10 · *Characterization of Buffalo/Cattle Interactions for Assessing Pathogen Transmission*

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Introduction

African buffalo (*Syncerus caffer*) and domestic cattle (*Bos taurus*, *B. indicus*) coexist in large tracks of Africa. Both are large bovid species (but see Chapter 2) that are principally grazers with similar body sizes, and therefore rely on and compete for the same natural resources. Savannas are an important biome in Africa that have been maintained for the last millennia by the interaction of wild herbivores, livestock and their herders. Human-induced fire and livestock dung-related nutrient cycling play an important role in the enrichment and heterogeneity of these habitats (Marshall et al., 2018). Savannas offer important grazing that is more or less degraded or constrained by the footprint of human activities, including agricultural expansion and the scarcity of surface water, especially during the dry season (Valls-Fox et al., 2018). Today, most savanna African buffalo populations live in protected areas (Chapter 4), often with no physical separation to prevent interactions with livestock living on the periphery of, and more and more frequently within, these protected areas. Savanna buffalo populations outside protected areas live in areas where they can also encounter livestock (e.g. Garissa district, Kenya). Interactions between buffalo and cattle have increased significantly during the second half of the twentieth century due to the wider use of anti-trypanosomiasis drugs and the reduction of the range of trypanosomiasis vectors, *Glossina* sp. This provided an opportunity for herders to penetrate into grazing areas where cattle previously would have simply died, including in protected areas of West, Central and Eastern Africa. As livestock populations in these regions grew, so

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did demand for grazing resources, increasing competition with crop producers and placing livestock in closer proximity to buffalo populations relatively isolated from them until recently (e.g. Cuisance, 1996). This phenomenon is not limited to savannas, as it can also be observed in rainforests in which forest buffalo (*S. c. nanus*) are increasingly interacting with intruding cattle.

Buffalo/cattle interactions are a source of conflict not only because both species compete for resources, but also due to the risk of disease transmission in both directions (Miguel et al., 2017). These interactions can contribute to the disease burden of small-scale livestock production systems as buffalo can maintain or spread some diseases detrimental to the health of cattle (e.g. tick-borne diseases, bovine tuberculosis; Caron et al. 2013; Chapter 9). Commercial livestock production, especially that intended for international trade, is very sensitive to some diseases that cannot be eradicated in buffalo, and therefore important trade regulations are imposed on producers depending on their exposition to buffalo/cattle interactions (e.g. foot and mouth disease, FMD; Scoones et al., 2010; Thomson et al., 2013; Chapter 12). Some of the diseases mentioned above are zoonoses, most of them hardly studied in African contexts and therefore with an (often unknown) impact on public health (e.g. Rift valley fever, brucellosis; Gadaga et al., 2016). Finally, the interactions work both ways, and cattle can transmit diseases that can threaten the survival of wildlife such as rinderpest, a cattle disease imported during European colonization that decimated wildlife populations in Africa (van Onselen, 1972; Chapter 12). Buffalo/cattle interactions are therefore an important aspect of the management of African savannas and forests with socioeconomic, environmental and political implications. For example, the success of Transfrontier Conservation Areas in southern Africa connecting parks across borders and promoting wildlife mobility can be weakened by sanitary regulations aiming to protect cattle production from transboundary animal diseases (Ferguson et al., 2013).

In this chapter, we will review the knowledge on the characterization of the buffalo/cattle interaction, the related ecology of pathogen transmission, and how this transmission can be modelled to improve the management and control of diseases. The geographical distribution of studies on buffalo/cattle interactions and the associated disease ecology is uneven, with almost none undertaken in rainforest habitats and most focused on savanna habitats in eastern and mainly southern Africa.

Characterizing the Buffalo/Cattle Interface

Wildlife/livestock interactions occur in wildlife/livestock interfaces that exist worldwide and represent a matter of concern for various reasons, including predation by wildlife, competition for resources, biodiversity conservation, cross-breeding and crop-raiding (Osofsky and Cleaveland, 2005). However, the risk of disease transmission at these interfaces has probably been the most burning issue in modern times (Kock, 2005). Frameworks to define and characterize these interfaces have also been proposed recently, including the definition of the interface that is used in this chapter: 'the physical space in which wild and domestic species, as well as humans, overlap in range and potentially interact' (Caron et al., 2021). They principally focus on defining the geographic (e.g. spatial), physical (hard–soft edge) and dynamics (e.g. seasonality, small-scale and interannual dynamics) properties of the interface to understand if, where and when wild and domestic species interact.

For both buffalo and cattle, access to scarce water and grazing resources in the savanna ecosystem, including agricultural fields (which attract buffalo), is the main driver of buffalo and cattle movements across their respective land-use boundaries (i.e. protected areas and communal land). In addition, rainfall, natural and human-induced fires, as well as human activities and infrastructure are key factors influencing the distribution of buffalo and cattle in space and time (Higgins et al., 2007; Cornélis et al., 2011; Naidoo et al. 2012; Ogutu et al., 2012). These movements determine a spatial use that may or may not trigger contact between buffalo and cattle and create the buffalo/cattle interface.

