Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Africa

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Contents

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Introduction

The African continent has been for centuries perceived as the lost Eden for wildlife populations. Some areas are indeed, home to the largest concentrations of large mammals in the world and harbor an incredibly high level of biodiversity. At the same time, this abundant and rich diversity of mammal hosts comes together with a large diversity of pathogens, many of which are the cause of the most threatening infectious human and animal diseases in the world today. Warthogs (*Phacochoerus africanus)* and soft ticks in East and Southern Africa represent the wild reservoirs of the African Swine Fever (ASF) virus, a virus threatening the world pig industry (Jori and Bastos 2009; Dixon et al. 2020). Similarly, buffalo (*Syncerus caffer*) populations in sub-Saharan Africa, are the main wild reservoir of Foot and Mouth Disease (FMD), considered as one of the major threats for the livestock industry in developed countries (Thomson et al. 2003; Knight-Jones and Rushton 2013). From the public health perspective, there is equally evidence that nonhuman primates from Central and West Africa forests were at the origin of the Human Immunodeficiency Virus (HIV), the largest human pandemic in the last century. Therefore, for the common public, Africa could be also easily be perceived as sources of pathogens of global importance.

In addition, Africa is intensively exposed to many and very serious development and environmental challenges that are progressively transforming natural environments and increasingly encroaching on wildlife populations. This is leading many wildlife populations towards a higher rate of interactions with anthropic compartments (humans and their domestic animals), rising the risk of emergence of new diseases and re-emergence of old diseases on new territories.

The development and globalization of Africa also involve new forms of wildlife exploitation, which are intensifying and expanding across the continent. Traditional subsistence hunting and bushmeat consumption are rapidly evolving towards organized commercial trade (Fig. 1b) to supply increasing consumption demands towards large cities in the continent and beyond (Van Vliet et al. 2016). Moreover, new forms of consumptive and non-consumptive wildlife exploitation activities are developing and generating new patterns of interaction between wildlife humans and their livestock.

This chapter reviews the changes and transformations of Africa, the conjunction of drivers that affect a diversity of interactions between wildlife, domestic animals, and humans, the main characteristics of those interactions, and the problems and consequences related to them.

Fig. 1 Wildlife utilization activities have developed in Africa in recent years. Different forms of wildlife exploitation such as cane rate farming in West Africa (left) and the bushmeat trade (right) have been expanding during recent decades in different parts of Africa and generating new forms of the interface between wild animals and the human environment (Photos: Ferran Jori)

History of the Wildlife-Livestock Interface in Africa

Major infectious animal diseases circulating at the wildlife-livestock interface have been historically interlinked and influencing each other in Africa. Rinderpest, one of the most destructive viral diseases circulating among ruminants, is a good example: Initially introduced from Asia in the late nineteenth century, it decimated millions of wild and domestic herbivores with very serious ecological, epidemiological, and social implications. The removal of approximately 90% of susceptible wild and domestic ruminants induced a dramatic shortage of animal protein availability resulting in the mass starvation of human populations in sub-Saharan Africa (Sunseri 2018). At the beginning of the twentieth century, the ruminant population was so small that pathogen transmission was limited and the burden of diseases circulating between domestic and wild ungulates such as FMD or animal trypanosomiasis (AAT) were reduced to historical low levels. From an ecological perspective, the lack of grazing pressure allowed the expansion of thick savannah vegetation, favoring abundant breeding grounds for tsetse fly populations and an increase in the prevalence of human and animal trypanosomiasis. As a result, human populations abandoned tsetse-infested areas in search of more comfortable living territories. These regions became exclusive wildlife habitats with negligible human presence, turning into African game reserves and national parks during colonial times.

Towards the middle of the twentieth century, the development of a vaccine against rinderpest allowed repeated mass vaccinations campaigns against this virus and resulted in an extraordinary recovery of wild and domestic ungulate populations, which expanded into new territories: a new and abundant wildlife-livestock interface was then restored. This situation favored the re-emergence of bovine diseases such as FMD and AAT across large parts of the continent in the second half of the twentieth century (Brito et al. 2016; Van den Bossche et al. 2010).

Ecological, Socioeconomical, and Geographical Drivers Affecting the Wildlife-Livestock Interface

Climate Change

The African continent is highly exposed to climate change and its mean annual temperature will increase more than +2 °C in the course of the present century (Pereira 2018). The greatest negative impacts on livestock are expected in grazing systems in arid and semi-arid areas. Exacerbated drought conditions will reduce forage and range productivity and may contribute to overgrazing and land degradation. This phenomenon can enhance competition for grazing lands, and water sources (Fig. 2), increasing the frequency of interactions between wild and domestic animals around those common and increasingly scarce resources such as vegetation

Fig. 2 Water points in arid environments congregate large numbers of species including different species of animals and humans. This congregation will increase with climate change (Photo: B. Faye)

cover, water surfaces, or pasture. The alteration of these climate-dependent resources may also force animals to adjust their migratory movements towards new ecosystems where they may encounter or introduce new pathogens (Altizer et al. 2011).

In addition, climate change is able to modify the distribution of many diseases and pathogens affecting wildlife and livestock, particularly vector-borne diseases. Warmer temperatures have an impact on the range patterns of vectors and their pathogens to new temperate or higher latitudes, exposing naïve host populations to new diseases (Kaeslin et al. 2012; Van den Bossche et al. 2010).

Climate change is reducing the distribution of tsetse fly habitat, allowing the expansion of cattle production in areas where it was previously limited by AAT, with several ecological, socioeconomic, and epidemiological implications (Anderson et al. 2011). One of them is for an instance an increase of conflicts between wildlife and livestock, which threaten the survival of top African predators such as lions or wild dogs (Carter et al. 2018; Easter et al. 2018).

Finally, climate change can have an impact on the immune status of animals due to heat or nutritional stress, increasing their susceptibility to parasites and pathogens, facilitating co-infection with multiple organisms, and the occurrence of clinical disease in normally resistant host species. This phenomenon has been recently observed in Serengeti lions (*Panthera leo nubica*) infected with canine distemper virus and with high levels of infection with *Babesia leo*, a usually non-pathogenic tick-borne parasite. This co-infection was suspected to be responsible for abnormal mortality events in lions in 1994 and 2001 (Dybas 2009).

