al., 2005, 2007; Nix et al., 2006). Similarities or differences between isolates recovered from wildlife and pigs in different geographical areas indicate the existence of the three types of transmission cycles previously described. Some isolates seem to be country-specific isolates while others occur across regions.

Genotype II was most likely introduced in Madagascar from Mozambique (Bastos et al., 2003; Gonzague et al., 2001), and remains the unique genotype occurring on the island. The ASFV isolate introduced in Mauritius was also found to belong to a group with other Genotype II viruses isolated in Mozambique and Madagascar between 1998 and 2007.

In contrast, all isolates from West Africa belong to Genotype I (Bastos et al., 2003), but some intra-group variability was recently demonstrated (Gallardo et al., 2009; Nix et al., 2006; Owolodun et al., 2010a; Phologane et al., 2005). The same Genotype I was found in sylvatic hosts in East and southern Africa (Boshoff et al., 2007; Lubisi et al., 2005).

Outside Africa, Genotype I was the only one found in Europe, America, and the Caribbean, until the recent introduction of a virus from Genotype II in Caucasus and Russia. Molecular analysis showed the likely origin of this introduction in Georgia was East Africa (Rowlands et al., 2008). Gallardo et al. (2009) showed that the Portuguese isolate Lisbon57 was identical to West African isolates, confirming the hypothesis of introduction from this region. However, Nix et al. (2006) showed some intra-Genotype I variation in isolates recovered from ticks in Portugal.

Considering this evidence, the genetic diversity in East and southern Africa has been attributed to the long-term evolution of ASFV within wildlife hosts. In contrast, the stability of viruses in West Africa and Madagascar has been interpreted as an indication of the absence of a sylvatic cycle (Costard et al., 2009c). The low genetic variation there and on other continents may be due to the lack of selective pressure when only pigs and/or *O. erraticus* are involved, possibly because they are not the original ASFV hosts (Chapman et al., 2008; de Villiers et al., 2010). One could argue that the genetic diversity may be also be influenced by co-infection with different isolates, subsequent reassortment and virus evolution, but it appears that different mechanisms prevent such co-infection (e.g. Bastos et al., 2004). Finally, the fact that genotype VIII in East Africa has only been isolated from domestic pigs (39 outbreaks) over a period of almost 25 years shows that the domestic cycle can occur independently of wildlife hosts in these regions (Lubisi et al., 2005).

5. Regional patterns

5.1. Europe

ASF has been eradicated from the Iberian Peninsula in the late 1990s, after 30 years of endemicity, thanks to rigorous control programmes (Arias et al., 2002b; Bech-Nielsen et al., 1993; Perez et al., 1998). A domestic and tick-pig cycle existed in both Spain and Portugal. In the Iberian Peninsula, wild boars were affected in a similar way to domestic pigs: the initially high morbidity and mortality rates decreased with time (Perez et al., 1998). The only long-term reservoir for the disease in Spain and Portugal was *O. erraticus* (Caiado et al., 1988; Oleaga-Perez et al., 1990).

In Sardinia, ASF is still endemic and affects domestic pigs, wild boar and feral pigs. Backyard, free-range production systems with shared grazing areas were found to increase the risk of outbreaks (Mannelli et al., 1997, 1998; Sanchez-Vizcaino et al., 2009), by facilitating disease transmission between pig herds and between pigs and wild boars. Ticks are absent from the island, where they are therefore not involved in the transmission or persistence of ASFV infection.

In the Caucasus region and Russian Federation, ASF causes acute disease in domestic pigs and wild boar (Beltran Alcrudo et al., 2008, 2009). The majority of pig farms in the area are backyard systems, except for Russia where the proportion of commercial farms is higher (FAO, 2010). Due to the general lack of biosecurity measures and poor implementation of disease control measures, the illegal movement of infected pigs and products, and the existence of areas of interaction between free-ranging pigs and wild boar, there is substantial risk that ASF may persist in these regions and/or spread to other areas of Europe (Costard et al., 2012a; EFSA, 2010a; FAO, 2012; Mur et al., 2012b,c,d; Sanchez-Vizcaino et al., 2012; Wieland et al., 2011), as illustrated by the recent detection of ASFV in meat products in northern Russia (ProMED, 2012) introduction of ASF into Ukraine (OIE, 2012).