In Africa, buffalo/cattle interfaces are found mainly in savanna ecosystems. Forest buffalo (*S. caffer nanus*) seldom interact with cattle, given their exclusive dwelling in forest habitats in which cattle husbandry seldom exists. However, recent changes in pastoral practices in Central Africa (e.g. south-west of the Central African Republic) have pushed cattle closer to forest buffalo habitat, especially during the dry season (Chardonnet, personal commmunication). In savannas, the buffalo/cattle interface can exist under the form of a 'hard edge', a type of interface found mainly in southern Africa and especially South Africa (e.g. the fence surrounding Kruger National Park on the South African side), but not exclusively (e.g. also in Botswana, Namibia; Figure 10.1). The remaining majority of the interfaces found in West, Central, Eastern and Southern Africa should be classified as 'symmetric soft interfaces' where both species can cross the edge and exploit resources a few kilometres maximum from the edge (Caron et al., 2021; see e.g. Figure 10.2). In

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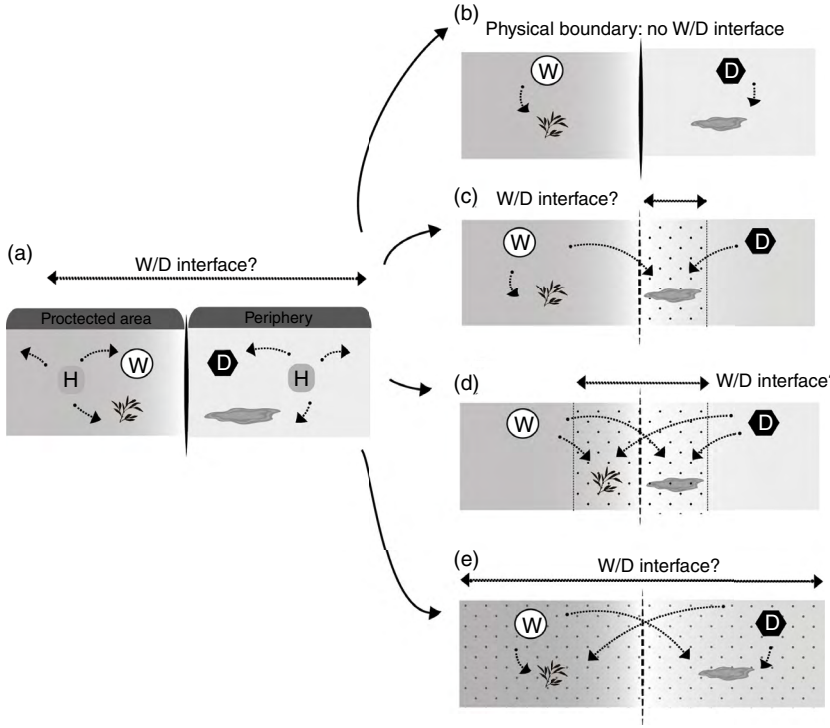

Figure 10.1 (a) Theoretical conceptual model of a wildlife/livestock (W/L) interface including wild buffalo (W) and domestic cattle (D) populations, human actors (H) as well as key landscape features including land-use boundaries (dark line separating a hypothetical protected area and its periphery) and key resources (pasture and surface water for example, represented by icons) that will help define hypotheses about the W/L interface (horizontal bidirectional arrow on top); the human component is only represented in panel (a) but it is assumed that the human driver is one of the most important to define W/L interfaces, defining cattle production practices, buffalo management and resource distribution. (b) Hard-edge interface: a fence or a natural impassable barrier (e.g. non-crossable river) limits the movements of buffalo and cattle: this is a hard edge; this type of interface is theoretical for many national park boundaries as animal movement-proof edges are rare. (c) Asymmetric semi-hard interface: only one of the two species (i.e. buffalo here) can cross the edge to use natural resources; the interface is limited to a small band in the cattle side; the reverse is of course also possible. (d) Symmetric soft interface: both species can cross the edge and exploit resources across the edge; this type of interface exists for many unfenced protected areas. (e) Diffuse interface: there is no edge and the home range of buffalo and cattle overlap extensively. In (c)–(e), the temporal dimension of the interface is crucial to understanding the dynamics of the interfaces. Adapted from Caron et al. (2021), with permission from Springer.

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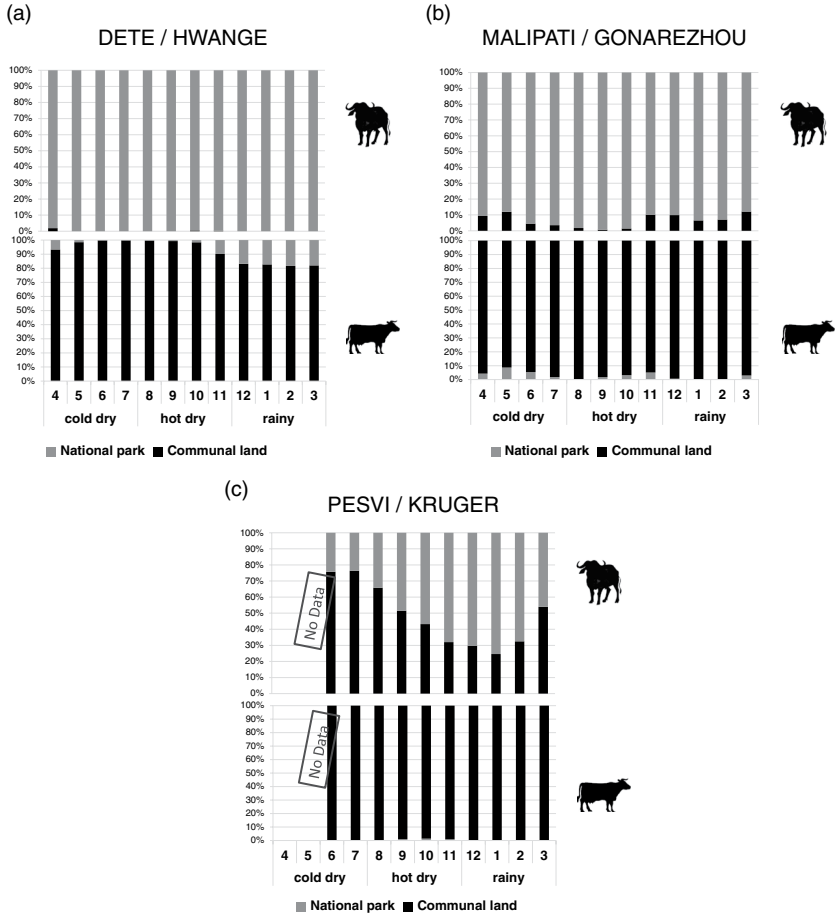

