The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health

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Contents

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Introduction

The past decades have been marked by infectious disease pandemics in humans and livestock whose origins were traced back to wildlife hosts (Cunningham et al. 2017; Jones et al. 2008) in areas where wildlife interacts directly or indirectly with domestic animals and humans: the “wildlife-livestock-human interface” areas. Wildlife reservoirs harbored microbial organisms or parasites that were mostly commensals or non-pathogenic in the wild reservoir species but became pathogenic for domestic species and eventually humans. Some of these organisms adapted to human hosts by chance through secondary epidemiological cycles via vectors or bridge species such as domesticated animals or peridomestic wildlife (i.e., living in and around human habitations), and now circulate among humans (see hereafter the definition and discussions for pathogen spill-over/spill-back events). Direct infection by pathogens from animals to humans (zoonosis) is a relatively rare event, and the proportion coming directly from wildlife is even more exceptional. However, when it occurs, it can be very serious as dramatically illustrated by the COVID-19 pandemic. Previous recent pandemics also had devastating impacts, claiming numerous lives and shaking entire communities, such as the Ebola outbreak that occurred in West Africa from 2014 to 2016 (Shiwani et al. 2017), which is presumed to originate from a wildlife reservoir (Coltart et al. 2017), possibly frugivorous bats (Leroy et al. 2005; Pourrut et al. 2005).

Infection of humans from wildlife has historically been related to occupational hazards, such as bushmeat hunting or consumption for Ebola virus on exposure to bat excreta through agricultural practices for Nipah virus. Pathogen spill-over seems to be associated with long-term practices that provide opportunity for the establishment and spread of infection in human communities through changing human landscapes and contact networks. What is more, anthropogenic impacts on ecological systems largely dictate the risk of spill-over and spread at the interface between humans and animals (Hassell et al. 2017). Biodiversity losses that affect pathogen maintenance and spill-over at wildlife-livestock-human interface often result from anthropogenic interventions (Keesing et al. 2006; Morand et al. 2014a). Changes in agricultural practices, domestic animal husbandry infrastructures, especially transportation networks, and artificial habitats as well as specific stressors, such as climate change, play important roles in triggering pathogen spill-overs at wildlife-livestock-human interfaces. The emergence of diseases in humans and domestic animals is therefore often linked to anthropogenic alterations of the structure of landscapes and species communities (e.g., Lambin et al. 2010). Current evidence also indicates that the same drivers are also responsible for the emergence of disease in wildlife, mostly due to direct exposure to domestic sources of infection and exposure to a wild source via human intervention such as the translocation of hosts (Tompkins et al. 2015).

The efficient management of epidemic events requires early detection and control of outbreaks where the initial transmission events occur, at the wildlife-livestock interface. The precise mechanisms and pathways of emergence of pathogens in humans and domestic animals from wild organisms are still poorly understood except in some well-studied cases such as Yellow Fever. Each emergence appears as an idiosyncratic event (Caron et al. 2012). The current reductionist approaches adopted to analyze the mechanisms at stake are unlikely to provide holistic and generic insights, because they only focus on parts of the system and fail to encompass all the complex interactions of very different nature (ecological, evolutionary, sociocultural) that are at play among wildlife, livestock, and humans in order to generate a "successful" disease emergence (Plowright et al. 2017). Mass pathogen discovery from wildlife species around the globe (Morse et al. 2012) will certainly lead to the discovery of "new" pathogens, the immense majority of which do not, and will probably never, represent a threat to humans, livestock, or even wildlife from which they originate. Even focusing on the "usual culprit" bat reservoir (Han et al. 2015) is of little predictive value for future emergence, unless we adopt a fully integrated approach to understand the infection dynamics within the hosts and the impacts of humans on the environment that change the likelihood for virus spill-over (Plowright et al. 2017; Smith and Wang 2013). Large-scale retrospective analysis of disease emergence events over the past decades highlighted regions of the world that have been disproportionally hit by disease emergence (e.g., "hotspots" (Jones et al. 2008)). They listed a number of correlative variables potentially associated with these greater odds of emergence, but this cannot be truly representative of all situations even if corrected for bias. Indeed, we are still far from understanding the mechanisms at stake and forecasting the next pandemic of emerging diseases will require more integrative social-ecological-evolutionary studies focusing on where the initial transmission events occur, the wildlife-livestock interface.

The transmission of pathogens from a wildlife source to domestic hosts involves complex mechanisms operating within diverse ecological communities, which are best analyzed through an ecological lens. Disease ecology is the study of host–pathogen interactions within the context of their environment and evolution. It is concerned with how interactions between species and with the abiotic components of their environment affect patterns and processes of infectious diseases. Several books are now considered as landmarks of the theoretical and empirical developments associating ecology and epidemiology in order to study and manage diseases in wildlife-livestock interface systems. Grenfell and Dobson (1995) offered the foundations for the ecological approach of infectious diseases in natural populations. Collinge and Ray (2006) proposed a community epidemiology perspective of disease transmission between wildlife and livestock. Disease–ecosystem relationships analyzed in Ostfeld et al. (2010) encompass both the role played by parasites in ecosystems, and vice versa. They have paved the way for further applications of ecological theories to disease management and policies. Since then, the emerging discipline of disease ecology has continued to develop, integrating different ecological perspectives: spatial and landscape, functional, community, evolutionary, and molecular ecology. Simultaneously, the human component of wildlife-livestock interfaces has received increasing attention. As we have entered the Era of Human-Induced Diseases (Chaber 2017), it is increasingly acknowledged that human activities (e.g., agricultural, industrial, recreational, and conservation) are largely shaping these interfaces, as will be illustrated below.

Local, regional, and even global processes affect the community of hosts composing the wildlife-livestock interface and their network of interactions, both of which impact pathogen transmission and persistence. The ecology of disease transmission at the wildlife/livestock interface addresses crucial questions such as (1) the effect of community composition, landscape, and human management on pathogen transmission, regulation, and maintenance at this interface; (2) the ecological interactions among host species and interspecies transmission rates, and (3) the impacts of infectious diseases on host populations, communities, humans ecosystems, and subsequently, sustainable land management and conservation. This chapter reviews the current evidence for pathogen transmission in wildlife-livestock interface areas. We use examples drawn from the experience of the co-authors to illustrate how advances in ecology have improved our ability to analyze the patterns of pathogen transmission among wildlife, livestock, and humans. We then analyze the mechanisms at stake, emphasizing the importance of ecological drivers, such as access to resources, competition, and predation, and the increasing evidence for the importance of anthropogenic drivers, such as agricultural and conservation practices. We conclude by emphasizing the necessity for an integrative socio-ecological approach for research and management of wildlife-livestock interfaces and discuss some opportunities and challenges.

The Transmission of Pathogens at Wildlife-Livestock-Human Interfaces

Direct and indirect interactions may result in the transmission of pathogens from wildlife to livestock, and from livestock to wildlife. The transmission of pathogens from livestock to wildlife, i.e., “spill-over” as defined here following Nugent (2011), or back from wildlife to livestock (i.e., “spill-back”; Nugent 2011) represents a series of epidemiological events at wildlife-livestock interfaces that are difficult to demonstrate empirically. Detecting pathogens in the putative hosts is not sufficient, as the epidemiological evidence for spill-over and spill-back should document the temporal sequence of infections: presence in initial host, subsequent transmission to the spill-over host, and transmission back to the initial host. This requires diagnostic and analytic tools that have been only recently available (e.g., phylogenetics) and in the absence of routine surveillance data for poorly known (wildlife) species, most spill-over events remain undetected, and even when they are, it is rarely possible to determine accurately when they have happened (Voyles et al. 2015). This section reviews and illustrates with several examples the epidemiological evidence for pathogen spill-over between wildlife-livestock and livestock-wildlife, and to/from humans.