Population Growth and Movements

Africa has one of the youngest human populations on Earth and its demographic growth in the next decades is likely to rise exponentially. Now home to 1.2 billion, the African population is expected to double to 2.5 billion by 2050, exceeding a growth of 42 million people per year. Conversely, the perspectives of protein production are inversely proportional, exposing many regions to an extremely serious challenge of the local sustainable food supply. Many of those areas include large surfaces of dry land and forested areas, where a combination of growing populations and land degradation are increasing the vulnerability of people to both economic and environmental changes (Van Vliet et al. 2016). While the rate of replacement of forested areas by pastoral systems is expected to decline between 2020 and 2050, the expansion of humid cropland systems at the expense of forest is expected to continue for decades ahead.

Another important impact of demographic growth is the increased frequency and number of migratory movements, which influence the exchanges of agricultural products. Those transactions can facilitate the long-distance spread of some pathogens, once localized in some areas of wildlife-livestock interface to distant territories. In this manner, strains of FMD originating from wildlife interface areas in Southern Africa have managed to cross country boundaries thousands of kilometers away, generating outbreaks in Northern African countries (Jori et al. 2016). At a larger trans-continental scale, African swine fever strains originating in warthog burrows have been introduced in Eastern Europe, generating huge economic losses to the pig industry (Quembo et al. 2017).

Rural Exodus

By 2050, more than two-thirds of the world's population will live in towns. Urbanization will primarily be the result of the expansion of the main megalopolis such as Lagos, Kinshasa, Cairo, or Luanda. One of the major challenges in this context, is how to feed those people sustainably, since the future will bring risks of non-renewable natural resource shortages. In forested Africa, cultural habits of wildlife consumption linked with demographic growth have driven the development of a very important bushmeat trade. This places at risk of extinction many vulnerable wildlife species and reduces at the same time the food supply of people dependent on these resources in rural forested source areas in the longer term (Van Vliet et al. 2016).

Deforestation

Across Africa, oil, gas, and mining projects are driving investments in new and improved infrastructure. Within these developments, forests are vulnerable to loss or severe degradation through conversion to agriculture or colonization by settlers seeking employment and other economic opportunities (Edwards et al. 2014). This trend is the cause of the disappearance of close to 90% of the West African forest during the last century. Given the extent and rate of forest fragmentation due to roadside farming and logging, up to 30% of Central African forests are expected to disappear by 2030. This process facilitates the overlapping of anthropic activities with natural habitats (Chukwuka et al. 2018) and the contact of humans and domestic animals with wildlife reservoirs, generating a higher rate of exposure of previously naïve host populations to new zoonotic pathogens (Wolfe et al. 2005). In addition, habitat destruction is conducting many endangered species to a serious situation of vulnerability because they are increasingly confronted with challenges of overexploitation and contacts with infectious pathogens from human or domestic animals, which can equally threaten their survival.

Characteristics Affecting the Wildlife Interface in Different African Regions

African Rainforests (Congo Basin, Remaining Forests in West Africa or East Africa)

African equatorial rainforests encompass a very high level of animal and plant biodiversity. The Congo Basin contains 20% of the world's tropical forests and supports the highest biodiversity of the continent. African tropical rainforests are separated into the Congo Basin in Central Africa, the Guinean Forests of West Africa, and some relics of forest on the East African Coastal area, which support rich wildlife populations, including numerous endemic species of high conservation priority (Mayaux et al. 2013). Nevertheless, forest habitats in East, Central, and West Africa are seriously encroached by highly dense human populations and their livestock and are exposed to tremendous pressure by commercial logging, slash-and-burn plantation agriculture, weak governance, industrial-scale mining or logging, and unsustainable bushmeat hunting (Nogherotto et al. 2013). In addition, many of these areas are often threatened by civil unrest and political conflicts, which add a further strain when refugees turn to the forests for shelter and firewood.

African Rangelands

African savannahs are distributed across the West African Sahel, Eastern, and Southern Africa. Most of sub-Saharan agriculture takes place in savannah areas, which support most of the cropland and pasture areas. Importantly, savannah landscapes are also home to the largest wild mammal populations on Earth. For this reason, large surfaces of these landscapes are devoted to transboundary conservation such as the Mara-Serengeti Ecosystem, the Kavango-Zambezi Transfrontier Conservation Area, or the W complex in West Africa. Although these processes are positive for wildlife conservation, they enhance the presence of common grounds where wildlife and livestock interact, generating new challenges for the control of shared infectious diseases (Thomson et al. 2013).

However, future changes in the climate could have an impact on these landscapes by increasing the number of droughts or increasing rainfall. Furthermore, another major threat for savannah habitats is the shift of agricultural practices towards intensification and conversion of very large areas of grassland into cropland. Unfortunately, all these biotic and abiotic changes are pushing rates of extinction of many large emblematic mammals of Africa to unprecedented and dramatic levels (Archer et al. 2018).

Transition Areas

Transition areas constitute a mosaic of habitats and climates extremely rich in biodiversity. A diversity of ecosystems changing from forested to open shrub savannah areas exists in coastal areas of Central Africa, West Africa, and East Africa. Highly diverse habitats are also found on the slopes of many high peaks such as Kilimanjaro, Mount Cameroon, or the boundaries of the Ethiopian plateau. These areas are particularly prone to interactions with wildlife because they host important human population densities with their domestic animals. Therefore, these transition areas are considered as hot spots for emerging zoonotic infectious diseases at the human-animal-ecosystems interface that have the potential to spread across borders such as Yellow Fever, Ebola Virus disease, Marburg Viral fever, Crimean Congo hemorrhagic fever, Hepatitis E virus, or Rift valley fever (Olivero et al. 2017).

African Deserts

Those include the Saharan region in North Africa and the Kalahari and Namib deserts in Southern Africa. Due to the lack of water, these habitats host a limited number of large mammal species, compared to other regions.

Interphase Between Phylogenetically Close Species

Phylogenetically close species such as wild and domestic ruminants or birds often share the same ecological spaces, similar resources, and a wider range of pathogens. This is for instance the case between wild and domestic bovids or between avian species.

The Ruminant Interface

Livestock production is a deeply rooted traditional activity and represents the cultural, socioeconomic, and nutritional basis of many agro-pastoral societies in Africa. The continent hosts almost 20% of the world cattle population (326 million heads), which has increased by 100 million heads since the beginning of the twenty-first century (Figs. 3 and 4). In the Sahelian regions of West, East, and northern Africa, small ruminants kept by rural agro-pastoral communities in mixed crop-livestock settlement areas, represent more than 60% of the continental mammal production (Fig. 3) and are a major source of income generation, despite the challenges posed by infectious diseases, land pressure and climate change (Otte et al. 2019).