Figure 10.2 Three asymmetric and seasonal interfaces in southern Africa characterized by GPS localizations of cattle and buffalo in protected areas or communal land used for extensive subsistence livestock farming. (a) The Dete/Sikumi Forest interface in Zimbabwe without any fence: a mainly asymmetric interface during the rainy season when cattle enter the protected Sikumi Forest. (b) The Malipati/Gonarezhou national park interface in Zimbabwe separated by the Mwenezi River that dries part of the year: asymmetric interface with buffalo entering the communal land most of the year but with some cattle incursions into the protected area during the cold-dry (and hot-dry) seasons. (c) The Pesvi/Kruger national park in Zimbabwe/South Africa separated by the (large) Limpopo River that dries part of the year: an asymmetric interface with buffalo entering the communal land most of the year but with seasonal variations (Miguel, 2012).

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practice, few 'diffuse interfaces', where both cattle and buffalo permanently coexist on the same production unit, currently exist in Africa. These may occur locally within extensive mixed ranches associating cattle and buffalo for diversified ecotourism, hunting and meat productions. However, veterinary regulations applicable in most African countries prevent such associations to protect livestock from buffalo-borne disease transmission that would put a high burden on meat production both from a production and regulatory perspective. Early attempts in southern Africa to produce 'disease-free' buffalo herds, which could be associated with cattle herds on the same ranges, proved technically and financially difficult to maintain in the long run. From a spatial perspective, other types of interfaces such as 'asymmetrical interfaces' can exist but are rare, despite their potential to promote buffalo/cattle coexistence systems. The asymmetry can, however, emerge from 'symmetric soft interfaces' and produce some opportunities for coexistence between buffalo and cattle. For example, where cattle are penned at night to protect them from natural predation or theft, buffalo can use this nocturnal temporal window to use space previously used by cattle (Miguel et al., 2017).

Characterizing wildlife/livestock interfaces has been the focus of recent research, supported by the development of technologies such as telemetry and remote sensing technologies (e.g. Richomme et al., 2006; Pruvot et al., 2014; Woodroffe et al., 2016; Campbell et al., 2019; Triguero-Ocana et al., 2021). To characterize interfaces, multidisciplinary approaches are often required. They can range from behavioural studies of wild and domestic species (e.g. telemetry or capture–marking–recapture techniques) to emerging non-invasive molecular techniques to assess the presence or absence of specific species (e.g. faecal or environmental sampling), as well as sociological studies to understand people's perceptions, knowledge and practices regarding the state and management of the interface. Focusing on the characterization of buffalo/cattle interfaces, satellite remote sensing (SRS) offers an array of methodologies to monitor, characterize and quantify how natural resources impact buffalo and cattle movements in their respective environments (Rumiano et al., 2020). Optical and radar SRS imagery can be used efficiently to discriminate surface water and land covers at a landscape scale due to a wide range of sensors, with various spatial and temporal resolutions available (Corbane et al., 2015; Bioresita et al., 2018; Huang et al., 2018). The effects of fire on vegetation can spatially and temporally be detected using vegetation spectral signature as their intrinsic characteristics change over time (Meng and Zhao, 2017). Whereas precipitation

can be measured with advanced infrared (IR), passive microwave (MW) and radar sensors provide a complementary alternative to in situ records (Camberlin et al., 2019). These SRS techniques are available to characterize interfaces across the range of buffalo and cattle in Africa at the spatial and temporal scale deemed most relevant to the issue at hand. Combining these SRS methodological approaches with telemetry studies on both species and the pastoralist and agro-pastoralist practices can provide a good understanding of buffalo/cattle interfaces.

Most of this research on wildlife/livestock interfaces has been done in the field of ecology (e.g. Hibert et al., 2010) and especially in the emergent field of disease ecology. The study of the ecology of pathogen and disease transmission at the wildlife/livestock interface seeks to: (1) understand the patterns of contact between wild and domestic species, especially the intensity and frequency of these contacts as well as their driving factors; (2) assess the proportion of these contacts that could trigger an 'infectious contact' defined as the interspecies transmission of a pathogen; and (3) model the host and pathogen population dynamics in this context and assess the efficiency of potential management options to mitigate or control diseases (de Garine-Wichatitksy et al., 2021).

Measuring Infectious Contact at the Buffalo/Contact Interface

Measuring Contacts between Two Species

Determining the relative location of two individuals to each other (e.g. individual cattle and buffalo) is the first step to be able to estimate if there is a risk of interspecies pathogen transmission. This risk will be defined by the evaluation of potential infectious contacts between two individuals. As the observation of infectious contact *per se* is almost impossible (i.e. pathogens are invisible to the naked eye), interspecies contacts are used as a proxy. For a given pathogen, a direct mode of transmission requires close contact between an infected and a healthy individual, that is both hosts are at the same place and at the same time (Bengis et al., 2002; Altizer et al., 2003). Indirect transmission can occur when a pathogen is excreted by the infected individuals in the environment at a specific location (e.g. directly on the ground or water) and subsequently infects a susceptible host using the same location after the infected host. Until recently, direct observation was the only way to determine the position of wild individuals, a time-consuming technique difficult to implement

on two species. The advent of satellite telemetry using a global positioning system (GPS) has transformed the possibility to assess the temporal and spatial positions of animals in a given area with high precision and temporal accuracy (Cagnacci and Urbano, 2008). This breakthrough in technology can generate a lot of data: a GPS collar collecting one GPS point every hour for two years will produce 17,520 locations of the individual in addition to its speed, the position of its head and the temperature among numerous data that can now be collected with captors integrated into the GPS collar. This technology has thus enabled new insights into the ecology of animal movements (e.g. patterns of biodiversity, ecological characteristics of individual species and ecosystem function; Kays et al., 2015; Eikelboom et al., 2021). Data describing the movements made by individual animals during their entire lifetime, and species-wide sampling from multiple populations, are now becoming available and offer new opportunities to measure and estimate contacts (Flack et al., 2016). Wielgus et al. (2020) used GPS telemetry to describe fission–fusion dynamics of buffalo in various groups at several sites. This example shows how GPS telemetry can define and improve species-inherent ecological behaviours that can potentially be used, by extension, to characterize intra- and interspecies contacts. Proximity loggers are another recently developed tool. While they only provide a measure of direct contacts between individuals (i.e. they detect and log events when tagged individuals are located within a predefined distance threshold; Böhm et al., 2009; Drewe et al., 2013), they cost considerably less than GPS collars. This allows a larger number of individuals of a given wildlife or livestock population to be equipped, depending on the difficulties and costs associated with the capture/fitting of the collars.

