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Drivers of foot-and-mouth disease in cattle at wild/domestic interface: Insights from farmers, buffalo and lions

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Abstract

Humans live increasingly in the proximity of natural areas, leading to increased interactions between people, their livestock and wildlife.

Aim: We explored the role of these interactions in the risk of disease transmission (foot-and-mouth disease [FMD]) between cattle and the African buffalo (the maintenance host) and how a top predator, the lion, may modulate these interactions.

Location: The interface of Hwange National Park (HNP) and surrounding communal lands, Zimbabwe.

Method: We combined a longitudinal serological cattle survey for FMD, GPS-collar data and cattle owners' interviews during four seasons in 2010–2011.

Results: Overall FMD incidence in cattle was low, but showed a peak during the rainy season. The incidence dynamic was significantly explained by cattle incursion into the protected area (i.e., buffer zone of 3 km inside HNP) and not by contacts with buffalo or contacts among cattle. These results suggest that FMD virus either survives in the environment or is transmitted by other ungulate groups or species. The analysis of incursion frequency in the buffer suggests that (1) buffalo and cattle are avoiding each other up to 2 months after one species track and that (2) lions make frequent incursions in the buffer few days to few weeks after buffalo had used it, whereas buffalo did not use areas occupied by lions. Lions could thus reduce the spatio-temporal overlap between cattle and buffalo in the interface, which could contribute to the low level of FMD incidence.

Main conclusions: During the rainy season, traditional herding practices push cattle away from growing crops near villages into the HNP but not during the dry season, suggesting that cattle owners may decide to rely on lower quality resources in the communal land in the dry season to avoid the risks of infection and/or predation in the HNP.

This study highlights the complex dynamics that operates at human/livestock/wildlife interfaces.

KEYWORDS

Africa, herding practices, human–wildlife coexistence, interspecific contacts, networks, space use

1 | INTRODUCTION

World-wide, increasing human populations and the associated re-source consumption and habitat fragmentation force humans and their domestic animals to live in increasing proximity to protected areas and wildlife (Wittemyer, Elsen, Bean, Burton, & Brashares, 2008). Protected areas are often delimited by soft and porous frontiers such as rivers or roads, and consequently, animal movements between protected areas and their periphery occur in both directions (Ferguson & Hanks, 2010). The interfaces between protected areas and surrounding communal lands are thus hotspots of potential interactions between people, their livestock and wildlife, often typified by human–wildlife conflicts including threat to human life (Packer, Ikanda, Kissui, & Kushnir, 2005), livestock depredation by carnivores (Kolowski & Holekamp, 2006), crop destruction by wild herbivores (Hoare, 1999), competition for shared resources (Mishra, Van Wieren, Ketner, Heitkonig, & Prins, 2004), hunting or illegal poaching (Nicholls, 2015) and disease transmission (Jones et al., 2008). Encroachment of human activities into wildlife habitats may have enhanced pathogen transfer between wildlife and domestic animals (Daszak, Cunningham, & Hyatt, 2000) and may have caused the emergence of several recent zoonoses (e.g., Ebola (Maron, 2014), MERS coronavirus (Azhar et al., 2014)). These interface areas raise significant public health and conservation issues globally (Woodroffe, Thirgood, & Rabinowitz, 2005).

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

In this study, we combined a unique dataset of simultaneous GPS-collar data of wild and domestic ungulates, and their natural predator, with livestock owners' interviews and an epidemiological survey of foot-and-mouth disease (FMD), in domestic hosts. We assessed the seasonal dynamics of the risk of FMD infection in a cattle population (*Bos taurus* and *Bos indicus)* living at the periphery of a protected area in Zimbabwe. FMD is a contagious disease caused by a virus characterized by complex transmission processes (Haydon, Woolhouse, & Kitching, 1997). Here, we explored the influence on FMD virus transmission to cattle of (1) the frequency at which cattle use the protected areas, (2) interspecific contacts between cattle and buffalo *(Syncerus caffer)* which is assumed to be the main reservoir of FMD (Thomson, Vosloo, & Bastos, 2003) and (3) intraspecific interactions among individuals from different cattle herds. At this interface, domestic cattle and African buffalo are at risk of predation by the African lion *(Panthera leo).* We eventually explored the potential modulating influence of lions' presence on interspecific interactions or on cattle incursion inside the protected area and thus the risk of disease transmission.

2 | METHODS AND MATERIALS

2.1 | Study area

The study was carried out at the northern periphery of Hwange National Park (HNP, ~15,000 km²; 35K 484826E; 794130S; Figure 1a). The edge of the national park is unfenced and thus permeable to movements of wild and domestic animals. HNP and surrounding protected areas host a large diversity of wild herbivore species (Chamaille-Jammes, Valeix, Bourgarel, Murindagomo, & Fritz, 2009) and are characterized by a relatively high abundance of large carnivores (e.g., 3.5 lion/100 km² (Loveridge, Hemson, Davidson, & Macdonald, 2010)). The mosaic of land use at the periphery of HNP is composed of Forestry Commission areas (Sikumi Forest), which are protected areas designated for sustainable use of natural resources, and communal areas. Activities in communal lands consist of subsistence farming with small-scale livestock production. At night, cattle herds are usually confined to enclosures located close to owners' houses. During the day, they are generally driven by a herder to grazing areas and water points. Entering national parks is forbidden throughout the year in Zimbabwe (Lindsey, Romanach, Tambling, Chartier, & Groom, 2011). However, the use of natural resources within the Forestry Commission area is more flexible, with permission granted to local communities for limited collection of deadwood and to a certain extent a tolerance for grazing within 3 km of the boundary.

According to these cultural practices, we restricted our analyses to an area encompassing a 3-km strip within protected lands (hereafter referred to as the "buffer") and the adjacent communal lands (Figure 1a). Overall, the vegetation is characterized by a woodland–bushland semi-arid savanna (Rogers, 1993). NDVI (Normalized Difference Vegetation Index) extracted from Landsat images (Landsat-7 2012/04/29, i.e., end of rainy season) was 13% in the buffer, whereas it was 5% in the first 3 km of communal lands, suggesting higher vegetation productivity and biomass in the buffer (Figure 1b, Google earth picture Cnes/Spot image 2012). Furthermore, the vegetation is less fragmented and less overgrazed in the buffer than in communal lands. Available surface water for animals is scattered over the landscape (Figure 1a), but water point density is three times higher in the buffer (0.25 water points per km²) than in the adjacent communal lands (0.08 water point per km²; including pans and boreholes). The mean annual rainfall is ~600 mm,
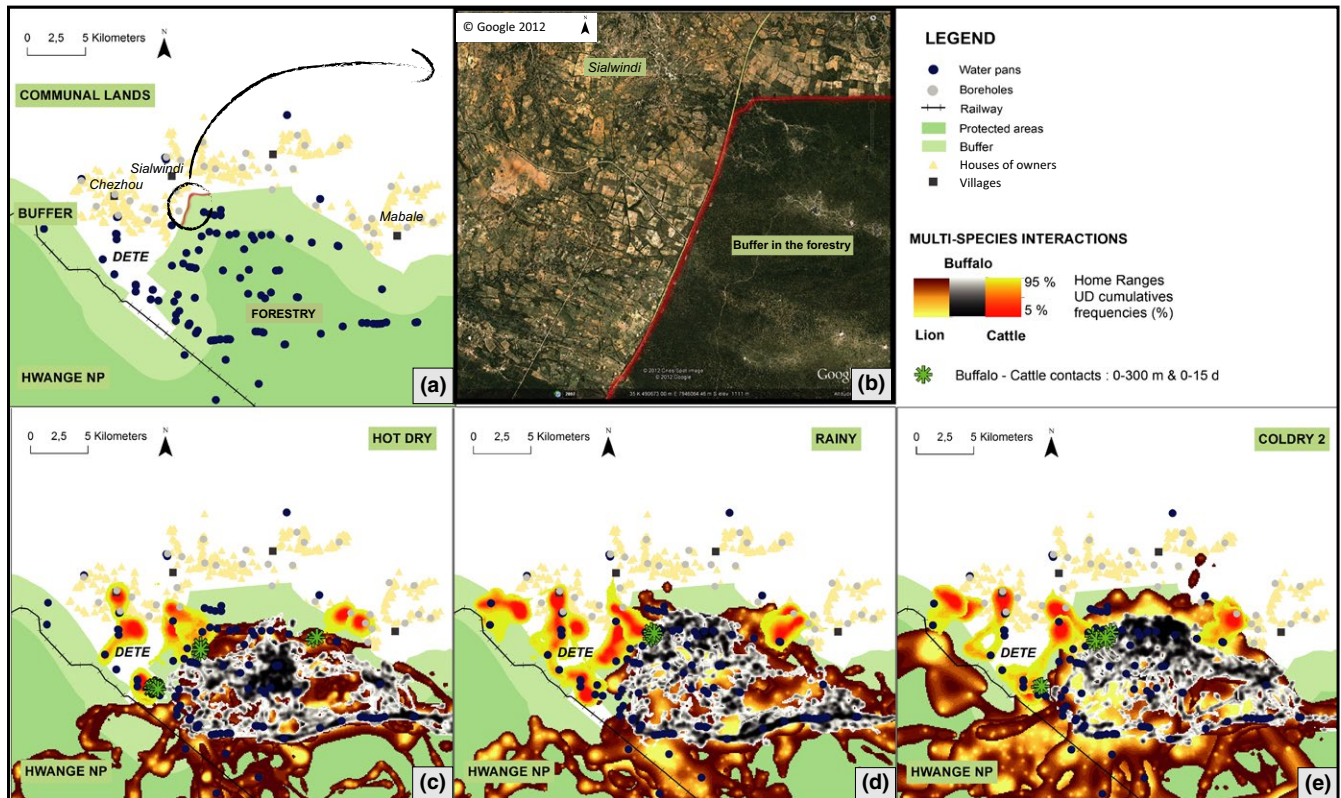
FIGURE 1 (a) Study area with the three compartments: protected areas (Hwange National Park (NP) and the Forestry), the buffer and communal lands. Chezhou, Sialwindi and Mabale are the three study villages and Dete the main town. (b) Google Earth picture showing examples of fields adjacent to wild areas close to Sialwindi village. See area highlighted by circle, narrow and red border in panel A (copyright Google earth – CNES spot image 2012). (c–e) Home range overlaps between the three species (buffalo–cattle–lion) in the three study seasons where GPS data were available (i.e., August 2010–August 2011). Green stars indicate the locations of the buffalo–cattle contacts defined with a spatio-temporal window of 0–300 metres and 0–15 days. The home range legend refers to the utilization distribution (UD) cumulative relative frequencies up to 95%: the value attributed to a given percentage, p, applies to the area comprised between p and p – 5% isopleths. Figure created with ArcGIS10.2. [Colour figure can be viewed at wileyonlinelibrary.com]