In many countries with deeply rooted pastoral culture, there is a traditional opposition between livestock production areas and territories protected for wildlife use (national parks and game reserves). Despite the substantial contribution of wildlife-based tourism (Fig. 5) to many African economies, demographic growth and climate change increase the dependence of livestock herders to areas rich in pasture and water and the competition with wildlife for natural resources (Gordon 2018). This competition is particularly acute at the boundaries of protected areas in savannah ecosystems, where agro-pastoral societies often share grazing spaces and water sources with wildlife populations (Miguel et al. 2017).

In this context, a diversity of wild and domestic large and small ruminants interact, sharing a diversity of diseases (Table 1). The wild domestic bovid interface in Africa is well described in the literature due to its role in the maintenance of many economically important infectious diseases such as FMD (Box 1), while information on diseases circulating between other wild and domestic ruminants species is scarcer (Mahapatra et al. 2015; Wambua et al. 2016).

Short Cycle Species (Pigs and Poultry)

Pigs and poultry are a crucial food source for rural populations in Africa due to their fast growth, quick turnover, and prolificacy. They both play very important roles in Africa by improving food security, reducing poverty, and providing employment.

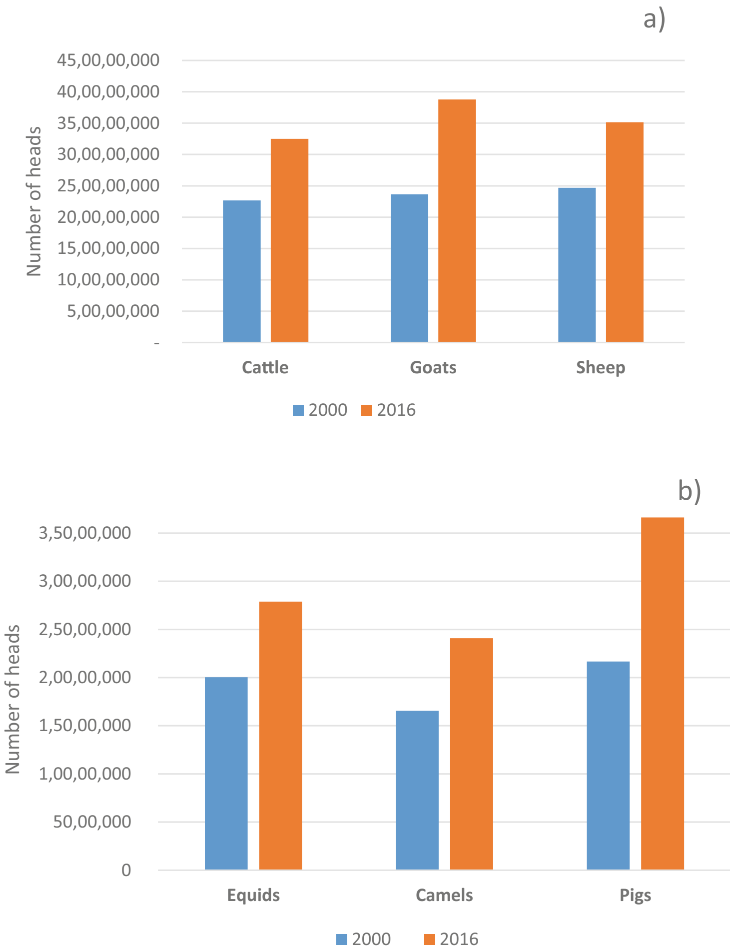

Fig. 3 Trend of the total numbers of live domestic mammals in the African continent since the beginning of the twenty-first century until 2016: (**a**) Ruminant species and (**b**) Non-ruminant species. (Source: FAOSTAT)

The Avian Interface

Chickens are the most numerous of all domestic animals raised in Africa. The vast majority of rural households keep chickens or other poultry species as a way to provide income, cheap proteins, or gifts for friends and families (Guèye 2000). Additionally, some countries such as South Africa, Egypt, Nigeria, or Ghana have developed modern poultry value chains for meat and eggs production.

Poultry production systems are classified into four categories (or sectors) based on the level of integration of operations, the level of biosecurity, and the type of marketing system. The category corresponding to village or backyard production

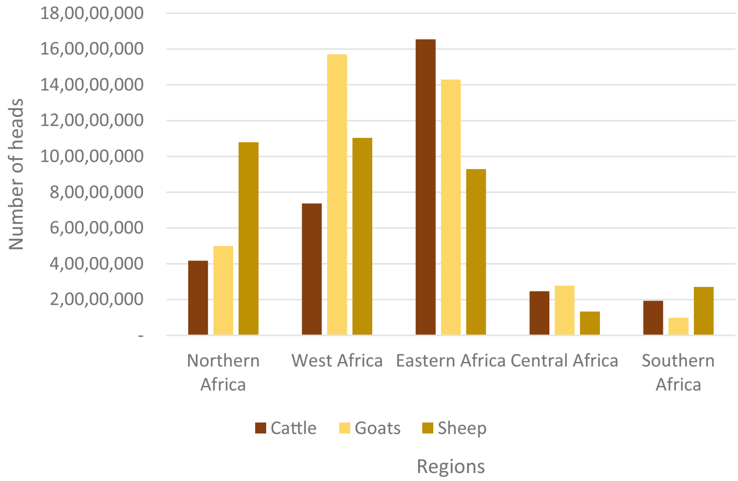

Fig. 4 Distribution of domestic ruminants per region in the African continent in 2016. Source: FAOSTAT (http://www.fao.org/faostat)

systems, with minimal biosecurity, is largely predominant in sub-Saharan Africa where it represents between 70 and 99% of the national poultry flock in most countries. This lack of biosecurity is characterized by free-roaming of poultry flocks and possible contacts with other animals including wild birds, which may have large consequences in terms of flock vulnerability to infectious diseases such as avian influenza (Box 1) or Newcastle disease (Molia et al. 2015). Transmission of other avian diseases is poorly covered by the research.

The Pig Interface

Although in lower figures than other domestic animals, pig numbers are growing steadily and have more than doubled in the last three decades, to supply meat to expanding urban markets. Current pig figures are estimated at 36.6 million heads (Fig. 3) mostly concentrated in Nigeria, South Africa, Mozambique, and Uganda. Despite being negligible in Northern Africa due to religious considerations, some West African predominantly Muslim countries (Senegal, Mali, or Burkina Faso) host large numbers of pigs kept by animist or Christian populations. The sector is characterized by (1) a high proportion of traditional, small scale, subsistence farmers mainly localized in rural areas, (2) a large-scale intensive pig farming mostly located in peri-urban areas to access the market of major cities, and (3) a whole range of production systems between those two extremes (Penrith et al. 2013). Interactions with wild suids can occur under traditional free-ranging domestic systems. Some studies suggest that direct contact between domestic pigs and warthogs is rare. However, serious shared diseases (ASF or AAT) are mostly transmitted by vectors such as argasid ticks or tsetse flies (Kukielka et al. 2016). Conversely, direct

Fig. 5 Wildlife tourism generates new opportunities for close encounters between African mammals such as banded mongooses (left), nonhuman primates (center) or antelopes (right), and human populations, and allowing for potential pathogen transmission on both directions. (Photos: Ferran Jori)

interactions between domestic pigs and bushpigs are suspected in different African areas. However, the nature of those interactions and the importance of other potential shared pathogens remain unknown (Jori et al. 2017).