Both technologies allow researchers to determine when, and for how long, two animals have been in proximity and, therefore, describe the contact patterns relevant for a directly or indirectly (only for GPS) transmitted pathogen. However, few studies on large herbivores occupying African savanna environments using these technologies have been conducted so far (Owen-Smith et al., 2020). These new technologies have several constraints that can potentially limit their use. The most apparent is the cost of recording units (until recently between €1500 and €2500 per buffalo unit) to be fitted to individual animals (until recently between €1500 and €2500 per buffalo unit) (Cooke et al., 2004) and the cost of the capture and then recapture to remove the collars (€1000–1500 per head). These devices are also not robust enough to study adult male buffalo and can be damaged by cattle during, for example, dipping for

tick-borne disease control (Caron, personal communication). Moreover, GPS telemetry can affect animal behaviour, survival and well-being in some instances, and its system function is influenced by environmental variables (e.g. climatic factors, habitat types, terrain roughness) and animal behaviour (e.g. movement, orientation of the collar) (Tomkiewicz et al., 2010). As a result, spatial inaccuracy of the acquired locations, and missing data in the form of failed location attempts, can potentially impact derived GPS telemetry data and lead to mistaken inferences on animal spatial behaviour, especially those involving movement paths and habitat selection (Frair et al., 2010). Finally, movement is a continuous process that can only be tracked by sampling, usually at constant time intervals. This sampling is constrained by the limits of the technology used (battery life), which forces a trade-off between the sampling frequency of the displacement and the duration of the tracking. This trade-off is especially important when working on contacts between two individuals as we can assume that most of these contacts occur between sampling points. However, telemetry technology is developing rapidly and future systems may overcome some of these constraints.

Contact Estimation at the Buffalo/Livestock Interface

Few studies have investigated wildlife/livestock contacts for epidemiological or other purposes. Some of the main models studied so far are: the interface between the European badger (*Meles meles*) and cattle in the UK in relation to bovine tuberculosis (e.g. Woodroffe et al., 2016; Campbell et al., 2019); the interface between wild boar (*Sus scrofa*) and cattle in relation to the same disease in Spain (e.g. Barasona et al., 2014; Triguero-Ocana et al., 2019); the interface between white-tailed deer (*Odocoileus virginianus*) and cattle in the United States in relation to bovine tuberculosis (Ribeiro-Lima et al., 2017); the interface between elk (*Cervus canadensis nelson*) and cattle in relation to brucellosis in the US (Proffitt et al., 2011); and the buffalo/cattle interface in relation to FMD and bovine tuberculosis (e.g. Miguel et al. 2013, 2017; Valls-Fox et al., 2018).

By combining telemetric and epidemiological approaches to sympatric cattle and buffalo, recent studies have provided good evidence that the contact rate with buffalo significantly influences FMD dynamics in cattle populations living at the periphery of conservation areas in Zimbabwe (Miguel et al., 2013, 2017). In the latter study, 36 GPS collars were deployed on African buffalo and cattle to assess proximity patterns at the

symmetric soft interface of three protected areas in Zimbabwe, namely Hwange and Gonarezhou in Zimbabwe and Kruger in South Africa. GPS acquired one location per hour and data collection ran between 14 and 17 months between 2010 and 2011. One head of cattle was equipped per herd (herd size averaged 12) on the assumption that the movement of one of the lead cows would significantly represent the daily movement of the herd. At night, cattle herds were penned in 'kraals' (a case of partial asymmetrical interface between cattle and buffalo at night; Figure 10.1) to protect them from predation and theft. Adult female buffalo were equipped and their movements were assumed to represent mixed herd movements (Chapter 6). To assess interspecies contacts relevant for FMD, direct and indirect contacts were calculated based on the buffalo–cattle dyad being: (1) at the same place together (i.e. direct contact); the 300 m radius accounts for GPS precision and herd size; or (2) one or the other being in a 300 m radius from a location of the other up to 15 days later; this spatial–temporal window was decided based on the potential survival of the FMD virus in the environment.

Contacts between buffalo and cattle varied between sites and seasons and individual cattle. Of importance, almost no direct contact was recorded during the entire study. The locations of indirect contacts were both inside the national parks and in the communal land and varied greatly between sites, with most of the spatial overlap occurring in the Kruger–Pesvi interface area (Pesvi is a small village across the Limpopo River in Zimbabwe, along the northern section of Kruger National Park; Figures 10.3 and 10.4). Contacts increased from the rainy season towards the late dry season.

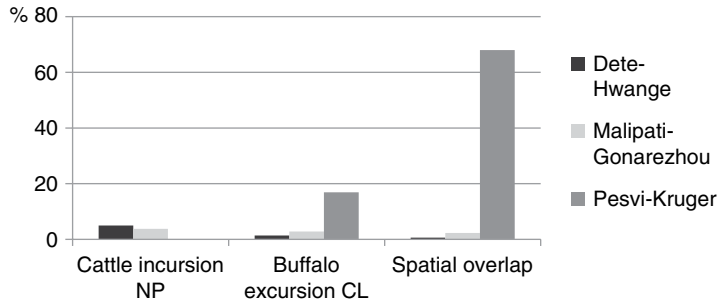

Figure 10.3 Percentage of cattle/buffalo contacts relative to sites and land-use (inside national park – NP – or inside the Communal Land – CL): during the study by Miguel et al. (2013).

