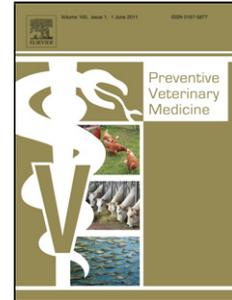


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Transmission of foot and mouth disease at the wildlife/livestock interface of the Kruger National Park, South Africa: can the risk be mitigated?

Running title: Risk of FMD at the Kruger National Park interface

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Highlights

- Since 2000, the efficacy of foot and mouth disease control at the interface between cattle and buffaloes at the edge of the Kruger National Park has deteriorated and needs urgent improvement.
- This quantitative risk assessment allowing to model the risk of FMD virus transmission between cattle and buffaloes at the edge of the KNP is based on ecological and epidemiological data and fits with past and current numbers of outbreaks.
- Including variability and uncertainty this model could be used as a tool for assessing control strategies and may be easily adapted to other transfrontier conservation parks in Southern Africa.
- Examples encompassing vaccination coverage (or efficacy), control of buffaloes' population in the park, control of buffaloes escaping the park are presented and discussed.

Summary

In Southern Africa, the African buffalo (*Syncerus caffer*) is the natural reservoir of foot and mouth disease (FMD). Contacts between this species and cattle are responsible for most of the FMD outbreaks in cattle at the edge of protected areas, which generate huge economic losses. During the late 1980's and 90's, the erection of veterinary cordon fences and the regular vaccination of cattle exposed to buffalo contact at the interface of the Kruger National Park (KNP), proved to be efficient to control and prevent FMD outbreaks in South Africa. However, since 2000, the efficiency of those measures has deteriorated, resulting in an increased rate of FMD outbreaks in cattle outside KNP, currently occurring more than once a year.

Based on retrospective ecological and epidemiological data, we developed a stochastic quantitative model to assess the annual risk of FMD virus (FMDV) transmission from buffalo to cattle herds present at the KNP interface. The model suggests that good immunization of approximately 75% of the cattle population combined with a reduction of buffalo/cattle contacts is an efficient combination to reduce FMDV transmission to one infective event every 5.5 years, emulating the epidemiological situation observed at the end of the 20th century, before current failure of control measures. The model also indicates that an increasing number of buffalo present in the KNP and crossing its boundaries, combined with a reduction in the vaccination coverage of cattle herds at the interface, increases 3-fold the risk of transmission (one infective event per year). The model proposed makes biological sense and provides a good representation of current knowledge of FMD ecology and epidemiology in Southern Africa which can be used to discuss with stakeholders on different management options to control FMD at the wildlife livestock interface and updated if new information becomes available. It also suggests that the control of FMD at the KNP interface is becoming increasingly challenging and will probably require alternative approaches to control this disease and its economic impact.

Keywords: African buffalo; Foot and mouth disease; transmission; risk assessment; modelling; Kruger National Park

Introduction

Foot and mouth disease (FMD) is considered one of the most important infectious animal diseases in the world, mainly because it inflicts severe economic losses due to the restrictions in trade of livestock and its products within infected countries (Thompson et al., 2002). In southern Africa, the epidemiology of this disease is substantially different than in other regions, mainly due to specific circulating strains (SAT1, SAT2 and SAT3) and the role of reservoir played by African buffalo (*Syncerus caffer*) populations (Vosloo et al., 2002; Vosloo and Thomson, 2004). This wild bovid is widespread in southern Africa's protected areas and represents a serious challenge for the control of FMD, particularly among cattle living in close proximity to natural habitats of buffalo. During the last decades of the 20th century, the implementation of specific control measures in exporting countries in the region, such as veterinary cordon fences and regular vaccination of cattle herds exposed to buffalo contacts, has managed to limit the occurrence of the disease in the region to less than one outbreak per decade. However, since 2000, the region has been experiencing a serious re-emergence of the disease (Baipoledi et al., 2004; Jori et al., 2009; Thomson et al., 2013a), with a frequency of at least one outbreak per year in areas where the disease was previously under control.

Epidemiological models are tools that provide useful insights into complex situations associated with the management of animal diseases at the wildlife/livestock interface (Miller et al., 2013) and are developed to improve our understanding on the effect of external inputs, through representation of the interactions between components of a complex system. Such tools can be helpful in discussions with (domestic and wild) animal health authorities and managers about the critical pathways of transmission and the assessment of different scenarios on disease outcomes in order to guide decisions. In that context, the development of stochastic epidemiological models that take into account the complex dynamics of FMDV have been modelled in the past, to estimate the risk of FMD transmission posed by different wildlife species in Zimbabwe and more recently, to take into account landscape heterogeneity, and climatic variability in the transmission of FMDV at the wildlife – livestock interface of Kruger National Park (KNP), (Dion and Lambin, 2012). In our study, we used a stochastic approach with the goal of integrating quantitative information of cattle and buffalo

movement across the veterinary cordon fence surrounding the KNP, and using available data accumulated by the animal health and wildlife authorities working at the interface of the KNP during the last two decades to measure the risk of FMD transmission in that area. The goal of the model was to estimate the annual probability of cattle becoming infected with FMDV at the interface of the KNP and to compare the impact of several mitigation measures on the annual occurrence of the disease during recent years.

Methods

STUDY AREA

The study area is the KNP wildlife/livestock interface, described in detail by Jori et al. (2009) and other authors (Van Schalkwyk et al., 2014). The KNP and adjacent private wildlife areas, inhabited by free-ranging buffalo populations, are recognised as the FMD-infected zones of the country (Figure 1). Adjacent to these fenced borders lies the buffer zone, mostly comprising communal farming areas, where rural communities graze their cattle and which is divided in two sections: i) a portion directly adjacent to the FMD infected zone, where cattle are vaccinated three times a year, referred to as the buffer zone with vaccination (BZV), and ii) a second portion adjacent to the BZV, where animals are not vaccinated but where increased livestock surveillance and movement control are implemented, known as the buffer zone without vaccination (BZNV). Adjacent to the latter is an inspection zone, where increased surveillance is implemented through the inspection of domestic livestock every 28 days. In the infected zone, BZV and BZNV, restrictions on animal movement are also enforced to prevent the occurrence and spread of outbreaks among cattle herds, while in the FMD-free zone (rest of South Africa), no restrictions are applied.

DEFINITION OF THE RISK AND MODEL FORMULATION

Since long distance air-borne transmission is extremely unlikely to occur in southern Africa (Sutmoller et al., 2000), we considered direct transmission as the main route of FMDV transmission between an infected and a susceptible animal.

The quantified risk (output of the model) was defined as the annual probability for at least one bovine from the BZV becoming infected with FMDV as a result of a contact with an infected wild buffalo from the KNP. This probability $P(I_{cbz})$, was modelled as follows:

$$P(I_{cbz}) = 1 - (1 - P_{cbz})^{n_{cbz}}$$

Where n_{cbz} is the number of cattle in the BZV and P_{cbz} the probability that one cattle head of this population becoming infected with FMDV from a buffalo transmitting virus.

