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CONTACTS IN THE WILD AND PATHOGENS SPILLOVER
English version: Introduction & Discussion

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INTRODUCTION

How to explain the AIDS pandemic of the 20th century? Interactions between humans and monkeys of equatorial African forests have existed for thousands of years in these regions of the world (Wrangham et al., 1999, Hahn et al., 2000, Wolfe et al. 2005). Hunting and wild animal consumption is an ancestral human practice leading to an increased risk of interspecific transmission of pathogens (i.e. host jump). However, the first host jump of the immunodeficiency virus was recorded in the 1930s (Korber et al. 2000) and the first human cases were not detected before 1980 in the United States. The virus was only identified few years later in France and on the American continent.

Using the AIDS case as an example to introduce this document illustrates the emergence or re-emergence of many human and animal infectious diseases since the early 80s (Woolhouse and Gowtage-Sequeria 2005). Such events of emergence follow on from a post-war period of relative ecological and epidemiological prosperity (“The Glorious Thirty”, 1950-1980 (Horiiuchi 1992)). Indeed, smallpox eradication, vaccination campaigns, mass antibiotic treatments, economic growth and full employment enabled a large segment of the world’s population (human and animal) to increase its expected life duration (Lee 2011). However, according to some experts, this indicator is nowadays in decline (Lutz et al. 2001). Why such a phenomenon? What are the key factors of emergence and spread of diseases such as AIDS in the 20th century?

The 80’s left a mark on recent social history and represent a transitional period with alternating cycles of progress and cycles of crises. Indeed, at the dawn of the 21st century, crises are many and various: financial (Masood 2009, Haldane and May 2011), climatic (Raupach et al., 2007, anonymous 2012), environmental (Hooper et al., 2012), spiritual, religious (Esteban et al., 2012), food-related (von Braun 2008, Garrett 2012) as well as health-related (Jones et al., 2008, Dobson 2009). The interdependence of these crises is certainly strong (Hulot 2004) and explain for a part new diseases like AIDS.

To continue with the example of AIDS and the reasons for its emergence in the 20th century, many factors have been advanced in the literature such as: (i) competition for space and resources (the building of roads led to increased human incursion into the forests of Central Africa and thus stimulated bush meat consumption), (ii) development of economic activity due to globalization and trade intensification between Equatorial Africa and the rest of the world, (iii) an increase in poverty (with the increase of prostitution activities through tourism and trade (Peeters et al., 2009), and (iv) potential consequences of past therapeutic actions (where mass antibiotic treatments of the 30s could potentially have freed hosts from their bacteria, making room for viruses (Grmek 1989)). Finally, a coincidence of events seems to have provided a favorable situation for the emergence of the virus at this time and in this context.

Thus, understanding the mechanisms of emergence, resurgence or spread of a pathogen between or within species seems to require the integration of many parameters derived from areas as distant as are veterinary, economics, social or ecological.

Our thesis focuses on a particular phenomenon that could generate emergencies and which study requires a pluridisciplinary framework. This phenomenon is the pathogen spillover between wild and domestic populations at the interface between protected and communal lands. However, before launching a study of such patho-systems, a corpus of historical, theoretical and methodological references must be presented. These contextual details will provide a better introduction to the study of these multifactorial processes.

Globalization of pathogens

The pathogen globalization phenomenon can be introduced through the example of European population history. Harsh weather conditions and strong competition for space have created complex societies. This complexity induces a need to organize around crop plants and domesticated farm animals (Diamond 2002). The need to organize, store resources during infertile periods, trade, build political organizations and create technological breakthroughs, generated structured societies with high human densities, organized around cities. These demographic conditions were one of the key factors of emergence of major infectious diseases such as smallpox, measles, influenza, typhus, bubonic plague and would determine the immune characteristics of the people of the old continent (Diamond 1997).

The first major contacts recorded between “new hosts - new pathogens” took place at the time of the biggest population movements, which occurred during the colonization of the New World by Europeans in the 15th century. European endemic diseases vanquished many populations on other continents. Pathogen transmission from “resistant” or “immune” to “non immune” populations was decisive in the conquest of these territories. The contrary was naturally observed in populations of settlers who suffered from African, Indian or Asian tropical diseases such as malaria or yellow fever.

A large number of pathogens have been globally dispersed through commercial and domestic trade that has been taking place for centuries, and especially since the 1930s (Brown and Howmoller 2002, Pepperell et al. 2011). Air transport development more easily and frequently connects people who are normally separated by thousands of kilometers. By allowing an international mixing of pathogens, these new physical connections gave rise to the phenomenon of “microbiological globalization” (“The microbial globalization world” (McMichael 2004).

Immunization and pathogen evolution

Along with trade intensification, mass antibiotherapy was established in human and animal populations after Fleming discovered penicillin in 1928. Major infectious diseases of the 19th century such as leprosy, tuberculosis and the plague could thus be combated in many countries. Large-scale public health actions were also carried out via vaccination campaigns. Yet nowadays, these two significant health advances may be victims of their own success and of their massive use.

In accordance with the laws of the co-evolutionary ‘arms race’ between two competing species (Lotka 1927) or the ‘model of the red queen’ (Carroll 1998), two opponents constantly acquire new adaptations to avoid being left behind by the other, through a sequence of reciprocal selective pressures (Gualde 2006). Today we are witnessing the phenomenon of bacterial resistance to antibiotics and the emergence of virulent strains against vaccination. Therapeutic ac-
INTRODUCTION

Assumptions
Power and effects of globalization (McMichael 2004) and new social organization and settlement phenomena are observed in some regions, emphasizing competition for water access (Harvell et al., 2009, Lafferty 2009, Ostfeld 2009, Randolph 2009). Competiton increases contacts between hosts, thus amplifying the spread of pathogens. (See Box 1 for more details).

Given the multiplicity of factors of disease emergence or reemergence (McMichael 2004), new transdisciplinary research fields were needed to better understand the mechanisms involved in such phenomena. Eco-epidemiology is one example of transdisciplinary field research that...
emerged at the end of the 20th century (Woolhouse and Gowtage-Sequeria 2005).

**Epidemiology and ecology: two complementary disciplines**

The term “epidemiology” can be found in the writings from 1855 onwards and describes a discipline aimed at studying the factors that influence health. The term “ecology” was defined in 1866 and describes a discipline aimed at studying relationships between organisms (CNRTL National Resource Centre textual and lexical). As described in **Figure 1**, there has been an intellectual mixing of the two disciplines since the 1960s. An exponential increase can be seen in the number of scientific articles published in the last century on these topics. The alliance between ecology and epidemiology was then formalized in the 80s after a few years of infancy.

Pathogens have often occupied a marginal position in ecological models (Thomas et al. 2007). However, they play an important role in the ecosystem functioning. MacArthur was a precursor of the empirical laws of ecology at global scale (MacArthur 1972, Hubbell 2001). These macro-ecological approaches are more systemic and inductive than the classical hypothetico-deductive ecological point of view. The aim of this new approach is to infer the processes that occur in the behavior of complex ecological systems. Over the past twenty years, this approach has gained popularity with the development of information technologies and data sharing. It has produced important computing capabilities and robust statistical analysis (Rohani and King 2010). Pathogens are among the major components of these complex systems. Indeed, they affect the survival and reproductive success of their hosts (Michalakis and Hochberg 1994). They thus represent key determinants of their selective value and their population dynamics. On the other hand, pathogens can alter the sexual, social and food behavior of their hosts (Agnew et al. 2000, Hurd 2009).

Ecology help to understand biotic and abiotic environmental influences on host-pathogen relationships.

In the following paragraphs, we will try to describe the contributions to epidemiology of various fields of ecology such as behavioral ecology, functional ecology, evolutionary ecology and community ecology.

**Contacts in epidemiology and spread of pathogens**

Mathematical models have been important in understanding the diffusion phenomena of a pathogen in a population (Anderson and May 1979). Without going into detail, it is important to grasp the basic elements of epidemiological process models to improve integration between theoretical and empirical approaches. These elements are presented in **Box 2**.

In these models, one of the parameters that most affects the probability of infection of susceptible individuals as well as the diffusion capacity of a pathogen, is the contact rate of a susceptible individual with an infected individual, and more generally with the pathogen (Anderson and May 1991, Keeling and Rohani 2007). But estimating contact rates is often hampered by the lack of data to quantify these interactions (Patz et al. 2004). Parameterization of the models describing the processes that govern the epidemiological dynamics is often based on assumptions regarding rate of contact. Such approximations can lead to erroneous conclusions (Smieszek 2009). The problem is particularly acute when studying the mechanisms governing the epidemiological dynamics in multi-specific contexts. Indeed, these models involve an assessment of the frequency of interactions between individuals belonging to the same species but also between species (Lloyd-Smith 2005, Perkins et al., 2009 Woodroffe et al. 2009).

The contribution of ecology to epidemiology may thus be very important to quantify contact frequency and to grasp the mechanisms that generate them. As these interactions are not static in time or space, their understanding involves the study of human or animal population movements.

**Contacts and movements**

Why move? In what direction? What are the decision-making processes of an individual subject to changes in its environment? The answers to these questions shed light on the mechanisms at work in generating the encounter between host and pathogen (potentially hosted by another host). Ecologists have developed techniques, concepts and theories to study the spatial distribution of individuals in a population and their movements.

Theories of habitat selection and optimal supply (‘Optimal Foraging Theory’ (MacArthur and Pianka 1966)) attempt to decipher the use by an individual of the habitat within its home range (Burt 1943) in terms of maximizing survival and reproductive success. They help in understanding the ultimate motivations in the phases of movement and stationing of individuals within their habitats.
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A population is composed of sensitive individuals (S) to the pathogen of study, of infected individuals (I) and of recovered individuals (R). At time t + 1, some of the sensitive individuals will be infected by the pathogen (S -> I). Some of the infected individuals will have recovered (I -> R) while some of the recovered individuals will again have become sensitive to the pathogen in the case of reversible immunity (R -> S). To model these transitions, parameters were defined to estimate the probability of an individual changing state.

