

1 Drivers of Foot and Mouth Disease in cattle at wild/domestic interface: insights from
2 farmers, buffalo and lions

3 Running title: Foot and Mouth Disease at wild/domestic interface

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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 4 seasons in 2010-11.

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 3km 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 (i) buffalo and cattle are avoiding each other up to two months after one species track and that (ii) 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

41 cattle owners may decide to rely on lower quality resources in the communal land in the dry
42 season to avoid the risks of infection and/or predation in the HNP.

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

45 **Ending:** Africa, Herding practices, Human-wildlife coexistence, Inter-specific contacts,
46 Networks, Space use

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52 **A.INTRODUCTION**

53 Worldwide, increasing human populations and the associated resource consumption and
54 habitat fragmentation force humans and their domestic animals to live in increasing proximity
55 to protected areas and wildlife (Wittemyer *et al.*, 2008). Protected areas are often delimited by
56 soft and porous frontiers such as rivers or roads, and consequently animal movements
57 between protected areas and their periphery occur in both directions (Ferguson & Hanks,
58 2010). The interfaces between protected areas and surrounding communal lands are thus
59 hotspots of potential interactions between people, their livestock and wildlife, often typified
60 by human-wildlife conflicts including threat to human life (Packer *et al.*, 2005), livestock
61 depredation by carnivores (Kolowski & Holekamp, 2006), crop destruction by wild
62 herbivores (Hoare, 1999), competition for shared resources (Mishra *et al.*, 2004), hunting or
63 illegal poaching (Nicholls, 2015) and disease transmission (Jones *et al.*, 2008). Encroachment
64 of human activities into wildlife habitats may have enhanced pathogen transfer between
65 wildlife and domestic animals (Daszak *et al.*, 2000) and may have caused the emergence of
66 several recent zoonoses (e.g. Ebola (Maron, 2014), MERS coronavirus (Azhar *et al.*, 2014)).
67 These interface areas raise significant public health and conservation issues globally
68 (Woodroffe *et al.*, 2005).

69 In Africa, where population growth is the highest and the populations living at the
70 edge of protected areas have increased dramatically in the recent past (Wittemyer *et al.*, 2008;
71 Bongaarts & Sinding, 2011), and where livestock plays a key-role in the livelihoods of rural
72 families (Herrero *et al.*, 2010), an understanding of where, when and why livestock interact
73 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 *et al.*, 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 *et al.*, 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 *et al.*, 2003), and (3) intra-specific 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.

A.METHODS AND MATERIALS

B.STUDY AREA

The study was carried out at the northern periphery of Hwange National Park (HNP, ~ 15000 km²; 35K 484826E; 794130S; Fig. 1 A). 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 *et al.*, 2009) and is characterized by a relatively high abundance of large carnivores (e.g. 3.5 lion/100km² (Loveridge *et al.*, 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 *et al.*, 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 3km of the boundary.

According to these cultural practices, we restricted our analyses to an area encompassing a 3km strip within protected lands (hereafter referred to as the "buffer") and the adjacent communal lands (Fig. 1 A). 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 (Fig. 1 B, 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 (Fig. 1 A) 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 ~ 600mm, 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-dry1, hot-dry, rainy, cold-dry2).

B.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 worldwide, only 7 serotypes of the virus have been identified. In Africa, the buffalo (*Syncerus caffer*) is the main wild local reservoir of FMD and have been reported to carry live virus for up to 5 years (Condy *et al.*, 1985). In southern Africa, 3 main FMD virus sero-types are frequently detected in domestic and wild populations: SAT1, SAT2 and SAT3 (Southern African Territories) (Rweyemamu *et al.*, 2008; Paton *et al.*, 2009), among which no cross-immunity has been observed. (Vosloo *et al.*, 2002; Thomson *et al.*, 2003; Grubman & Baxt, 2004; Paton *et al.*, 2009; Ayebazibwe *et al.*, 2010).