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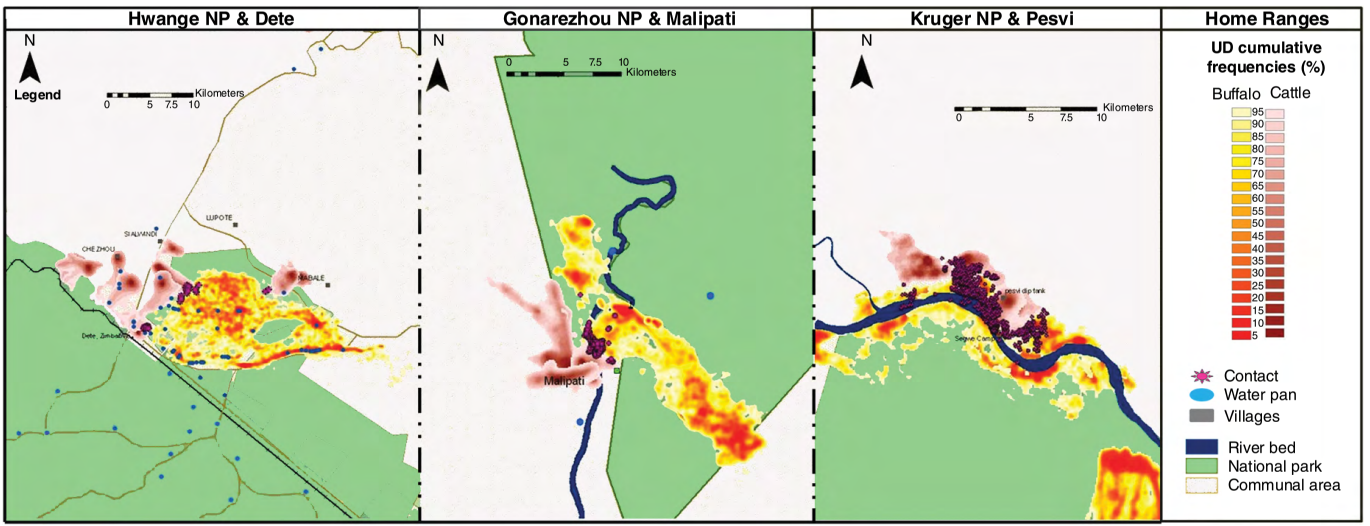

Figure 10.4 Maps of cattle and buffalo home ranges (red-brown and red-yellow, respectively) and contacts at three national parks (NP) borders in southern Africa (KAZA-TFCA: Hwange–Dete and GL-TFCA: Gonarezhou–Malipati and Kruger–Pesvi). The locations of contact events between cattle and buffalo are represented by pink stars (i.e. cattle position recorded within 300 m of a buffalo position less than 15 days after the buffalo position has been recorded). Source: Miguel (2012).

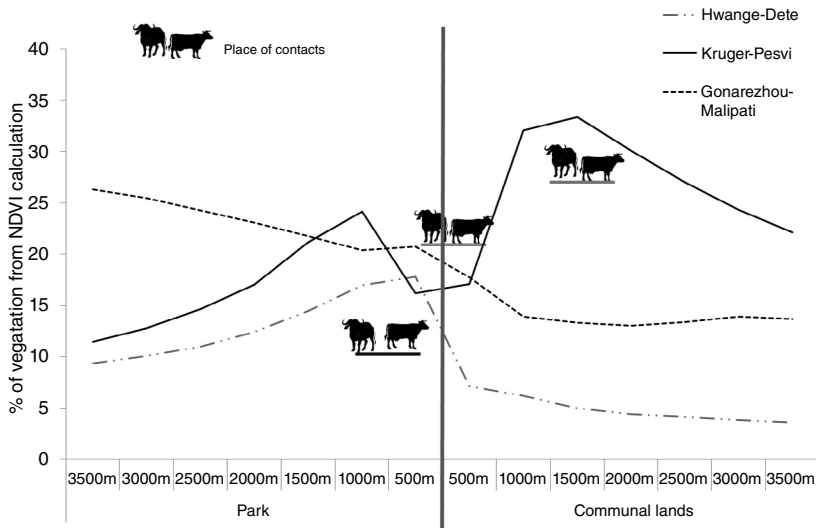

Figure 10.5 NDVI estimations (lines) in communal lands and protected areas of the three sites studied in relation to the distance from the interface (dark vertical line). The cattle and buffalo pictogram illustrates the localizations of the contacts between the two species and the line below these pictograms represents the 95 per cent range of these contacts. Source: Miguel (2012).

Because buffalo and livestock use similar resources, particularly water and grazing areas during the dry season, they use similar habitats, which explains the contact patterns observed. Quantitative observations of the density of vegetation on each side of the boundaries (National Park/Communal Land) were obtained, for the three interfaces, using satellite images and the calculation of NDVI (Normalized Difference Vegetation Index). Although NDVI does not allow grassland to be distinguished from shrubland and forest areas, this index can be used to measure the plant phenology and by extention, the distribution of available vegetation in communal lands and adjacent protected areas. High variability in terms of habitat use was observed across sites with NDVI structuring the buffalo habitat use. When NDVI was higher outside the protected areas (Kruger–Pesvi interface), buffalo exited from the Kruger NP boundaries to range inside the communal land areas (Figure 10.5).