5.2. Africa

As mentioned previously, 3 cycles of ASF transmission exist in East and southern Africa. Sylvatic cycles with sporadic emergence in domestic pigs have been described in these regions, for example in Kenya and South Africa (Heuschele and Coggins, 1965b; Pini and Hurter, 1975), where Genotypes I, X and XX isolates were recovered from warthogs and ticks found nearby to affected pig farms. In Malawi, the existence of both tick-pig and domestic cycles has been demonstrated: in the endemic central region of the country, ASF was shown to affect farms with soft ticks in areas devoid of warthogs (Haresnape, 1984; Haresnape et al., 1985, 1987, 1988; Haresnape and Mamu, 1986; Haresnape and Wilkinson, 1989). In these areas, high seroprevalences were observed, including the detection of antibodies in apparently healthy animals, while outbreaks in the non-endemic, southern area of Malawi caused high mortality in pigs and did not involve ticks (Allaway et al., 1995; Edelsten and Chinombo, 1995; Haresnape, 1984; Haresnape and Wilkinson, 1989). In Zambia, the studies by Wilkinson et al. (1988) and Samui et al. (1996) suggest the existence of a domestic cycle, with sylvatic cycles restricted to national parks and their adjacent areas. In Mozmbique, ASF is endemic in regions close to Malawi and Zambia (Penrith et al., 2007) but outbreaks are reported throughout the country. A sylvatic cycle may occur in some national parks and be the cause for important pig losses in the surrounding areas (C. Quembo, personal communication).

In West Africa, the domestic cycle is the only one involved in the persistence of the disease (Sanchez-Vizcaino et al., 2009). In Senegal, Cameroon and Nigeria, there is evidence of the maintenance of the disease in domestic pig populations, with decreased mortality rates and chronic carriers. When ASF is (re-)introduced into non-endemic areas of the region, it causes outbreaks with high morbidity and mortality rates. In Senegal, epidemiological studies and molecular typing suggest that warthogs and *O. sonrai* ticks are unlikely to be involved in the transmission of the disease (Bastos et al., 2003; Jori et al., 2007; Vial et al., 2007). High serological prevalence was found in farms where animals did not exhibit clinical signs (Etter et al., 2011). In Nigeria, ASF is present in most agro-ecological zones of the country where it is considered endemic (Fasina et al., 2010; Otesile et al., 2005; Owolodun et al., 2010b). High mortality rates characterised outbreaks in the first years following initial introduction in the country (Babalobi et al., 2007; Odemuyiwa et al., 2000; Otesile et al., 2005), but decreased mortality and high seroprevalence in apparently healthy animals are now observed (Fasina et al., 2010; Owolodun et al., 2010b). Ticks are absent from domestic settings; ASFV has been detected on

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rare occasions in captive wild suids (Luther et al., 2007; Taylor et al., 1977) but never in naturally occurring wild suid populations. In Cameroon, ASF is endemic in the South, in the absence of warthogs and ticks in domestic settings (Awa et al., 1999; Ekue and Wilkinson, 1990). As with Nigeria, the initial mortality rates were around 80%, but now isolates of various virulence are circulating (Ekue and Wilkinson, 2000). In West Africa, formal and informal trade of pigs and pork products are likely to be the major means of dissemination of the disease at both local and regional levels.

In Madagascar, recent studies suggest that ASF is restricted to the domestic pig population, with seasonal peaks of ASF and mostly unspecific symptoms reported by farmers. An abattoir survey conducted in 2006 found up to a quarter of slaughtered pigs infected with ASFV (Costard et al., 2009b). Pig farming systems and practices within the pig production sector facilitate the spread and persistence of the disease, such as trade of pigs on live animal markets, absence of quarantine, natural service breeding, lack of appropriate slaughter facilities, and emergency sale of pigs in case of suspicion of ASF (Costard et al., 2009a,b, 2012b; Randriamparany et al., 2005). Both bushpigs and *O. moubata* ticks are present on the island (Roger et al., 2001), but no evidence of bushpig-ASFV or bushpig-tick was detected (Jori et al., 2007; Ravaomanana et al., 2010, 2011). Molecular epidemiology supports these findings, with all circulating viruses belonging to Genotype II (Bastos et al., 2003). As in other endemic settings, morbidity and mortality rates have decreased, and subclinical or chronic cases facilitate the persistence and transmission of ASF.

6. Conclusion

African swine fever is a complex disease with severe socio-economic consequences. The disease has a high potential for expansion to new areas where it can then rapidly spread and persist if early detection and strict control measures are not implemented. The disease distribution and recent spread to the Caucasus and Eastern Europe illustrate well the threat ASF poses to the pig production sector worldwide. ASF presents a complex epidemiology with the existence of different patterns, which depend on host and vector species densities and interrelationships, and are thus influenced by livestock production system characteristics and ticks and wild pig habitat. In this context, prevention and control of the infection requires good understanding of its epidemiology, so that targeted measures can be instigated.

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