Wildlife-to-Livestock

Historically, protecting livestock from wildlife diseases has been used as a prime justification for confining and extirpating wildlife reservoirs from rangelands that they shared with livestock. For instance, the control of trypanosomosis in Southern Africa during the first half of the twentieth century resulted in the culling of over one million wild ungulates, most of them in vain from an epidemiological point of view as they belonged to species such as the African Elephant (*Loxodonta africana*), Sable Antelope (*Hippotragus niger*), or Common Ostrich (*Struthio camelus*) that do not play a significant role in maintaining the parasite (Matthiessen and Douthwaite 1985).

However, there are a number of well-documented cases for which wildlife populations have been demonstrated to act as maintenance hosts (sensu Haydon et al. 2002) of diseases affecting livestock (Bengis et al. 2002). Foot-and-mouth disease (FMD) provides an appropriate model to illustrate the complexity and the need for integrated ecological studies at wildlife-livestock interfaces mainly in Southern Africa (Brahmbhatt et al. 2012). This disease has important economic impacts and constrains exporting countries to implement massive control programs (e.g., through culling or vaccination (Paton et al. 2009). It is widespread worldwide and has been earmarked by the World Organization for Animal Health (OIE) as a target for eradication from the globe.

In Africa, several strains of FMD virus are circulating within a community of host species, including African buffalo *(Syncerus caffer),* impala *(Aepyceros melampus),* greater kudu (*Tragelaphus strepsiceros)*, common warthog *(Phacochoerus africanus),* cattle (*Bos taurus* and *Bos indicus*), and small domestic ruminants. All can be involved in the circulation of FMD (Lefèvre et al. 2010). The respective roles and relative importance of each species in a system associating wildlife and livestock are difficult to quantify and disentangle. The African buffalo is assumed to be the natural reservoir of the virus, as it can be infected without apparent symptoms and maintain the virus within populations, whereas cattle can also maintain the virus, and develop clinical signs including mouth ulcers and foot wounds and a decrease in milk production (OIE 2009). However, because the host communities include very diverse species and wildlife-livestock interactions are very complex and dynamic, several aspects of FMD in interface areas in Africa still remain unclear (seasonal dynamics, strains circulating, virulence according to the inter-specific contacts) (Miguel 2012; Tekleghiorghis et al. 2016).

In 2010–2011, a study was carried out in Zimbabwe at different interfaces to quantify the frequency of contacts between African buffalo and cattle (Miguel et al. 2013) in relation to the availability of natural resources (vegetation and water), anthropogenic activities (crop fields and settlements) (Miguel 2012) and predation pressure (Miguel et al. 2017b). A total of 36 GPS collars were deployed on African buffalo and cattle at 3 sites to assess contact patterns at the periphery of 3 protected areas in Zimbabwe. Simultaneously, a longitudinal survey of 300 cattle with five repeated sampling sessions on known individuals during 16 months was undertaken.

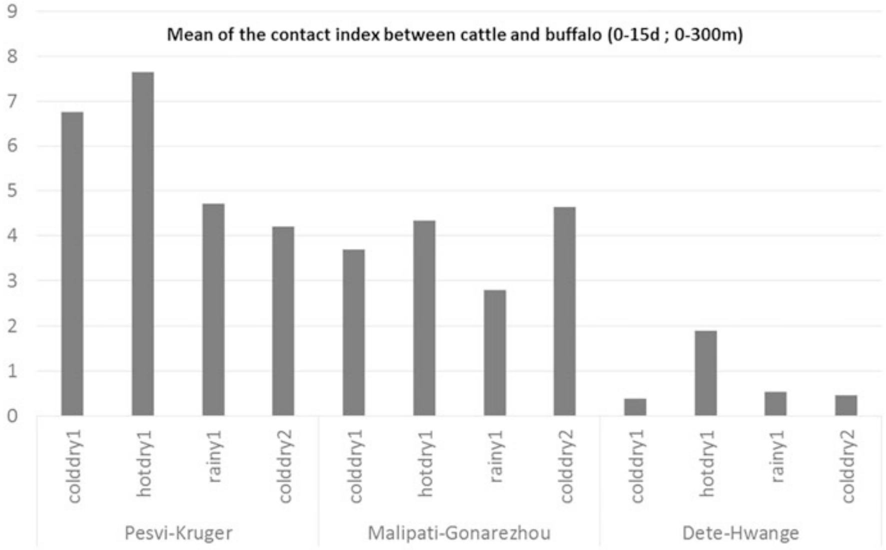


Fig. 1 Seasonal variations in indirect contact rates between African buffalo and cattle in three different interfaces between rural/protected areas in Zimbabwe. Potentially infective contacts were defined when a cattle location was recorded within 300 m of a buffalo location and less than 15 days after the buffalo location had been recorded. More details in Miguel et al. (2013)

Immunological assays (ELISAs), that allowed tracking the production of antibodies following infection or vaccination, were used to assess serological transitions (i.e., incidence and reversion) in the surveyed cattle.

Simultaneous GPS tracking of sympatric cattle and buffalo revealed significant differences in contact patterns across areas (Fig. 1). Although the permeability of the boundaries was similar in the 3 interface sites (unfenced or extensively damaged fence) and the animal densities almost equivalent (Miguel 2012), very different contact rates were observed in terms of frequency. However, the seasonal patterns of contacts were similar among sites with the lowest contacts during the rainy season, and usually reaching a maximum during the hot (or cold) -dry season. This seasonality suggests that contacts between cattle and buffalo are driven by resource availability, as will be explored further in paragraph 3.3.

The results also demonstrated that the probability of cattle FMD serological incidence (antibodies acquisition) was positively associated to the frequency of contacts with buffalos (Fig. 2). On the contrary, serological reversion (i.e., loss of antibodies) was negatively associated to the frequency of buffalo–cattle contacts (Fig. 1b). As direct contacts (i.e., at the same time, at the same place) were almost never recorded, the results suggest that the survival of FMD viruses in the environment is high enough for delayed contacts to generate virus spill-over from buffalo to cattle, or that transmission occurred by unrecorded individuals and/or species. Furthermore, in spite of strong serological evidence for infection events, no clinical signs for FMD were detected in the monitored cattle populations during the course of

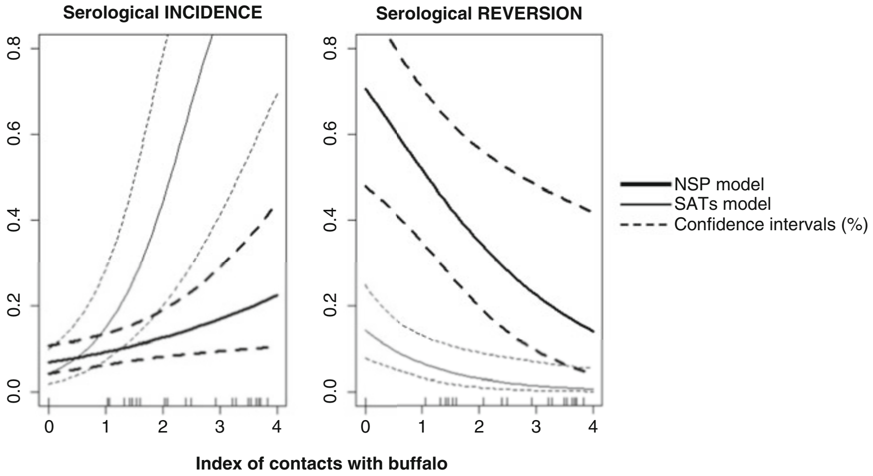


Fig. 2 Serological incidence and reversion probabilities of foot and mouth antibodies in cattle populations depending on the buffalo–cattle contact rate. Non Structural Proteins (NSP) for "natural antibodies" and SATs (South African Territories) for "natural" and "vaccinal" antibodies. The lines at the bottom of the figure represent the data used from GPS devices to estimate the index of contact among cattle and buffalo (For more details see (Miguel et al. 2013)

the study, which tends to support the idea of a silent virus circulation in some areas of southern Africa.