The infection force, lambda \(\lambda\), governs transitions from a sensitive individual to an infected state. A parameter \(\beta\) is the parameter \(\lambda\) which distinguishes the rate of infectious contacts between individuals. This parameter \(\beta\) is itself a function of two parameters: \(c\) and \(p\), with \(c\) being the rate of contact between individuals and \(p\) the probability that the contact is infectious. \(\beta\) can be thus written as follows: \(\beta = c \log (1-p)\). The recovery rate, gamma \(\gamma\), governs individual transitions from an infected to a recovered state.

In this illustrative example, we will assume that population \(N\) is stable and contains only sensitive, infected, and recovered individuals. Such as \(N = S + I + R\). Naturally models can be more complex and integrate narrower levels of transition (e.g. birth and mortality rate). Compartments can also be added such as individuals in the incubation period or vaccinated individuals.

In epidemiology, two modes of pathogen transmission are distinguished:

1. Density-dependent transmissions applied to highly contagious diseases such as FMD or influenza (Haydon et al. 1997). Host density influences the number of potentially infectious contacts between hosts. The contact rate increases with the abundance of hosts (McCallum et al. 2001), thus increasing the value of the infection force \(\lambda\) and the basic reproductive rate \(R_0\) (proxy of disease spread). The infection force takes the following form: \(\lambda = \beta I\).

2. Frequency-dependent transmission such as sexually transmitted diseases. The number of hosts in the population does not influence the number of potentially infectious contacts. Contacts between individuals occur at a constant frequency, independent of density. The infection force then takes the following form: \(\lambda = \beta I / N\). Thus the infection force is no longer proportional to the number of patients in the host population but to the proportion of patients in the population (McCallum et al. 2001).

Naturally, the presentation of these two modes of transmission simplifies the complexity of biological systems in order to improve their understanding. However, the majority of pathogen dissemination strategies are found between density- and frequency-dependence.

This understanding is potentially important in the field of epidemiology because it identifies and characterizes risk areas in terms of meeting between host and pathogen.

For example, the health risk may in some cases be a determining factor in the habitat selection process. A host defense strategy, other than immunity, which is less invasive and referred to as prophylactic, would consist in avoiding infection risk sites.

This strategy would involve risk perception and fine adjustment of host behavior, especially in regard to their movements (Rohr et al. 2009). For instance, Ezenwa (2004) showed the existence of selective food patch behavior in some wild ungulates, these patches being far from antelope defecation areas that are rich in nematode larvae (Ezenwa 2004). Infection avoidance behaviors by hosts are however less common than selection behavior by parasites to reach their hosts. ‘The arms race’ between hosts and parasites to meet or avoid each other, is often to the advantage of the parasite. Avoidance is difficult for the host because parasite recognition systems are limited, unlike their alert systems in response to predators. Conversely, certain areas could be selected for their therapeutic effects: the selection and use of medicinal plants for prophylactic or curative purposes in primates or ungulates such as elephants or rhinoceroses (Lozano 1998, Aufrreiter et al. 2001).

At a broader scale, the ecological niche concept, mathematically formalized by Hutchinson (Hutchinson 1953) as a hypervolume or envelope where each dimension of the space is a resource (food, materials, etc.) or a condition (temperature, rainfall, etc.) of the environment can be applied to hosts, parasites, pathogens and vectors to identify areas in which coexistence is possible. This concept has especially been used to map the risk of emergence of vector-borne diseases under future scenarios of climate change (Estrada-Pena 2008).

Parasitism and the immune system

The acquisition and persistence of immunity are fundamental parameters for epidemiological dynamics and are important factors in the emergence of diseases. However, the development of immunity represents an investment of energy (Schmid 2003) weighed against investments in other functions that are also involved in the survival and reproductive success of individuals. Therefore, investment in immune function is modulated by factors such as food availability (Chew and Park 2004), the need to invest in breeding activities (Apanius 1998) or physiological stress induced by adverse environmental conditions. The immune system is thus highly dependent on the environment in which the individual lives (Lochmiller Deerenberg 2000). Environmental influences induce a strong heterogeneity of individual immune responses (Frank 2002). Integrating functional eco-immunology into epidemiology may have a part to play in studying this phenomenon.

Natural selection, the evolution of life history traits, and adaptation as addressed by evolutionary ecology are very important concepts for the understanding of immunity phenomena. Indeed, natural selection is the driving force behind changes in virulence and the ability for a pathogen to spread, because of the selective pressures caused by the immune system of their hosts (see above, the model the Red Queen). For example,
incomplete immunity in a population induced by an imperfect vaccine can induce a shift in the virulence of the parasite toward the highest levels (Gandon). Symmetrically, the immune adaptation of a host population to its exposed pathogens is a fundamental element in understanding epidemiological dynamics and, more specifically, emergences. Indeed, the selection pressures exerted by parasites on host immune responses affect the susceptibility of host populations to different pathogens. A host population usually exposed to common strains of a pathogen may be strongly affected by the introduction of a rarer strain (Aaron et al. 2004).

Although the role of immunology in natural populations is increasingly integrated into the ecology of infectious diseases (Grenfell and Dobson 1995, Hudson 2002), phenomena of pathogen adaptation to the complex multi host immune context are still largely under-researched. In particular, immune responses associated with the spillover of pathogens between wild and domestic species remain to be explored.

**Using the concepts of population ecology in the study of epidemiological processes within fragmented host populations**

Major work has been conducted in eco-epidemiology in recent years on human measles and pertussis based on a series of long-term data (Rohani and King 2010). These longitudinal empirical studies have investigated the spatiotemporal dynamics of these diseases using concepts from population ecology.

The first concept is that of “metapopulation.” A metapopulation is a network of spatially distinct subpopulations connected via movement of individuals. Metapopulations generally occupy fragmented habitats and are characterized by a dynamic occupation of habitat fragments governed by colonization and local extinctions. Colonization and extinctions depend on (1) the carrying capacity of each habitat fragment (i.e. the number of individuals that can occupy each fragment is a function of the size of the fragment) and (2) the flow of individuals between habitat fragments. By transposing the metapopulation concept to epidemiology in the 1960s the critical community size (‘CCS’) could be defined. The ‘CCS’ defines a threshold population size below which a pathogen can persist over time without external inputs of contaminated cases (Bartlett 1957, Black 1966). Metapopulation models in epidemiology have subsequently been refined by integrating the densities of subpopulations and their connectivity (Cliff and Haggett 1995).

Another concept from ecology, ‘source-sink’ dynamics (Kirstan 2003) was subsequently used in the late 90s to develop “cities-villages” models to describe the dynamics of epidemics and the extinction of measles and pertussis phenomena in a system consisting of three variable-sized cities in England. In these models a pathogen cannot persist for long in too small a subpopulation but can be regularly introduced by stochastic processes of encounter with infected individuals from subpopulations of larger sizes. Megacities are then sub-population “sources” that permanently harbor pathogens and occasionally supply smaller host populations described as “sinks” (Rohani et al. 1999). In addition to the size of host subpopulations, their connectivity is a key parameter in these models of epidemiological processes in structured host populations (Black, 1966, Cliff and Haggett 1995).

**Integrating community ecology in the study of multi-host systems**

One potentially valuable contribution of ecology to epidemiology is to consider the biotic environment in the study of interactions between host and pathogen. Since the beginning of this century, eco-epidemiology has integrated the scale of host, vector and pathogen communities, in disease diffusion mechanisms. The effect of biodiversity on the risk of disease transmission has been at the heart of scientific interest over the past ten years. Describing this type of relationship is a challenge with strong theoretical and ethical implications. The consequences in terms of ecosystem management are considerable. One question that has aroused considerable controversy focuses on the relationship between the diversity of hosts or vectors and the prevalence of one or several disease(s) in an ecosystem. Does an increase in the host or vector diversity of a pathogen dilute (Schmidt and Ostfeld 2001, Begon 2008) or amplify the prevalence of this pathogen?

The risk of infection depends on many factors such as modes of transmission of pathogens or the composition of host community and relative ability of the host in transmitting the pathogen (Keesing et al. 2006). These effects naturally become more complex with the addition of new elements to the chain of transmission such as vectors or the environment (LoGiudice et al. 2003, Keesing 2006, Roche et al. 2011). Many research results now support a dilution effect in the transmission of a pathogen when susceptible host composition is diverse (see Box 2 for the conditions of application). However, this effect is extremely critical especially concerning (1) the repeatability of the empirical models used (2) the difficulty of rigorously estimating host or vector population densities (Allan et al. 2003, Randolph and Dobson 2012) (3) and the difficulty of distinguishing the dilution effect from the density or competition effect between species (Lotka-Volterra), which leads to lower densities of each species and consequently a decrease in the prevalence of associated pathogens (Begon 2008).

Dobson in 2004 theoretically formalized the dilution effect using models describing the epidemiological process (see Box 3) (Dobson 2004). He thus highlights the role of the susceptibility of the host community and the mode of transmission of the pathogen considered in the process of dilution (Figure 2). In contrast, the study of Power and Mitchell 2004 reveals a higher prevalence of a pathogen under study after adding species to the community. However, the discussion in this study is more about the composition of the community than its richness. Indeed, the prevalence was completely conditioned by the presence in the community of a highly competent host (Power and Mitchell 2004b).