Table 1 Summary of identified interfaces between phylogenetically close wild and domestic species

Identified interface	Area/Region	Specific/Major diseases at the interface	References
Wild-domestic carnivores	East Africa Zambia, Ethiopia	Distemper	Berentsen et al. (2013), Gordon et al. (2015)
	Tanzania	Rabies	Lembo et al. (2008), Sillero-Zubiri et al. (2016)
	East Africa	Babesiosis	Dybas (2009)
	Zambia	Canine parvovirus	Berentsen et al. (2013)
	East Africa Botswana	Feline immunodeficiency virus	Roelke et al. (2009)
Wild-domestic Bovids	Botswana	Brucellosis	Alexander et al. (2012)
	South Africa Zimbabwe Zambia Tanzania	Bovine tuberculosis	Hlokwe et al. (2016)
	Southern Africa	Foot and mouth disease	Brito et al. (2016), Jori et al. (2009)
	Southern Africa Eastern Africa	Tick-borne diseases	Van der Bosche et al. (2010) Espinaze et al. (2018)
	Southern and Eastern Africa	Malignant catarrhal fever	Swai et al. (2013), Wambua et al. (2016)
	Eastern Africa Southern Africa	Bovine Trypanosomiasis	Anderson et al. (2011) Auty et al. (2012)
Wild and domestic equids	Southern Africa	African horse sickness	Gordon et al. (2013)
Wild domestic pigs	Mozambique	African swine fever virus	Quembo et al. (2016)
		Trypanosoma spp	Anderson et al. (2011), Jori et al. (2017)
		Trichinella spp.	Jori et al. (2017)
Wild domestic birds	South Africa Mali	Avian influenza	Abolnik et al. (2016)
		Newcastle disease	Molia et al. (2015)
Small ruminant interface	Kenya	RVF	Lembo et al. (2013)
	Zimbabwe	Anthrax	Mwakapeje et al. (2018)

The Carnivore Interface

A wide diversity of small and large wild carnivore species share savannah and forest ecosystems in Africa. With the encroachment of wildlife habitats, new ecologic landscapes dominated by human activities with an increased presence of domestic dogs and cats facilitate interactions between wild and domestic carnivores and the circulation of a diversity of pathogens (Table 1). Studies on pathogens among domestic dogs at the carnivore interface are more common than for cats. Some retrospective studies in the selected shared ecosystem, suggest that the dynamics of those pathogens at the interface are variable, depending on the geographical location, the available wild and domestic carnivore population density and distribution (Gordon et al. 2015; Lembo et al. 2008). Theoretically, implementation of control measures such as vaccination or deworming can reduce the circulation of pathogens in domestic carnivores at the interface. However, in practice, dogs and cats in rural African communities rarely receive veterinary attention from their owners.

The Equine Interface

There are almost 28 million domestic equids in Africa, mostly located in East and West Africa. African horse sickness is transmitted by arthropods and does not require direct contact between wild and domestic species. Information on other shared diseases is limited (Horak et al. 2017). Direct interactions between domestic equids (donkeys, horses, and mules) and zebras (*Equus* spp.) are described and biologically possible, although in natural conditions, they are limited. The expansion of game farms in Southern Africa can increase the availability of virus from natural sources. However, vaccination can prevent infection in domestic equids (Gordon et al. 2013). Although occurring outside the African continent, movements of wild equines from Africa to zoological collections in, have triggered the emergence of African horse sickness outbreaks among equine populations of Europe(Sánchez-Matamoros et al. 2016) and more recently in Thailand.

Interface Between Phylogenetically Distant Species

Interactions between species that are not genetically close can also occur when a generalist pathogen circulates in a multi-host ecosystem or in the case of man-driven ecosystem or habitat transformations.

The Multi-Species Interface

In multi-host ecosystems hosting a large diversity of mammals, generalist pathogens find numerous opportunities to cross-species barriers. In Southern or Eastern African mixed grazing systems, domestic and wild mammals are highly connected, facilitating cross-infestation of a diversity of species with common pathogens (Abu Samra et al. 2013; Espinaze et al. 2018). *Mycobacterium bovis* (Hlokwe et al. 2016) in the Kruger National Park affects an increasing range of wild species over the years (Hlokwe et al. 2014) and to a lesser extent, FMD (Box 3) can affect a diversity of ungulates in multi-host African savannah ecosystems (Casey et al. 2014). In Kenya, serological surveillance among wildlife populations after Rift Valley Fever outbreaks provides evidence of exposure of a large community of wild and domestic mammal hosts to the virus (Britch et al. 2013). Environmental contamination of soil or water with some infectious pathogens such as *Bacillus anthracis* can generate outbreaks affecting a diversity of wild and domestic mammals and humans in a diversity of habitats including forest and savannahs (Mwakapeje et al. 2018; Hoffmann et al. 2017).

New Interfaces in Africa

Current patterns of change in the African continent enhance the occurrence of contacts between species of different genera. Living in different ecological niches, phylogenetically distant species have fewer common pathogens because they seldom encounter each other in natural environments. However, man-driven ecological transformations and social changes are facilitating new forms of interaction between wildlife and anthropogenic environments.

The Human-Wildlife Interface

The wildlife-human disease transmission is particularly relevant in sub-Saharan Africa considering the important poverty levels, the abundance of wildlife populations, and diversity of opportunities of interaction between humans and animals with or without the participation of domestic animals (Tables 1, 2 and 3). Pathogen transmission can occur through bushmeat hunting (Fig. 6) (Filippone et al. 2015), game butchering and cooking (Rimoin et al. 2017), collection of carcasses (Monroe et al. 2015), holding wild pets, the practice of certain traditional rituals or medical practices and exposure to bites from hunted species or their arthropod vectors. These opportunities are more common in forested areas where there is less availability of domestic animal protein and the exploitation of wildlife for food is more widespread.