Livestock-to-Wildlife

Until the 1970s, the impact of parasites and pathogens on wildlife populations was largely overlooked (Grenfell and Gulland 1995), and academics, managers, and even the general public perceived wildlife as being resistant to the parasites and pathogens they have coevolved with (de Garine-Wichatitsky et al. 2014). It is only recently that the impact of diseases on biodiversity conservation has been recognized and has gained attention from researchers and conservation organizations (Smith et al. 2009). According to the IUCN Red List of Threatened Species™ (Version 5.2 downloaded 2 March 2018), up to 20.7% of the 1.424 terrestrial mammal species classified as threatened may be impacted to some level by diseases, although Threat Category 8 which accounts for disease risks also includes "invasive and other problematic species." Nevertheless, there is no doubt that interactions between wildlife and livestock are an avenue for pathogen transmission in both directions, and that domesticated animals do also play the role of reservoir for a number of infections that have had significant and detrimental effects on wildlife species, populations, and ecosystems.

Fig. 3 Saiga antelope (*Saiga tatarica*) carcasses after mass mortality event in Kazakhstan in 2017. (photo@ Association for the Conservation of Biodiversity, Kazakhstan, Biosafety Institute, Gvardeskiy RK, Royal Veterinary College, London, UK)

The most well-documented of these are the morbillivirus infections: rinderpest, peste des petits ruminants, and distemper. The first two are pertinent to artiodactyls and food animals. Rinderpest caused massive mortalities in cattle over 5 centuries across Eurasia and in the 19th–20th centuries in Africa. Cattle populations were the maintenance hosts. This occurred alongside colonization and introduction of infected cattle from Eurasia. The Great Pandemic as it was called, spread the virus across the whole continent and entire ecosystems like the Serengeti changed. Key stone species, such as African Buffalo and Blue Wildebeest (*Connochaetes taurinus*) declined, and the removal of bulk grazers from African savannah ecosystems resulted in a dramatic vegetation shift. This change in vegetation composition and structure, and its reversal when the disease was eliminated, have been well documented (Dobson et al. 2011; Holdo et al. 2009). After the eradication of rinderpest, around 2003 (officially declared globally absent in nature in 2011), the less well-known virus Peste des petits ruminants emerged in ruminants and spread widely from West Africa to East and southern Africa. The virus perhaps partly filled the ecological niche emptied by the eradication of rinderpest and eventually spilled from domestic small ruminants into wildlife. To date, it has caused little harm in wildlife in Africa, but in Asia in 2017 it nearly destroyed the last remaining population of the Saiga Antelope (Mongolian subspecies, *Saiga tatarica mongolica)* when over 60% of the remaining 10,000 antelope died (Kock et al. 2018) (Fig. 3). Prior to this event, an effort to eliminate the virus from livestock involved some 11 million vaccinations. But little consideration was given to the risks to wildlife over this period by national or international agencies. This lack of consideration contributed to its spill-over to the saiga antelope as no extra precautions were taken to buffer these populations more intensively.

Livestock-to-Wildlife, and Back?

As discussed earlier, interface areas may lead to the transmission of pathogens and parasites from wildlife to livestock, as documented for several diseases of economic importance a long time ago, and also from livestock to wildlife, which was only acknowledged more recently. This was partly due to technical difficulties in collecting ecological and epidemiological data from free-roaming wild animals. However, despite recent significant methodological and technical advances (molecular ecology, spatial ecology; see Chapter "Collecting data to assess the interactions between livestock and wildlife"), little attention has been given to successive spill-over and spill-back events between sympatric hosts over time.

Bovine tuberculosis (bTB) at the wildlife-livestock interface provides a good case study of this complexity (Fig. 4). First globally, the disease has spread and spilled-

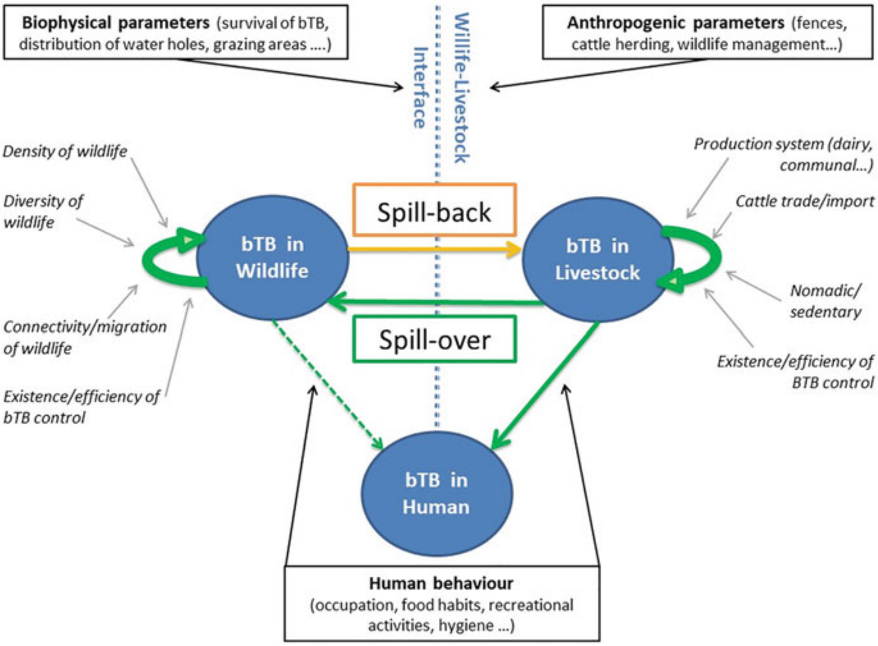


Fig. 4 Biophysical and anthropogenic drivers of bTB spill-over and spill-back across wildlife-livestock interfaces (adapted from de Garine-Wichatitsky et al. 2013c). Green and orange arrows indicate the direction and the width is proportional to the frequency of pathogen transmission (dotted arrow indicates that spill-over from wildlife is suspected but not documented to our knowledge)