with three seasons commonly distinguished: the rainy season (mid-November–March), the cold dry season (April–July) and the hot dry season (August–mid-November). The study period extended from April 2010 to August 2011 (i.e., cold dry 1, hot dry, rainy, cold dry 2).

2.2 | Foot-and-mouth disease (fmd) dynamics

This disease is due to an *aphthovirus* that can infect ungulates and is highly contagious (Haydon et al., 1997). Although FMD is widespread world-wide, only seven serotypes of the virus have been identified. In Africa, the buffalo (*Syncerus caffer*) is the main wild local reservoir of FMD and has been reported to carry live virus for up to 5 years (Condy, Hedger, Hamblin, & Barnett, 1985). In southern Africa, three main FMD virus serotypes are frequently detected in domestic and wild populations: SAT1, SAT2 and SAT3 (Southern African Territories) (Paton, Sumption, & Charleston, 2009; Rweyemamu et al., 2008), among which no cross-immunity has been observed. (Ayebazibwe et al., 2010; Grubman & Baxt, 2004; Paton et al., 2009; Thomson et al., 2003; Vosloo, Bastos, Sangare, Hargreaves, & Thomson, 2002).

A direct transmission pathway is well documented in the literature, with infection by oral inhalation of viral particles during close contact

between two hosts (OIE, 2009). Indirect transmission through contact with contaminated ground or water is also possible, even in semi-arid regions (Lefèvre, Blancou, Chermette, & Uilenberg, 2010), although this has never been quantified under natural conditions in a savanna ecosystem.

Little is known about the production and persistence of antibodies produced following natural FMD infection in wild and domestic hosts in southern Africa. In the literature, the natural antibodies appear after 7 or 14 days post-infection and they could persist in the host for almost 3 years (Charleston, 2011; Cloete, Dungu, Van Staden, Ismail-Cassim, & Vosloo, 2008; Grubman & Baxt, 2004; Paton et al., 2009; Thomson et al., 2003).

No FMD outbreak was recorded in cattle by the veterinary services during our study despite year long, biweekly to monthly surveillance, and thus, no vaccination campaign was undertaken in the Hwange district. Additionally, the FMD seropositivity rate in buffalo from HNP was estimated in 2009 at 80% on 15 individuals, confirming the reservoir role of buffalo in this region. The Wildlife Research Unit in Zimbabwe used the Liquid Phase Blocking ELISA test to detect SAT1, SAT2 and SAT 3 in accordance with the SADC (Southern African Development Community) harmonized protocol accredited by

the norm ISO 17025. This estimation is in close to what is observed in buffalo from the Gonarezhou NP and Kruger NP where prevalence rate was estimated at 94% and 100%, respectively (see (Miguel et al., 2013)).

2.2.1 | Epidemiological survey

An individual-scale longitudinal serological survey on 110 cattle from 11 cattle herds, selected so as to cover a relatively extended stretch of the interface, was undertaken to describe the dynamics of FMD serological incidence (i.e., acquisition of antibodies after infection). The cattle population in this area is estimated at 4,850 heads (see Appendix in (Miguel et al., 2013) for more statistics). Three of four villages were selected for their proximity to the protected area (see Chezhou, Sialwindi and Mabale in Figure 1a). In each cattle herd, the serological survey was conducted on 10 randomly chosen ear-tagged adults (males and females). Ten animals represent almost 80% of a herd in this agrosystem (see (Miguel et al., 2013), for more statistics). The 110 cattle were blood sampled every 4 months when possible during the 16-month study period. ELISA commercial test (PrioCHECK® FMDV NS) was applied on each sample to detect FMD antibodies. The ELISA commercial test detects the antibodies produced following natural viral replication, irrespective of the virus serotype, but does not detect vaccine antibodies (Moonen, van der Linde, Chenard, & Dekker, 2004). The specificity and sensitivity of the test are estimated to be 98.1% and 97.2%, respectively (Brocchi et al., 2006). We assumed that a transition from seronegative to seropositive status between two sampling sessions reflected the occurrence of a natural infection event between the two sessions.

2.2.2 | Statistical models for spatial and temporal incidence variation

Serological incidence of FMD in cattle was modelled according to season, village and age. The dependent variable was binary: the serological status of an individual (cattle) either changed or remained unchanged during a time interval. The statistical models used were generalized linear mixed models (GLMM) with binomial error structures. In this analysis, the elementary statistical unit was defined by an individual cattle and a time interval over which serological status transition could be documented for that cattle. Because the same individual could produce more than one pair of successive serological records, and because individuals were aggregated in herds, a herd random effect was included to account for pseudoreplication. Finally, because not all cattle were sampled at each of the five sampling sessions and consequently the time between two sampling sessions varied from 4 to 8 months, a complementary log–log link function was used and the log of the length of the time interval was included as an offset in the models (Fortin, Bedard, DeBlois, & Meunier, 2008). Goodness of fit was assessed with the Pearson overdispersion test (Bolker et al., 2009). Model selection was performed using Akaike information criterion (Bolker et al., 2009; Burnham & Anderson, 2002).

These analyses were performed with R free software (R development core team, 2011) and using the 'glmmPQL' package.

2.3 | FMD Routes of transmission

2.3.1 | Environmental transmission

GPS UHF collars (manufactured by African Wildlife Tracking) were fitted simultaneously to 11 cattle (adult females) with one collared cattle in each of the 11 herds monitored for FMD serological incidence. Given the way, cattle are managed locally and the highly gregarious behaviour of cattle, the single collared cow in a herd was considered representative of the movements of the entire herd. GPS were scheduled to acquire one position per hour during the day from 06:00 to 18:00. Seasonal home ranges were determined using the movement-based kernel density estimation method (Benhamou & Cornelis, 2010) (Cumming & Cornelis, 2012), allowing the visualization of seasonal cattle distribution in the landscape. Analyses were performed with R software using the 'adehabitat HR', 'rgdal' and 'raster' packages. Maps were created using ArcGIS (version 10; ESRI Inc., Redlands, California). To investigate cattle exposure to FMD virus resulting from frequenting areas used by buffalo and other wild ungulates, an 'incursion index' inside the buffer was computed. The index is the ratio of the number of GPS locations recorded in the buffer zone to the total number of GPS locations recorded over 24 hrs.