Monitoring zoonotic spillover events dynamics in remote regions can be extremely laborious and challenging. In the case of Ebola, for instance, the natural life cycle of the virus, the role of reservoir species (wild or domestic), and the

Table 2 Cases of multi-species transmission at the wildlife-livestock interface

Rabies	Lembo et al. (2008)
Distemper	Berentsen et al. (2013)
Bovine tuberculosis	Hlokwe et al. (2014, 2016)
Foot and mouth disease	Casey et al. (2014)
Cryptosporidium spp	Abu Samra et al. (2013)
Peste des Petits ruminants	Lembo et al. (2013)
Rift Valley fever	Evans et al. (2008)

Table 3 Cases of pathogen transmission into wildlife populations from humans and livestock in Africa

Wildlife species	Area	Specific pathogen	References
Mongoose	Botswana	*Mycobacterium tuberculosis* *M. mungo*	Flint et al. (2016)
Multi-hosts	South Africa	*Mycobacterium bovis*	Hlokwe et al. (2016)
Mountain Gorilla	Rwanda	Metapneumovirus	Palacios et al. (2011)
African Buffalo	Zimbabwe	FMD virus	Casey et al. (2014), Brito et al. (2016)
Nonhuman primates	South Africa	Cytomegalovirus, hepatitis A virus *Cryptosporidium* spp. *Giardia* spp	Drewe et al. (2012), Odeniran et al. (2018)

interspecies transmission dynamics remain largely unknown. Direct contact of human index cases with some wild animal sources was clearly reported in at least eight Ebola outbreaks, providing some strong indication of zoonotic transmission from wild animal species (Leroy et al. 2005). Similarly, the role of domestic livestock in Ebola virus epidemiology remains unknown. Pigs (*Sus suis*) are the only known domestic animals to be naturally susceptible to Ebola-like viruses, with the ability to transmit them to other pigs as well as to nonhuman primates (Atherstone et al. 2017).

The Camel Interface

Except for national parks situated in arid lands where camel herds (*Camelus dromedarius*) are common, (e.g., Awash National Park in Ethiopia), interactions between camels and wild species are scarce, the density of antelopes in the desert being low, and wild camels' populations (only in Central Asia) almost extinct. However, some global changes affect traditional camel production:

1. Climate change is leading to the expansion of the camel farming systems to southern parts of Sahelian countries (Central African Republic, Uganda, Tanzania, Cameroon, or Senegal) and longer transhumance migration routes.
2. Traditional camel farming systems become more sedentary to be closer to town markets (for camel milk and meat), increasing the interface with peri-urban wild species such as bats or rodents.
3. Increasing regional demand in camel meat generates trade movements of live camels from the Sahel to North Africa and from the Horn of Africa to the Arabian Peninsula (Faye et al. 2012).

Fig. 6 Wildlife interactions in rural areas of Africa are common through hunting or by keeping wildlife as pets: (**a**) Hunters transporting a bush pig (*Potamochoerus larvatus*) in Madagascar (Sophie Molia); (**b**) Village boy playing with a hunted bat in Guinee Conakry (Helene de Nys); (**c**) Cormoran kept as a pet bird in Mali (Sophie Molia)

These changes facilitate new forms of interactions between camels and other domestic or wild species and have the potential to impact on public health and the dissemination of transboundary diseases. For instance, the cohabitation between camels and small ruminants facilitated the emergence of PPR outbreaks in camels in Ethiopia or of the Rift Valley Fever outbreak in Mauritania (Roger et al. 2000). Similarly, it could have contributed to the emergence and spread of MERS-COV in the Middle East (Box 2).

New Interfaces through Different Wildlife Utilization

Any new form of wildlife utilization, consumptive or not, can generate new situations of interaction between wildlife and other hosts. Growing industries based on wildlife such as tourism or game production have increased in the last decades and represent new opportunities for the circulation of pathogens between wildlife and human or domestic animal hosts.

Wildlife Tourism

Every year millions of persons travel to some of the approximately 400 national parks and reserves in Africa to experience a diversity of activities that allow some degree of contact with wildlife species. Tourism contributes more than 8% to the GDP in Namibia, Zimbabwe, and Tanzania, 4–8% to Ethiopia, Kenya, Uganda, Rwanda, and Botswana (UNCTAD 2017). This industry generates new and unprecedented pathways of disease transmission between humans and wildlife (Odeniran et al. 2018). Indeed, repeated exposure of animals to human presence can alter their behavior, cognitive reactions, and immune responses increasing the probability of cross-species transmission between humans and wildlife. There is, for instance, evidence that elephant-back safari camps facilitate the risk of infection of elephants with human strains of *Mycobacterium tuberculosis* and *M. bovis.* Similarly, herds of banded mongooses (*Mungos mungo*) habituated to tourist camps in Southern Africa have become infected with tuberculous mycobacteria from human or domestic animal origin (Flint et al. 2016; Rosen et al. 2018). In addition, safari camps generate closer contacts between humans and habituated nonhuman primates such as baboons (*Papio* spp.) and vervet monkeys (*Chlorocebus pygerythrus*), facilitating the transmission of infectious and parasitic diseases between the two groups (Drewe et al. 2012; Odeniran et al. 2018) which have the capacity to challenge human health and biodiversity conservation.

Wildlife Production. A New Growing Interface

Global changes have enhanced the shortage of animal protein and the need to explore the development of new protein sources. Wildlife production creates new opportunities for interaction between wild species, domestic animals, and humans. In West Africa, the domestication of the greater cane rat (*Thryonomys swiderianus*), an extremely popular large edible rodent (Jori et al. 1995) has allowed the development of several thousands of small-scale farmers. This activity generates a potential new interface between domestic and wild rodents in close contact with humans that have received little scientific attention to date (Fig. 1a).

In Southern Africa, a flourishing wildlife industry based on mixed-ranching of several species of antelopes in private properties has been expanding in the last decade. Since the year 2000, more than 14,000 game ranches are reported, covering an area >200,000 km^2 and harboring between 16 and 20 million wild mammals (Child et al. 2012; Lindsey et al. 2013).

As an example, the extensive nature of ostrich (*Struthio camelus*) production systems in South Africa bears the continual risk of point introductions of avian influenza virus (AIV) from wild birds (Abolnik et al. 2016).