Since this event can happen through two independent and compatible events, I_{cbz} will be the result of the union of two probabilities: the probability (PA) that a bovine gets infected by a buffalo escaping from the KNP into the communal grazing areas of the BZV and, the probability (PB) that a bovine enters the KNP and becomes infected through contacts with buffalo in the park. According to probability laws, the union of PA and PB is equal to the sum of both probabilities minus the product of those probabilities (Saporta, 2006). Therefore, $I_{cbz} = (PA+PB)-(PA*PB)$.

The pathway of events considered in the model is based on a preliminary qualitative risk assessment (Jori et al., 2009) illustrated in Figure 2.

The release assessment considered the annual probability for a buffalo to excrete FMDV. Most young buffalo, which are usually born during midsummer (November-February), become infected between 3 and 6 months of age (Thomson and Bastos, 2004), when maternal antibodies wane (Bengis et al., 1986). By the time they reach one year of age, almost 90% have been infected and show circulating antibodies to the three SAT type viruses (Thomson et al., 1992), and most surveys of buffalo in KNP and surrounding protected areas show FMD seroprevalence values that range between 80 and 90% (Jori et al., 2014). In the acute stages of infection, young buffalo excrete FMDV in roughly the same quantities and by the same routes as infected cattle and become highly contagious (Gainaru et al., 1986). Within 15 days of infection, the virus can no longer be recovered from the tissues, secretions or excretions, with the exception of cells in the pharyngeal mucosa, where the virus may persist for extended periods of time, resulting in carrier buffalos (Condy et al., 1985).

Therefore, the annual probability for a buffalo becoming infected, and excreting FMDV (P_i in Figure 2) can occur as the result of 3 event probabilities:

- i) A young weaned buffalo younger than one year is infected and becomes viraemic (P 1.1)
- ii) A young weaned buffalo younger than one year has become infected and becomes a carrier, after this period of viraemia (P 1.2.)
- iii) A buffalo older than one year has become a carrier, after becoming infected during the first year of his life (P 1.3.)

As a result of the two different scenarios proposed, P_A and P_B were assessed on the basis of historical data collected by wildlife management authorities and the Veterinary Services from the study area as well as from recent published literature (Table I)

The exposure assessment focused on the probability of livestock becoming infected as a result of infectious contacts with excreting buffaloes. Potential scenarios of transmission involving other wildlife (antelope) species or small ruminants were not considered in our study since the transmission of FMDV from buffalo to cattle is the most common scenario (Jori et al., 2009; Tekleghiorghis et al., 2014) in the Southern African context, the other domestic and wild species playing a minor role in FMD transmission (Jori et al., 2009; Weaver et al., 2013).

DEFINITION OF DISTRIBUTIONS FOR INPUT VARIABLES

Buffalo population in the KNP (Pop)

According to the census data produced annually by KNP management authorities, the KNP buffalo population almost tripled between 1985 and 2011 (Figure 3). These data were modelled using a normal distribution in which μ was the mean population of buffaloes in the KNP between 1985 and 2005 and σ was the standard deviation of this sample. The same data sources provided the mean number of buffalo calves (0-1 year old) per year between 1985 and 2005, which were modelled as another normal distribution. The number of adult buffalo was calculated as the difference between the total number of buffalo and the number of young. This allowed estimating the probability for a given buffalo from the KNP being younger (P_y) or older than one year (P_a).

Probability for a buffalo to be excreting FMDV (P 1.1)

In the model, we assumed that infection and potential transmission of the three SAT type viruses could occur as three separate processes, as suggested in other similar risk assessments (Sutmoller et al., 2000). For a young buffalo to become infected, it needs to lose the immunity provided by maternal antibodies which happens right after the weaning process (Thomson et al., 1992). According to the literature (Thomson and Bastos, 2004; Vosloo and Thomson, 2004), we determined that for an African buffalo from KNP to excrete FMDV (P1.1.), the following event chain needs to occur: a buffalo from KNP needs to be young (probability P_y), needs to be weaned (probability P_w), it needs to become infected with FMDV (probability P_{yi}) and it needs to find itself in a period of viraemia after the infection (P_e).

$$P1.1.=P_y*P_w*P_{yi}*P_e$$

Details on the calculation of prevalence and excretion of FMDV depending on the age of weaning and the days of viraemia can be found in Table I and Appendix I of Supplementary material.

Probability for a buffalo to be carrier of FMDV (P_c)

After the viraemic period, FMDV can still be isolated from the oropharyngeal fluid in a small proportion of individuals defined as carriers (Moonen and Schriver, 2000). Therefore, we distinguished two types of buffalo carriers that we named young and adult carriers, depending on their age (before or after the first year of life) and we defined P1.2 and P1.3 as the probabilities for a buffalo to be a young carrier and an adult carrier, respectively.

We defined the as P1.2 (probability for a buffalo to be young and carrier) was calculated as the product of the probability for a given buffalo being younger than one year (P_y), the probability to be weaned, the probability of a buffalo becoming infected during the second 6 months of life (P_{yi}), the probability of this animal not being in the period of viraemia ($1-P_e$) and the probability of being a carrier (P_c):

$$P1.2.=P_y * \frac{(12 - A_w)}{12} * \frac{Pr_{6-12} - (1 - P_{w6-12}) * Pr_{0-6}}{P_{w6-12}} * (1 - P_e) * P_c$$

In the same manner, P1.3. (the probability for buffalo to be adult and carrier) was calculated as the product of the probability to be older than one year (P_a) by the probability for an adult to be infected ($P_{r_{ad}}$), and by the probability for an infected buffalo becoming a carrier (P_c). We consider that infected adult buffalo results of infection during the first year of age, or do not become infected

$$P1.3. = P_a * P_{r_{ad}} * P_c$$

Additional details of the calculation of these probabilities are given in Appendix II of the supplementary material.

Probability of buffaloes escaping from KNP (P_{bcf})

The annual number of buffaloes escaping from the KNP was obtained from historical data recorded between 2002 and 2007 by the National Veterinary Services and wildlife authorities, operating outside and inside the KNP, respectively. We did not take into account the data from 2000 and 2001 because those years experienced massive buffalo evasions due to exceptionally high rainfall and were subsequently considered as rare events (Bruckner et al., 2002; Jori et al., 2009; Van Schalkwyk et al., 2014). Therefore, the average number of stray buffalo escaping from KNP during that period was evaluated at 70 individuals per year. We assumed that in the absence of those rare events, the probability for a buffalo to escape from the KNP was proportional to the total KNP buffalo population size and performed a logistic regression to obtain a model of this probability. Then, out of the same set of data, we calculated the probability for an adult buffalo (P_{caf}) or a young buffalo (P_{cyf}) to cross the fence (See supplementary material, Appendix III).

In summary, assuming that becoming infected and crossing the fence were two independent events, the release assessment of virus outside the KNP considered the 3 following probabilities:

- Release probability outside the KNP for a young excreting buffalo P1

$$P1 = P1.1. * P_{cyf}$$

- Release probability outside the KNP for a young carrier buffalo P2

$$P2 = P1.2. * P_{cyf}$$

- Release probability outside the KNP for a adult carrier buffalo P3

$P_3 = P_{1.3} * P_{caf}$

Probability for an individual bovine head to be in contact with buffalo outside the KNP (P_{coo}).