Host diversity and interaction strongly influence epidemiological dynamics. It thus seems worthwhile to broaden the spectrum of studies involving one pathogen or one host to wider scales such as multi-host and multi-pathogen scales. This change of multispecific scale (Guegan, Constantine) naturally leads to an enlargement of the complexity of the analyses and interpretations but seems necessary to address the health and interconnected issues detailed above.
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BOX 3: DILUTION EFFECT

The application of the dilution effect is subject to four conditions (Roche 2008, Roche and Guegan 2011):

1. the vector species must have generalist trophic behavior,
2. transmission of the pathogen should not be vertical,
3. the susceptibility of different host species of the community must be variable and finally
4. the most sensitive host species must also be the most abundant. This set of conditions naturally decreases the applicability of such a model, but would explain some epidemiological systems. As shown in (Figure 2) basal reproduction rate R0 grows with an increase of specific richness, host abundance and contact rates for density-dependent diseases. Symmetrically, an increase in specific richness is accompanied by an increase in low-skilled individuals thus decreasing R0 in case of frequency-dependent disease transmission.

Predation as an interaction modulator

In ecology, too many studies have so far focused on the direct, lethal consequences of predators on their prey (Rosenzweig and MacArthur 1963). But over the last ten years, some studies have considered the indirect effects of the presence of predators in the landscape, for example in terms of the prey’s increased vigilance activities to the detriment of feeding behaviors (Creel et al. 2007) (McCauley et al. 2011). Indeed, low densities of predators could induce specific behaviors in prey, with serious consequences for their survival. It was even suggested that the indirect costs of predation could surpass those of the direct effects of predation at the population level (Schmitz et al., 1997, Preisser EL 2008).

One of the indirect predation effects could affect the sanitary health of prey populations. Recent theoretical studies suggest that predation may reduce the level of prevalence of a disease in an ecosystem (Holt and Roy 2008). Under these assumptions, infected individuals are the prey of choice for predators and therefore suffer from higher mortality due to predation compared to healthy individuals. According to Packer (Packer et al., 2003), predator control may have indirect consequences on prey populations. Such theoretical suggestions indicate that the disappearance of predators could reduce the proportion of healthy individuals in prey populations. Predators would play a decisive role in maintaining ecological and epidemiological equilibriums.

A more subtle effect of predation may influence the transmission of pathogens between domestic and wild hosts. Indeed, fear of the wolf has strongly structured the cognitive representation and use of nature in humans. Different European stories between the 17th and 19th centuries whereby parents warn children of the dangers associated with the presence of predators in the wild are good illustrations of this phenomenon. We can quote, “Little Red Riding Hood” (Perrault 1698), “The wolf and the seven kids” (Brother Grimm 1812) or “The Three Little Pigs” (James Orchard Hilliwell-Phillipps 1843). The anecdotal example of the story “Deep in the Woods” that exists in many countries (England, Greece, Spain, the United States with a bear variant) supports this demonstration. Africa is no exception: Alexander McCaul, brings together African stories in the book ‘The girl who marries a lion’ and describes the ambiguous relations that bind man and wildlife. Because of this association between wild areas and risk of predation, the presence of predators in a natural area could severely restrict the use of this space by humans and thus reduce the transmission of pathogens between wild and domestic hosts.

The research problematic

Southern countries: ‘areas of interest’ in the study of ‘wild-domestic’ transmissions? The case of Africa

We have seen that the transfer of pathogens between host species has probably largely accounted for the emergence or re-emergence of diseases in domestic animals and humans since the 1980s. Models of the relative risks of infectious diseases and of interspecific transmission of pathogens frequently target Southern countries. They thus define certain areas as ‘hot spots’ for certain transfers of pathogens (Jones KE. 2008).

In this context, we will focus our interest on Africa, although the issue of interspecies transmis-
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Africa, a continent where the competition for space is often accompanied by habitat fragmentation.

The strong growth of crop areas, livestock activities and the expansion of cities into the countryside are just some of the factors that exacerbate the conflictual relationship between man and nature (Wittermyer et al., 2008, Craigie et al. 2010). Combined with global changes, which project an intensification of rainfall in equatorial regions and aridification in other parts of the continent (Giannini et al., 2008), such anthropogenic pressure significantly threatens the sustainability of African ecosystems, including the Savannah (Kay 1997, Ogutu and Owen-Smith 2003, Odadi 2011).

Africa, continent that passed the one billion inhabitants mark in 2010 could reach the 2 billion threshold in 2050. Africa, a continent where more than 4 million km² of land is protected (Chape et al., 2005, Wittemyer et al. 2008), and where a wide diversity of herbivores and carnivores still exist (Fritz and Loison 2006, Fritz et al. 2011). Africa, a continent where the competition for space is often accompanied by habitat fragmentation.

The objectives of the thesis

We have developed this project to work on issues related to the transmission of pathogens from wild ‘reservoir’ populations to domestic ‘sensitive’ populations. We have focused on the interface between a wild compartment (protected area) and an anthropogenic compartment (cultural areas) in southern Africa. We focused on the phenomenon of FMD transmission between the African wild buffalo (Syncerus caffer) and the domestic cow (Bos taurus, Bos indicus). The African buffalo is considered to be the natural reservoir of the disease in this region (Thomson 2003).

This parasitic biological model is not emerging, but its endemicity allows the study of interspecies transmission phenomena in an area that is potentially conducive to other emergences. We were particularly interested in the relations-

Table 1: Overview of disease transmissions between wild and domestic vertebrates and the type of ecotone involved (Despommier, 2007)

<table>
<thead>
<tr>
<th>Diseases</th>
<th>Wild</th>
<th>Domestic</th>
<th>Affect Human</th>
<th>Ecotone</th>
<th>Ref</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avian flu</td>
<td>Wild birds</td>
<td>Domestic birds</td>
<td>Yes</td>
<td>Settlement - Agriculture - Aquatic habitat</td>
<td>(Olsen et al. 2006)</td>
</tr>
<tr>
<td>Tuberculosis</td>
<td>Badger</td>
<td>Cattle</td>
<td>Yes</td>
<td>Settlement - Agriculture - Natural Habitat</td>
<td>(Donegely et al. 2006)</td>
</tr>
<tr>
<td>Nipah virus</td>
<td>Bats</td>
<td>Cattle</td>
<td>Yes</td>
<td>Settlement - Agriculture - Natural Habitat</td>
<td>(Drozak et al. 2012)</td>
</tr>
<tr>
<td>Ebola</td>
<td>Bats</td>
<td>Cattle</td>
<td>Yes</td>
<td>Settlement - Natural Habitat</td>
<td>(Leroy et al. 2005)</td>
</tr>
<tr>
<td>HIV</td>
<td>Monkeys</td>
<td>Cattle</td>
<td>Yes</td>
<td>Settlement - Natural Habitat</td>
<td>(Hahn et al. 2000)</td>
</tr>
<tr>
<td>yellow fever</td>
<td>Monkeys</td>
<td>Cattle</td>
<td>Yes</td>
<td>Settlement - Natural Habitat</td>
<td>(Barrett and Mounth 2003)</td>
</tr>
<tr>
<td>Brucellosis</td>
<td>Elk, bison</td>
<td>Cattle</td>
<td>Yes</td>
<td>Settlement - Natural Habitat</td>
<td>(Kilpatrick et al. 2009)</td>
</tr>
<tr>
<td>Rabies</td>
<td>Vertebrates</td>
<td>Dogs</td>
<td>Yes</td>
<td>Settlement - Natural Habitat</td>
<td>(Holmala and Kukkala 2006)</td>
</tr>
</tbody>
</table>

Table 1: Overview of disease transmissions between wild and domestic vertebrates and the type of ecotone involved (Despommier, 2007)

Figure 3: Pictogram of wild-domestic-human interface and factors underlaying the risk of disease transmissions from wild to domestic animals (hatched area) with, between brackets, corresponding section numbers in the manuscript (inspired from Daszak 2000)

- Pathogens introduction - ‘spillover’ (1;2;3)
- Ressource competition (2)
- Biodiversity loss and trophic chain perturbation (2;4)

Wild – Domestic Interface :
- Direct transmission (1;2;3)
- Environmental transmission (1;3)
- Vector transmission (4)
hip between interspecific interactions and virus transmission. We described the temporality of inter-
actions and factors associated with meetings or avoidance between the two sympatric spe-
cies. Intra-specific interactions in the home com-
partment were also described to characterize the
contact network, and the heterogeneity of risk of
infection in this compartment. Finally, we also
considered the influence of host diversity in this
area on the presence of vectors and the risk of
vector-borne disease transmission. A summary
of our approach is given in Figure 3

Our approach was mainly empirical, being based
on collected data whose conditions could not
be controlled and which therefore is imperfect
by nature. However, we have tried to link these
data to theory (Restif et al. 2012). To do so, we
mainly relied on theories and concepts of eco-
epidemiology presented in the introduction of
this document.

In this document, our work is presented in four
sections.

We began by compiling an inventory of the di-
seases present in each population to estimate
the potential risk of pathogen transmission be-
 tween the two host species considered (epide-
miological context).

Secondly, we quantified the interactions and
analyzed the influence of wild-domestic contacts
on the dynamics of infection in the domestic po-
population. At this stage, we also tried to clarify
the virus modes of transmission (direct and / or
indirect via the environment), the immune res-
ponses of domestic populations to infection by
a pathogen from the wild compartment and we
evaluated the effectiveness of vaccination cam-
paigns (Section 1).

Thirdly, we focused on the ecological and social
determinants of the wild / domestic interactions.
A description of the “landscape” description at
the interface (water availability and vegetation)
helped to inform our thinking. We then supple-
mented this work with two additional studies:
one aimed at understanding how wild areas are
perceived by livestock farmers living at the inter-
face, and the other aiming to assess the role of
predators in the use of wild areas by the livestock
(Section 2).