over to wildlife through intercontinental cattle movements, mainly using primary and secondary colonial routes (Smith 2011). In southern Africa, the introduction of multiple strains in the ecosystem through cattle importation is a typical example (Michel et al. 2008). The subsequent spread and spill-over to wildlife are not fully understood in the region. However, it is estimated that bTB spilled-over from cattle populations to the buffalo population in Kruger National Park (KNP) in the early 1960s in the southern part of the park, across the unfenced Crocodile River (Bengis et al. 1996; De Vos et al. 2001). The main hypothesis points to a single bTB spill-over event from cattle to buffalo (Michel et al. 2009). Subsequently, the disease spread across the KNP buffalo population and to buffalo populations across countries within the Great Limpopo TransFrontier Conservation Area (Caron et al. 2016; de Garine-Wichatitsky et al. 2010). Until recently, no spill-back events to cattle were detected despite investigations in several cattle populations separated physically or not from infected buffalo populations in South Africa and Zimbabwe (de Garine-Wichatitksy et al. 2013c). However, in 2015, Musoke et al. (2015) reported the first description of bTB in cattle on the periphery of KNP across a hard fence, with a wildlife, mostly probably buffalo strain of bTB, indicating a spill-back event. Buffalo straying from the KNP boundary into the communal land across African elephant- or flood-made breaks in the fence provide a good hypothesis to explain this spill-back event (van Schalkwyk et al. 2016). The pathogen and subsequent disease transmission risk across this wildlife-livestock interface in the Great Limpopo TFCA is, therefore, real both ways and threatens bTB naïve cattle and wildlife populations, notably in Zimbabwe (Caron et al. 2016; Kock et al. 2014).

These two-way exchanges of bTB across wildlife-livestock interfaces have been described in other contexts: Eurasian Badger (*Meles meles*) in England and probably other continental European countries (Payne et al. 2012); Wild Boar (*Sus scrofa*) and Red Deer (*Cervus elaphus*) in Spain (Gortázar et al. 2010); White-tailed Deer (*Odocoileus virginianus*) in the USA (Palmer et al. 2012); brushtail possum in New Zealand (Coleman and Cooke 2001). In each of these cases, it is assumed that bTB was introduced by cattle into wildlife and the subsequent control of bTB in cattle reversed the risk of pathogen transmission across the interface. Gortázar et al. (2010) documented in details the succession of management options taken that led to the current situation in Southern Spain, where bTB is emerging in overabundant wild ungulates and spilling-back into cattle, which could apply in very similar situations for most of continental Europe and North America.

Wildlife-to-Livestock-to-Humans

Following the Nipah, Hendra, and Severe Acute Respiratory Syndrome (SARS) epidemics, and various publications on the subject of zoonoses (Jones et al. 2008), the general public and nonspecialist members of the research and academic world have come to realize that most human pathogens and parasites originate from animals, especially from wildlife in the case of emerging infectious diseases. This was not a surprise for evolutionary biologists, as humans have evolved in proximity to animals for a long time, especially with domestic animals with whom they may exchange pathogens and parasites frequently and through diverse transmission modes (Cleaveland et al. 2001). Morand et al. (2014b) have demonstrated the importance of time since domestication in determining the number of pathogens and parasites that have spilled-over to humans. Humans, of course, engage in direct physical or indirect contact with their livestock in a variety of ways, from husbandry to consumption, providing continuous opportunities for pathogen spill-over. Although such direct and indirect interactions between humans and wildlife are less common, there is circumstantial evidence that wildlife represent a direct source of human pathogens or spill-over of organisms which can lead to what is described as a pathogen jump, with the organism establishing in its new host. This can occur with or without any livestock species playing the role of "bridge" (Caron et al. 2015). However, documenting the circumstances that lead to the emergence in humans of a new pathogen and identifying the animal source of the pathogen is a difficult task. It necessitates a combination of efficient laboratory and field investigations, which may prove problematic when the suspected emergence occurs in countries with limited resources or areas difficult to access.

The latest pandemic threat, the Middle East Respiratory Syndrome Coronavirus (MERS-CoV), provides an illustration of the challenges encountered to elucidate the role played by putative livestock and wildlife species in the transmission of a zoonotic pathogen. In September 2012, a novel coronavirus, MERS-CoV was identified from a patient with a fatal viral pneumonia in Saudi Arabia. This coronavirus was genetically related to the SARS coronavirus that emerged in southern China in 2002 (Hilgenfeld and Peiris 2013). As of February 19, 2018, 2143 human cases had been reported to the World Health Organization with at least 750 deaths (WHO World Health Organization. 2018). Most zoonotic infections have occurred in the Arabian Peninsula, particularly in Saudi Arabia, although nosocomial outbreaks arising from returning travellers have been reported from Europe, North America, Africa, and Asia.

Dromedary camels (*Camelus dromedaries*) have been confirmed to be the source of human infection (Al-Tawfiq and Memish 2014) of MERS-CoV (Chu et al. 2014). Alraddadi et al. (2016) showed that direct exposure to dromedary camels and particularly milking camels were associated with MERS-CoV human illness in Saudi Arabia (Alraddadi et al. 2016). Secondary infections in humans have been reported, especially within nosocomial settings or to a smaller extent, within households (Assiri et al. 2013). The genetic analyses confirmed that the long-term MERS-CoV evolution occurs exclusively in camels, whereas humans act as a transient, and ultimately terminal host. Spill-over events are frequent and the virus has been introduced into humans several hundreds of times in Saudi Arabia leading to occasional outbreak amplification according to specific "environmental" conditions, which are still unknown (Dudas et al. 2018).

So far MERS-CoV has not been detected in wild animals, such as birds (Perera et al. 2013) or feral camels (Crameri et al. 2015). Some short fragments of the virus genome almost identical to MERS-CoV were found in bats (Kim et al. 2016; Memish et al. 2013) but the role that these hosts may play in the epidemiology of the disease, if any, is not confirmed. In domestic hosts, however, the MERS-CoV has been investigated in numerous species (horse, cattle, pig, goat, chicken, water buffalo *Bubalus bubalis*, and bactrian camel *Camelus bactrianus*) and all specimens were negatives (Funk et al. 2016; Miguel et al. 2016b). By contrast, the virus is circulating actively in dromedary camels (Miguel et al. 2016a, 2017a). Retrospectively, collected serum samples provide evidence that this virus has been infecting camels in East Africa for many decades (Muller et al. 2014). However, so far, it is not clear whether transmission of MERS-CoV to humans is occurring in Africa or not; and the role played by the usual culprits, bats, as compared to camels and human practices are not clear either.