Surface water distribution among study sites varied significantly. Two river systems for Pesvi–Kruger (Limpopo River) and Malipati–Gonarezhou (Nuanetsi River) flow part of the year and only offer a few stagnant pools of water during the dry season. In Dete–Hwange,

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scattered water pans provide water across the year, with their number decreasing as the dry season proceeds. This contrast in water distribution patterns could explain the difference in contact rates between the three study areas. For example, in the Hwange–Dete study site, cattle and buffalo preferred open grassland habitats found close to water. During the rainy season, cattle entered the protected forest area daily, pushed by herders to avoid feeding on the crops growing just outside the protected forest border, and buffalo avoided cattle completely. During the dry season, when cattle ranged further into the protected area in search of forage, buffalo and cattle spatial overlap increased as water dependence took precedence over avoidance (Valls-Fox et al., 2018).

The role of lions in buffalo–cattle contacts was also explored in the same study site (Miguel et al., 2017). Buffalo and cattle avoided the use of the same pasture up to 2 months after one species had used a specific location. Lions made frequent incursions in the interaction zone a few days to weeks after buffalo had used that zone and buffalo avoided areas recently used by lions. Lions could therefore impact the spatiotemporal overlap between cattle and buffalo and therefore buffalo–cattle contacts.

Finally, buffalo/cattle contacts were structured by land-use and resource gradients (mainly water and grazing) as well as the presence of wild predators. The small sample size of these studies (i.e. a few individuals tracked for a dozen months) limits the extrapolation of results at population levels. However, this limit is somehow attenuated by the gregarious organization of both buffalo (in mixed herds) and cattle (in managed herds) for which the movements of a few individuals represent the behaviour of the herd.

From Interspecies Contact to Infectious Contact

Besides direct contacts, the capacity of the pathogen to survive in the environment and to be able to infect another host will determine the temporal window in which transmission can occur. The same applies to vector-borne transmission (e.g. arthropod-borne) with the difference that a spatial window will need to be taken into account in addition to the temporal window to account for the potential mobility of the vector in the environment (Dougherty et al., 2018).

Infectious contacts, that is contacts that result in the transmission of one or more pathogens, are invisible ecological processes that are currently impossible to characterize in real-time. An assessment of contacts

as presented in the previous section provides some information about the spatial and temporal dynamics of infectious transmission but cannot be directly translated into an assessment of infectious contacts. For example, in the study by Miguel et al. (2013), the GPS protocol at the buffalo/cattle interface was completed by a longitudinal survey of 300 cattle, with five repeated sampling sessions undertaken on known individuals over 16 months. Immunological assays, which allow the production of antibodies following infection or vaccination to be tracked, were used to assess serological transitions (i.e. incidence and reversion) in the surveyed cattle. The incidence in the cattle populations of FMD antibodies produced following infection varied among sites and as a function of contact rates with African buffalo. The incidence was higher for sites with higher contact rates between the two species and varied according to the season.

The use of genomics on hosts and pathogens can help in inferring infectious contacts and their direction. Kamath et al. (2016) in the Greater Yellowstone ecosystem estimated the date and the frequency of brucellosis introduction events and found that the disease was introduced into elk (a.k.a. wapiti, *Cervus elaphus*) from cattle in this region at least five times. The diffusion rate varies among *Brucella* lineages and over time. They were also able to estimate the direction of transmission between hosts from different species with 12 host transitions from bison (*Bison bison*) to elk, and five from elk to bison. However, up to now, such a large-scale study using both telemetry and pathogen genetic studies has not been implemented for the characterization of buffalo/cattle interfaces (but see Musoke et al., 2015).

Space–Time Window as a Proxy of Modes of Transmission

Infectious diseases spread through transmission routes between hosts, and each pathogen can use one or more modes of transmission to 'jump' from one host to another. Therefore, as seen for FMD in the previous section, the pathogen of interest and its specific mode(s) of transmission will define the space–time window in which a pathogen can spread from an infected to a susceptible host. The behaviour of both hosts (e.g. cattle and buffalo), the characteristic of the pathogen, and, when relevant, the ecology of the vector will therefore be crucial to estimating the risk of interspecies pathogen spread. This also means that a given contact network between buffalo and cattle can produce very different risks of interspecies spread when considering pathogens with different modes of

transmission and similar risks when the modes of transmission and the characteristic of two pathogens are converging. Finally, the data collection method also can impact the quality of the assessment.

To define contacts responsible for FMD transmission between buffalo and cattle, Miguel et al. (2013) used a spatial window of 300 m and a temporal window of 15 days. The spatial window took into account both the inaccuracy of the GPS measure and the ability of and cattle to move during a one-hour period. The temporal window accounted for the potential environmental transmission of the virus. Bovine tuberculosis is most often transmitted by respiratory routes, requiring close contact between buffalo and cattle, but the pathogen also can spread by indirect contacts, as the mycobacteria *Mycobacterium bovis* can survive in faeces for up to 1 month in natural conditions in southern Africa (Tanner and Michel, 1999). A space–time window to assess the probability of bovine tuberculosis transmission between buffalo and cattle (or vice versa) must take into account direct contacts between both hosts, as well as indirect contacts, with up to 30-day intervals to reflect the survival of the pathogen in faeces. Therefore, a single data set of contact patterns between buffalo and cattle will result in different estimations of the risks of pathogen transmission between species depending on the modes of transmission of the pathogen considered.

Modelling Pathogen Transmission at the Buffalo/Cattle Interface

The dynamics of pathogens in multi-species assemblages are complex. They are influenced by the interaction of each host–pathogen dyad (e.g. morbidity, mortality rate), host population dynamics (e.g. social dynamics, size of groups, intergroup contacts) and interspecies contacts. Various approaches exist to model each of these components, but they have yet to be integrated to produce a holistic model of the buffalo/cattle interface. Here we present examples of modelling approaches to buffalo and cattle population dynamics as well as of interspecies contacts that could support the integration of a pathogen or disease transmission model.