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 *et al.*, 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. (Thomson *et al.*, 2003; Grubman & Baxt, 2004; Cloete *et al.*, 2008; Paton *et al.*, 2009; Charleston, 2011)

No FMD outbreak was recorded in cattle by the veterinary services during our study despite year long, bi-weekly 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 to 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 %, in respectively (see (Miguel *et al.*, 2013a))

C.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 4850 heads (see appendix in (Miguel *et al.*, 2013b) for more statistics). Three out of four villages were selected for their proximity to the protected area (see Chezhou, Sialwindi and Mabale in Fig. 1 A). 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.*, 2013b) 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 *et al.*, 2004). Antibodies against FMD in cattle population are usually produced 7-14 days following infection (Grubman & Baxt, 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.

C.Statistical models for spatial and temporal incidence variation

Serological incidence of FMD in cattle was modeled 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 pseudo-replication. Finally, because not all cattle were sampled at each of the 5 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 *et al.*, 2008). Goodness of fit was assessed with the Pearson over-dispersion test (Bolker *et al.*, 2009). Model selection was performed using Akaike Information Criterion (Burnham & Anderson, 2002; Bolker *et al.*, 2009). These analyses were performed with R free software (R development core team, 2011) and using the ‘glmmPQL’ package.

B.FMD ROUTES OF TRANSMISSION

C.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 behavior 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 hours.

C. Inter-specific 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 3 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 hours a day. A potentially infective contact was considered to occur whenever a cattle’s position was recorded within 300m of a buffalo’s position less than 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.*, 2013b). 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.*, 2013b). 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’.

C.Intra-specific transmission

Interviews with cattle owners were done 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 equaling 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 done with R and with the ‘sna package’.

C. Modeling the routes of transmission

We modeled 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.

B. LION AS A MODULATOR OF ENVIRONMENTAL and / or INTER-SPECIFIC TRANSMISSIONS?

Data from GPS collars fitted on 10 lions (3 adult females and 7 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 were 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 auto-correlation within time series and cross-correlation among time series were examined using the acf (Auto-correlation Function) and ccf (Cross Correlation Function) functions of the mgcv package in R (Shumway & Stoffer, 2010).

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280 **A.RESULTS**

281 **B.FMD DYNAMICS**

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

290 **B.ENVIRONMENTAL TRANSMISSION**

291 Cattle spent most of their time in communal lands (80-95% of the GPS positions) (Fig. 1
292 CDE). Cattle incursions into the buffer were more frequent during the rainy season (see the
293 highest kernel density in red on Fig. 1 D and Fig. 3 A; see also Appendix S1 for the individual
294 level data).

295 **B.INTER-SPECIFIC TRANSMISSION**

296 Buffalo were never observed in the communal lands where human are settled (Fig. 1 CDE),
297 but they consistently used the buffer throughout the year (Fig. 3 B). The cattle-buffalo contact
298 index was however very low (172 contacts documented compared to 90,238 and 72,601
299 positions recorded for cattle and buffalo, respectively) with a relative peak in November when

most contacts occurred within 500m of a water point (see the contact locations illustrated with green stars in Fig. 1 CDE and the temporal distribution of contacts in Fig. 4 A). Less than 2% of contacts occurred within a temporal window of 24h, 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 (Fig. 4 B). Conversely, only 5 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.

B.INTRA-SPECIFIC 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 during the rainy season with high network density values (i.e. 0.31 in Chezhou, 0.34 in Sialwindi and 0.33 in Mabale) (Fig. 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.

B.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 (Fig. 6).

B. LION AS A MODULATOR OF ENVIRONMENTAL AND / OR INTER-SPECIFIC TRANSMISSIONS?

C. Kernel

Overall, lions used primarily protected areas but they also used to a lesser extent the buffer in all seasons (Fig. 1 CDE and Fig. 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 Fig. 1 D and E).