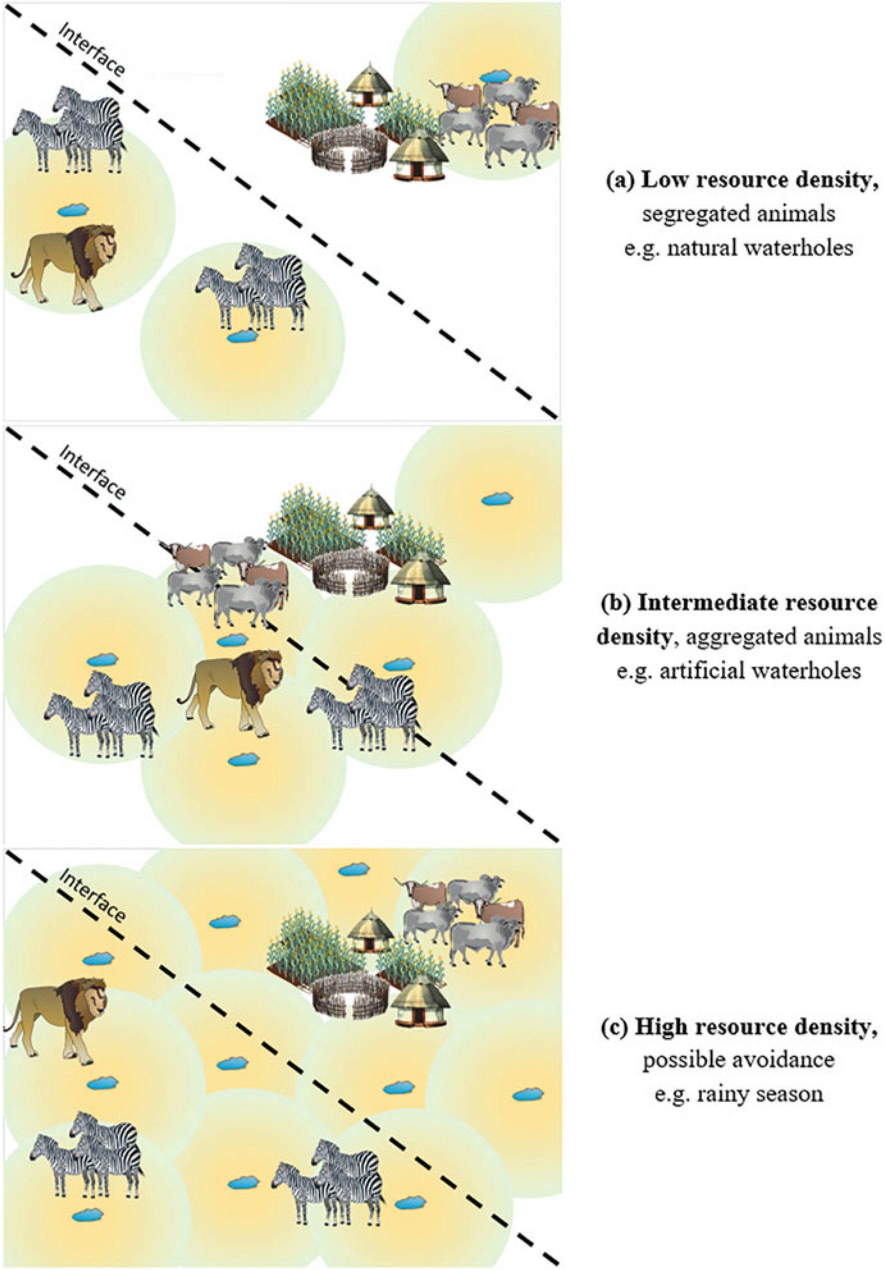
Ecological Drivers of Wildlife-Livestock Interactions

Whether direct or indirect, pathogen transmission between wildlife and livestock results from the use of shared areas (Miguel et al. 2013; Woodroffe et al. 2016). Understanding the ecological and anthropogenic drivers of species distribution at broad scales and animal movement at fine scales will enhance our ability to model wildlife-livestock interactions and the likelihood of disease transmission. In this section, we present evidence of bottom-up effects of resource availability (Section “Resource Availability Drives Wildlife-Livestock Interactions”) and top-down effects of predation (Section “Predation”), anthropogenic drivers are discussed in the following Section (Anthropogenic Drivers of Wildlife-Livestock Interactions).

Resource Availability Drives Wildlife-Livestock Interactions

Wildlife use of interface areas is highly idiosyncratic. Camera trap surveys of large mammals in Southeast Asian forests have shown that some species strongly avoid human disturbances, whereas others appear to select areas that have been subjected to logging and thus appear to be attracted by the human-wildlife interface (Brodie et al. 2015). Underlying these idiosyncratic responses, resource preference can be used as one of the key predictors of wildlife-livestock interactions. Foraging resources are a primary driver of habitat selection; however, multiple resource requirements must be considered to fully understand transmission patterns. The transmission of bovine tuberculosis between cattle and badgers in European pastures illustrates these complex interactions. Badgers favor pasture/forest ecotones that provide prime foraging grounds (pastures) as well as refuge areas (forest) where they can escape predation and dig safe burrows, despite behavioral avoidance of cattle by badgers, contamination may occur by the shared use of a contaminated environment (Woodroffe et al. 2016).

Domestic and wild herbivores are particularly prone to disease transmission due to their phylogenetic proximity and their similar resource requirements (Fig. 5).



(a) Low resource density,
segregated animals
e.g. natural waterholes

(b) Intermediate resource density, aggregated animals
e.g. artificial waterholes

(c) High resource density,
possible avoidance
e.g. rainy season

Fig. 5 Resource-driven encounters between wildlife, livestock, and predators at an African wildlife/livestock interface (adapted from Borchering et al. 2017)

Despite dietary niche partitioning, large herbivores consume a number of shared plant species. Dietary overlap is greater for species with similar body size and proportional grass consumption (Kartzinel et al. 2015). Thus, in African rangelands domestic species such as cattle are more likely to compete with similar-sized ruminant grazers such as African buffalo than browsers (e.g., Greater Kudu), nonruminant grazers (e.g., zebra, *Equus quagga*), or very large (e.g., African elephant) or very small (e.g., duikers and subfamily *Cephalophinae*) herbivore species. Grazed ecosystems are also characterized by positive feedbacks between herbivores and their resource base. Both competition and facilitation provide mechanisms that may increase or decrease the likelihood of direct (contact) or indirect (environmental) disease transmission. Competing herbivores may seek out the same resource patches or segregate into different patches due to competitive exclusion. In extensive farming systems in southern Spain, Wild Boar density is positively correlated with cattle density but negatively correlated with domestic pig density (Carrasco-Garcia et al. 2016). East-African savannas, short grass grazers such as Blue Wildebeest select areas grazed by livestock, whereas bulk grazers such as African Buffalo avoid these areas (Bhola et al. 2012; Tyrrell et al. 2017). In turn, facilitation may lead herbivores to share resource patches such as grazing lawns or use these areas in sequence due to post-grazing regeneration (Odadi et al. 2011).

Although domestic and wild herbivores can share foraging resources, when resources are abundant and widely distributed, free ranging wild herbivores generally avoid mingling with livestock due to direct competition (Riginos et al. 2012) or fear of humans. However, the behavioral response of each species differs. For instance, in a dystrophic savannah system in Zimbabwe, African Buffalo nearly completely avoid cattle at the home range scale whereas elephant bulls favor temporal niche shift, allowing their home range to overlap with cattle by avoiding direct encounters during the day and using the shared range during the night (Valls-Fox et al. 2018a, b). These differences imply that each species may play a different role in pathogen transmission networks at livestock-wildlife interfaces (VanderWaal et al. 2014).