Despite their diversity, different wildlife production initiatives face similar problems. The development of the sector is often faster than the conception of guidelines and legal requirements to regulate its value chain. This situation affects the implementation of surveillance programs and monitoring of animal movements in game farms, which can have a huge impact on the risk of disease emergence and spread among a naïve population. The intensification in the production and the frequent mixing of individuals from different origins for trade or translocation exposes exploited wildlife species to stress and immunosuppression. These factors, together with the lack of availability of performant and validated diagnostic tests limit the capacity to routinely monitor disease in wildlife species (Hlokwe et al. 2016), facilitate the emergence of unsuspected infections such as avian Influenza in ostrich farms (Abolnik et al. 2016), or the emergence of rabies outbreaks in captive kudu (*Tragelaphus strepsiceros*) populations in Namibia (Mansfield et al. 2006; Scott et al. 2013). Poor education of animal handlers on management and handling of the game, lack of quarantine facilities, drug misuse, and poor record keeping can equally have a significant effect on the prevalence of wildlife pathogens in captive wildlife populations.

Problems and Impacts Related to Wildlife-Livestock Coexistence

Human Wildlife Conflicts

Human wildlife conflicts (HWC) are defined as any interaction between humans and wildlife resulting in negative socioeconomic impacts in human communities, the conservation of wildlife populations, or their environment (Madden 2004). HWC usually implies several negative outcomes such as the loss of human and animal lives, crop damage, habitat destruction, predation on livestock, and serious reduction of wildlife populations at the edge of protected areas in Africa or their habitats (Penteriani et al. 2016; Williams et al. 2017). The fact that rural communities living in this context are seldom compensated for socioeconomic losses incurred by wildlife contribute to exacerbate negative perceptions of wildlife among human communities and the perpetuation of HWC. Diseases circulating at the wildlife-livestock interface and affecting livestock such as FMD, act as an additional trigger of HWC.

With human population growth in Africa and the need for land facilitating encroachment into natural areas, we can anticipate an increase in HWC (including disease emergence) in wildlife and livestock populations.

Implications of HWC for Conservation

HWC contribute to generate a negative perception among rural communities cohabitating with wildlife at the edge of protected areas and can jeopardize conservation efforts (Kahler and Gore 2015; Matseketsa et al. 2019). Large African predators such as lions, leopards (*Panthera pardus*) or African wild dogs (*Lycaon pictus*), or cheetahs (*Acinonyx jubatus*) often pay a very serious price to HWC since livestock owners often eliminate raiders. One of the most commonly used practices to achieve this purpose is poisoning, which has a dramatic environmental impact because it can also affect other species. This widespread use of poison represents for instance one of the main causes of drastic vulture declines in Africa together with the use of environmentally toxic veterinary drugs such as diclofenac. Subsequently, this decline in scavenger numbers can have serious impacts on the removal of carcasses from diseased animals and the deterioration of environmental health.

Disease Transmission and Its Implications

Disease transmission is considered as another form of HWC. In many instances, outbreaks of diseases of wildlife origin among livestock populations from rural communities living at the edge of protected areas can jeopardize the peaceful cohabitation between wildlife and livestock interests in Southern or East Africa (Swai et al. 2013; Thomson et al. 2013; Wambua et al. 2016). Scientific research has abundantly covered some diseases at this interface in Africa in the last few years (avian influenza, rabies or FMD, or BTB). However, the list of diseases has increased in the last decades (Tables 1, 2, and 3) as wild and anthropic ecosystems become more intermingled. The majority of them are poorly investigated despite their suspected impact on domestic animals, public health, and the conservation of wild species.

Implications of Disease Transmission for Human, Domestic Animal, and Wildlife Health

Except for some specific animal diseases, the impact of diseases circulating at the interface with livestock is seldom quantified and, in many cases, completely unknown. In any case, it clearly goes beyond morbidity and mortality in livestock and has numerous socioeconomic implications such as the cost of diagnosis, control, and treatment, loss of man-power, negative social and psychological status, and indirect effects to commercial markets (Knight-Jones and Rushton 2013). The impact is even higher if we take into consideration the public health perspective of zoonotic diseases (Welburn et al. 2015). In the case of Africa, the widespread circulation of HIV increases the vulnerability of human populations to many wildlife-borne zoonotic infections.

As seen earlier with several examples, increasing proximity between domestic and wild hosts also puts wildlife populations at risk of disease outbreaks. Over a quarter of domestic mammal pathogens are infectious to wildlife species and their spillover to natural ecosystems can have variable levels of impact on wildlife populations (Cleaveland et al. 2001). There is evidence of transmission of bovine tuberculosis, brucellosis, or FMD from livestock to wildlife populations in Southern and East African ecosystems. The introduction of bovine tuberculosis in African rangelands has generated a chronic devastating impact in a diversity of wild species sharing the same environment (Hlokwe et al. 2016). Great apes such as the endangered mountain gorilla or some chimpanzee populations are highly susceptible to respiratory pathogens carried by humans such as human metapneumoviruses, human respiratory syncytial viruses, and *Streptococcus pneumoniae*, being able to cause high morbidity and mortality rates in great ape populations (Calvignac-Spencer et al. 2012; Köndgen et al. 2017; Palacios et al. 2011).

Management Practices to Reduce the Risk of Disease Transmission at the Interface

Adequate management practices to prevent disease spread at the wildlife-domestic animal-human interface are crucial.

Fencing and Zoning

One proposed solution to protect both people and wildlife from the negative outcomes of HWC is the physical separation of both populations through the erection of fences. However, there are numerous social, economic, and conservation drawbacks to fencing large areas In dryland ecosystems, fences prevent the mobility of animal populations and can have very serious ecological impacts on migratory species such as zebra and wildebeest (Durant et al. 2015). Historically, fences started to be erected in South Africa in the 1950s in order to separate livestock from wildlife, once it became scientifically evident that the African buffalo represented a wild reservoir of Foot and Mouth Disease (Jori et al. 2009; Thomson et al. 2003).

During the 1980s, South Africa started establishing disease-free areas based on the guidelines of the World Animal Health Organization (OIE), in order to be able to export livestock and beef commodities from areas where FMD had been eradicated (Thomson et al. 2013). These FMD-free zones were achieved through the use of fences to separate livestock from infected wildlife, repeated annual vaccination of livestock herds, and strict control in animal movements. This approach, known as commodity-based trade, successfully increased beef exports from South Africa and was subsequently adopted by other exporting countries in the region such as Namibia, Botswana, or Zimbabwe. However, fences are more than just physical barriers. Despite having a significant ecological impact on the migrant population of wild herbivores, they also influence economic growth and development enhancing social and economic discrimination between disease-free exporting areas and infected areas where rural communities are unable to export and sell their livestock at competitive prices (Naziri et al. 2015).