Contact Network and Graph Models

Contact networks, where individuals are represented as nodes and interactions between them as edges, expand the relevance of epidemiological

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models by capturing the patterns of interaction between individuals (Hamede et al., 2009, 2012; Yin et al., 2020). However, realism and precision can limit the applicability of contact data to general contexts (White et al., 2015), especially as contact networks are rarely fully described for wildlife species. To address these issues, we can infer the rules behind the generation of contacts within the network and use them to extrapolate the contact structure in the entire population. Exponential random graphs models (ERGMs) provide an appropriate framework to do so. The purpose of ERGMs is to describe parsimoniously the local forces that shape the global structure of a network (Silk et al., 2017, 2018). To this end, a network data set may be considered as the response variable in a regression model, where the predictors are based on individual traits (gender, age, group), such as 'the propensity for individuals of the same sex to form partnerships', or structural metrics of the network (degree, two-stars, triads), such as 'the propensity for individuals to form a cluster'. The information gleaned from the use of an ERGM may thus be used to understand how contact networks are generated and to simulate new random realizations of networks that retain the essential properties of the observed network, which can be used to simulate disease dynamics (Reynolds et al., 2015). Such an approach was attempted using the GPS data of 84 collared African buffalo from four populations (Wielgus et al., 2020). Unfortunately, no non-random structure of contact was found within the sampled networks because they were missing individuals representing, for example, adult males or juveniles. Nevertheless, ERGMs hold great potential for pathogen transmission modelling within buffalo populations if GPS data from a significant number of individuals within the same population can be sampled for several years.

Spatialized Mechanistic Modelling Approaches

Spatial models integrating the environmental drivers of buffalo and cattle mobility can be developed to assess the potential contacts between the two species and their variations in space and time. For example, the Ocelet domain-specific language and open modelling platform (www.ocelet.fr), based on the tool of interaction graphs (Degenne and Seen, 2016), allows the implementation of spatialized mechanistic modelling approaches (e.g. Grégoire et al., 2003) that connect 'entities' of different nature (e.g. buffalo, cattle, water bodies, grazing areas), define their interactions (e.g. interspecies relations, species-natural

resources dependencies), and simulate their spatiotemporal dynamics. As a result, such models allow the assessment and visualization of the location and frequency of potential contacts between different species based on a wide range of variables that can evolve through time (e.g. animal behaviour, natural resources distribution, human-based social and economic processes, pathogen transmission). Such an approach was used to simulate the impact of the surface water spatial distributions and its seasonal variation on African buffalo movements in a given area (Rumiano et al., 2021; Figure 10.6). From there, cattle movements can be added to assess the potential contact areas between the two species (Rumiano et al., in prep.), provided that ecological empirical knowledge on focal species is available to feed the model and determine its design. Of note, GPS telemetry data collected from previous works (Miguel et al., 2013; Valls-Fox et al., 2018) provide necessary information for calibration (conceptual phase) and validation (assessment phase) of the models.

Combining Host Contact and Pathogen Transmission

Once interspecies host population dynamics have been modelled using one of the methodologies presented above, pathogen data can then be coupled with host population modelling to better understand the relationship between environmental drivers, host contacts and pathogen dynamics. This coupling will resolve an important limitation of most epidemiological models that assume homogeneous mixing between naïve and infected hosts, and thus omit the heterogeneity of host behaviour (Lloyd-Smith, 2005; Paull et al., 2012). Thus far, the use of such applications in disease ecology has been limited, especially at an interspecies level, despite the importance of interspecies contact patterns on pathogen transmission and the impact of infection on host behaviour (Dougherty et al., 2018). New insights into buffalo social dynamics will modify the dynamics of pathogens spread in buffalo groups (Chapter 6; Wielgus et al., 2020, 2021). Gregarious species with connected and unfragmented social units (classical definition of a mixed herd) should facilitate pathogen spread compared to gregarious species with a higher level of fusion–fission dynamics (Sah et al., 2017). Similarly, these fusion–fission patterns will have an impact on the risk of pathogen spread between cattle and buffalo (both ways) at interface areas.