In situations of resource limitation, key resources distributed in discrete localized patches create hotspots where animals aggregate, acting as hubs in epidemiological networks. In tropical savanna ecosystems, most herbivore species are water dependent and their distribution is constrained by access to water, particularly during the dry season (Ogutu et al. 2014). Seasonal variation in resource availability reveal similar patterns across ecosystems, resource-driven encounters increase when resources become scarce (Barasona et al. 2014; Kaszta et al. 2018; Valls-Fox et al. 2018a, b; Zengeya et al. 2015) due to the limited mobility of animals that are forced to share the remaining key resource patches. Counterintuitively, when resources are very scarce, increasing resource availability can increase spatial overlap and contacts (Borchering et al. 2017). To explain this pattern, Borchering et al. (2017) provide a mechanism based on the assumption that animals have a limited movement radius around their core home range. As a result, when resources are sparse each animal or group of animals use different resource patches that are too far apart for them to interact (Fig. 6a). When resource density increases, animals have access to multiple

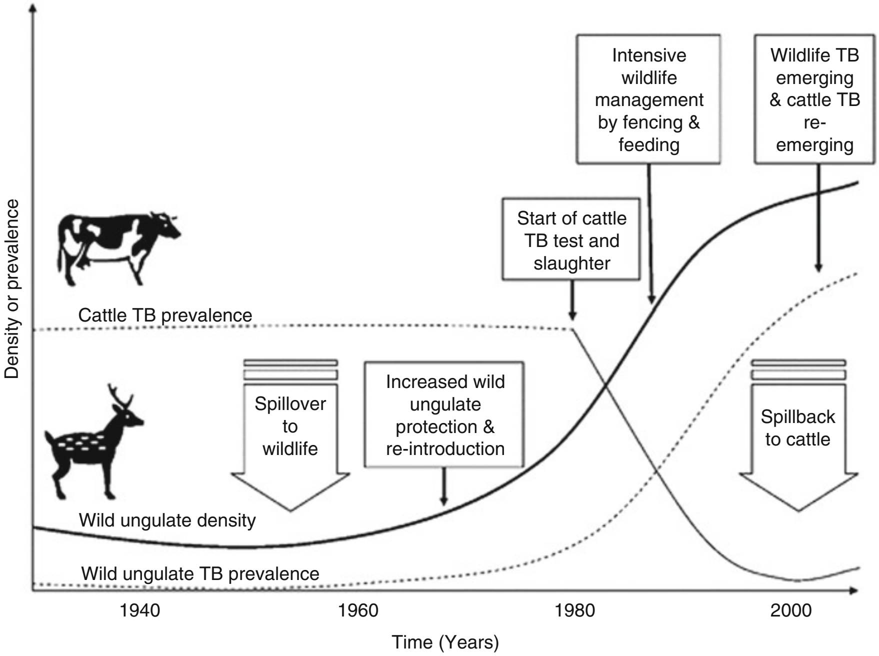


Fig. 6 Evolution of bovine tuberculosis prevalence and transmission (spill-over and spill-back), in livestock and wildlife populations in southern Spain (reproduced from Gortázar et al. 2010). The solid line represents the demographic trend of wildlife (mainly Wild Boar *Sus scrofa* and Red Deer *Cervus elaphus*). Dotted lines represent bTB prevalence in cattle and wildlife

patches and are likely to come in contact with one another particularly if these patches are located close to the interface (Fig. 6b). As resource density increases more (Fig. 6c), animals can adopt a more flexible behavior and avoid encounters. Managing key resources, such as waterholes, at domestic-wildlife interfaces may substantially reduce the probability of contact (Barasona et al. 2014; Valls-Fox et al. 2018a, b). Direct management of livestock movement patterns accounting may be used to limit contact at the most risky areas (such as forest/pasture ecotones that may be used for hay) or at critical time periods. However, top-down mechanisms such as predation risk may modify these patterns, as will be illustrated in the next paragraph.

Predation

The presence of large carnivores is likely to affect habitat use by herbivores (Valeix et al. 2009) and may indirectly influence where interactions occur (e.g., Fig. 6), and consequently disease transmission between sympatric hosts. For instance, a study in Yellowstone National Park, USA, discussed the potential for gray wolf (*Canis* *lupus*) restoration to decrease the spatio-temporal overlap between bison and elk and decrease the transmission risk for brucellosis (Proffitt et al. 2010).

In Africa, where human population growth is high, especially at the edge of protected areas (Bongaarts and Sinding 2011; Wittemyer et al. 2008), and where livestock plays a key role in the livelihoods of rural families (Herrero et al. 2010), an understanding of where, when, and why livestock interact with wildlife is a priority (du Toit 2011). The use of space by cattle in African rangelands is likely to reflect the trade-offs between potential benefits (i.e., access to resources such as water and grazing) and potential costs for livestock owners, including the risk of predation by wild carnivores (Kuiper et al. 2015), disease transmission from wild reservoirs (de Garine-Wichatitsky et al. 2013b), and fines or confiscation of livestock grazing illegally inside protected areas. These potential costs may thus influence husbandry decisions, such as when and for how long livestock are allowed to graze within protected areas (Alexander and McNutt 2010). These decisions are likely to influence the different disease transmission hubs, from wild to domestic hosts or inversely, through direct interactions, the environment and/or vectors evolving in wild or anthropized areas. Further, the presence of large carnivores is likely to affect habitat use by herbivores (Valeix et al. 2009), and may indirectly influence where interactions and consequently disease transmission between sympatric hosts occur (Proffitt et al. 2010).

A recent study explored the potentially modulating influence of African Lion (*Panthera leo*) presence on interspecific interactions on cattle incursions inside a protected area and thus the risk of disease transmission (Miguel et al. 2017b). They combined a longitudinal serological cattle survey for FMD, GPS-collar data from three sympatric species (lion, buffalo, and cattle), and cattle owner interviews in Zimbabwe. No sign of significant short-term interactions (i.e., time window of 24 h) was found between cattle and lion, although they frequently used the same areas. More interestingly, the analysis of incursion frequency time series revealed that lions made frequent incursions in the buffer between rural and protected areas a few days to a few weeks after buffalo had used it, suggesting a potential attraction effect of buffalo on lions. Not only did lions use the buffer a short time after buffalo (3 days), but also after longer time lags (up to 40 days). Conversely, buffalo, the main prey for lions in this ecosystem (Davidson et al. 2013), did not use the buffer zone when it had been occupied by lions a few weeks before, which suggests avoidance of lions by buffalos, but at a temporal scale that is not traditionally considered. Under such scenarios, lions could play a role of “natural barrier” between sympatric species by reducing the spatio-temporal overlap between cattle and buffalo in the buffer zone, consequently reducing the likelihood of direct or indirect contacts and subsequent transmission risk of diseases like FMD (Miguel et al. 2013; Miguel et al. 2017b; Proffitt et al. 2010).

The results also showed that cattle entered the buffer zone of the protected area almost exclusively during the rainy season, which was also observed in a similar ecosystem in Zimbabwe (Kuiper et al. 2015). This pattern is informative at three levels. First, the rainy season coincides with the season when resources (grazing and water) are the most abundant and allow access to a larger home range (“ecological driver"). In addition, cattle can substantially damage crops and are driven into the buffer zone away from the communal areas during the growing season ("anthropogenic driver") (Perrotton et al. 2017). The amount of agricultural work required, and the necessity to keep cattle herds out of growing fields, encourage cattle herds to be grazed away from communal lands and hence more into the buffer zone (Murwira et al. 2013). After crop harvest, cattle are often fed with crop residues in fields during the early dry season, which constrains cattle movements to areas closer to villages and farther from protected areas as described in Perrotton et al. (2017). The availability of resources (vegetation and surface water) inside protected areas should be attractive for cattle owners during the dry season. At this time, surface water is scarce and grass is rare or trampled in the vicinity of homesteads and driving cattle inside the protected areas would represent an opportunity (Prins 1996; Zengeya et al. 2011). However, the buffer zone was not used by cattle during the dry season. This suggests that cattle owners decide to rely on lower-quality resources in the communal land, maybe in order to avoid the risks of infection with FMD virus or tick-borne diseases, and/or predation in the protected area. It has been shown that cattle are more often killed by lions during the rainy season than during the dry season. Indeed, seasonal use of protected areas during the crop-growing season increases vulnerability of cattle to lion depredation (Kuiper et al. 2015). The optimized strategy for cattle herders at the wildlife-livestock interface might be to decrease the likelihood of livestock depredation by avoiding the use of protected areas when the constraints in communal lands are acceptable (i.e., when the crop residues are available). Considering that the risk of being fined for entering the protected area is the same throughout the year, this effect alone does not explain the seasonal variations of cattle buffer use. Contrary to what was found in other similar ecosystems with less predation pressure (Caron et al. 2013; Miguel et al. 2013; Zvidzai et al. 2013), the study showed that the rainy season was the key season for pathogen transmission risk and exposure to predation (Miguel et al. 2017b).