The numbers of cattle in the BZV were modelled as a livestock population ranging from 70 000 to 100 000 head based on the different data found in the literature and provided by the National Veterinary authorities outside the KNP (Brahmbhatt et al., 2012; Stevens et al., 2007).

The probability of cattle and buffalo being in close proximity outside the KNP was calculated using data gathered through a questionnaire performed among 113 cattle farmers from a specific location adjacent to the KNP fence in October 2007 (Abu Samra et al., 2012). Contact was defined as the fact of buffalo and cattle being in a common area measuring approximately the size of 0.7 ha. On that occasion, 30 out of 113 farmers declared having observed buffalo in their grazing area and 18 of them declared having seen the two species in contact and gave an indication of the time of contact observed (Abu Samra et al., 2012). We used this information to model the probability of observing a contact (P_{coo}). To take into account that contacts could occur between one buffalo and several individuals of a cattle herd, we considered the probability for a single buffalo to be in contact with at least one animal of the herd through the following formula:

$$P_{coo} = 1 - (1 - P_{cooh})^{n_{ch}}$$

where P_{cooh} was the probability for a single buffalo to be in contact with a cattle herd and n_{ch} the average size of a cattle herd modeled as a lognormal distribution and standard deviation of the cattle herd size observed in the study area where the questionnaire was implemented (cf. Table 1).

The time of contact observed by farmers in minutes was reported as maximum and minimum time intervals and was modelled as a uniform distribution between these values for each reported interval. The mean time of contact was modelled as a discrete distribution in which the uniform distribution of each time interval was considered a possible value and was combined with the probability weight provided by the proportion of farmers having reported this time interval (Vose, 2004).

Probability for an individual bovine head to be in contact with buffalo inside the KNP (P_{coi}).

The questionnaire implemented among 113 small scale farmers outside the KNP (Abu Samra et al., 2012), gathered data about the number of farmers (n=13) that declared taking their livestock inside the KNP for drinking several days a year. We assessed the probability of one bovine entering the KNP as a Beta distribution (r+1; n-r+1) in which “r” represented the total number of events i.e. the number of days per year that farmers declared driving their cattle into the KNP for drinking and “n” represented the total number of days that this event could have occurred in one year (Vose 2004). The probability of cattle and buffalo becoming in contact in the KNP was gathered by a questionnaire implemented among fence workers to assess the permeability of the 70% of the KNP Western boundary veterinary fence (Jori et al., 2011). This data set allowed us to quantify the number of days that every fence worker reported the observation of contacts during the previous year (r), and the number of possible days that this event could have been observed by the totality of persons interviewed (n). We then used a Beta distribution, as described above, to model this parameter. The mean time of contact between buffalo and cattle inside the KNP as reported by KNP fence workers (Jori et al., 2011), was modelled as a discrete distribution of each observed time interval. To take into account the occurrence of contacts between several individuals of each herd (buffalo and cattle) at water sources in the KNP, we calculated the probability for an individual from a cattle herd to come into contact with at least one individual of the buffalo herd when they would come across each other, P_{coi} , using the following formula:

$$P_{coi} = 1 - (1 - P_{coih})^{n_h}$$

where P_{coih} represented the probability for an individual bovine to be in contact with a buffalo herd and n_h the average buffalo herd size modeled as a lognormal distribution obtained from KNP buffalo census data.

PROBABILITY OF DISEASE TRANSMISSION AFTER CONTACT BETWEEN BUFFALO AND CATTLE (Pt)

The probability of transmitting FMDV following a contact between buffalo and cattle was calculated differently for a young (Ptyc) or adult carrier (Ptac) buffalo and for an excreting buffalo (Ptye). For carriers, we used the transmission rate parameter quantified by Tenzin et al. (2008), estimated at

0.0148 infections per month (likelihood-based confidence interval: 0.004625–0.0341). This variable was calculated from published experiments with buffalo and other domestic ruminants and the authors found no difference in the risk incurred by a domestic or wild FMDV carrier. We considered the transmission rate for a young excreting buffalo to be 100% efficient as observed in experimental cattle infections (Orsel et al., 2007; Orsel et al., 2005). Since conditions in the field are different than in experimental conditions and the SAT strains are different from the O strains used in these experiments (Orsel et al., 2007; Orsel et al., 2005), we conditioned this rate of transmission to the time of contact. Therefore, for times of contact longer than 6 hours, we considered a transmission of 100% and for contacts of 6 hours or shorter we assumed that transmission only occurred in 50% of the cases.

Concerning the susceptibility of cattle to infection through a contact with an excreting buffalo, we considered that vaccinated livestock were protected against FMDV infection in 100% of cases, while non-vaccinated cattle were entirely susceptible. The vaccination coverage of the cattle population in the BZV was modeled using a normal distribution according to the reports of vaccination campaigns provided by the official Veterinary Services operating in the BZV between 1996 and 2006, which ranged between 64% and 86%.

MODEL ENVIRONMENT AND SOFTWARE

The model was run 10,000 times using a Latin Hypercube simulation using the software package @Risk (@Risk version 5.5.0 Professional edition, 2009, © Palisade Corporation, 31 Decker Road, Newfield, NY) add-in for Microsoft Excel (© Microsoft Office Professional Edition, 2010).

SENSITIVITY ANALYSIS AND MODEL EXPERIMENTATION

To identify which inputs had the greatest effect on the variation of the final output and to assess the possible effects of variability and uncertainty of the input data on the model outcomes, a sensitivity analysis using least-squares regression coefficients was performed. Based on previous literature on risk assessment models (Martinez-Lopez et al., 2008; Mur et al., 2012), we considered regression coefficients (β) with values higher than 0.1, having a significant influence in the final output of the model.

In addition, in order to experiment further with the model and assess its sensitivity to the most common control strategies of FMD, we ran different scenarios modifying key input parameters such as i) the number of buffalo escaping from KNP to simulate potential changes in fence permeability or ii) the number of buffaloes living in the KNP to simulate an increase in the buffalo population, iii) the number of animals vaccinated to simulate changes in vaccine efficiency and vi) a combination of those scenarios. The value of each of those parameters was systematically varied in 5 steps using 5000 iterations/step from minimum and maximum values, while keeping constant all other variables at their base values.

Results

Numeric probabilities of the model with 90% confidence intervals are provided in Table 2. In general, the probabilities for any category of buffalo crossing the KNP fence were very low. The mean annual probability for a buffalo to be an FMD carrier and to leave the KNP (adult or young) was estimated at $240 \cdot 10^{-5}$ while the mean annual probability for a buffalo to be young, excreting FMDV and leaving the KNP was $3.6 \cdot 10^{-5}$. This suggests that it is approximately 67 times more likely for a buffalo to be carrier and to leave the KNP than for a young buffalo to be viraemic, excreting FMD virus and crossing the KNP fence.