Fourthly we explored interactions within the do-
mestic population in order to describe the intra-
specific contact networks in which pathogens
from wildlife can spread (Section 3).

Fifth, we developed a community ecology-ba-
sed approach to understand the relationship bet-
 tween host diversity and parasitic risk (Section 4).

Finally, after concluding on these studies, we de-
veloped perspectives that attempt to feed both
fundamental and applied future research.
OBJECTIVES

QUESTIONS AND RESEARCH
OBJECTIVES OF THE THESIS

Question? Do domestic animal populations in proximity to wild populations share pathogens with the wild compartment?
Objectives: Characterize a range of pathogens in wild/domestic populations with and without interaction and compare infestation intensity. Pathogen spectrum between the buffalo and the cow. Exploratory study.

Question? Does the occurrence of disease in “sensitive” domestic populations depend on the intensity of contact with the wild “reservoir” population?
Objectives: Characterize the intensity of wild/domestic interactions and simultaneously study the incidence of FMD in sensitive domestic populations. Use FMD as an epidemiological marker of wild to domestic transmission. The case of FMD between buffalo and cattle. Section 1

Question? Do wild and domestic interactions vary according to season and distribution of resources in the landscape?
Objectives: Characterize interactions per season and available resources. Sections 1 and 2

Question? Do wild and domestic interactions vary according to the presence of predators in the wild compartment?
Objectives: Characterize the incursion of domestic populations into the wild compartment according to the presence of predators. Case of lion, buffalo and cattle. Section 2

Question? Does the intensity of intra-species interaction in a sensitive population condition the diffusion of a pathogen from the wild to the domestic compartment?
Objectives: Characterize the network of cooperation between livestock farmers according to herding strategies and seasons in the periphery of protected areas. Section 3

Question? Are the diversity and abundance of wild and/or domestic hosts amplification factors in the abundance and/or diversity of associated vectors.
Objectives: Characterize the vector populations (i.e. abundance and diversity) at the interface (co-existence between wild/domestic population), in protected area (wild population) and communal area (domestic population). The case of FMD. Section 4

To go further…

Before starting the next section, which focuses more on host species ecology and resource distribution in the landscape to explain interspecific contacts, it is important to point out the limitations of our study.

Two points may be particularly open to criticism:

The first limit concerns serological analyses. As ELISA used to detect antibodies directed against antigens SAT2, did not work, our ability to describe the seasonal dynamics of FMD virus on our sites was impaired. According to FAO and OIE recommendations resulting from an FMD conference that took place in Bangkok in June 2012, this serotype would experience a significant spread on the African continent (e.g. emergence of serotype in Egypt and Libya). Aliquots are still stored in veterinary service freezers in Zimbabwe. It would thus be interesting to retest them once the calibration phase is improved.

A second limit also concerns serological analyses but as a reflection of virological analyses. After all these steps of biological and statistical analysis, we can conclude on correlations (i.e. incidence and antibody reversion rates versus contact rates) but we cannot assert that these correlations indicate viral circulation between these sympatric species (e.g. problems of sensitivity and specificity of serological tests). Yet we remain convinced that antibody detection between two sampling sessions is a very good proxy.

However, had we been able to simultaneously isolate strains of virus circulating in cattle and buffalo, we could have described pathogen diffusion (or ‘spillover’) between these two species with greater certainty and precision. Genetics would then inform us on the phylogenetic relationship of isolated virus in wild and domestic populations. However, given the logistic difficulties associated with field conditions, virus isolation is a rare event under natural conditions in southern Africa.

In addition, the fact that domestic individuals present very few symptoms makes the task even more difficult. Finally, the cost of molecular analyses, besides the uncertainty of their results, currently reduces the net benefit that such protocols would present compared to serology, which remains inexpensive and easy to apply in situ.
To go further…

At the end of the two preceding sections, we progress on defining the various factors that govern wild/domestic interactions of the interface and pathogen spillover. We are then able to build a conceptual model of cattle and buffalo movement at the interface. This model identifies factors and constraints that influence decisions regarding the use of communal and protected areas throughout the seasons. This conceptual model is presented in figure 39-A, where we point out the central question for the two sympatric species: “Should I stay at home or go further afield”? Constraints detailed in the preceding paragraphs are vegetation, water, parasites, predation, border type, and human presence (i.e. poaching, culture, national park rangers). Following this description, the next step could be to build an explicit dynamic spatial model of cattle behavior and breeding strategies. Figure 39-B outlines this new modeling stage, where we see the information layers required to implement a model of this type. These models could allow us to simulate scenarios and to dynamically observe the behavior of the various factors identified. For example, in the eventuality of climate change, we could develop scenarios of severe drought drying up most water points in the middle of the dry season. These models would thus help to describe alternative herbivore behavior and estimate the potential risk of pathogen transmission.

Many steps still need to be validated in order to produce such models able to support the decision-making and management of these interfaces. However focusing on such objectives helps to build better protocols and improve data collection, pooling and information capitalization. Figure 40 illustrates this model applied to the Dete-Hwange interface for which we compiled and analyzed the most information. In the dry season (Figure 40, A), despite the theoretical attractiveness of the park in terms of its vegetation and water, the main strategy adopted is to remain in communal lands because of potential predation pressure (or otherwise, as estimated by national park rangers). Conversely, during the rainy season (Figure 40, B) despite the fact that pressure on resources decreases and that pressure on predation is maintained, the principal strategy adopted was incursion into protected area. Agricultural constraint in communal lands would thus generate a switch in the cost/benefit trade-off.

To go further…

Social network analysis can be conducted on the basis of inexpensive data collection and help to identify periods, places and herds presenting strong health risks. These analyses are even more relevant when diseases are “density dependent” and/or zoonotic and/or weakly detected. The implementation of these protocols in southern countries could significantly improve the monitoring and control of diseases by veterinary services. Indeed prioritization of areas, seasons and farmer groups which present high health risks, would help to reduce the costs allocated to the control of animal diseases. This budget reduction could afford to repeat observations on the groups presenting the most risk in order to rapidly detect the emergence, in the domestic compartment, of pathogens coming from the wild reservoir. For buffalo, the spread of bovine tuberculosis from South Africa to Zimbabwe between 1950 and 2008 is a current and illustrative example (figure 46). Pathogen spillover from buffalo to cattle may have significant health consequences in Zimbabwe, a country whose human population is highly immuno-depressed because of the AIDS epidemic that has been raging for many years (Gregson et al. 2006).
To go further …

Estimation of parasite abundance, whose detection rates are low and whose gregarious ecology implies an interdependence of detection events, generates statistical issues. Implementing algorithms in statistical tools allowing the use of zero inflated negative binomial distribution (such as the site occupancy model with PRESENCE), would improve the modeling of rare events. However, at the time of writing this manuscript, we can indicate that this function now seems to be implemented on R (free software unmarked package).

Another improvement of statistical tools, in parasite study with detection issues, could be to aggregate estimated coefficients using generalized linear mixed models. Implementing such an index would help to adjust confidence intervals around estimates and better integrate species biology in estimation models of density or presence.

Finally, continuing to support the idea of a dilution effect from host diversity on macro-parasite density, it seems crucial to repeat these measurements on inter and intra annual scales. A more detailed description of host community in each compartment (i.e. diversity and density of macro and micro mammals) also seems indispensable.
Our results reflect similar studies

Studies published to date on interspecific pathogen transmission are either:

(1) about the transfer of pathogens from domestic to wild animals in the aim of conserving endangered species (Haydon et al. 2006). A case in point is the vaccination of the last subpopulations of Ethiopian wolves against the rabies virus, hosted in populations of domestic dogs on the periphery of the conservation area.

Or (2) the transfer of pathogens between wild animals, again in the aim of conservation. We can cite the example of brucellosis transmission among populations of elk and bison in Yellowstone National Park in the United States (Proffitt et al. 2010).

Or else (3), the transfer of pathogens from wild to domestic from the public health standpoint. Two studies are referred to here that are emblematic in this respect. First, once again referring to the Yellowstone system, the risk of the spread of brucellosis in bison cattle (Kilpatrick et al. 2009). And secondly, the study of the spread of TB between badgers (i.e. population reservoir) and cattle in England (Donnelly et al. 2006).

Multiple determinants of spillover risk, process complexity and difficulty of generalization

Through these examples, we can see that interactions between wild and domestic ungulates in Africa are still largely unexplored. Our results thus provide key empirical information to shed more light on this unknown area. They provide the link between contacts and the transfer of pathogens from wild to domestic populations. Our study addresses both economic issues and conservation goals. It also opens perspectives on public health issues. In our study, like those mentioned above, contacts and spatial coverage are central to thinking about interfaces; mixed areas whose management raises a number of environmental, economic and epidemiological issues.

Figure 49 provides a schematic synthesis of the various results obtained during this PhD on pathogen transmission interfaces between rural areas and those dedicated to the protection and conservation of wildlife. Note that the studies are presented in detail in the appendices and the results they have produced have been summarized in the preceding four sections. The estimates obtained in this thesis of rates of contact between buffalo and cattle and the serological incidence of FMD show that the risk of pathogen transmission from buffalo to cattle varies between our study sites. They also show that seasonal and spatial patterns of contact and impact vary. Contact between cattle and buffalo occur in rural areas, protected areas or their interfaces depending on the site considered. The peak incidence of FMD in livestock populations does

Figure 49: Summary of empirical results produced to describe the drivers of inter-specific infections at the interface between communal lands and protected areas. (A) FMD incidence in cattle populations (i.e. more cases) increases with contacts rates between these cattle populations and the reservoir populations (i.e. buffalo) (Section 3) and with the frequency of incursions into the protected areas (Sections 1 & 3). We also explored the influence of within and between species contacts of drivers such as climatic conditions and predation pressure. The effect of seasonal climatic conditions differed among study sites (i.e. dotted and plain lines). (B) We undertook a preliminary investigation of the relationship between host biodiversity and parasite density in protected, rural and interface landscape compartments Section 4.)
not occur in the same season at all sites. We have tried to identify the processes and determinants governing these epidemiological and ecological patterns of contact and incidence.