Predator–prey–host interactions, the availability of resources driven by seasonality and human herding practices adapting or reacting to the perceived state of the system, all influence FMD transmission to cattle. The risk of pathogen spill-over between sympatric host populations is restricted to limited areas at specific seasons, and avoidance of predators could potentially be manipulated in order to mitigate interspecific disease transmission. A better picture of the patho-ecosystem would require an understanding of how cattle owners make their herding decisions and according to which clues and perceived risks: disease, predation, or risk of fines? The integration between biological and social sciences is therefore necessary to better understand and manage the risk of disease transmission at complex wildlife-livestock-human interfaces, which are hotspots in the context of emerging infectious diseases (Woolhouse and Gowtage-Sequeria 2005).

Anthropogenic Drivers of Wildlife-Livestock Interactions

In the "Era of Human-induced Diseases" (Chaber 2017), there are numerous examples of how human activities may have a profound influence on disease epidemiology in interface areas (Daszak et al. 2001; Jones et al. 2013). The management of wildlife populations, inside or outside protected areas, and the associated recreational and economic activities, have a direct or indirect impact on wildlife-livestock interactions and pathogen transmission among them. Similarly, livestock belongs to farmers, whose management practices are the results of changing demographic, economic, and socio-cultural parameters, with direct and indirect consequences for wildlife-livestock interactions and disease transmission. Livestock health policies and management have evolved over the past decades, at a different pace and with contrasting results in industrialized versus developing countries. But one general trend is the increasing recognition of the importance of integrated cross-sectoral management of animal health (Binot et al. 2015) and including environmental and wildlife conservation agencies.

The links between livestock and wildlife health, and the associated risks for public health, livestock production, and wildlife conservation have been reviewed for Europe by Gortázar et al. (2006). The evolution of bTB in cattle and wildlife populations in southern Spain over the past century (Gortázar et al. 2010) illustrates these relationships and their implications for management (Fig. 6). After an initial decrease of bTB prevalence in cattle following the test-and-slaughter control program established during the early 1980s, the prevalence reached very low levels during the early 2000s and started rising again. This trend was not completely unexpected from an epidemiological point of view, as it was partly attributed to bTB spill-back from increasingly abundant wildlife. The active conservation of game species put in place after the 1970s resulted in an increase in wild ungulate densities. High levels of bTB prevalence have thereafter been recorded in wild ungulates in central and southern Spain, maintaining a multi-host system of bTB transmission that more than likely involves the livestock populations (Gortázar et al. 2010).

Similar epidemiological situations for bTB could arise in the future in other regions, particularly in Europe and North America that experience comparable increases in wildlife populations. Beyond the particular case of this disease, the following sections will illustrate the complex and far-reaching influences of human activities on wildlife-livestock interface areas adopting two different perspectives: protected area management and pastoralism.

Management of Protected Areas

Wildlife-livestock interfaces have evolved in the last centuries under various social, economic, and demographic pressures, often driven by factors that were independent or distantly related to biodiversity conservation (Andersson et al. 2013), and at an increasing pace in the last decades with the creation of protected areas. The next section will describe how the evolution of livestock management (e.g., pastoral activities in Africa), has profoundly transformed disease ecology at the interface. But we must also consider the other side of the coin and evaluate how the remaining "natural landscapes" kept by humans under some level of protection (e.g., national parks, hunting reserves, and conservancies) have evolved throughout the twentieth century and what were the consequences for wildlife-livestock interfaces.

The emergence of the conservation paradigm in the twentieth century, which created reserves and national parks, has impacted the remaining natural landscape in several ways. First, it created land use boundaries around the protected "natural landscape." De facto, these land use boundaries created a virtual wildlife-livestock interface that would evolve according to the socio-ecological context. Land use boundaries lead to different regulations being applied on each side of the boundary. On the protected side, the control of human activities (from tourism only to a wider array of activities such as natural resource collection or cattle grazing) modified the wildlife-livestock-human interactions. In addition, the management of protected areas includes modifying the environment through the creation of water holes, roads, and camps, and the impacts of these on wildlife ecology and distribution as well as on the (limited) human activities within the protected area must be considered.

For example, the impact of logging roads in Central African forests on increasing wildlife trade has been demonstrated (Burivalova et al. 2014). Similarly in southern Africa, African buffalo populations are negatively impacted by the human footprint within protected areas (Naidoo et al. 2012). Therefore, the management of protected areas has consequences on wildlife-livestock interactions and on pathogen and disease transmission. In Central Africa, the great ape tourism industry that constitutes an important source of funding for conservation at the country level, has created a human/great ape interface that promotes exchange of bacterial species (Rwego et al. 2008). Ultimately this transmission of pathogens between humans and apes may threaten great ape conservation (Goldberg et al. 2008).

A classical model of land use management around protected areas to mitigate human-wildlife conflicts is to surround the core national park with other types of protected areas (e.g., controlled hunting zones) that will buffer the impact of human activities inside the protected area and conversely decrease human-wildlife conflicts negatively affecting surrounding rural areas. A more recent model, developed mostly in southern Africa and progressively expanding in East Africa, relies on the creation of "TransFrontier Conservation Areas" (TFCAs). TFCAs interconnect protected areas (under different land uses) and rural landscapes in a vision to integrate biodiversity conservation and local rural development (Cumming et al. 2013). By promoting wildlife population connectivity and a more socio-ecosystemic approach of the landscape, these initiatives should lead to a better management of wildlife-livestock interactions, and thus reduce the risk of pathogen transmission at these interfaces. These positive outcomes will take time to emerge but the health issues in TFCAs have been highlighted as important and potential threats to the TFCA initiatives (de Garine-Wichatitsky et al. 2013a; Osofsky 2005).

The proximity of protected areas impacts the risk of pathogen transmission to livestock. In fact, this risk of transmission at the wildlife-livestock interface has been a major driver for the establishment and management of protected areas, which have often been established in marginal agricultural lands for that very reason (Andersson and Cumming 2013; Cross et al. 2007). But disease management at wildlife-livestock interfaces has evolved, and elimination of wildlife is increasingly considered an unacceptable solution. The control of FMD (see Section "Wildlife-to-Livestock") could arguably be considered one of the major constraints to the coexistence of livestock and wildlife in southern Africa (Ferguson et al. 2013). Strict land policies on animal movement controls (e.g., fencing) have sometimes locally solved the problem when they have been strictly applied (Thomson 1995). The lack of sustainability of these control options and the indirect costs they induce have raised concerns for decades among conservationists (e.g., Taylor and Martin 1987). Even the best maintained fences cannot restrain the movements of all wild animals (Dion et al. 2011; Sutmoller et al. 2000).