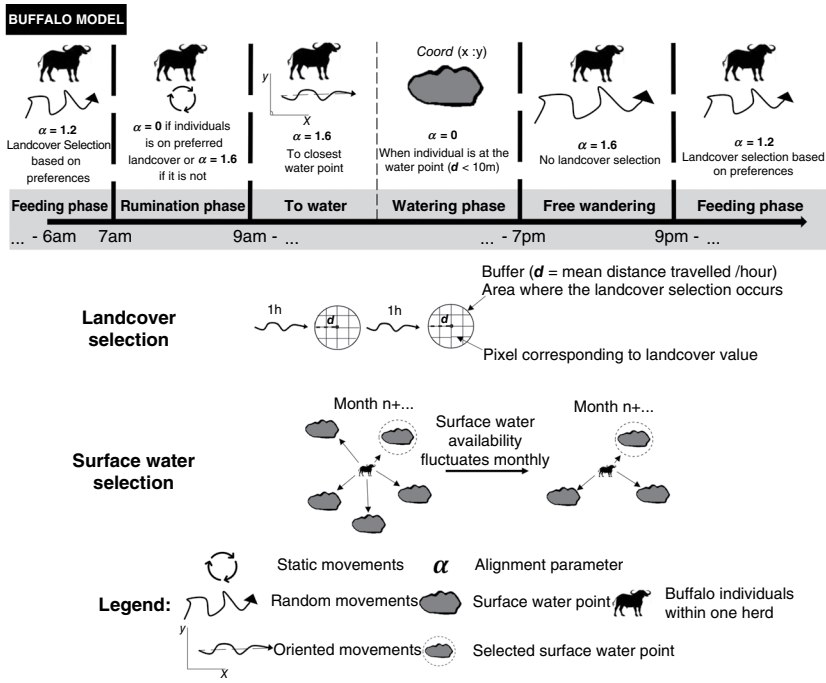

Figure 10.6 Designed mechanistic model of buffalo movements according to surface water seasonality, geographic location and type of land cover. This movement model is divided into five behavioural phases per 24-hour period (Feeding phase, Rumination phase, To water phase, Watering phase, Free wandering phase) that are based on buffalo behaviour (i.e. median speed per hour) derived from collected telemetry data of three study sites (Miguel et al., 2013; Valls-Fox et al., 2018). All individuals move from their starting location to the next at discrete time steps by a fixed distance, their direction defined for each time step as an angle. This angle is correlated to the alignment (α) of each individual with respect to their close neighbours, thus allowing simulation of a collective movement of interdependent individuals (Grégoire et al., 2003). The value given to α will determine the behaviour of the buffalo. During the 'Feeding phase', the buffalo will move until they reach a 'feeding' land cover type. During the 'Rumination phase', the buffalo stay in motion in the same land cover type. For these two behavioural phases, land cover selections occur within a determined buffer area corresponding to the mean distance travelled per hour (Rumiano et al., in prep.). In the 'To water phase', buffalo move towards the closest surface water (varies seasonally) from the buffalo's herd centroid position at the beginning of the phase. Once buffalo individuals are within 10 m of the targeted surface water point, the 'Watering phase' starts and all individuals stop their movements. During the 'Free wandering' phase, buffalo move freely in space. Land cover and surface water have been characterized at the landscape scale (10 m of spatial resolution) using supervised and unsupervised classifications on a selected time series of Sentinel-2 satellite images (Rumiano, 2021). The spatialized classifications have then been integrated into the model thanks to the spatial modelling language Ocelet (Degenne and Seen, 2016).

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Perspectives and Conclusion

Buffalo and cattle interactions and the sustainability of the systems that maintain both species are relevant to the coexistence between humans and nature in Africa. The potential spillover and spillback of pathogens between sympatric buffalo and cattle populations threaten biodiversity conservation, local and national agricultural economies and public health. If buffalo and cattle are to coexist in an open landscape, the sanitary risk will need to be managed according to a new paradigm relative to the level and types of risks that are acceptable. Currently, production systems have not managed to conceive a management process in which both species coexist (Chapters 12 and 14).

Different spatial models of animal movement, contact and interaction taking into account biotic and abiotic ecological features as well as behavioural mechanisms have been developed in recent years (Rastetter et al., 2003; Moorcroft 2012; Westley et al. 2018). Nonetheless, there is a need to further develop mechanistic animal movement, contact and interaction models that integrate independent and validated environmental SRS data enabling landscape-scale analysis of interspecies contact and interaction. Such models could benefit from the integration of especially characterized environmental SRS data while extending their application capacities to different environmental and ecological contexts (Neumann et al., 2015; Rumiano et al., 2020). Several SRS methodologies have already been developed to characterize spatial and temporal variations of environmental drivers, such as surface water (Naidoo et al., 2020) and vegetation (Zengeya et al., 2015), in relation to buffalo and cattle movements. By allowing the characterization of these environmental drivers at the landscape scale, SRS can improve the understanding of buffalo/cattle contacts and associated disease transmission estimations where in-situ environmental data are lacking.

Mechanistic models, even if they involve significant development and implementation costs, are less dependent on a correlation between ecological processes and environment properties than empirical modelling approaches (Dormann et al., 2012). By mathematically simulating interactions and mutual constraints among animal species, mechanistic models improve the transferability to different environments (Kearney and Porter, 2009). Such models can therefore be adapted specifically for interspecies contacts and interactions by improving focal species ecological behaviour simulations regarding habitat selection and spatial and temporal distributions of natural resources. Advances in GPS telemetry, such as decreasing size, weight and cost of tags, computing power enhancement, and improving battery autonomy and durability, are allowing this

technology to be used more efficiently on an expanded range of animal species, but also on animal population subcategories (e.g. female, juvenile, male) while increasing their temporal resolution (Kays et al., 2015). Improved GPS telemetry technology combined with the rapid growth of SRS use in functional ecology and the enhancement of specialized mechanistic models offer tremendous potential for evaluating inter-species interactions (Rumiano, 2021). This type of approach can prove to be very valuable in environments such as the buffalo/cattle interfaces in African savannas that are limited in terms of natural resources, highly sensitive to climate condition fluctuations and prone to constant changes in land-use/management practices.

Despite the limits and constraints of these studies, the understanding of buffalo/cattle interactions is crucial to managing the interface and mitigating its negative consequences. Modelling is important to investigate the consequences of some management options that cannot be tested in situ. For example, as resources drive these interactions, appropriate water management could reduce contacts between buffalo and cattle (e.g. Mwakiwa et al., 2013; Hilbers et al., 2015). One could suggest manipulating cattle management practices or buffalo behaviours, taking into consideration ethical aspects of animal welfare and transdisciplinary approaches when working with local stakeholders. Modelling also can be important to explore how these interactions will evolve: buffalo/cattle interactions are a moving target as both cattle herding (e.g. pastoralism and agro-pastoralism) and wildlife populations are currently adapting to changing environments (e.g. climate change, human demographic explosion, global markets; Kock et al., 2014). Modelling can also trigger essential discussions and debates between different actors (e.g. scientists, breeders, political institutions, etc.) and different research disciplines. This implies a participatory platform potentially allowing the integration of virtuous solutions for all (e.g. One Health).

In combination with other emerging initiatives such as commodity-based trade in southern Africa (Thomson et al., 2013), the management of buffalo/cattle interactions can be a pillar of a sustainable coexistence between humans and nature in African landscapes (du Toit et al., 2017). The current focus of the study of these interfaces in southern Africa (and to a lesser extent to East Africa) calls for more studies in different contexts including pastoralism of Central Africa, and different biomes including rainforests in which encroachment by cattle creates new types of interfaces.

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