As the occurrence of inter-and intra-species contact is closely related to the use of areas by buffalo and cattle, we explored the processes and determinants governing these uses. We have tried to describe how the distribution of resources (i.e. pasture and water) and predators determine the movement and stationing of cattle and buffalo in the landscape. The sites varied considerably in terms of certain features of the landscape and the animal communities that occupy it. Our study sites differ in terms of type of distribution of water resources, with two sites characterized by distribution in the form of a major river and one site with distribution in the form of water points dispersed in the landscape. We also highlighted the significant differences between sites in regard to the distribution of forage resources between the various areas (i.e. protected areas, interface). Finally, our results suggest that the processes of habitat selection by wild and domestic ungulates differ depending on whether predation pressure is high or low.

We also looked at the processes and epidemiological determinants at work in each of our study sites. We characterized the effects of serological vaccination applied to only two of our three study sites. We also questioned the relative importance in each of our study sites of the two possible interspecific routes of transmission of the FMD virus, the direct route and the environmental route.

Finally, a simultaneous study of contrasting sites by combining epidemiological approaches with ecological approaches allowed us to identify situations in which the risk of transmission is low and other situations in which these risks are higher (Figure 50). Thus, the risk of transmission between species appears to be reduced by a wide spatial dispersion and a good balance between protected and rural areas of the key resources for herbivores, especially water but also grazing areas, high predation pressure limiting spatial overlap between sympatric species of prey and relatively high anthropogenic pressure on the borders of protected areas generating enough ‘disturbance’ to keep wild populations away from communal areas.

One of our conclusions is that health risks in general and emergence in particular, cannot be predicted purely on the basis of correlative approaches (e.g. Ezenwa 2007). In fact, only an understanding of the processes involved will allow us to develop mechanism models that are capable of predicting the various risks linked to the coexistence of wild and domestic species (Kee Ling 2002, LaDeau 2011, Restif 2012). This type of tool could be useful in predicting the health consequences under different scenarios (i) a worsening economic crisis accompanied by increased anthropic pressure at the edge of protected areas (Guerbois et al. Submitted), (ii) climate change resulting in the aridification of savannah ecosystems (Giannini et al., 2008) or (iii) the disappearance of large carnivore populations in these ecosystems (Packer et al., 1991, Bauer 2008).

In the following paragraphs, we attempt to identify the tasks involved in understanding the ecological and epidemiological factors governing interspecific pathogen transmission. We will also identify research avenues to improve this understanding.

Ecological processes and determinants

Understanding land occupation and use

Understanding the processes that govern the occupancy and habitat use by two sympatric populations is crucial in predicting the risk of interspecies transmission (Kilpatrick et al. 2009). A very good example of the importance of these processes is provided by the case of bovine TB transmission between badgers and cattle in the UK. Culling part of the badger population in order to control the disease would have resulted in increasing the size of the home ranges of badgers. This increase would epidemiologically connect herds of cattle that were previously isolated. Thus, culling some of the badger population resulted in an increase in the prevalence rate of TB in some herds of cattle (Donnelly et al., 2006; Jenkins et al. 2007).

In the African context of this PhD, we developed protocols for the best estimate of interspecific contacts. Two methods were used to characterize these interactions: (1) a matrix of contacts and (2) overlap area coverage. However, a third method of quantifying interactions, more rooted in understanding the movements of monitored animals, could be developed using GPS data. The results of section 3 show that the movement of cattle does not seem to be random and that areas with high nutrient values, in particular, are selected after integrating various constraints (e.g. predation, human presence) (Sinclair 1977 McNaughton 1985). In this context, the Resource Selection Function methods (Boyce and McDonald 1999) or K-select (Calenge et al. 2005) could be used to characterize the habitats selected or counter-selected by the studied species, using...
biophysical parameters (i.e. topography, vegetation) or anthropogenic parameters (i.e. fields, barriers). These methods compare the observed frequencies of use of different habitat types within the home range of individuals, with expected frequencies of use under so-called "null" hypothesis (i.e. without selection or avoidance). They would identify the habitat types strongly selected by two animal populations. These habitat types undoubtedly present favorable conditions for interspecies transmission. In addition, in situations where several species in a community are monitored by telemetric techniques, it may be possible to consider the presence of predators or competitors as characteristic of the habitat of a given species. Although integrating these mobile elements into habitat selection analysis certainly involves significant technical difficulties (Mc Loughlin 2010), they appear to provide a much better understanding of the processes governing land use.

However, this type of analysis requires the acquisition of detailed, high spatial resolution data on the biophysical characteristics of the landscape (Lambin et al. 2010). In some areas, such information is still difficult to obtain. Satellite images may help to overcome these limitations. However, the analysis of a remote sensing signal requires validation in situ for the best attribution of habitat classes to spatial units (Curran 1985). Also in areas subject to highly seasonal climatic conditions, habitat should be characterized dynamically (McLoughlin 2010).

Creating maps of interaction and infection risks would greatly increase our power of analysis by allowing us to move from individual to landscape scale. Areas and periods of risk of disease transmission could then be represented and characterized (Brook and McLachlan 2009).

Placing epidemiological interactions between two species in the context of their communities.

In many epidemiological systems the relationships between host species and pathogen are influenced by other components of the communities to which they belong (e.g. LaDeau 2011). A recent publication on the transmission of brucellosis between populations of elk and bison in Yellowstone National Park (Proffitt et al., 2010), remarkably illustrates the value of not restricting the study to host populations when observing interspecies transmission. Indeed this study shows that the re-introduction of wolves could limit spatial overlap between bison and elk, thus limiting the transmission of brucellosis between these two species. (Packer et al. 2003b).

This type of situation could also occur in the African context of our own study. In addition to an approach centered on two host species (i.e. cattle and buffalo) and their shared pathogen (i.e. FMD), we tried to place our study in the broader context of animal communities. We thus examined the role of a predator, the lion, in modulating buffalo-cattle interactions. Like the study mentioned above our results suggest that high predation pressures may limit the interactions between cattle and buffaloes thus reducing the transmission of pathogens between these two species.

The investigation of interspecies FMD transmission processes, by adopting a community level perspective could be extended to questioning the existence of communities of wild and domestic ungulate species capable of establish an epidemiological bridge between buffalo and cattle, commonly known as ‘bridge species’ (Caron et al. 2012b). Indeed, the ungulate communities occupying our study sites include species such as the impala (Bastos et al. 2000) (Aepyceros melampus), greater kudu (Tragelaphus strepsiceros) or warthog (Phacochoerus africanus), identified in the literature as potentially excreting infectious particles of FMD (Anderson et al., 1993, Thomson et al. 2003). The role of these species seems particularly important in exploring situations such as the Dete-Hwange site, where despite the apparent lack of contact between potentially infectious buffalo and cattle, the transmission of FMD virus between these two species does appear to exist.

We also initiated a more holistic approach to health risk by trying to assess the influence of host diversity on the density of parasites that are pathogen vectors (e.g. ticks) (Figure 49.8). Such community level approaches are still embryonic, but need to be developed. Indeed, this specific study could be used as a preliminary step in setting up a more ambitious protocol for a longitudinal monitoring of tick communities in the vicinity of water points. Moreover, understanding the relationship between the characteristics of host population and tick communities would also require a description of the host community for the immature stages of ticks, such as small mammals, birds or reptiles (Walker et al., Zieger et al. 1998).

Sociological processes and determinants that are still unknown

Our research shows that the eco-epidemiological approach alone is not sufficient to understand interactions among populations of cattle and buffalo. Indeed, the multiplicity of observed patterns (as detailed in the preceding paragraphs) is probably due in part to the variety of livestock practices. Understanding human behavior is difficult without the appropriate sociological studies.

In our context, there is insufficient historical description of the conditions of access to certain areas, in accordance with the administrative laws and permissive arrangements granted by traditional power, to fully grasp the mechanisms of land use at these interfaces. Another important step appears to be the understanding of the relationships binding man to his stock. After analyzing our results, we investigated the competitive mechanisms between humans and domestic animals in the struggle for land. In effect, observations made at the Dete-Hwange interface of the strategies used to keep cattle away from cultivation land, at the risk of greater exposure to predation, affected our thinking on this matter. Cost / benefit analyses of livestock rearing strategies in wild / domestic interface areas are still largely under-documented. They are however crucial to understanding the process of disease spread in these hybrid zones.

Epidemiological processes and determinants

We can question the relevance of FMD as a biological model for the study of mechanisms of pathogen transmission in the wild - domestic interface. Regular circulation of the virus in the hosts leads to frequent detection of events (Bruckner et al., 2004 Rweyemamu et al., 2008, Caron et al. 2010). From this point of view, FMD is an interesting model. However, despite the historic nature of the disease, some elements of its epidemiology are still unknown in tropical ecosystems (FAO / OIE 2012). These uncertainties restricted the possibility of drawing strong conclusions from our serological monitoring in absence of experimental protocols. However, our results
open up some interesting hypotheses. Let us consider two rather unexpected results. First, over a relatively short time (4-8 months) we observed high rates of loss of the antibodies produced in response to infection (i.e. antibodies detected by the NSP) (section 1 - Appendix 2). These high rates of serological reversion are inconsistent with the information in the literature suggesting that antibodies produced after infection persist for several years (Grubman and Bax 2004, Paton et al., 2009 Charleston, 2011) (Figure 10). The second surprising result is the presence of FMD antibodies among individuals in areas of the country where no outbreak was declared and where no symptoms were detected by the veterinary services. This result could indicate an imperfection in the surveillance system but also indicates a potential silent circulation of the virus (Kennedy et al. 1984b) (i.e. serological incidence from two independent sources of diagnostics: NSP and SATs for KAZA region). Such circulation could have important consequences for the optimization of control strategies across the country (Jori et al. 2009a).