Evolution of Pastoralism and Consequences for Wildlife-Livestock Coexistence in Africa

With its human population exploding, the speed of change in the socioeconomic and political landscapes in Africa is hard to comprehend, with far-reaching consequences for wildlife-livestock coexistence. Predictions during the early 2000s were for an African population in 2020 of 1 billion; the figure in 2016 was already 1.2 billion, while meat consumption (livestock excluding fish) was estimated to reach ten million kg by 2020, the true figure being closer to 16 million kg by 2013 (Desiere et al. 2018). The demand for meat will rise in Sub-Saharan Africa and pending shortages cannot be taken up entirely by traditional livestock systems and rangelands, but the traditional livestock production sector will play a significant role. The ongoing "tragedy of the commons" for competitive use of disputed rangelands involves land grabbing for crop agriculture, irrigation schemes, and hydroelectric or extractive industries, usually promoted by State and private actors. Pastoral communities are squeezing into less and less land for livestock, changing water and forage dynamics, and driving socioeconomic decline.

One strategy for pastoralists in the face of this loss of open resources is to reduce livestock numbers, diversify livelihoods and practices, and inevitably sedentarise, if not permanently, at least on a more frequent basis by shifting to agro-pastoralism or mixed livestock and cropping land use. These communities have the opportunity to develop more sophisticated socioeconomic models and become part of the conservation management system, which is to match stocking densities to resource availability rather than the age old "as many as will survive" policy of traditional nomadic pastoralism. This change diversifies the livelihoods of these communities beyond herding, including settlement in market towns to process livestock rather than relying on itinerant traders (e.g., Mangesho et al. 2017) and using mobile phone technologies to gather market information and trade directly rather than through middlemen. These new developments add much needed value to their economy. Diversification of these communities into a wider landscape and range of work activities is inevitable under these pressures and opportunities. It enables adaptation and compensation for loss of assets or resource access, including (sometimes remote and part time) employment in other sectors in both urban and rural environments, with remittance supporting at-risk family groups such as the youth and elderly in rural rangelands. To some extent, this inevitably leads to more sedentary livestock, cattle and small stock, and associated land degradation, which was uncommon in nomadic systems.

Another pressure on pastoral communities is that traders increasingly demand a different animal product than the tough "rangy" livestock of old, and this is being promoted and achieved through the introduction of "so-called improved genetics" for indigenous breeds or replacement of traditional stock altogether. The main externality of this change is increasing vulnerabilities to and expression of disease, with the trade-offs being increased milk or meat products and more marketable meat. Traditional livestock have shown considerable resilience to diseases, especially indigenous breeds. They have developed tolerances to a range of pathogens in the ecosystems they have occupied for millennia and co-evolved with. Pathogens, which can devastate imported livestock (e.g., *Bos taurus* European breeds) and often did during colonial times, include FMD, trypanosomiasis, theileriosis, bTB, and many others. These diseases are endemic in traditional livestock, but they result in relatively mild conditions with minimal impact. Examples of this include the resilience among Maasai cattle against FMD in Kenya and Tanzania, bTB resistance in Ethiopian breeds of cattle, Ankole cattle in Uganda, and resistance to trypanosome infection amongst the dwarf cattle breeds of West Africa (Ameni et al. 2007; Meunier et al. 2017). With a fundamental shift from traditional livestock, not only will there be more pathogens circulating but more virulent variants will undoubtedly emerge. This will lead to economic loss, increased costs for control, and more impacts of pathogens on wildlife.

Pathogens, which historically spilled from wildlife into indigenous livestock to little negative effect, more often promoting endemic stability and co-evolution, are no longer tolerated where economic losses from disease arise among more vulnerable breeds. This leads to a more exclusionary management of stock and wildlife typified by the emergence of the livestock and wildlife sectors in colonial southern Africa over the twentieth century, where the introduction of European breeds promoted high loads of pathogens like bTB, FMD, and other pathogens (see Section "Livestock-to-Wildlife, and Back?"). This has also led to industrialization of wildlife systems and conservation concerns over genetic manipulation of wildlife for commercial purposes. In addition, rising profiles of disease in tightly managed wildlife can increase risks to livestock systems. Changing political circumstances in the southern African countries are beginning to reverse this process to some extent, with the abandonment of fencing as a tool in some areas with full agreement from the veterinary authorities. Global agendas change and the shift to sustainability is now at the core of development (United Nations 2016). This allows for a fresh look at pastoralism in the food system and its contribution to future food and nutrition security in Africa, with less impact on the climate and environment. Pastoralism is not an outdated agricultural system, quite the reverse, it may resolve many of the challenges currently faced by the food system, biodiversity conservation, and the environment. More attention should be given to a One Health approach considering livestock, wildlife, humans, and environment to achieve a fair balance and mutual benefits across sectors and particularly when implementing disease control measures.

Way Forward: Toward Socio-Ecological Management of Wildlife-Livestock Interfaces

As illustrated throughout this chapter, wildlife-livestock interfaces are very complex and dynamic systems, where spill-over/spill-back of pathogens is at the core of disease ecology problematics. Pathogens must overcome a hierarchical series of barriers to cause spill-over infections, as recently illustrated for zoonotic pathogens by Plowright et al. (2017). Understanding how pathogens spread among complex multi-host systems through these barriers, in time and space, and identifying the drivers of wild and domestic host movements and contacts requires multiple disciplines and approaches, a combination of ecology (behavioral, community, molecular, spatial), epidemiology, and social sciences. The fact that spill-over and spill-back events are not occurring with the same frequencies and intensities is probably a widespread phenomenon (“asymmetric interfaces”), which should be explored more thoroughly, with potentially great implications for the management of diseases in interface areas.

Understanding how these barriers are functionally and quantitatively linked, and how they interact in space and time, will substantially improve our ability to predict or prevent spill-over events (Plowright et al. 2017). And several major conceptual and methodological advances have been made in various ecological fields during recent years, which provide us with unprecedented capacities to characterize pathogens, hosts, and vectors, track their movements and dispersal from molecular to population and landscape levels, and model disease spread (see Chapters “Collecting Data to Assess the Interactions Between Livestock and Wildlife” and “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field”). But there is still a need for integrated holistic models linking demographic and societal factors to land use and land cover changes whose associated ecological factors help explain disease emergence (Wilcox and Gubler 2005) and the circulation of pathogens in interface areas. Despite considerable attention given over the past decade to One Health and EcoHealth approaches (e.g., Roger et al. 2016; Zinsstag et al. 2011), the interdisciplinary integration of ecological, biomedical, and social sciences into a single discipline of “disease socio-ecology" still remains a major research frontier relative to challenges at the wildlife-livestock interface (see Chapter "Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field").

To sum, the main challenge ahead for improved wildlife-livestock disease management is not merely technical or even conceptual. It will necessitate a radical shift in attitudes toward wildlife, which should be considered more as an asset than a problem to be controlled (du Toit et al. 2017), and the strategic use of ecological complementarities between livestock and wildlife to promote coexistence (Fynn et al. 2016). Pathogen transmission between sympatric hosts is inevitable, especially between wild and domestic species that are taxonomically related. Further, eradicating diseases from wildlife populations is very difficult, and has rarely been successful. The history of the interface, where livestock and wildlife are framed in terms of conflict only and not synergy, is full of examples where veterinary interventions have largely exacerbated disease impacts or created catastrophic externalities for biodiversity conservation across the globe. A more socio-ecological understanding of disease is vital to fulfil human ambitions for sustainable systems into the future, to sustain both culturally, economically, and ecologically valuable livestock and wildlife populations.

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