2.3.2 | Interspecific transmission

Wildlife census data (Zimbabwe Parks and Wildlife Management Authority, CNRS unpublished data), field expertise and aerial searches during the capture revealed that only one herd of buffalo (~250 heads) was likely to be in contact with the GPS-equipped cattle herds. Three GPS UHF collars were fitted to three adult females in this buffalo herd. The spatial overlap between the collared buffalo was high with a mean of 81.6% (range: 79–84%), suggesting that the three collared individuals were reasonably representative of the movements of the main buffalo herd frequenting the study area but not necessarily of smaller splinter groups or resident bachelor herds. GPS positions were taken on an hourly basis 24 hrs a day. A potentially infective contact was considered to occur whenever a cattle's position was recorded within 300 m of a buffalo's position and 15 days after the buffalo's position had been recorded. The chosen time window corresponds to the conservative assumption that the virus can survive in the environment for 15 days under the semi-arid climatic conditions characteristic of the study area (Lefèvre et al., 2010; Miguel et al., 2013). The spatial window was chosen by considering that the collared buffalo represented the herd, that GPS precision was imperfect, and that the collared individuals may have moved during the hour between two consecutive positions. An analysis of the sensitivity of contact frequency to the size of the spatio-temporal window used for defining contact is presented in (Miguel et al., 2013). Contact rates were computed as the number of contacts relative to the number of cattle–buffalo position pairs to make unbiased contact rate comparisons and take into account the seasonal variation in GPS acquisition rates and number of GPS collars deployed. Because these rates

were extremely low, they were multiplied by 10^8. The resulting index is hereafter referred to as the 'cattle–buffalo contact index'.

2.3.3 | Intraspecific transmission

Interviews with cattle owners were carried out by the veterinarian officers in charge in the Hwange area with one central question to depict the seasonal herding strategies: Which areas do you select for livestock drinking activities during each season? The localizations of homestead and of the water points (pans and boreholes) identified during the interviews were thereafter registered with GPS devices. Based on interviews, seasonal networks of cattle herd contacts at water points were described. In these undirected networks, each node represents a cattle herd and ties connect herds using the same water points during the same season. A node-level connectivity index, the degree, was computed for each herd and each season. The degree is the number of ties of a node with all the other nodes (*i.e.*, the number of herds which are in contact with a focal herd through shared water points). Two network-level indexes, the connectivity and the density, were also computed. The connectivity measures the social cohesion of a group at a general level. A network is said "connected" (connectivity equalling 1) if there is at least one path between every pair of nodes in the network. The density is the number of existing ties in the network divided by the number of potential ties. In our context, cattle herds are managed for health care by veterinary in charge in each village and are not in contact with cattle from other villages. Networks analyses were carried out with R and with the 'sna package'.

2.3.4 | Modelling the routes of transmission

We modelled serological incidence of FMD in cattle according to (1) cattle incursion index into the buffer, (2) 'cattle–buffalo contact index', (3) cattle interaction index with the cattle herd degrees and (4) the cattle network density index. The statistical models used were GLMM as described above in the "statistical models for spatial and temporal incidence variation" section.

2.4 | Lion as a modulator of environmental and/or interspecific transmissions?

Data from GPS collars fitted on 10 lions (three adult females and seven adult males) were used. Most lion groups in the study area were collared (80% of the lion groups seen in the study area included one collared individual during the study period – unpublished data). GPS fitted on lions was scheduled to acquire one position per hour during the night from 18:00 to 6:00 when they are active (Schaller, 1972). To depict the role of lions on the use of the buffer by cattle and the risk of cattle–buffalo contacts, the daily buffer incursion index was computed for cattle, buffalo and lions (see above). Smoothing was applied to each of the three time series in order to visualize low frequency fluctuations of the buffer incursion index. Smoothed curves were estimated using general additive models (GAMs) with the mgcv package in R (Crawley, 2012). Patterns of

autocorrelation within time series and cross-correlation among time series were examined using the acf (Autocorrelation Function) and ccf (Cross-correlation Function) functions of the mgcv package in R (Shumway & Stoffer, 2010).

3 | RESULTS

3.1 | FMD dynamics

Overall, FMD serological prevalence in cattle was low with 8.5% (95% CI: 5.8–11.2%), compared to the level of prevalence in similar ecosystems as for instance at the border of the Kruger National Park with 30.6% (95% CI: 22.6–38.6) (see (Miguel et al., 2013)). Among the candidate models for the description of the spatial and temporal variation in FMD serological incidence in cattle, the lowest AIC model included only the effect of season. Adding the effects of cattle age and of the village where the herd was located did not decrease the model's AIC (Model 1 in Table 1). The serological incidence of FMD in cattle was higher during the rainy season (Figure 2).

3.2 | Environmental transmission

Cattle spent most of their time in communal lands (80%–95% of the GPS positions) (Figure 1 CDE). Cattle incursions into the buffer were more frequent during the rainy season (see the highest kernel density in red on Figures 1d and 3a; see also Appendix S1 for the individual level data).

TABLE 1 Model selection for the FMD serological incidence ("incid") modelling in the cattle population in the Hwange system

	AIC
Model 1	
Incid ~ season	154.1
Incid ~ villages + season	157.1
Incid ~ villages + season + age	158.8
Incid ~ constant	186.3
Model 2	
Incid ~ incursion	172.8
Incid ~ incursion + buffalo contacts + owner degrees	175.1
Incid ~ incursion + age	174.6
Incid ~ constant	186.3
Incid ~ network densities	187.1
Incid ~ owner degrees	188.3
Incid ~ buffalo contacts	187.7

Model 1 depicts spatio-temporal variations with season, village and age as candidate explanatory variables. Model 2 depicts the potential drivers of FMD serological incidence with cattle incursion inside the protected area ("incursion"), contacts with buffalo ("buffalo contacts") and interactions with other cattle (variables "owner degrees" and "network densities"—see text for details) as explanatory variables. All the models included herd identity as a random effect and an offset to account for variation in the duration of the period between two sampling sessions.
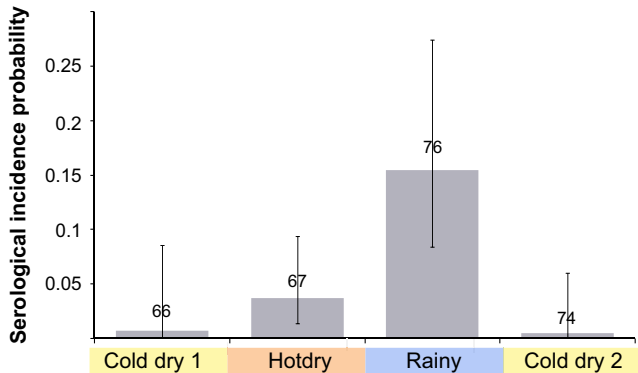
FIGURE 2 Foot-and-mouth disease incidence (with standard errors and sample size) in cattle across seasons for the period April 2010 (start of cold dry 1) – August 2011 (end of cold dry 2) in the Hwange system. Figure created with R studio software. [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Interspecific Transmission

Buffalo were never observed in the communal lands where human are settled (Figure 1c–e), but they consistently used the buffer throughout the year (Figure 3b). The cattle–buffalo contact index was, however, very low (172 contacts documented compared to 90,238 and 72,601 positions recorded for cattle and buffalo, respectively) with a relative peak in November when most contacts occurred within 500 m of a water point (see the contact locations illustrated with green stars in Figure 1c–e and the temporal distribution of contacts in Figure 4a). Less than 2% of contacts occurred within a temporal window of 24 hr, 19% within 5 days and 49% within 10 days. All the tracked buffalo are recorded as having been in contact with cattle according to our definition of contacts (Figure 4b). Conversely, only five of the 11 tracked cattle herds have been in contact with buffalo and with variable frequencies as illustrated by the thickness and the number of the links from nodes in Figure 4b.