These two results should trigger thinking about the evolution of host-parasite relationships in endemic situations. Cattle and buffalo have shared common land and pathogens in these parts of the world for decade (Diamond 2002). Co-evolutionary mechanisms could have potentially shaped the characteristics of the host immune system and the life history traits of the pathogens. These mechanisms may have selected pathogens with low levels of virulence and hosts that are weakly invested in irreversible immune defense mechanisms (Gandon et al. 2001) in favor of less demanding immune memory mechanisms that are sufficient to fight against mild, chronic infections (Roitt et al. 2002, Schmid-Hempel 2003, Netea et al. 2011) (1). Note that in the context of environmental transmission and attenuated virulence domestic host populations may also play the role of secondary reservoir populations of the disease. These findings also have major implications for controlling the spread of the virus in a region. A second question arising from our work focuses on the modes of transmission of FMD virus. Indeed, our telemetric monitoring suggests that direct contacts between cattle and buffalo are extremely rare. Despite the virtual absence of direct contact, the serological incidence of FMD seems to be associated with the asynchrony presence of buffalo and cattle in common areas. We therefore believe that indirect transmission via the environment plays an important role in the transmission of FMD virus from buffalo to cattle. As indicated in the findings of our first study (Appendix 1), these results are quite unexpected. The existence of such a mode of indirect transmission may have evolutionary implications that are particularly useful epidemiologically. Indeed, a recent theoretical study (Roche et al., 2011) suggests that the ability of a pathogen to be transmitted both directly and indirectly could lead to the evolutionary stable coexistence of several strains within the same population. However, these strains would maintain different levels of virulence. The author also refers to high and low pathogenic strains of influenza viruses coexisting within bird populations (Chen et al., 2005, Olsen et al. 2006). Environmental transmission would be a more conservative strategy and allow the survival of a weakly virulent strain. Conversely, direct transmission is associated with more virulent strains.

To return to our context of FMD transmission between wild and domestic populations, we know that different strains of FMD: SAT1, SAT2 and SAT3 circulate in the reservoir host population (i.e. wild buffalo) (Thomson et al. 2003, Caron et al. 2012a). Given the existence of such serotype diversity, we can ask whether the mode of interaction between populations of buffalo and cattle differentially influence the transmission of the strains of virus hosted by the reservoir population. Some observations support this hypothesis. The existence of direct interactions on the Pesvi-Kruger site (see figure 21) could favor viral strains that are relatively virulent but have little ability to survive in the environment. This could explain the detection of potential symptoms (i.e. ulcers on the tongue) on certain individuals at the Pesvi-Kruger interface during the sampling campaign in July 2010. Moreover, as noted above, a vaccination campaign was set up in this area at this time. In contrast, only indirect interactions at the Dete – Hwange site could foster strains of low virulence but which are able to survive in the environment. This could explain why no symptoms were detected in populations of cattle on the Dete- Hwange site despite zero serological incidence during the rainy season.

Testing this type of hypothesis would mean characterizing the viral strains circulating in the buffalo and cattle populations. This could be done through serological testing to differentiate FMD virus serotypes. The SATs tests we used would allow for this but are unable to distinguish vaccine antibodies from infectious antibodies. The use of vaccination in both study areas thus complicates the interpretation of such serological monitoring (i.e. across serotype). Therefore, and echoing the conclusion of section 1, isolation of the strains circulating in buffalo and cattle populations at the different interfaces, would seem to be a crucial step in understanding the routes of transmission of these interface pathogens.

DISCUSSION

Is the risk of interspecies transmission the only component in the risk of emergence?

Our work focused on the risk of interspecies spillover of an endemic pathogen. But, does this risk translate as a risk of emergence?

Two steps must occur to result in the emergence of a pathogen in a population (Childs et al., 2007, Caron et al. 2012b): (1) the emergence of the pathogen stricto sensu in a target population (i.e. population of interest) from interspecies spillover from non-target populations (Haydon et al. 2002). (2) the amplification of the epidemic phase in the target population involving a high proportion of available susceptible hosts. Host availability is ensured by high densities in the population.

Through network analysis we noted that, in our African context, there is a close link between the level of anthropization in an environment, connectivity, and the risk of pathogen spread (section 3). When a pathogen, whose mode of transmission is density dependent, is introduced into a strongly connected host population, it spreads very quickly (McCallum et al. 2001). Thus a highly anthropic system but with weak wild-domestic interaction (i.e. Dete Hwange-) is considered low risk in terms of pathogen spillover. It could, however, become a site of emergence after introduction of a pathogen, although introductory events are rare (Figure 50).

Conversely, a more ‘rustic’ system where wild / domestic hosts share much of their habitat and where anthropogenic pressure is low (i.e. Pesvi-Kruger) does not necessarily represent a higher risk of emergence. The isolation and (supposed) low connectivity of such populations does not necessarily allow for the amplification and spread of the pathogen within
domestic populations even if introduction to these populations is common (Figure 50).

**Integrative models of the epidemiological process: the potential contribution of mechanistic models in understanding epidemiological dynamics**

As discussed in the preceding paragraphs, the assessment of emergence risk, and health risks in general, in interface contexts requires integrating the inter- and intra-species pathogen transmission processes (Choisy et al. 2007). To achieve such a goal, it is particularly interesting to conceptualize complex systems studied in the form of models (LaDeau 2011, Restif 2012). Figure 51 presents a model of the epidemiological dynamics of our study systems. As the figure shows, the work presented in this thesis could initiate the parameterization of such models. Our longitudinal study of infection antibodies (i.e. NSP test) provides information on the probabilities of transition from ‘sensitive’ state to ‘infected’ state (λ: force of infection) and ‘recovered immune’ state to ‘susceptible’ state. Telemetric monitoring of buffalo and cattle could estimate one component of the force of infection: interspecific contact rates. An analysis of the cattle herd network would provide information about another component of the force of infection i.e. intra-specific contact rate in the cattle population. Finally, longitudinal serological monitoring with NSP tests and SATs provides information on the transition probabilities from ‘sensitive’ state to the ‘recovered immune’ state generated by vaccination. Note that our empirical approaches also lead to a description of these parameters between sites, depending on the season and as a function of determinants such as resource distribution type or predation pressure. The figure 51 also measures what is required for a complete characterization of the epidemiological system composed of buffalo and cattle populations. In particular, epidemiological processes within buffalo populations are still largely unknown. In an extremely rigorous approach, a validation step would have to be included in the process of parameterization of these models. This step would require the acquisition of dynamic epidemiological data (description of the distribution of individuals in a population in the various epidemiological states on different dates) independent from the data used to estimate the model parameters to avoid any tautological effect.

Once fully configured and validated, such models are used to describe the composition of the population in terms of epidemiological status on any given date thus allowing the identification of periods or sites of epidemic, extinction or endemic (Haydon et al., 2004, Choisy et al. 2007). These models can also be used to estimate key parameters of the epidemiology of the pathogen, such as R0 (Mishra et al. 2011). Sensitivity analysis can finally be conducted to provide decision support tools to understand or simulate epidemiological dynamics under different scenarios (e.g. climate change or territorial changes) (Mbah and Gilligan 2011, Ferguson and Van Kerkhove 2012).

**Figure 51**: Integrated modeling from field to computer in eco-epidemiology (Lloyd-Smith et al. 2009). Box (A) shows how data were collected in the field and statistically modeled. Box (B) shows the dynamical SIR modeling and how the information presented in Box A can be used to parameterize it (dotted arrows). One output of the SIR model is the description of the dynamics of three epidemiological compartments. Box (C) Dynamical models allow evaluating key epidemiological parameters (e.g. R0). These models are also useful to predict future trends and help decision makers. Such predictions can be derived from sensitivity analyses on key parameters under different scenario. Finally these models are crucial to estimate the best control strategies to apply (vaccination, disease prevention or culling) and adapt surveillances strategies.
The contribution of statistical models to interpreting serological data

In the course of this PhD, we faced the challenge of interpreting serological data. An important approach in our study is the use of more sophisticated statistical models to overcome this obstacle. In accordance with this perspective, one type of statistical model seems particularly interesting. These are state-space models (LaDeau 2011). These models simultaneously estimate the parameters that govern the transitions between states (i.e. epidemiological states) and the parameters linking observations to states (Conn & Cooch 2004, McClintock et al. 2010). Based on the data we have obtained (i.e. sequences of NSP serological results and SATs), these models could be used to estimate the parameters that link these results to actual epidemiological states (susceptible, infected, recovered). More specifically, the test performance parameters and parameters that govern the transitions between epidemiological states could be estimated (i.e. force of infection, probability of seroconversion after infection or vaccination, probability of seroreversion), (Faustino et al. 2004, Conn & Cooch 2009, McClintock et al. 2010). This type of statistical modeling seems to be particularly interesting for the study of diseases in the south because it also allows for the processing of incomplete monitoring data (Jennelle 2007).

Control of FMD, in the process of eradication?