Control in Targeted Hosts

In general, the control of pathogens is rarely implemented in free-ranging wildlife populations, with the exception of valuable animals in game ranches or the case of extremely endangered wildlife populations such as the Ethiopian wolves (Sillero-Zubiri et al. 2016). In other circumstances, wildlife-borne infectious and parasitic diseases are controlled through vaccination or control measures implemented in human or livestock populations. Treatment of livestock with acaricides is recommended to prevent tick-borne diseases at the edge of protected areas (Espinaze et al. 2018). Dog vaccination is the strategy of choice to prevent rabies cases in domestic carnivores and humans (Lembo et al. 2008) and the vaccination of ruminant populations is common to prevent the spread of outbreaks of Rinderpest, Rift Valley Fever or FMD in East or Southern Africa (Jori et al. 2009; Roeder et al. 2013).

Surveillance at the Interface

In Africa, active surveillance of wildlife populations takes place in exceptional situations because it often requires expensive equipment and specialized expertise, which is only available in a few selected countries in Southern and East Africa where the wildlife sector contributes substantially to national economies (Fig. 7). In the majority of African countries, funds to monitor disease in wildlife are very limited and passive surveillance approaches are the method of choice. They often involve the participation of local communities or staff working in wildlife departments or protected areas. A common approach is the collection and analysis of wildlife carcasses found in natural habitats (Lembo et al. 2008). The availability of mobile phone technologies in recent years helps to overcome the constraints of poor physical infrastructure by real-time transmission of field observations such as unexpected mortalities or reports of carcass findings (Karimuribo et al. 2017).

In countries where wildlife management and capture expertise is lacking, cooperation with hunters for the collection of animal samples in bushmeat networks (Fig. 1) can be a cheaper way to collect wildlife specimens (Ravaomanana et al. 2011). However, one should be cautious in avoiding incentives for hunting, which would be legally and ethically questionable. The collection and conservation of samples in remote areas is nowadays easier with filter papers (Picard-Meyer et al. 2007; Smit et al. 2014). However, this approach is only suitable for the detection of certain pathogens and the availability of validated tests for disease detection in wildlife samples remains a major constraint for wildlife surveillance (Hlokwe et al. 2014; Jori et al. 2014).

In order to prevent the introduction of pathogens into new territories, a comprehensive risk analysis approach should be implemented before any translocation or relocation of animals for wildlife management or game farming purposes (Hartley and Sainsbury 2017).

In case of new emerging outbreaks, genomic technologies based on new generation sequencing can rapidly identify new viruses and pathogens in the most remote areas on the planet and facilitate the identification of reservoir species and the pathogen dynamics among different host populations (Gardy and Loman 2017).

Fig. 7 Wildlife management skills lack in the majority of African countries. High wildlife management and capture skills are very efficient to monitor the health of wildlife populations. However, they are only available in a minority of countries in East and West Africa, where the wildlife industry contributes substantially to the national economies. The large majority of African countries lack this kind of expertise, which is out of their financial reach. Innovative and cheaper ways to obtain wildlife health information are needed (Photos: Ferran Jori)

Raising Awareness among Exposed Stakeholders

Awareness among stakeholders about risk practices and their mitigation is a useful approach to prevent the transmission of wildlife pathogens to livestock. The risk of African swine fever in Southern Africa is highly associated with free-ranging pigs interacting with the soft tick in warthog habitats. To prevent infection of domestic pigs by infected tick bites, important efforts are deployed to raise awareness about the importance of increasing biosecurity in pig farms (Penrith et al. 2013). This practice has the advantage to reduce the transmission of other zoonotic diseases such as trichinellosis or hydatidosis.

In another context, awareness about the importance of global health and the potential health risks related to different types of interaction with wildlife within protected areas, tourist camps, exposed rural communities and different sectors of the wildlife industry is instrumental to facilitate proper surveillance, reporting, and implementation of preventive measures among the exposed human population (Jori et al. 2014).

Future Directions for Improving Health Management at the Wildlife-Livestock-Human Interface

Community Based Natural Resource Management (CBNRM) projects in Africa promote the integration of conservation of natural resources with rural development by empowering communities in their right to use and manage their natural resources and wildlife populations. The benefits from wildlife-based activities (tourism or sport hunting) are reinvested in community development activities. This approach, which promotes the concept that rural communities will protect wildlife if they can benefit from it, has met some success in Southern African countries like Namibia and Zimbabwe (Lindsey et al. 2009, 2013).

The concept of commodity-based trade is based on the principle that beef commodities that follow certain manufacturing procedures such as deboning, removing the lymph nodes, maturing, or heating meat beef products reduce to negligible the probability of spreading FMD through beef products trade (Thomson et al. 2013). Wildlife conservation organizations have promoted the implementation of this approach in the Southern Africa Development Community (SADC)region as a way to facilitate the trade of beef products originating from rural communities living at the edge of protected areas, and therefore potentially infected with FMD virus through their contacts with wildlife-infected species. Indeed, the development of such trade has the potential to improve benefits derived from rural livestock production, attenuating the conflict derived from cohabitation between wildlife and livestock (Thomson et al. 2013). However, in practice, the socioeconomic and technical feasibility of this approach requires demonstrative data through several pilot projects, and this is a long-term on-going process that will only yield results in a few years.

Conclusion

Africa is the last place on Earth with a significant presence and variety of large mammals and has extraordinary levels of biodiversity. Nevertheless, the continent is transforming quickly, and these changes generate a huge biodiversity loss and threaten nature's contribution to human livelihoods. The drivers of change in the African continent are all on the rise and we can anticipate an exponential growth of interactions between wildlife, livestock, and people, with serious implications in the level of conflict and in disease emerging events. In this confrontation, wildlife is likely to pay a heavy tribute in terms of species conservation, if no action is taken to highlight the potential value of wildlife and ecosystem services to improve human livelihoods and empower local rural economies. New formulas and approaches to promote cohabitation and resilience between natural ecosystems and farming systems, need to be tested and successes disseminated at national, regional, and continental levels to promote new ways of acting and thinking. In that sense, initiatives that have met some levels of success in increasing benefits from wildlife for local rural communities should be monitored, assessed, and disseminated (Lindsey et al. 2009; Thomson et al. 2013).

From the disease perspective, zoonotic pathogens from wildlife origin are more likely to emerge from forested areas while transboundary animal disease events are more likely to come from interactions between livestock, humans, and wildlife in savannah areas. However, the risk of unexpected events resulting from new wildlife use activities should not be underestimated. Mitigating the risk of emergence and increasing protection against pathogens requires research for understanding disease transmission dynamics. The use of high technologies such as new generation genetics, geomatics, and new diagnostic techniques can provide some specific epidemiological answers. However, sophisticated expensive technologies that most countries will not be able to apply are not necessarily sustainable solutions at the large scale. Surveillance and prevention methods need to be technically simple, have a limited cost, and be accompanied by awareness and capacity building campaigns. They also need to be adapted to the new types of wildlife interface developing in Africa.