3.4 | Intraspecific transmission

All the cattle owners registered at the regional veterinary service (450 owners owning 2914 cattle and representing more than 60% of the regional cattle population) were interviewed and geolocalized. Regarding the interactions between cattle herds through the use of water points, the herds from a same village are fully connected
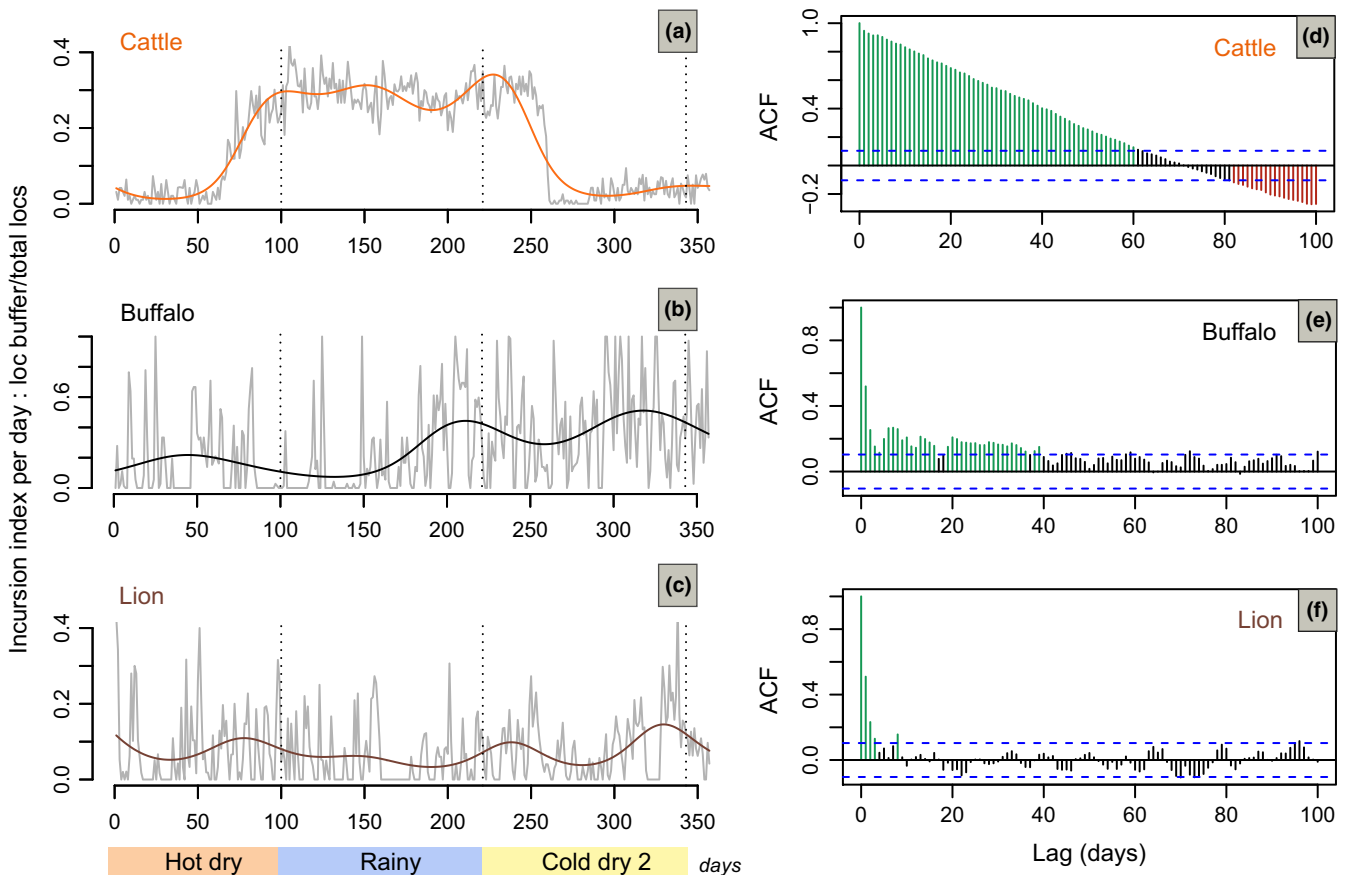

FIGURE 3 (a–c) Time series of buffer use by the three study species. The lines represent the smoothed curves to visualize low frequency fluctuations of the buffer incursion index. (d–f) Autocorrelation Functions (ACF) show the correlation coefficients of buffer incursion index for each species on day d and with a day lag varying from 0 to +100 days. The blue dotted lines indicate the significance threshold. The green and red colours indicate, respectively, a positive and negative significant correlation. Figure created with R studio software. [Colour figure can be viewed at wileyonlinelibrary.com]
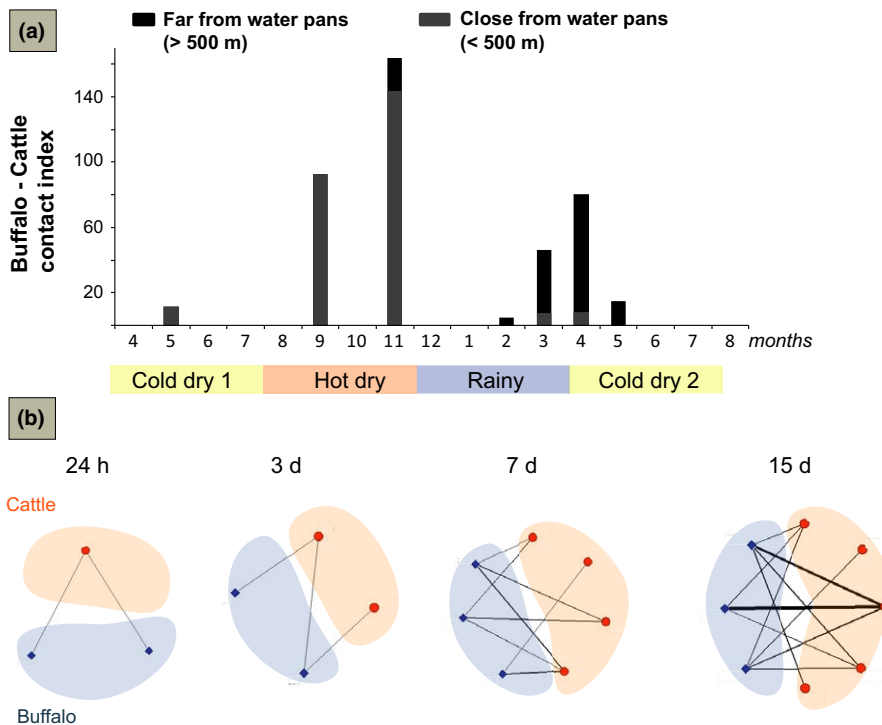
FIGURE 4 (a) Seasonal changes, from April 2010 to August 2011, of the buffalo–cattle contact index with an indication of where contacts occurred depending on distance to water pans (b) cattle–buffalo contacts at the individual scale according to a range of temporal windows (24 hr, 3 days, 7 days and 15 days) and for a fixed spatial window (300 m). The blue diamonds and numbers represent the buffalo tracked with GPS, and the red circles and numbers represent the study cattle. The thickness of the links is proportional to the contact intensity between two nodes. Figure created with R studio software. [Colour figure can be viewed at wileyonlinelibrary.com]

during the rainy season with high network density values (i.e., 0.31 in Chezhou, 0.34 in Sialwindi and 0.33 in Mabale) (Figure 5 and Table 2). Inversely the three networks are disconnected during the cold dry season with lower density values and almost the same pattern is observed during the hot dry season. At the node scale (i.e., the herd), the mean degree over cattle herds was 0.47 (ranging from 0.11 to 0.93) during the rainy season, 0.38 (ranging from 0.11 to 0.88), during the cold dry season and 0.44 (ranging from 0.11 to 0.88) during the hot dry season.

3.5 | Routes of transmission

Among the candidate models for the description of the influence of potential transmission routes on FMD incidence in cattle, the lowest AIC model included only the effect of the frequency of incursion into the protected area (Model 2 in Table 1). Adding the effects of the cattle–buffalo contact index of the cattle herd degree in the network of cattle herd contacts or of the density of that network did not decrease the model's AIC (Model 2 in Table 1). Serological incidence of FMD was higher in herds where and during the time periods when incursions into the protected area were more frequent (Figure 6).