In view of the results of sections 1 and 2, emphasis can be placed on two elements to improve the control of FMD in cattle in Zimbabwe: (1) improve vaccination coverage which barely reaches 30% in some regions of the country (Appendix 2) and (2) renew the cycles of vaccination recommended in endemic areas (i.e. every 6 months) by circular zoning around the risk areas constituted by the interfaces between rural and conserved areas spaces. These seemingly trivial tips actually echo the skills of the veterinary services that have controlled FMD in the country for decades. The economic recovery that has taken place over the last 2 years will undoubtedly revive these skills, which will be supported by international institutions such as FAO, OIE and SADC (Box 7). However, the strategies to manage the current situation need to be adapted and new components must be integrated.

Firstly, the barriers once erected to separate wild populations from domestic populations have now fallen down for the most part. In addition, the cost / benefits analyses for replacing and maintaining these barriers seriously question their value (Ferguson and Hanks 2010). Secondly, it seems that the goal of controlling FMD must include thinking about the effects of the vaccination campaigns applied for decades in Zimbabwe (see box on the history of the country) on the selection and evolution of strains of FMD virus. One might indeed ask whether the use of vaccines composed of the three serotypes circulating in the region (1 Bot SAT 1/68 - SAT 2 ZIM S/81 - Zim 4/81 for the year of study) (Fogg in 2010) does not generate selection pressures favoring the emergence of new strains (see paragraph on vaccination in the introduction) (Levin et al. 1999). Serotypes that are uncommon in the region, such as serotype 0 already detected in South Africa, can thus emerge or re-emerge. (Sangare et al. 2001, Bruckner et al. 2002). These selection pressures should be better taken into account by the animal health services when defining control strategies (Mackinnon and Read 2004). Thus, a systematic characterization of strains of FMD virus should be carried out when outbreaks occur in livestock populations. It would also be valuable to conduct serological surveillance and to search and characterize the viruses circulating in buffalo populations. Moreover, as some strains appear to circulate undetected, it would probably be useful to conduct serological surveillance activities even in apparently free areas. This work on characterizing the strains of FMD virus circulating in different populations would certainly result in optimally adapted vaccines (Haydon et al. 2004).

We also question the adhesion of rural populations to control measures in these contexts of subsistence agriculture on the periphery of national parks. Is there sufficient motivation for a farmer to travel many kilometers on foot with his cattle to participate in an immunization session? This is unlikely given (1) that the cattle develop very few symptoms of the virus, (2) the productivity of the herd seems little affected, (3) the trade of livestock products is limited to the local market (i.e. low prices) as international institutions are lobbying hard to prevent trade across-borders, and finally (4) the most basic provision is often lacking for the human population (i.e. latrines, drinking water and basic medical care). A colleague has said elsewhere in the literature that in Zimbabwe there is a marked discrepancy between the number of animal health facilities in villages and the number of human health facilities (Appendix 4).

This discrepancy highlights the economic past of a country based on beef rearing in large ‘white farmer’ farms. The aim of the FMD control strategies at the time was to contain the disease in some areas in order to protect others. This raises the issue of defining which population to protect. In publications by authors closely involved in these issues of interface and man-fauna conflict it is common to find quotes such as: ‘the views and needs of local people are ignored or overlooked’; ‘Local priorities are not consulted’; ‘The voice of communities is seldom heard’ (Andersson et al., 2012 deGarineWichatitsky et al. 2012). This type of quotation illustrates the gap between local, national and international issues and the difficulty in reconciling these issues (Mukamuri et al. 2012).

Interface management: wild versus anthropic areas: how to coexist? Keys for management

In previous sections we considered the implications and scientific perspectives of our study on FMD epidemiology in contexts of wild-domestic coexistence. We now propose to discuss the practical implications of our work in terms of monitoring and health checks. We are aware that a truly relevant assessment of these implications would require management, socio-economic and political science skills that go beyond the scope of this thesis. We propose, however, to list some areas of reflection.
**Box 7: Control of Foot and Mouth Disease**

**FAO and OIE perspective (FAO/OIE 2012)**
Countries that are virus-free are still threatened by an outbreak whose combined losses would run to billions rather than millions. FMD is a major obstacle to the international trade of animals and animal products. However, FMD is more than a disease affecting international trade or a threat to certain countries. The consequences for the South have been underestimated. ‘Infected’ countries are excluded from lucrative export. The disease has a negative impact on the local or regional trade of food of animal origin. Consequently, economic development is affected by this virus at different scales, from farmer to urban production chain. It is recognized that improving control strategies for FMD promotes the control of other animal diseases by improving veterinary infrastructure and husbandry practices. FMD control is part of the broader control of Transboundary Animal Diseases (GF-TADs). The main objective is to improve animal production and marketing in the South to alleviate poverty. Specific objectives rely on the capacity of veterinary services and infrastructure. To eradicate the disease or at least provide good control of its spread, 4 points were identified (i) the availability of good diagnostic laboratories (ii) appropriate vaccines for the viruses circulating in the region (iii) an adapted epidemiological surveillance system and (iv) good partnerships between private and public interests.

**Perspective of SADC – Southern African Development Community (Thomson, G. 2008)**
http://www.youtube.com/watch?v=9oH6wBlEZIU

Eradication of the disease would be associated with the eradication of the wild buffalo population, which is unthinkable today, from an economic, ecological or ethical standpoint. Thus a community of stakeholders, SADC (Managers, Veterinarians, researchers), is calling for a relaxation of the legislation on the export of beef from endemic areas. They want to work from outside the borders of a country, after specific packaging of beef products (bone removal and PH manipulation). These packaging efforts would guarantee the absence of virus in the meat. According to the SADC more flexible legislation would reduce poverty, allow better integration of the activities of subsistence breeders and ensure the sustainability of conservation efforts and transfrontier parks.

**Improve surveillance strategies?**
In this dissertation, we also looked at a method of analysis to take into account the uncertainty surrounding detection events using methods of site occupancy and capture-recapture. This approach taken from ecology has already proved its worth in estimating macro-parasite density in a medium (Appendix 5), but could also be highly relevant in detecting micro-parasites.

**Sampling and data analysis methods taking uncertainty into account**
It is obvious that in many developing countries diagnostic capabilities are limited and the data available for epidemiological surveillance is patchy. The resulting uncertainty degrades the performance of surveillance systems (Vergne 2012). Optimized sampling and analysis could improve performance in these contexts (McClintock 2010). Indeed, methods such as the ‘site occupancy’ models in section 4 of this paper (Mackenzie and Royle, 2005), to describe the occupancy and density of ticks around water points could be adapted to issues of pathogenic presence in epidemiological units such as herds. These methods describe the epidemiological status of a population taking pathogen detectability into account. They could for example be used to describe the prevalence of a pathogen at herd level. Indeed, a longitudinal monitoring could be developed for several herds. At regular intervals and in each herd, a number of animals (not necessarily the entire herd and not necessarily the same animals at each session) would be tested for the pathogen. For a given session, each animal would thus represent a possibility of pathogen detection. Each tested animal would be a repetition of the detection attempt. Analysis of the data generated by this type of protocol by models of the ‘site occupancy’ type, would estimate the probability of presence of the pathogen in a herd (i.e. prevalence at herd level) and the probability of detection of the pathogen in an animal if the pathogen is present in the herd. Note that for a test with good sensitivity and specificity, the probability of detection could be interpreted as intra-herd prevalence. If this type of protocol is repeated at regular intervals, these models are able to estimate the parameters of the epidemiological dynamics of epidemiological units (i.e. herds in our example), in other words, the probability of colonization and local extinction of the pathogen. In addition, the selection of herd breeders to include in this type of longitudinal monitoring could be based on the network analysis detailed in section 3. More generally speaking, such methods of sampling and analysis provide a rigorous description of the epidemiological status of a population without resorting to exhaustive sampling. They would thus be very useful in the context of developing countries where resources allocated to monitoring are limited.

**Reliance on endemic disease surveillance to improve the detection of emerging outbreaks**
A particularly thorny aspect of risk emergence surveillance is that it relates to rare events. This usually means the surveillance of an event that may occur in the future (Cleaveland et al. 2007). It seems appropriate to focus efforts on monitoring that which already exists to better understand unknown phenomena such as emergence...
Indeed, working on endemic situations, as we have been able to do with FMD, helps to identify the gaps and needs of a surveillance system on at least two levels. Firstly, any flaws can be picked up in the transmission of information in the outbreak communication chain (i.e. from the farmer, to veterinary services, to the Ministry of Health and to international institutions). Secondly, work based on what already exists enhances the capacity of laboratories, allowing them to gain independence and international recognition. This capacity building needs to be strongly supported by international institutions such as FAO, OIE, WHO and the World Bank.

All these elements, taken together, will provide the necessary skills for early detection of emerging pathogens in populations (animal and human) and thus limit their spread (Figure 52). The argument for the sustainability of surveillance activities based on endemic situations, naturally contradicts emergency action in the event of crisis.

Participatory methods

Increasingly sophisticated methods are now able to identify zones of pathogen emergence or circulation (i.e. satellites (Bouyer et al., 2006), (Beck et al. 2000), Internet (Scarpino et al. 2012)). However, pathogen detection by local health services is lagging behind (Halliday et al. 2012). The detection and biological analysis capabilities of some laboratories, particularly in the south, are often limited. To remedy the lack of means, participatory diagnosis methods are increasingly implemented. Mobile technology (i.e. mobile phones) which has affected all strata of the world’s population in less than 20 years (Boretos 2007), is an excellent vector of information. And the Open Mobile Consortium (OMC) uses numerous applications (e.g. Frontline SMS, Nokia Data, Epi Surveyor) to share ‘open access’ health information under standardized nomenclatures (Aanensen et al. 2009). This participatory mobile surveillance, which can be applied to rural contexts, is undoubtedly a key asset for improving surveillance strategies in the South (Robertson et al. 2010, Lin and Heffernan 2011).