Considering a good vaccination coverage of 75% in the cattle population at the BZV, a buffalo population with a mean value of 23 400 individuals and an average of 70 buffalo escaping from the KNP annually, the mean annual risk of having at least one bovine infected by buffalo outside the KNP (P_A) was a probability of 0.08 [0.002; 0.34]_{95%} (Figure 4a), while the mean probability of a bovine being infected by entering the KNP (P_B) was 1.25 times higher (0.11 [0.031; 0.236]_{95%}) (Figure 4b). Nevertheless the variation of P_A is 1.5 higher than the variation of P_B meaning that the combination of uncertainty and variability is higher for P_A . The combined risk of both events (the probability of at least one bovine becoming infected at the KNP interface) was 0.18 [0.043; 0.481] (Figure 4c). This mean value suggests that a transmission from buffalo to cattle in the circumstances described above

(which are similar to the epidemiological background in the study area before the year 2000) would occur on average once every 5.5 years.

SENSITIVITY ANALYSIS

The results of the crude sensitivity analysis are shown in Figure 4d. The parameters having the greatest impact on the variation in the risk of transmission were the age of infection of young buffalo ($r=0.43$), the parameters of the logistic regression linking the KNP buffalo population and the number of animals escaping ($r=0.32$ and $r=0.34$), the number of days of viraemia for infected buffalo ($r=0.23$), the probability for a young buffalo to leave the KNP ($r=0.21$) and the time of contact ($r=0.17$).

SCENARIO PLAYING

Scenario playing permitted to fix some parameters with a high uncertainty and to explore specifically their impact on the variation of the final probability. Scenario playing provided evidence that the model is sensitive to the parameters representing the control strategies for FMD in the region, such as veterinary cordon fences and vaccination (Figure 5a). The effects of a KNP buffalo population increase up to a level of 45 000 individuals (comparable to the KNP buffalo population in 2014) increased the compiled risk 1.7-fold, representing one transmission incident every 3.3 years (Figure 5a). The second scenario represented the possible impact of changes in the number of escaped of buffaloes from 70 to 750 individuals; in such a case of a massive escape of buffaloes as it could occur in case of year with high rainfall causing numerous floods, the compiled risk also increased 1.7-fold (Figure 5a). The third scenario simulated the impact of a reduction in vaccination coverage to 25% (Figure 5a), in which the risk increased 2.2-fold. When we combined all 3 events together with the most unfavourable values of these parameters, the calculated risk increased 3.4 times with respect to the original output, representing one transmission incident every year (Figure 5b).

Discussion

Considering the increasing importance of wildlife reservoirs in the epidemiology of infectious animal diseases, studies that integrate ecological and epidemiological data to estimate pathogen transmission at the wildlife livestock interface are instrumental to explore potential management or control strategies (Miller et al., 2013). Recently, some authors have developed sophisticated spatially explicit models to assess the risk of FMDV outbreaks outside KNP. Those models took into account landscape heterogeneity and spatially represented contacts between buffaloes and cattle essentially outside the KNP interface (Dion and Lambin, 2012; Dion et al., 2011). Our model is different since i) it simplified the KNP interface landscape as a whole homogenous unit and ii) integrated more detailed information on FMDV transmission between buffalo and cattle based on updated available literature and data.

Our model shows that at individual level and based on available published literature, the probability for a carrier buffalo (either young or adult) to transmit FMD to a susceptible bovine is extremely low while transmission between young excreting animals and a susceptible bovine are 95 times more likely to occur. In other words, the probability for a young excreting buffalo to infect cattle is comparatively much more important mainly due to the very low transmission rate of carrier buffalo.

Our model also suggests that, based on data from localised questionnaires, interactions between cattle and buffalo are 1.25 times more likely to occur inside the KNP when cattle herds enter or drinking and share water sources with buffalo herds than when small groups of buffalo escape from the KNP and roam in communal grazing lands interacting with cattle. The main difference is that contacts between buffalo and cattle herds around water sources inside KNP should allow a larger number of domestic and wild individuals to interact with each other, increasing the probability of transmission between individuals whereas outside KNP, contacts mostly occur between one or two escaped buffaloes (Van Schalkwyk et al., 2014) and scattered herds of grazing cattle. From that perspective, a realistic option to mitigate the risk of FMD emergence would be to influence communal farmer's behaviour to prevent cattle herds from getting inside the KNP. According to the model, if these management options would achieve to reduce by two the probability of a cattle head entering the KNP, the overall risk of FMD transmission to cattle would be reduced by 30% (data not shown).

One of the main challenges in the development of epidemiological models in natural populations often results from a limited understanding of how contact between wildlife and livestock occurs and how it leads to effective pathogen transmission (Lloyd-Smith et al., 2009). The assumptions under which the model was constructed are described in detail in the supplementary material section (Appendix IV). However, a fundamental assumption in the model was that FMD transmission between cattle and buffalo could occur if they shared the same environment within a specific space and for a certain amount of time. The maximum space frame considered for a contact to occur in the different questionnaires implemented (Abu Samra et al., 2012; Jori et al., 2011) being the size of a local soccer field (approximately 0.7 ha) and the time window considered for a contact ranging between 30 min and 1 day were considered plausible scenarios.

Some of the inputs based on a limited number of observations and thus, modelled integrating an important level of uncertainty, could have influenced the variation of the final estimated risk (Figure 4D). The sensitivity analysis reflected this influence with some parameters such as the ones of the logistic regression heavily influencing the variation of the results. The high impact of the uncertainty linked with the parameters of the logistic regression on the final variation explained also the difference in the range of the confidence interval between P_A (Probability of a bovine becoming infected outside KNP), which includes a logistic regression formula, and P_B (Probability of a bovine becoming infected inside KNP) for which the logistic regression formula is not included. Therefore the comparison between P_A and P_B should be interpreted with caution. Other parameters such as the age of infection or the number of days of viraemia, are influenced by a high variability, which is clearly not reducible. In the model, according to field data from KNP (Thomson et al., 1992), we considered that animals became infected by all three SAT types before the age of one year. We assumed those three infections occurred as separate events, which increased by three the time of viraemia in days (Sutmoller et al., 2000). In the unlikely case, that these three infection processes would occur at the same time, the risk of transmission would be reduced by two (data not shown). The probability for a young buffalo to leave the park differs due to the variation between the numbers of animal escaping observed on different years. This variation is equally influenced by variability (different animals with different behaviour from one year to the other and different observers between years) and uncertainty

(due to the fact that this parameter is an extrapolation of a survey done on a part of the fence). The variation on the time of contact is influenced by uncertainty due to the scarce number of observed contacts that we extrapolated to the whole population of animals, which could potentially interact. However, our model is adaptable and has the capacity to integrate new information on some of the inputs when it becomes available.