3.6 | Lion as a modulator of environmental and/or interspecific transmissions?

3.6.1 | Kernel

Overall, lions used primarily protected areas, but they also used to a lesser extent the buffer in all seasons (Figures 1 c–e and 3c; see also Appendix S2 for the individual level data). They were recorded on rare

occasions in the communal lands with slightly higher proportions in cold dry 2 season when large fractions of the density kernel are located in the buffer areas (in golden in Figure 1d and e).

3.6.2 | Time series and autocorrelograms

The time series and the autocorrelograms for buffer incursion frequency revealed very different temporal variation patterns for cattle, lions and buffalo (Figure 3). The time series of the buffer incursion index for cattle showed small amplitude short-term variation and large amplitude seasonal fluctuations. Incursions were frequent from the end of the hot dry season until the beginning the cold dry season through the entire rainy season (Figure 3a). This pattern resulted in an autocorrelogram showing strong positive autocorrelation extending as far as 50 days implying that cattle incursion frequency could be predicted over a long time period from current incursion frequency (Figure 3d). This contrasts strongly with the pattern of lion incursion. Lion incursion index showed no clear seasonal variation but large short-term variation (Figure 3c). This pattern resulted in an autocorrelogram with positive autocorrelation persisting only over a few days implying that current lion incursion frequency could inform future lion incursion frequency over a couple of days only (Figure 3f). The pattern for buffalo was intermediate showing both relatively large seasonal fluctuations (with higher frequency from the second half of the rainy season until the end of the cold dry season) as well as large short-term fluctuations (Figure 3b). This pattern resulted in an autocorrelogram with weak but significant positive autocorrelation persisting over 40 days (Figure 3e). The predictability of buffalo incursion frequency was longer than that of lions but shorter than that of cattle.
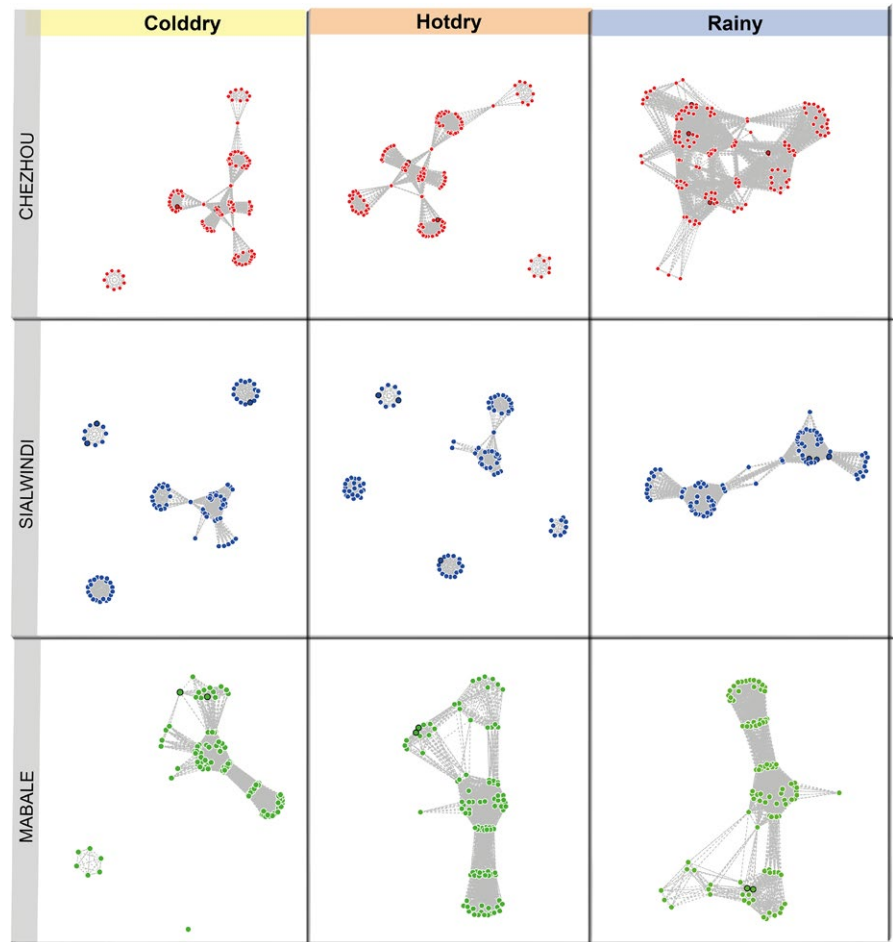
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FIGURE 5 Cattle owners uni-modal networks where nodes represent owners and links represent the water points use (i.e., borehole and natural pans) for each study village and season. The cattle herds tracked by GPS are represented by black circles. Figure created with R studio software. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Connectivity and density estimates of cattle networks by season and village

	Rainy season		Cold dry season		Hot dry season		All seasons	
	Connectivity	Density	Connectivity	Density	Connectivity	Density	Connectivity	Density
Chezhou	1	0.31	0.87	0.20	0.87	0.20	1	0.36
Sialwindi	1	0.34	0.37	0.21	0.28	0.17	1	0.34
Mabale	1	0.33	0.86	0.34	1	0.35	1	0.39

3.6.3 | Cross-correlation functions

The cross-correlograms highlight the synchrony (or the asynchrony) of buffer incursion frequencies, which could ultimately indicate attraction or avoidance between the study species. The cross-correlogram between buffalo and cattle (i.e., correlation of cattle incursion frequency at day 0 with buffalo incursion frequency at varying lags) showed negative correlations from a negative lag of 50 days to a positive lag of 40 days (Figure 7a). This indicates that cattle did not use the buffer zone when buffalo had been using it frequently up to 2 months before and that buffalo did not use the buffer zone when cattle had been using it up to 1 month before (which could suggest avoidance between these two species). The cross-correlation pattern most likely results from the asynchronous seasonal patterns of buffer zone incursion frequency by cattle and buffalo which could be partly influenced the presence of the other species but which are also likely to be determined by other drivers.

The cross-correlogram between lions and buffalo (i.e., correlation of buffalo incursion frequency at day 0 with lion incursion frequency at varying lags) showed negative correlations at lags −25 to −20 days and positive correlations at lags +3 + 13, +15 and +30 to +35 days (Figure 7b). This indicates that buffalo did not use the buffer zone when lions had been using it frequently 3 weeks before and interestingly that lions tended to use the buffer zone when buffalo had been using it over the 4 last weeks. This pattern is also visible on the smoothed time series where peaks of buffer incursion frequency by lions lag behind peaks of buffer incursion frequency by buffalo (Figure 3b,c).
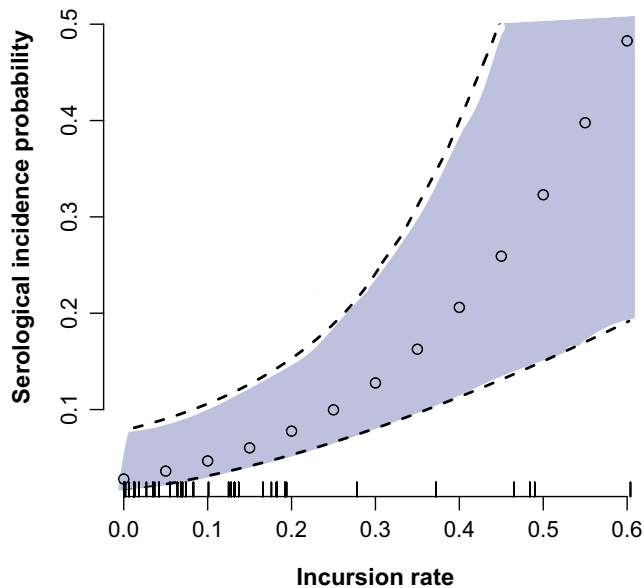
FIGURE 6 FMD incidence probability according to cattle incursion into the buffer area. Dots indicate the incidence estimations; dotted lines, the confidence intervals; and ticks along the x-axis, the values of the cattle incursion in the data. Figure created with R studio software. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Landscape of infection at the wildlife/livestock interface