C. Time series and auto-correlograms

The time series and the auto-correlograms for buffer incursion frequency revealed very different temporal variation patterns for cattle, lions and buffalo (Fig. 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 (Fig. 3 A). This pattern resulted in an auto-correlogram 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 (Fig. 3 D). This contrasts strongly with the pattern of lion incursion. Lion incursion index showed no clear seasonal variation but large short-term

variation (Fig. 3 C). This pattern resulted in an auto-correlogram 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 (Fig. 3 F). 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 (Fig. 3 B). This pattern resulted in an auto-correlogram with weak but significant positive autocorrelation persisting over 40 days (Fig. 3 E). The predictability of buffalo incursion frequency was longer than that of lions but shorter than that of cattle.

C. 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 (Fig. 7 A). 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

369 +35 days (Fig. 7 B). This indicates that buffalo did not use the buffer zone when lions had
370 been using it frequently 3 weeks before and interestingly that lions tended to use the buffer
371 zone when buffalo had been using it over the 4 last weeks. This pattern is also visible on the
372 smoothed time series where peaks of buffer incursion frequency by lions lag behind peaks of
373 buffer incursion frequency by buffalo (Fig. 3 B C).

A.DISCUSSION

B.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.*, 2013b). 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 patho-ecosystem, our study of incidence (and reversion see (Miguel *et al.*, 2013b) for more details) patterns demonstrate that the FMD antibodies is 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 intra-specific 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 *et al.*, 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 behaviors 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 that 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 accounted for by long sero-conversion 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 *et al.*, 2015b). 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 *et al.*, 2015a) or single adult animals (van Schalkwyk *et al.*, 2016) that could also play a significant role in FMD dynamics.

B.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 auto-correlogram 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 *et al.*, 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).

B.HUMAN BEHAVIOR 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 *et al.*, 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.*, 2013b; Zvidzai *et al.*, 2013), our study shows that the rainy season is the key season for foot-and-mouth disease transmission and potential exposure to predation.

A.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 patho-ecosystem would require an understanding of how cattle owners take their herding decisions and according to which clues and perceived risks: disease, predation or

493 risk of zoonoses? The integration between biological and social sciences is therefore necessary to
494 better understand and manage the risk of disease transmission at complex
495 human/livestock/wildlife interfaces which are hotspots in the context of emerging infectious
496 diseases (Woolhouse & Gowtage-Sequeria, 2005). Recently, Iversen and collaborators
497 showed interesting results on the integration of community-based / participatory surveillance
498 to delineate disease outbreak and predict transmission risk (Iversen *et al.*, 2016)

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A.AUTHORISATIONS 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 license from the Zimbabwe Veterinary Association, Wildlife Group (Veterinary Committee) and Medicines Control Authority, Zimbabwe (license 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 Arrêté préfectoral n°DDPP69-2014-011 (agrément d’un établissement utilisateur / éleveur

524 fournisseur d'animaux utilisés à des fins scientifiques). Animal handling and care protocols
525 were carried out in accordance with approved guidelines

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

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693 **BIOSKETCH**

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

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TABLES

Table 1. Model selection for the FMD serological incidence (“incid”) modeling in the cattle population in the Hwange system. 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.

Model 1	AIC
incid ~ season	154,1
incid ~ villages + season	157,1
incid ~ villages + season + age	158,8
incid ~ constant	186,3
 Model 2	 AIC
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
incid ~ diptank	189,8

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

FIGURE LEGENDS

Figure 1. (A) Study area with the 3 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 pannel A** (copyright Google earth - CNES spot image 2012). **(C-D-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 meters 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.

Figure 2. Foot and Mouth Disease incidence (with standard errors and sample size) in cattle across seasons for the period April 2010-August 2011 in the Hwange system. Figure created with R studio software.

Figure 3. A-B-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-E-F: Auto-correlation 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 colors indicate

respectively a positive and negative significant correlation. Figure created with R studio software.

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** (24h, 3 days, 7 days, and 15 days) **and for a fixed spatial window** (300m). 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.

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.

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.

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

763 dotted lines indicate the significance threshold. The green and red colors indicate respectively
764 a positive and negative significant correlation. Figure created with R studio software.

765