The work presented here illustrates well the multifactorial nature of FMD re-emergence at the interface of the KNP and the results are well validated by historical data of reported FMD outbreaks from the study area. The model clearly shows that with good immunity of cattle herds and a limitation in the number of contacts between cattle and buffalo, the mean risk of transmission can be reduced from 1 transmission event /year to 1 event every 5.5 years (mean of the risk distribution = 0.18). This matches well with the limited number of outbreaks (only two between 1987 and 1999) reported in the literature (Bruckner et al., 2002; Jori et al., 2009; Thomson et al., 2013a), when the implementation of veterinary fences and bi-annual vaccination of cattle at the BZV successfully mitigated FMD occurrence. However, since the year 2000, the number of outbreaks at the KNP interface has increased almost 5-fold, with at least 14 reported outbreaks between then and 2014 (Figure 1). Our model shows how several ecological or management factors (increase of wildlife populations, combined with a reduction in the immunization of cattle) could have contributed to an increase in the risk of FMD transmission. Populations of elephants and buffaloes in KNP have been increasing exponentially since the mid-1990s and are nowadays higher than ever in KNP history (Figure 3). This abundance of buffaloes in the KNP is likely to increase the quantity of virus available and the number of animals likely to cross the park boundaries in case of fence damage, thereby increasing the probability of an infected (excreting or carrier) buffalo escaping its natural habitat and establishing an infective contact with susceptible cattle. Veterinary fences were specifically developed to prevent those contacts (Thomson et al., 2003) and their success in mitigating FMD transmission during the last two decades has promoted their spread across other countries in southern Africa, despite a highly controversial impact on wildlife populations (Woodroffe et al., 2014). In addition, although not integrated directly in the model, the increase of elephant populations in the KNP (Figure 3),

considered as one of the major causes of fence damage in the KNP (Jori et al., 2011; Jori et al., 2009). Therefore a reduction of elephant population is likely to decrease the number of fence gaps, reducing the number of escaped buffalo and the potential disease transmission to cattle in the BZV. Some control of elephant populations based on culling has been implemented in the past (Van Aarde et al., 1999). Similarly, the model equally suggests that a decrease in the number of buffaloes by 50% would reduce the risk of FMD transmission by two fold (Figure 5a). However, culling of large mammals is highly controversial; current KNP management options do not include this possibility in the short term and largely rely on the removal of artificial water supplies (Lange, 2008). Therefore, since substantial buffalo and elephant declines are unlikely to occur in the short term, it is likely that infectious contacts between buffalo and livestock at the interface of the KNP will increase progressively with the growth of those large mammal populations.

Although the possibility of controlling and eventually eradicating FMD with existing vaccines has been demonstrated in Europe and large parts of South America, this achievement is utopic in southern Africa due to the high genetic variability within and between the SAT serotypes circulating in buffalo populations (Bastos et al., 2003; Teklehiorghis et al., 2014; Vosloo et al., 2005) and due to the large buffalo populations remaining in the southern African region. During the late 1980's and 1990's in South Africa, this challenge was met through the production of vaccines synthesized from strains collected directly from KNP buffalo populations, which ensured better matching and protection of cattle against potential exposure of FMDV strains circulating at the interface. This measure, combined with a good prevention of wildlife/cattle physical contacts, resulted in successful control of FMD, confirmed by absence limited number of reported FMD outbreaks during that period (Thomson et al., 2013a) an is confirmed by other model.

However South Africa stopped its national vaccine production at the beginning of the 21st century. Since then, currently used vaccines in southern Africa are produced by a single manufacturer out of a pool of viruses which are not specific against KNP strains. This results in commercial vaccines that are less efficient against circulating strains than those used a decade ago (Thomson et al., 2013a), undoubtedly contributing to FMD re-emergence in the Southern African region. In our model, since data on the efficiency of vaccines was not available, we simplified this issue by assuming that the

vaccine was 100% efficient, and used the rate of vaccination coverage in the herd as a proxy of vaccine efficiency. Therefore, changes in the efficiency of vaccination were simulated through a variation in the herd vaccination coverage.

The production of more efficient vaccines, produced out of KNP circulating strains could potentially improve the situation, but in practice this option becomes expensive and commercially unrealistic at a regional scale. In addition, the lack of benefits for communal farmers living at the KNP interface would remain an issue likely to impact on the vaccination coverage of the herds and the immunological control of the disease. This progressive deterioration in the control of the disease also seems to be the trend in other countries in the region, with devastating economic losses for the beef industry and limited prospects for reverting the situation in the mid term. In addition, the increasing development of transfrontier conservation areas (TFCA's) in southern Africa will facilitate more contacts between buffalo and cattle and complicate attempts to reduce the number of FMD outbreaks (Teklehiorghis et al., 2014; Thomson et al., 2013a). This situation justifies the need to explore alternative solutions to the problem. One of such alternatives that is progressively gaining acceptance, is the implementation of the commodity based trade concept, consisting of the production and trade of safe, FMDV-free manufactured beef commodities, despite their being produced in FMD infected areas (Thomson et al., 2013a; Thomson et al., 2013a; Thomson et al., 2013b; Weaver et al., 2013). If this concept is successfully applied in southern Africa, it has the potential to reduce the challenge of wildlife-livestock cohabitation at the interface of protected areas.

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Figure Captions

Figure 1: Map of the study area showing the number of FMD outbreaks that occurred between 1990 and 2010.