In spite of cattle incursions into the protected area, FMD serological incidence observed in the study cattle population was unexpectedly low compared to similar interface areas elsewhere (Miguel et al., 2013). Nevertheless, our results showed a pronounced seasonality in FMD incidence peaking during the rainy season and coinciding with the period when cattle most frequently entered the protected forestry land. In this pathoecosystem, our study of incidence (and reversion see (Miguel et al., 2013) for more details) patterns demonstrate

that the FMD antibodies are not lifelong and that an individual can be infected several times during the year. The social network analyses on cattle owner herding strategies showed that network connectivity and density were higher in the rainy season, but these variables were not the most influential to explain the incidence of FMD in cattle. We cannot rule out that our sample sizes were not large enough but so far intraspecific interactions do not appear to be the main drivers of the FMD dynamics in cattle at wild/domestic interface. The seasonal dynamics of FMD can neither be explained by the contacts between cattle and buffalo. Indeed, contacts between cattle and buffalo occurred mainly at the end of the hot dry season (i.e., November) in the vicinity of water points when surface-water availability strongly constrains herbivore distribution (Redfern, Grant, Biggs, & Getz, 2003), compared to later in the rainy season when buffalo are more evenly distributed over the landscape. Additionally, these interspecific contacts, potentially resulting in infection, were also limited because the seasonal fluctuations of buffer incursion frequency by cattle and buffalo were asynchronous. Cattle frequently used the buffer zone from the second half of the hot dry season, throughout the rainy season and until the beginning of the cold dry season, while buffalo frequently used the buffer zone mainly during the cold dry season but avoided it over most of the rainy season. Such asynchronous patterns could partially result from spatial avoidance behaviours by buffalo triggered by perturbations associated with the presence of cattle herders in the protected area. Spatial separation between cattle and buffalo has previously been assessed in the W regional park in West Africa through the analysis of animal localization data collected during two aerial surveys in 2002 and 2003 (Hibert et al., 2010). This previous study detected, although in only one of the two study years, spatial separation between cattle and buffalo could result from buffalo avoiding cattle. However, in the present as well as in this former study, other drivers, such as resource distribution within the protected area and the communal area, are probably at least as important in determining seasonal pattern of cattle and buffalo incursion frequency in the different landscape compartments.

The time-lag between cattle–buffalo contacts (i.e., hot dry season) and the peak of FMD incidence (i.e., rainy season) is not likely to be
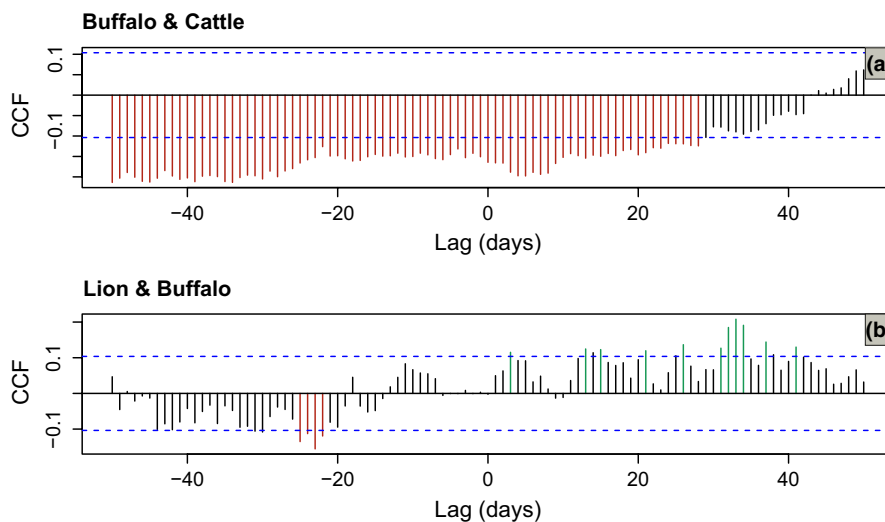

FIGURE 7 Cross-correlation Functions for species 1 (sp. 1) versus species 2 (sp. 2) show the correlation coefficients of buffer incursion index of species 2 on day d with buffer incursion index of species 1 on day d+lag with lag varying from −50 to +50 days. The blue dotted lines indicate the significance threshold. The green and red colours indicate, respectively, a positive and negative significant correlation. Figure created with R studio software. [Colour figure can be viewed at wileyonlinelibrary.com]

accounted for by long seroconversion time. Indeed, FMD antibodies are produced shortly after infection (Grubman & Baxt, 2004) and no significant lag between infection and serological conversion was expected (i.e., no longer than 14 days). There are three alternative and non-exclusive interpretations for this lag. The first is that virus survival in the environment is high enough for cattle to become infected when they use areas where buffalo have been present some time before (i.e., longer than the 15 days used for the temporal window that defines direct or delayed contacts). The second is that wild ungulate species other than buffalo, such as impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*), could play a role as secondary reservoirs of the FMD (Thomson et al., 2003) or function as bridge populations that generate epidemiological links between buffalo and cattle populations (Caron, Cappelle, Cumming, de Garine-Wichatitsky, & Gaidet, 2015). Under such scenarios, the frequent cattle incursions during the rainy season in areas used previously or concomitantly by reservoir and/or bridge population(s) could explain the peak of FMD incidence in cattle population during that season. Unfortunately, our study was not designed to be able to assess the role of other herbivore populations in the epidemiology of FMD. Nevertheless, these other herbivore species were present in the study interface and could have potentially played a role in disease transmission. Thirdly, the study did not allow us to assess the role of small unmonitored buffalo groups (such as bachelor herds) (Caron, Cornelis, Foggin, Hofmeyr, & de Garine-Wichatitsky, 2016) or single adult animals (van Schalkwyk et al., 2016) that could also play a significant role in FMD dynamics.

4.2 | Landscape of fear

In this study, we tested the hypothesis that predators could modulate the likelihood of encounters between livestock and wild herbivores, and ultimately influence pathogen transmission between them. We did not detect any significant and reasonable relationship at short term between cattle and lion. However, lions and cattle are frequently using the same area. More interestingly, the analysis of incursion frequency time series revealed that lions made frequent incursions in the buffer few days to few weeks after buffalo had used it, suggesting a potential attraction effect of buffalo on lions. If this is the case, it is noteworthy that lions use the buffer not only shortly after buffalo had used it (3 days), but also after longer time-lags (up to 40 days). The buffalo autocorrelogram showed weak but significant positive autocorrelation persisting over 40 days. Conversely, buffalo, which are the main prey for lions in the Hwange ecosystem (Davidson et al., 2013), did not use the buffer zone when it had been occupied by lions a few weeks before, which could suggest an avoidance of lions by buffalo but at a temporal scale that is not traditionally considered. Such results (even if the value of the correlations are not very high) pave the way for future research to test the scenario whereby lions and buffalo are engaged in a "predator–prey space game" at the landscape scale as revealed in other species (Johnson, de Roode, & Fenton, 2015), and encourage for the investigation of several temporal scales. Under such scenario, lions might play a role of natural barrier between sympatric species by reducing the spatio-temporal overlap between cattle and

buffalo in the buffer zone, and consequently the likelihood of direct or indirect contacts, which will ultimately influence FMD transmission (Proffitt et al., 2010).

4.3 | Human behaviour and seasonality

Our results showed that cattle entered the buffer of the protected area almost exclusively during the rainy season in this part of the Hwange system as it was observed in similar ecosystem in Zimbabwe (Kuiper et al., 2015). This pattern is informative at three levels. First, the rainy season coincides not only with the season when resources (grazing and water) are the most abundant and allow access to a larger home range but also with the ploughing and the crop growing and harvesting period in communal areas. The amount of agricultural work required and the necessity to keep cattle herds out of growing fields encourage unmanned cattle herds to graze away from communal lands and hence more into the buffer zone (Murwira, 2012). After harvest, cattle are fed on crop residues in fields during the early dry season which constrains cattle movements to areas closer to villages and further from protected areas as it was described in (Kuiper et al., 2015). Second, we might have expected the resource availability (vegetation and surface water) in protected areas to be attractive for cattle owners during the dry season. At this time, surface water is scarce and grass is rare or trampled in the vicinity of homesteads and driving cattle inside the protected areas would be an opportunity (Prins, 1996; Zengeya, Murwira, & de Garine-Wichatitsky, 2011). However, the buffer was not used by cattle during the dry season. This suggests that cattle owners decide to rely on lower quality resources in the communal land, maybe to avoid the risks of infection, not only from FMD virus but also tick diseases which are a burden for farmers, and/or predation in the protected area. It has been shown that cattle are more frequently killed by lions during the wet season than during the dry season. Indeed, "seasonal use of protected areas during growing season increases vulnerability of cattle to lion depredation" (Kuiper et al., 2015). The optimized strategy for cattle herders at the wildlife/livestock interface might be to decrease the likelihood of livestock depredation by avoiding the use of protected areas when the constraints in communal lands are acceptable (i.e., when the crop period is finished). Considering that the risk of being fined for entering the protected area is the same throughout the year, we assume that this effect could not explain the seasonal variation of the cattle buffer use. Third, conversely to the intuitive idea that the dry season is a risky period for disease transmission, as it was shown in similar ecosystems with a lesser predation pressure (Caron et al., 2013; Miguel et al., 2013; Zvidzai, Murwira, Caron, & de Garine-Wichatitsky, 2013), our study shows that the rainy season is the key season for foot-and-mouth disease transmission and potential exposure to predation.

