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Review

Review of the sylvatic cycle of African swine fever in sub-Saharan Africa and the Indian ocean

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ABSTRACT

African swine fever (ASF) is a major limiting factor for pig production in most of the countries in Sub-Saharan Africa and the Indian Ocean. In the absence of vaccine, a good understanding of the ecology and epidemiology of the disease is fundamental to implement effective control measures. In selected countries of Southern and East Africa, the association between *Ornithodoros moubata* ticks and warthogs has been described in detail in the literature. However, for many other countries in the region, information related to the sylvatic cycle is lacking or incomplete. In West African countries, for instance, the role of wild pigs in the epidemiology of ASF has never been demonstrated and the existence and potential impact of a sylvatic cycle involving an association between soft ticks and warthogs is questionable. In other countries, other wild pig species such as the bushpigs (*Potamochoerus* spp.) can also be asymptomatically infected by the virus but their role in the epidemiology of the disease is unclear and might differ according to geographic regions. In addition, the methods and techniques required to study the role of wild hosts in ASF virus (ASFV) epidemiology and ecology are very specific and differ from the more traditional methods to study domestic pigs or other tick species. The aim of this review is (i) to provide a descriptive list of the methodologies implemented to study the role of wild hosts in African swine fever, (ii) to compile the available knowledge about the sylvatic cycle of ASFV in different regions of Sub-Saharan Africa and the Indian Ocean in addition to the one that has been described for East and Southern Africa, and (iii) to discuss current methodologies and available knowledge in order to identify new orientations for further field and experimental surveys.

Contents

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1. Introduction

African Swine Fever (ASF), caused by a DNA virus of the Family *Asfarviridae*, is one of the most serious diseases of domestic pigs in Africa. The virus is extremely contagious and the lack of an efficient vaccine, together with the involvement of wild hosts able to maintain the virus and the existence of large free-ranging populations of domestic pigs are considered the major constraints for the control and the eradication of the disease. ASF remains an endemic problem in Madagascar and many countries in Africa and there is evidence that this represents a threat to the pig population and the rural economy of other continents and regions. It is for instance the case with the introduction and spread of ASFV from Southern Africa to Madagascar in 1998 (Bastos et al., 2003; Roger et al., 2001), to Mauritius in 2007 (Lubisi et al., 2009) and more recently into the Caucasus and Russia (Rowlands et al., 2008). In the absence of an effective vaccine, the only possibility to mitigate the transmission and spread of the disease is to implement sanitary control measures based on a solid knowledge of its epidemiology. However, this is complex and complicated by the fact that many aspects regarding the role of the wild hosts and tick vectors involved in the sylvatic cycle of the infection remain unknown. In addition, their contribution as reservoirs and vectors of the disease may vary in different continents or regions. Wild suids – warthogs (*Phacochoerus* spp.) and bushpigs (*Potamochoerus* spp.) – on one hand, and soft ticks of the genus *Ornithodoros* on the other hand, are considered the natural hosts in the sylvatic cycle in Africa and potentially in the Indian Ocean. Although the specific relationship between warthogs and soft ticks is extremely well described in the literature for East and Southern Africa (Plowright, 1981; Plowright et al., 1994; Thomson, 1985), it needs to be determined for the rest of the African continent and the Indian Ocean.

The fact that warthogs occurred in all the countries in Africa where ASF had been diagnosed in domestic pigs was noted by Thomson (1985). However, infection of warthogs with ASFV and association between *Ornithodoros moubata* complex ticks and warthogs was only established in countries in East and Southern Africa (Penrith et al., 2004b; Thomson, 1985). Findings in other countries have failed to provide convincing evidence of the warthog/tick sylvatic cycle and have demonstrated maintenance of ASFV in domestic pigs (Penrith et al., 2004b). The bushpig has been considered to be of less importance in the epidemiology of ASF than the warthog but since it is nocturnal and elusive, information on this species is much scarcer. The latter species has been suspected to be a reservoir of ASFV in areas where there are no warthogs, but where the virus is endemic (Haresnape et al., 1985). The blood virus levels in an infected bushpig are high enough to infect both the soft ticks and domestic pigs (Anderson et al., 1998). However, bushpigs do not live in burrows and therefore do not get into contact with the endophilous soft ticks naturally (Costard et al., 2009). It is reported by local inhabitants that natural interbreeding can occur between bushpigs and free ranging domestic pigs if they meet in the same areas, but scientific confirmation for this has not been provided (Jori and Bastos, 2009). It has been speculated that hybrids, if they exist, could become asymptomatic carriers among domestic pigs and thereby maintain the spread of the virus, because pure breed bushpigs do not show any clinical signs (Jori and Bastos, 2009). Bushpigs are hunted for their meat in many African countries and in Madagascar, and leftovers fed to domestic pigs could lead to infection if the virus amount in the tissues is high enough (Jori and Bastos, 2009).

In East and Southern Africa and the Indian Ocean, tick vectors of ASFV belong to the *Ornithodoros moubata* complex of species, while in North and West Africa they belong to the *Ornithodoros erraticus* group. The first group has been re-described by Walton (1962) and includes four different species: *O. moubata sensu stricto* (Fig. 1) and *O. porcinus* that are confirmed to be vectors and natural reservoirs of ASFV, and *O. compactus* and *O. apertus* that do not feed on suids. According to this author, the first two species are morphologically and ecologically distinct, although for both of them a wild strain that colonizes warthog burrows and a domestic strain colonizing pig pens and human dwellings have been described. In East Africa, the wild *O. porcinus porcinus* and the domestic *O. porcinus domesticus* were morphologically differentiated (Walton, 1962). The second group (Fig. 2) was first described as a sub-genus named *Theriodorus* (Pospelova-Strom, 1953) and includes *O. erraticus* and *O. sonrai*, which have both been found naturally infected by ASFV. *O. alactagalis* and *O. nereensis* also belong to this group but their role regarding ASF transmission is unknown. Because the systematics of both groups remains unclear in several parts of Africa, with suspected hybridization of species in sympatric zones, the classification above will be used in this paper. A recent molecular investigation of *Ornithodoros* from East and Southern Africa suggested a more parsimonious classification (Bastos et al., 2009). However, it is clear that further taxonomic investigations are needed at molecular level to arrive at a final taxonomic classification of *Ornithodoros*.

Based on investigations in East and Southern Africa, it was established that *Ornithodoros* soft ticks live in warthog burrows and transmit ASFV to immature warthogs, which develop sufficiently high levels of viremia to infect other ticks. Infected ticks would occasionally be transported by adult warthogs from natural to farmed areas where they are able to bite and infect domestic pigs, providing a pathway between sylvatic and domestic cycles (Plowright et al., 1994). Further investigations in other African and European countries have shown the existence of many diverse epidemiological situations, where soft ticks may only colonize domestic pig premises, maintaining ASFV by feeding exclusively on domestic pigs (Haresnape et al., 1985; Sanchez Botija, 1963). Equally, in the light of comparative virus investigations, it appears that the sylvatic cycle has acted as a source of new more diverse and virulent virus isolates for the domestic cycle since the greatest genetic variation, with a high number of genotypes, occurs in East and Southern Africa (Lubisi et al., 2005; Nix et al., 2006). However, the persistence of ASFV in local *Ornithodoros* ticks in Portugal and Spain demonstrates that new maintenance cycles may arise when the virus is introduced into new areas where suitable vectors are present, and this could equally occur if suitable vectors are