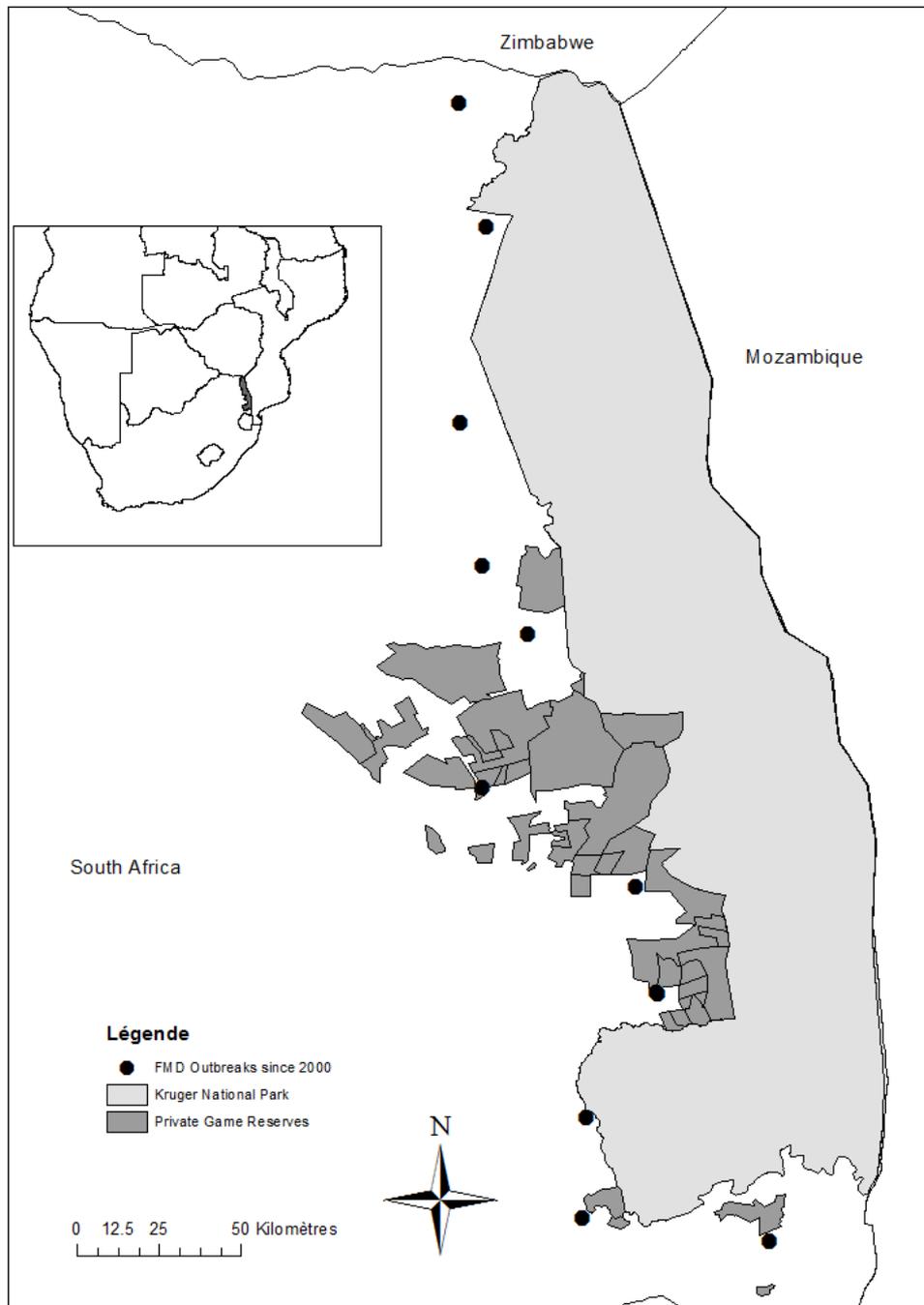


Figure 2: Event pathway of transmission of FMDV between buffalo and cattle at the wildlife/livestock interface of KNP with $P_i = P_{1.1} + P_{1.2} + P_{1.3}$

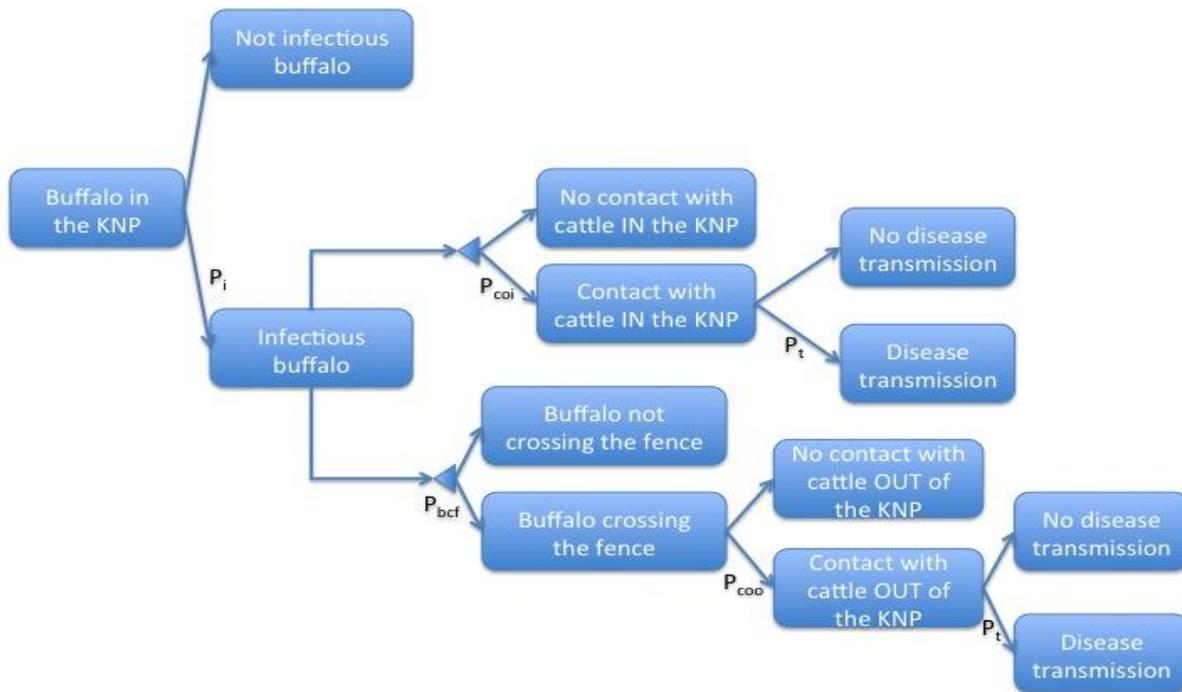


Figure 3: Trends in the buffalo and elephant population in KNP between 1995 and 2011 showing an increase of more than 100% during that period (Source: SanParks)