5 | CONCLUSION

In conclusion, our study brings scientific elements to consider that predator–prey–host interactions, the availability of resources driven

by seasonality and human herding practices adapting/reacting to the perceived state of the system influence FMD transmission. The risk of pathogen spillover between sympatric host populations is restricted to limited areas at specific seasons and predators could mitigate interspecific disease transmission. A better picture of the pathoecosystem would require an understanding of how cattle owners take their herding decisions and according to which clues and perceived risks: disease, predation or risk of fines? The integration between biological and social sciences is therefore necessary to better understand and manage the risk of disease transmission at complex human/livestock/wildlife interfaces which are hotpots in the context of emerging infectious diseases (Woolhouse & Gowtage-Sequeria, 2005). Recently, Iverson and collaborators showed interesting results on the integration of community-based/participatory surveillance to delineate disease outbreak and predict transmission risk (Iverson, Forbes, Simard, Soos, & Gilchrist, 2016).

6 | AUTHORIZATIONS AND PERMISSIONS

Experiments with animals: All experiments were performed in accordance with relevant guidelines and regulation. All procedures were approved by (i) the Zimbabwe Parks and Wildlife Management Authority (Permit numbers: REF: DM/Gen/(T) 23(1)(c)(ii): 25/2010, 06/2011, PERMIT NO.: 23(1) (c) (ii) 05/2011/01/2010); (ii) under licence from the Zimbabwe Veterinary Association, Wildlife Group (Veterinary Committee) and Medicines Control Authority, Zimbabwe (licence numbers: Elliot: 2010/18, 2011/04; Hunt: 2010/03, 2011/02,; Loveridge: 2010/04, 2011/03; Stapelkamp: 2010/05, 2011/01) (iii) and (iv) the Arreté préfectoral n°DDPP69-2014-011 (agrément d'un établissement utilisateur/éleveur fournisseur d'animaux utilisés à des fins scientifiques). Animal handling and care protocols were carried out in accordance with approved guidelines.

Experiment with humans: All experiments were performed in accordance with relevant guidelines and regulation. All procedures were undertaken with the permission of the Hwange District Administrator and approved by the Permit No 19/03/2010. A written informed consent was obtained from all subjects involved in the project.

AUTHOR CONTRIBUTIONS

EM, HF, MDGW, AC, VG and MV designed the study; EM did the field work for the cattle project (data collection + biological analyses); HF, MDGW, AC and EM collected the buffalo data; BS collected the lion data; FN did the social network analyses; VG and EM did all the other statistical analyses; EM, VG and MV drafted the manuscript and other authors revised it; HF manages the research programme of the Hwange French CNRS-INEE LTER; AJL and DWM manage the Hwange Lion Research project.

REFERENCES

Alexander, K. A., & McNutt, J. W. (2010). Human behavior influences infectious disease emergence at the human-animal interface. *Frontiers in Ecology and Environment*, *8*, 522–526.

Ayebazibwe, C., Mwiine, F.N., Tjornehoj, K., Balinda, S.N., Muwanika, V.B., Okurut, A.R.A., … Alexandersen, S. (2010). The role of African buffalos (*syncerus caffer*) in the maintenance of foot-and-mouth disease in Uganda. *BMC Veterinary Research*, *6*, 54.

Azhar, E. I., El-Kafrawy, S. A., Farraj, S. A., Hassan, A. M., Al-Saeed, M. S., Hashem, A. M., & Madani, T. A. (2014). Evidence for camel-to-human transmission of MERS coronavirus. *New England Journal of Medicine*, *370*, 2499–2505.

Benhamou, S., & Cornelis, D. (2010). Incorporating movements behaviors and barriers to improve Kernel home range space use estimates. *Journal of Wildlife Management*, *74*, 1353–1360.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135.

Bongaarts, J., & Sinding, S. (2011). Population policy in transition in the developing world. *Science*, *333*, 574–576.

Brocchi, E., Bergmann, I. E., Dekker, A., Paton, D. J., Sammin, D. J., Greiner, M., … De Clercq, K. (2006). Comparative evaluation of six ELISAs for the detection of antibodies to the non-structural proteins of foot-and-mouth disease virus. *Vaccine*, *24*, 6966–6979.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer, Verlag.

Caron, A., Cappelle, J., Cumming, G. S., de Garine-Wichatitsky, M., & Gaidet, N. (2015). Bridge hosts, a missing link for disease ecology in multi-host systems. *Veterinary Research*, *46*, 83.

Caron, A., Cornelis, D., Foggin, C., Hofmeyr, M., & de Garine-Wichatitsky, M. (2016). Transboundary conservation areas, African buffalo movements and animal diseases. *Emerging Infectious Diseases*, *22*, 277–280.

Caron, A., Miguel, E., Gomo, C., Makaya, P., Pfukenyi, D. M., Foggin, C., … de Garine-Wichatitsky, M. (2013). Relationship between burden of infection in ungulate populations and wildlife/livestock interfaces. *Epidemiology & Infection*, *141*, 1522–1535.

Chamaille-Jammes, S., Valeix, M., Bourgarel, M., Murindagomo, F., & Fritz, H. (2009). Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. *African Journal of Ecology*, *47*, 804–808.

Charleston, B. (2011). Relationship between clinical signs and transmission of an infectious disease and the implications for control. *Science*, *332*, 1263.

Cloete, M., Dungu, B., Van Staden, L. I., Ismail-Cassim, N., & Vosloo, W. (2008). Evaluation of different adjuvants for foot-and-mouth disease

vaccine containing all the SAT serotypes. *Onderstepoort Journal of Veterinary Research*, 75, 17–31.

Condy, J. B., Hedger, R. S., Hamblin, C., & Barnett, I. T. (1985). The duration of the foot-and-mouth disease virus carrier state in African buffalo (i) in the individual animal and (ii) in a free-living herd. *Comparative Immunology, Microbiology and Infectious Diseases*, 8, 259–265.

Crawley, M. J. (ed.) (2012). *The R book*. John Wiley & Sons The Atrium: Southern Gate, Chichester, West Sussex, England.

Cumming, G. S., & Cornelis, D. (2012). Quantitative comparison and selection of home range metrics for telemetry data. *Diversity and Distributions*, 18, 1057–1065.

Daszak, P., Cunningham, A. A., & Hyatt, A. D. (2000). Emerging infectious diseases of wildlife- Threats to biodiversity and human health. *Science*, 287, 443–449.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., & MacDonald, D. (2013). Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PLoS ONE*, 8(2), e55182. https://doi.org/10.1371/journal.pone.0055182, e55182

Ferguson, K., & Hanks, J. (2010). Fencing Impacts: A review of the environmental, social and economic impacts of game and veterinary fencing in Africa with particular reference to the Great Limpopo and Kavango-Zambezi transfrontier Conservation Areas. In: *University of Pretoria – Mammal Research Institute*, Pretoria.

Fortin, M., Bedard, S., DeBlois, J., & Meunier, S. (2008). Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Quebec, Canada. *Annals of Forest Science*, 65, 205.

de Garine-Wichatitsky, M., Miguel, E., Mukamuri, B., Garine-Wichatitsky, E., Wencelius, J., Manjengwa, J., ... Caron, A. (2013). Coexisting with wildlife in Transfrontier Conservation Areas in Zimbabwe: Cattle owners' awareness of disease risks and perception of the role played by wildlife. *Comparative Immunology Microbiology and Infectious Diseases*, 36, 321–332.