Enhance regional development to limit wild-domestic interaction?

Can contact between wild and domestic species be prevented? The trend in Southern Africa suggests that Wild / Domestic interactions are not about to diminish. Indeed, the increased connectivity of conservation areas through the creation of transfrontier parks is producing a mosaic of landscapes where man and nature coexist more than ever. From the livestock farmer’s standpoint, wildlife causes disruption and its economic benefits are practically nil in the ecosystems studied (Guerbois 2012). However, the way that people living in the periphery represent nature seems to be more complex than it would appear at first sight or purely on the basis of a cost-benefit analysis (Mukamuri et al. 2012). Recent studies show that the local human populations have a fairly positive representation of wildlife, one that incorporates symbolic capital and refers to the patrimony of these species (Guerbois 2012). Coexistence therefore seems possible in areas where wildlife is part of the landscape and where tolerance toward it seems high. It is interesting to compare this with northern countries, where the reindroduction of wildlife produces a real landscape of fear among those who interact with species such as wolves or bears (Garric 2012b). In these areas, men seem to have lost the ties binding them to wildlife and reindroduction results in real problems of governance between the state, farmers associations and nature conservation (Garric 2012a).

In Sub-Saharan Africa, 330 million young people will reach working age in 2025. Two thirds live in rural areas. For this population, the size of the U.S. population today, agriculture will be a major focus of activity (Losch 2012). With the prospect of the increase and intensification of zones of wild / domestic interaction, we propose considering regional development measures to reconcile conservation objectives (i.e. opening up areas with transfrontier parks and the survival of wild populations) with those of population development in the south (i.e. decreasing health risks and improving livestock). It is important to bear in mind that we are speaking about a southern country in economic and political crisis. The means of investment in regional development on a rural are expected to greatly increase the fragility.

**DISCUSSION**

**BEFORE**

| 1. | Livestock should be confined at night in a part of the communal area away from the park boundary. Confinement could be shared between |
| 2. | A relative anthropic pressure should be applied in close proximity to the boundary that is strong enough to create a ‘disturbance’ and induce ‘avoidance’ (Erb et al., 2012, Silva-Rodriguez and Sieving 2012). |
| 3. | Confine domestic animals after the household with top protection to decrease the risk of predation, |
| 4. | Build water through with pumped water not accessible for wild herbivores and allow the creation of water points (Littell 2011). |
| 5. | The notion of risk must be associated with incursions into an unreserved area. |

**AFTER?**

**Figure 53 : Land management possibilities at the periphery of national parks:** (1) create open spaces without resource (like tyre road) between national park and communal lands with difficulties to cross for species, (2) maintain anthropogenic pressure at the border of national parks to create a disturbance effect, (3) confine domestic animals after the household with top protection to decrease the risk of predation, (4) build water through with pumped water not accessible for wild herbivores and (5) allow lands and spreading in confined community lands. In the case of a river separating the wild and domestic lands, the problem is more complex but the construction of boreholes and barrier around lands could to decrease the dependence to key strategic water points. Symmetrically, the construction of a matrix of pumped water holes inside the national park could considerably decrease the contacts between wild and domestic animals.
farmers to increase surveillance efforts. containment areas could have roofing to reduce the risk of predation (Ogada et al., 2003 Kgathi et al. 2012).

4. More boreholes should be drilled in the periphery area. Troughs could be made. Using a water pump to supply them would reduce their attractiveness to wild herbivores, as the water would only be available after pumping.

5. Pooling certain lands and leaving land fallow would increase the productivity of grazing areas. Accompanied by methods such as manure spreading, the spatial reorganization of land use would improve soil quality (Baudron et al. 2012). This would enable a switch from totally extensive subsistence farming, in the face of extremely limited resources, to extensive subsistence farming but whose surveillance, protection and improvement strengths could be shared and managed at community (i.e. village) level as opposed to breeder level. All these proposals naturally require a thorough analysis of the cost / benefits and consequences of such management actions. However, pilot studies could be implemented on the ground to test their effectiveness. Note that these guidelines follow the same trend as those recommended by the NGO WWF (World Wildlife Fund) in their human wildlife conflict manual (WWF 2005). Some illustrations from this document have been reproduced here, moreover, to support our argument (Figure X). Finally, we wish to emphasize the fact that alleviating poverty on the edge of conservation areas seems to be a prerequisite for improving the wild / domestic coexistence (McMichael 2004).

Protect to be protected?
The design of our research protocol has attempted to shed light on current scientific discussions about conserving biodiversity (Balmford et al., 2002, Bellard et al. 2012). Our thinking, from a health point of view, emphasizes the potential benefits of diverse ecosystems in two main areas. First, maintaining higher trophic levels in the food chain such as large predators seems to reduce contact between wild and domestic ungulates. According to our assumptions and conclusions, predation would modulate domestic incursions into the wild compartment (Proffitt et al. 2010). Predation indirectly modulates the coexistence of competing species. Second, a diverse community of hosts appears to reduce the parasite load in an environment. Host diversity would create a dilution effect, reducing the abundance of parasites. Lower abundance naturally reduces contact between hosts and parasites and thus the associated risk of infection.

Our study offers points for discussion on the paradigm of the last decade, i.e. ‘protect in order to be protected’ (Keesing et al., 2010, Roche et al. 2012). This is of course subject to controversy, especially in regard to the interest it has generated in the media or among donors (Randolph and Dobson 2012). As examined in previous sections, our studies need to be repeated over time to reach a significant conclusion in terms of effects. However, despite the lack of repeatability of our measurements and the exploratory nature of our analyses, we can only endorse the relevance of this type of argument from an ethical viewpoint. It is a paradigm that extols the virtues of a complex and diverse world. Even if the concept of balance is questionable in the case of an ecosystem which by essence is always subject to disturbances by nature (Folke 2006). The speed with which changes have occurred in recent decades has led to a significant imbalance in the competition game between hosts and parasites. The alteration of trophic chains together with a crisis of extinction and a soaring human population have radically changed selection pressures in recent decades. Disruption of this balance between hosts and parasites occurs on time scales that are too short to accommodate adaptive mechanisms. Thus a tentative approach, advocating the reduction of anthropogenic pressures on ecosystems seems sensible from the perspective of co-evolutionary relationships between hosts and pathogens.
Emerging or re-emerging diseases in human populations have increased over the last thirty years. Since 70% of such diseases are caused by pathogens originating from animal hosts (i.e. Ebola, AIDS, and avian influenza), this increase has prompted the study of eco-epidemiological systems that occur at the interface between human and animal populations (i.e. wild and/or domestic). Contacts between hosts are particularly important factors in these systems since they result in pathogen transmission among individuals and, therefore, disease diffusion within and among populations.

We used foot-and-mouth disease (FMD) as a model to study pathogen transmission from wild to domestic populations. As the African buffalo (Syncerus caffer) is the presumed reservoir of this highly contagious disease, we examined the conditions in which the virus was transmitted to cattle sensitive to the disease (Bos taurus and Bos indicus) at the borders of African national parks; these areas are interfaces between anthropogenic and protected areas in which animals can move freely.

In the context of this Ph.D., four protocols were implemented between 2010 and 2011 in Zimbabwe. First, 36 GPS (Global Positioning System) collars were placed on cattle and buffalo in order to describe and analyze cattle their movements across the landscape as well as to quantify interspecific contacts. In one of the study sites, eleven collars were attached to one of the predators of these ungulates: the lion (Panthera leo). By integrating the predator guild into our telemetry protocols, we could examine the potential changes in spatial use by cattle and buffalo in response to predator presence and their consequences for contact dynamics and interspecific pathogen transmission. Second, a longitudinal serological survey was conducted in which tagged individuals were sampled repeatedly over the course of different seasons. Anti-FMD antibodies were detected using ELISA. Third, to characterize contacts within the domestic host population, interviews were conducted with cattle owners regarding their husbandry practices across seasons (i.e. descriptions of grazing and watering areas as well as herd mixing). Fourth, to describe the potential role of host diversity in ecosystem infection risks, macroparasite density (i.e. ticks) was estimated for landscape compartments that contrasted in terms of potential hosts present (i.e. (i) wild, (ii) domestic and wild, and (iii) domestic only).

Our study primarily shows the following results. (1) Interspecific interaction rates, as estimated by telemetry, vary between sites and have a pronounced seasonality (peak occurs during the hot dry season). (2) Resource distribution (i.e. water and grazing areas) seems to condition the frequency and distribution of these contacts in the different landscape compartments. (3) Cattle incursion frequencies into protected areas and the frequency and intensity of contact with buffalo significantly positively affect the probability of foot-and-mouth antibody acquisition in cattle. The probability of antibody loss in cattle is also a function of diminished rates of interaction with buffalo. (4) Intraspecific interaction densities positively influence FMD serological incidence in cattle. (5) Top predator presence in the landscape could limit cattle incursion into protected areas and reduce the likelihood of their being infected by wild host populations. (6) Finally, the estimated densities of two macroparasite genera, the ticks Rhipicephalus sp. and Amblyomma sp., in the vegetation were higher in communal spaces where there was no interaction with wild hosts and where host species richness was weak.

The results of this study on the interspecific transmission of pathogens between wild and domestic populations in tropical ecosystems encourage the exploration of research topics that are still largely unexplored, including the evolution of virulence transmission modes of pathogens hosted by sympatric wild and domestic populations. Individual control mechanisms deployed against pathogens (i.e. immunity resulting from natural exposure and/or vaccination) are also discussed in this thesis. Finally, this work generates questions about biodiversity's role in species interactions and its potential dilution or amplification effects on macroparasite abundance.