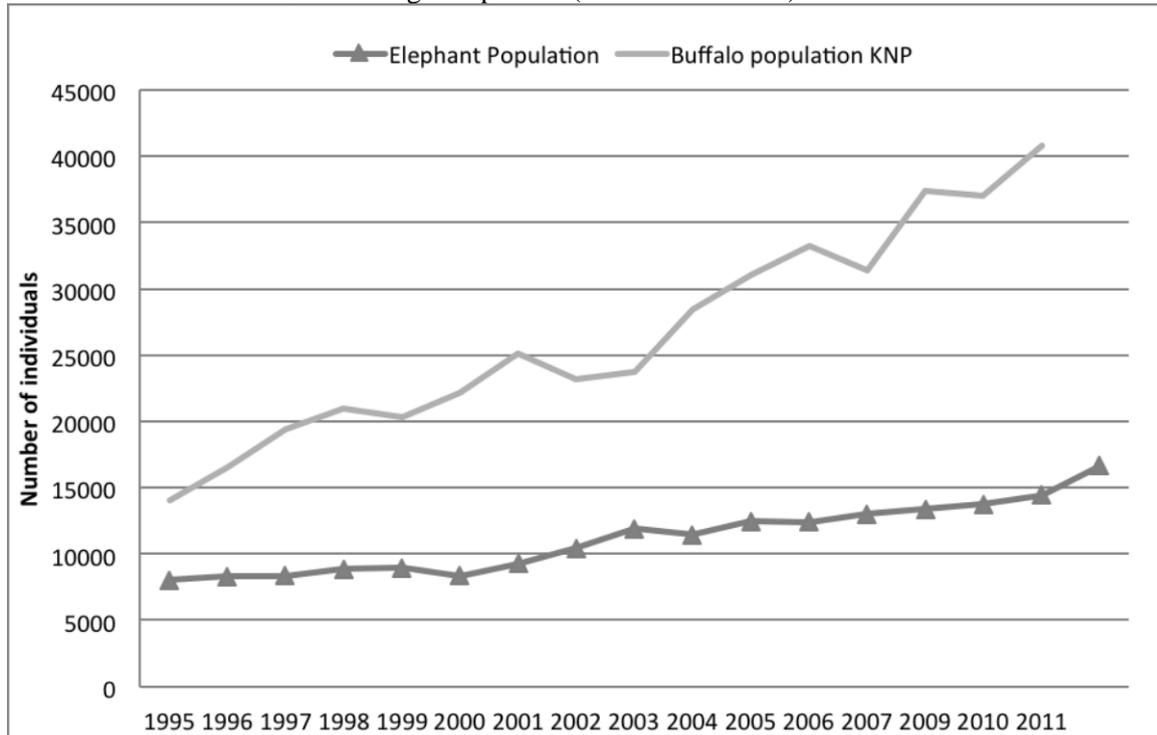
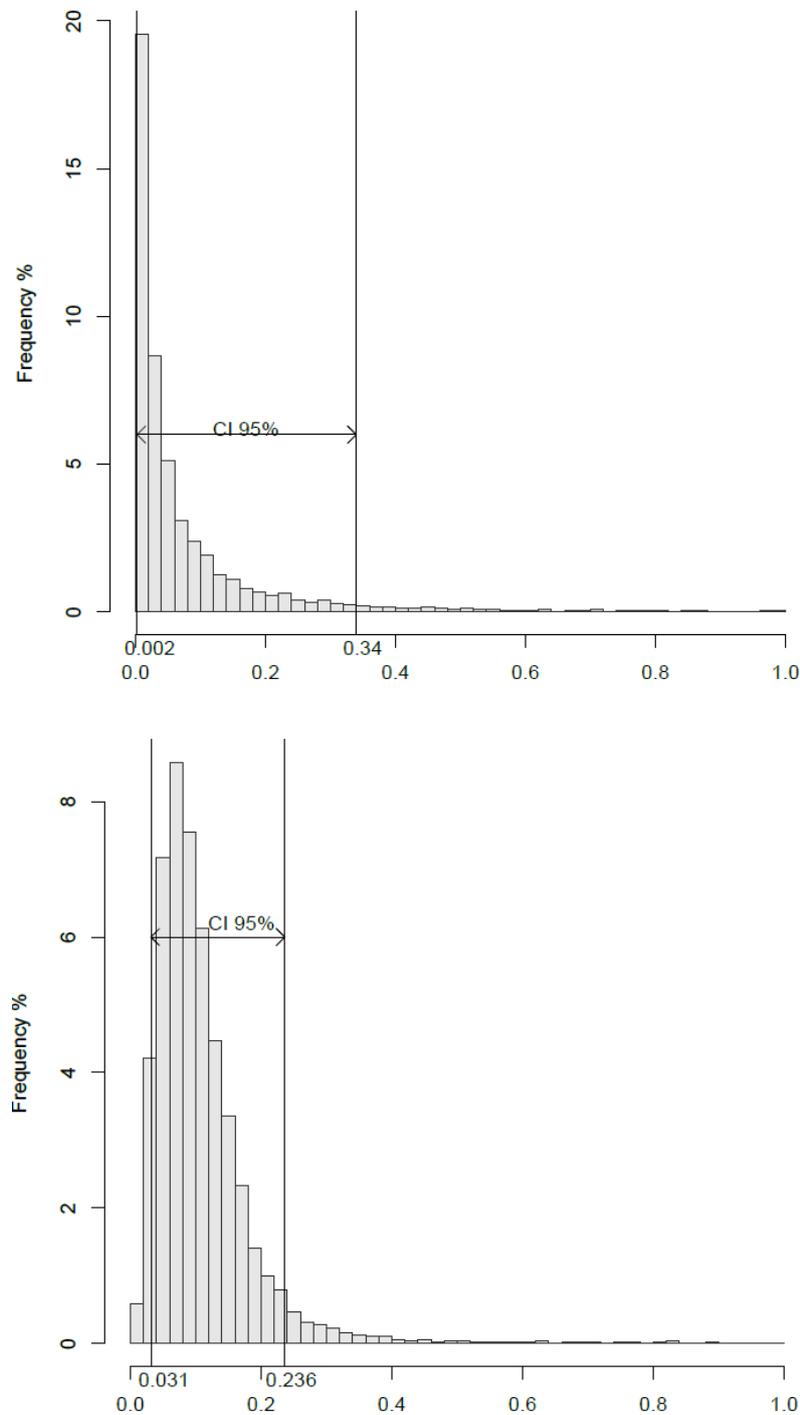


Figure 4: Model outputs for the different scenarios of transmission at the wildlife/livestock interface of the KNP. Annual probability of buffalo to cattle transmission A) outside and B) inside the KNP, C) Combined probabilities taking into account both scenarios and D) Crude sensitivity analysis showing correlation coefficients of inputs having a major influence in the final output. Only correlation coefficients > 0.1 are shown.