The concept of the interface in all its dimensions is complex and susceptible to change together with the evolution of African landscapes. In that sense, capacity building in wildlife health and management, sustainable use of wildlife, and new paradigms of system thinking applied to health management such as the concept of One Health or Ecohealth are instrumental to expose young generations to new ideas, change perceptions, and design and experiment new practical solutions. There is a growing need for investigating new methods to facilitate the integration of different disciplines in order to improve the understanding of complex socio-ecosystems which require multiple and diverse disciplines and solutions.

Box 1 Avian Influenza in Africa

Avian influenza has had a large negative socioeconomic impact in Africa. The arrival of highly pathogenic avian influenza (HPAI) virus type H5N1 in 2006 and its subsequent spread to 17 countries has caused the loss of hundreds of millions of poultry, either by death or culling, and has killed 122 humans mainly in Egypt (Ekong et al. 2018). Outbreaks of HPAI virus H5N2 in 2004, 2006, and 2011 in South Africa have also been very detrimental with up to 10% of the country's domestic ostrich population being lost (van Helden et al. 2016).

The interface between domestic and wild birds has played a key role in the propagation of avian influenza. AI viruses find periodically their way in Africa via wild birds migrating from Eurasian regions. They then circulate among populations of wild birds and are transmitted to domestic fowl by direct contact or through the contamination of surface water, river muds, and wetland banks (Gaidet and Caron 2016). A wild bird origin of HPAI strains causing outbreaks in domestic birds has been demonstrated in Nigeria and South Africa by molecular phylogenotyping (Abolnik et al. 2016). Similarly in Egypt, a migratory common teal (*Anas crecca*) sampled in the Nile delta was found infected with a H5N1virus, closely related to the parent of the group of viruses responsible for subsequent outbreaks in poultry and humans (Saad et al. 2007).

Further spread within or among countries is then largely due to trade, both legal and illegal, of poultry and poultry products as well as to the limited biosecurity of the traditional poultry breeding systems in Africa (Van den Berg 2009). In Africa, the biosecurity of small-scale poultry is unlikely to improve in the short term because its popularity is based on its very limited inputs in terms of food and facilities. To prevent cases of HPAI in humans, it is necessary to rapidly control outbreaks in poultry and to raise awareness among stakeholders (poultry farmers, collectors, market sellers, and consumers) about risk mitigation measures. These include sourcing poultry from outbreak-free areas, avoiding close cohabitation of humans and poultry, and wearing personal protective equipment (gloves, masks) when handling domestic fowl and poultry products (Van Kerkhove et al. 2011).

Box 2 Mers-CoV Emergence Could Be the Result of an Unexpected Wildlife-Livestock Interface

The MERS-coronavirus was described for the first time in a man in Saudi Arabia in June 2012 and subsequently in many other countries, mostly in the Middle East (Gossner et al. 2016). By the end of 2017, 2102 human cases of MERS-CoV including 733 fatalities were confirmed. Camels and bats were suspected as the main reservoirs of this new coronavirus. The bats are at the origin of many diseases and different investigations showed that 5.3–24.9% of the bats were positive to MERS-CoV. However, the bats existing in Saudi Arabia belong to other species than those tested, and finally, it was concluded that MERS-CoV was not transmitted through bats (Memish et al. 2013). Camels were found serologically positive to MERS-CoV in almost 100% of samples from the Middle East, confirming the wide circulation of the virus among the camel population, but without clear clinical expression of the disease. It was concluded that camels could act as a reservoir of the virus, especially in North Africa and the Middle East where camel farming is culturally important. The incidence of MERS-CoV in humans was 15 times higher in camel shepherds and 23 times higher in camel slaughterhouse workers than in the general population (Al-Osail and Al-Wazzah 2017). The MERS-Cov isolated in camel was identical to the human CoV while MERS-CoV does not infect other domestic species, including Bactrian camel and small camelids (Miguel et al. 2016). However, despite the high seroprevalence observed in camel populations from North Africa (up to 100%) for more than 30 years, no camel-human transmission case has been demonstrated to date. This data suggests that the transmission of the virus from camel to human is unclear and the role of other small mammals (rodents) deserves further investigation.

Box 3 The Different Sides of FMD at the Wildlife-Livestock Interphase in Africa

Foot and Mouth Disease (FMD) affects over 70 species of domestic and wild cloven-hoofed animals and is caused by an RNA virus from the family *Picornaviridae* that exists as seven serotypes (O, A, C, Asia 1, SAT1, SAT2, and SAT3). FMD is one of the most feared transboundary animal diseases, it is highly contagious and can survive sub-clinically for several years in persistently infected animals called "carriers." In Southern African beef exporting countries, FMD is mitigated in livestock populations and the African buffalo is considered the major ancestral maintenance host of SAT serotypes. Other wild ungulates only act as spillover hosts rather than

(continued)

Box 3 (continued)
maintenance populations and occasionally, high-density impala populations are involved as intermediate hosts between buffalo and cattle (Vosloo et al. 2009) Experimental evidence of FMD transmission from buffalo to cattle is lacking, however, it has been repeatedly demonstrated by field data and molecular phylogenetics (Bastos et al. 2003; Vosloo et al. 2006). East Africa, encompasses the highest numbers of wild ruminant and livestock populations in the continent, harboring a large continuum pool of wild and domestic susceptible hosts, rich in potential interactions between buffalo, other wildlife, and livestock species (Casey et al. 2014). In West and Central Africa, the wildlife-livestock interface has received very little attention to date. Recent investigations show that some African buffalo populations are infected with SAT1, SAT2, A, and O (Di Nardo et al. 2015). Their capacity to act as a reservoir of FMD for cattle requires further investigation, although it is probably circumscribed, to those few regions where viable buffalo populations are maintained.

Overall, the prospects of immunological control of the disease in sub-Saharan Africa are extremely challenging. Current vaccines for SAT viruses produce short-term immunity (often less than 6 months), are not cross-protective and thermosensitive. In Southern Africa, traditional methods of control such as veterinary fences are confronted by the development of Transfrontier Conservation Areas, which facilitate animal movements and wildlife-livestock interactions (Jori and Etter 2016). In East Africa, the broad spectrum of wild and domestic hosts and large and scale of animal movements creates an ideal scene for the emergence of a diversity of strains (Casey et al. 2014). In this context, non-geographic approaches of FMD control such as commodity-based trade, have the potential to provide access to beef African producers and allow a more balanced cohabitation between conservation and livestock development interests (Thomson et al. 2013).

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