Grubman, M. J., & Baxt, B. (2004). Foot-and-mouth disease. *Clinical Microbiology Reviews*, 17, 465.

Haydon, D. T., Woolhouse, M. E. J., & Kitching, R. P. (1997). An analysis of foot-and-mouth-disease epidemics in the UK. *Ima Journal of Mathematics Applied in Medicine and Biology*, 14, 1–9.

Herrero, M., Thornton, P. K., Notenbaert, A. M., Wood, S., Msangi, S., Freeman, H. A., ... Rosegrant, M. (2010). Smart investments in sustainable food production: Revisiting mixed crop-livestock systems. *Science*, 327, 822–825.

Hibert, F., Calenge, C., Fritz, H., Maillard, D., Bouché, P., Ipavec, A., ... de Visscher, M.-N. (2010). Spatial avoidance of invading pastoral cattle by wild ungulates: Insights from using point process statistics. *Biodiversity and Conservation*, 19, 2003–2024.

Hoare, R. E. (1999). Determinants of human-elephant conflict in a land-use mosaic. *Journal of Applied Ecology*, 36, 689–700.

Iverson, S. A., Forbes, M. R., Simard, M., Soos, C., & Gilchrist, H. G. (2016). Avian Cholera emergence in Arctic-nesting northern Common Eiders: Using community-based, participatory surveillance to delineate disease outbreak patterns and predict transmission risk. *Ecology and Society*, 21, 12.

Johnson, P. T. J., de Roode, J. C., & Fenton, A. (2015). Why infectious disease research needs community ecology. *Science*, 349, 4–349.

Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. *Nature*, 451, 990–994.

Kolowski, J. M., & Holekamp, K. E. (2006). Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation*, 128, 529–541.

Kuiper, T. R., Loveridge, A. J., Parker, D. M., Johnson, P. J., Hunt, J. E., Stapelkamp, B., ... Macdonald, D. W. (2015). Seasonal herding practices influence predation on domestic stock by African lions along a protected area boundary. *Biological Conservation*, 191, 546–554.

Lefèvre, P. C., Blancou, J., Chermette, R., & Uilenberg, G. (2010). *General considerations Viral diseases. Infectious and parasitic diseases of livestock*. Edition TEC & DOC, Lavoisier, Paris.

Lindsey, P. A., Romanach, S. S., Tambling, K., Chartier, K., & Groom, R. (2011). Ecological and financial impacts of illegal bushmeat trade in Zimbabwe. *Oryx*, 45, 96–111.

Loveridge, A. J., Hemson, G., Davidson, Z., & Macdonald, D. W. (2010). *African lions on the edge: reserve boundaries as 'attractive sinks'*.

Maron, D. F. (2014). New clues to where the Ebola epidemic started. In: Nature. International weekly journal of science, doi:10.1038/nature.2014.16651.

Miguel, E., Grosbois, V., Caron, A., Boulinier, T., Fritz, H., & Cornélis, D. (2013). Contacts and foot and mouth disease transmission from wild to domestic bovines in Africa. *Ecosphere*, 4, art51.

Mishra, C., Van Wieren, S. E., Ketner, P., Heitkonig, I. M. A., & Prins, H. H. T. (2004). Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. *Journal of Applied Ecology*, 41, 344–354.

Moonen, P., van der Linde, E., Chenard, G., & Dekker, A. (2004). Comparable sensitivity and specificity in three commercially available ELISAs to differentiate between cattle infected with or vaccinated against foot-and-mouth disease virus. *Veterinary Microbiology*, 99, 93–101.

Murwira, A., de Garine-Wichatitsky, M., Zengeya, F., Poshiwa, X., Matema, S., Caron, A., Guerbois, C., Hellard, E., & Fritz, H., (2013). Resource gradients and movements across the edge of transfrontier parks. In: Transfrontier conservation areas: People living on the edge. Londres, Royaume- Uni: Earthscan Publications.

Nicholls, H. (2015). *Charismatic lion's death highlights struggles of conservation scientists*.

OIE (2009). Foot and mouth disease : Aetiology Epidemiology Diagnosis Prevention and Control References. OIE Technical Disease Cards.. *Technical disease cards*, October

Packer, C., Ikanda, D., Kissui, B., & Kushnir, H. (2005). Lion attacks on humans in Tanzania – Understanding the timing and distribution of attacks on rural communities will help to prevent them. *Nature*, 436, 927–928.

Paton, D. J., Sumption, K. J., & Charleston, B. (2009). Options for control of foot-and-mouth disease: Knowledge, capability and policy. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364, 2657–2667.

Prins, H. H. T. (1996). *Ecology and behaviour of the African Buffalo*. London, UK: Chapman & Hall.

Proffitt, K. M., White, P. J., & Garrott, R. A. (2010). Spatio-temporal overlap between Yellowstone bison and elk – implications of wolf restoration and other factors for brucellosis transmission risk. *Journal of Applied Ecology*, 47, 281–289.

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84, 2092–2107.

Rogers, C. M. L. (1993). A woody vegetation survey of Hwange National Park. Report, Department of National Parks and Wildlife Management. Harare: Zimbabwe.

Rweyemamu, M., Roeder, P., Mackay, D., Sumption, K., Brownlie, J., Leforban, Y., ... Saraiva, V. (2008). Epidemiological patterns of foot-and-mouth disease worldwide. *Transboundary and Emerging Diseases*, 55, 57–72.

van Schalkwyk, O. L., Knobel, D. L., De Clercq, E. M., De Pus, C., Hendrickx, G., & Van den Bossche, P. (2016). Description of Events Where African Buffaloes (*Syncerus caffer*) Strayed from the Endemic Foot-and-Mouth Disease Zone in South Africa, 1998-2008. *Transbound Emerg Dis*, 63, 333–347.

Schaller, G. (1972). *The Serengeti lion. A study of predator-prey relations*.

Shumway, R. H., & Stoffer, D. S. (2010). *Time series analysis and its applications: With R examples*. University of California, Davis; University of Pittsburgh, Pittsburgh : Springer Science & Business Media.

Thomson, G. R., Vosloo, W., & Bastos, A. D. (2003). Foot and mouth disease in wildlife. *Virus Research*, 91, 145–161.

du Toit, J. T. (2011). Coexisting with Cattle. *Science*, 333, 1710–1711.

Valeix, M., Loveridge, A. J., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, *90*, 23–30.

Vosloo, W., Bastos, A. D., Sangare, O., Hargreaves, S. K., & Thomson, G. R. (2002). Review of the status and control of foot and mouth disease in sub-Saharan Africa. *Revue Scientifique et Technique de l'OIE*, *21*, 437–449.

Wittemyer, G., Elsen, P., Bean, W. T., Burton, A. C. O., & Brashares, J. S. (2008). Accelerated human population growth at protected area edges. *Science*, *321*, 123–126.

Woodroffe, R., Thirgood, S. J., & Rabinowitz, A. (2005). *People and wildlife: Conflict or co-existence?* Cambridge, UK: Cambridge University Press.

Woolhouse, M. J. E., & Gowtage-Sequeria, S. (2005). Host range and emerging and reemerging pathogens. *Emerging Infectious Diseases*, *11*, 1842–1847.

Zengeya, F., Murwira, A., & de Garine-Wichatitsky, M. (2011). An IKONOS-based comparison of methods to estimate cattle home ranges in a semi-arid landscape of southern Africa. *International Journal of Remote Sensing*, *32*, 7805–7826.

Zvidzai, M., Murwira, A., Caron, A., & de Garine-Wichatitsky, M. (2013). Waterhole use patterns at the wildlife/livestock interface in a semi-arid savanna of Southern Africa. *International Journal of Development and Sustainability -Special Issue: Development and Sustainability in Africa – Part 2*, *2*, 455–471 in press.

BIOSKETCH

The research of Eve Miguel is mainly focused on pathogen spillover at the wild/domestic/human interface. In particularly, she is interested on animal/human behaviours which lead to disease epidemic. Usually she is trying to depict spatial interactions among species and seasonal pattern to understand the epidemiology of the disease. Her background is ecology and evolution, but she has been collaborating with veterinary, wildlife manager, modeller, epidemiologist and sociologist.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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