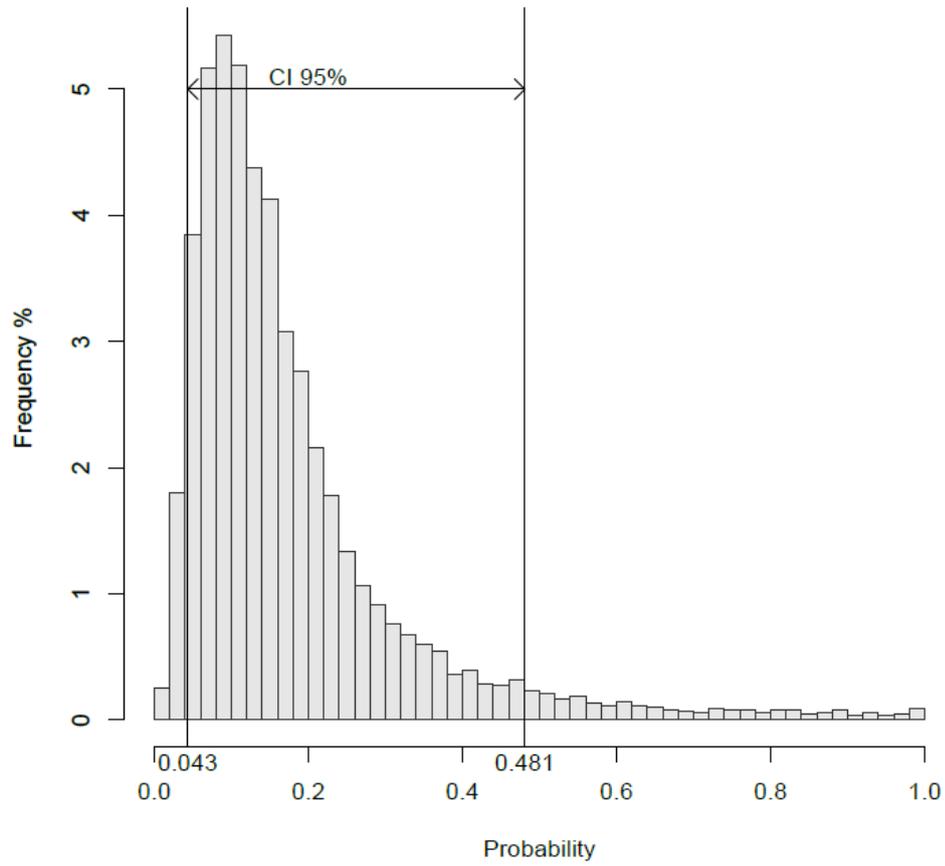
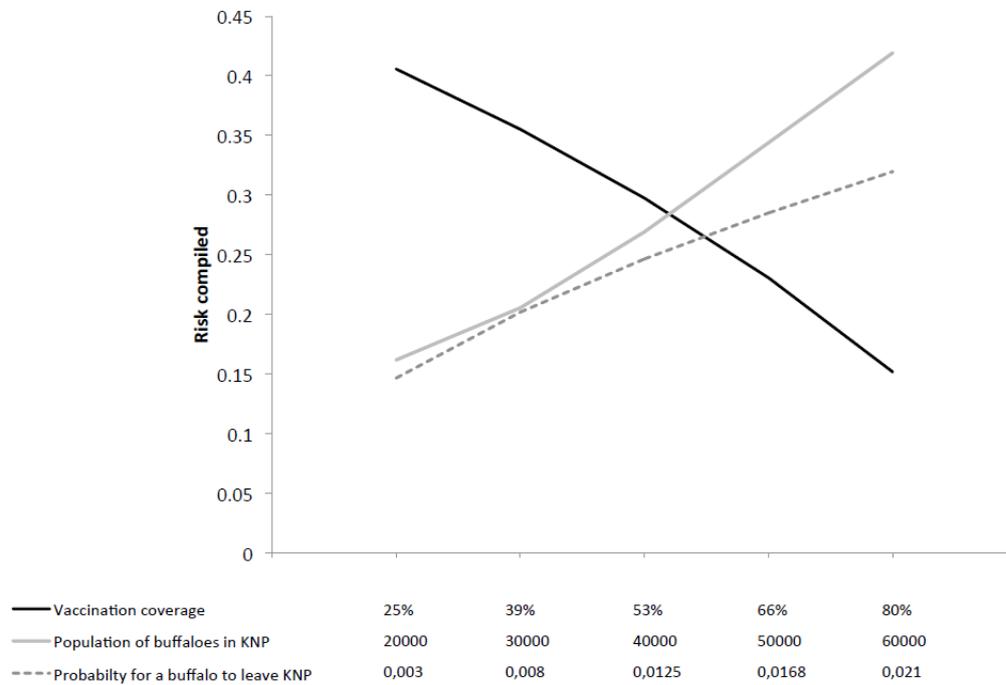
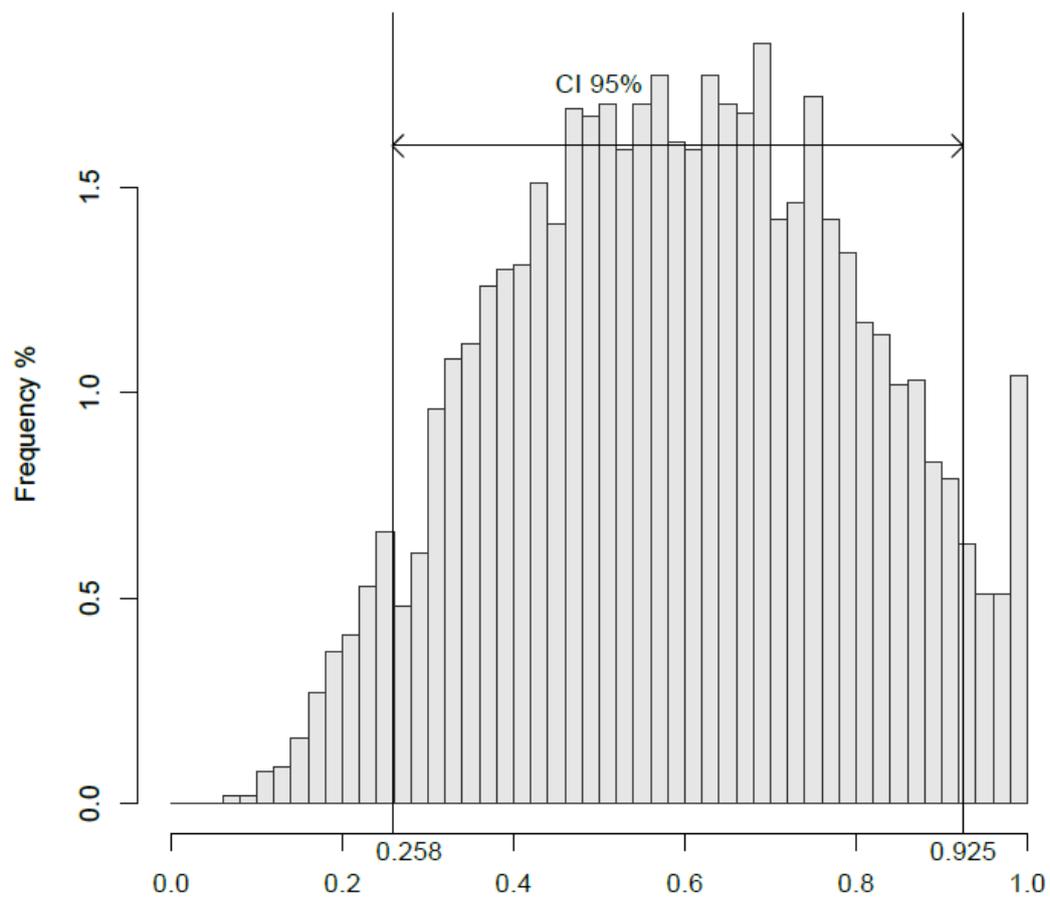


Figure 5: A) Scenario playing showing mean annual risk for FMDV transmission if the herd immunity changes between 25% and 80%, KNP buffalo population changes between 20 000 to 60 000 individuals, and if the annual probability for a buffalo escaping from the KNP changes between 0.003 (70 animals escaping per year) and 0.021 (500 animals escaping per year). B) Risk distribution when playing all the worst scenarios of the previous values together.





Tables

Table I: Inputs (distributions and values) used in the model with their respective sources of information.

Notation	Definition	Distribution type, @Risk Function and calculated values applied in the model	Source
P_{op}	Number of buffalo in the KNP	Normal Distribution RiskNormal(m, s) m=23377, s=5293	KNP Census Data (1985-2005)
n_{cbz}	Number of cattle in the buffer zone of KNP	Pert Distribution RiskPert(min,most_likely,max) min=70000, most likely= 85000, max= 100000	Jori et al., 2009 Brahmbatt et al, 2010 Stevens et al., 2007
A_w	Age of weaning for a young buffalo	Pert Distribution RiskPert(min,most_likely,max) min=6, most likely= 8, max=12	Bengis et al., 1986
Pr_{0-6}	Prevalence of FMD in buffalo younger than 6 months reflecting maternal antibodies	Beta distribution RiskBeta(α_1 , α_2) $\alpha_1 =42$, $\alpha_2=4$	Thomson et al, 1992
Pr_{6-12}	Prevalence of FMD in young buffalo from 6-12 months	Beta distribution RiskBeta(α_1 , α_2) $\alpha_1 =20$, $\alpha_2=4$	Thomson et al, 1992
P_y	Proportion of young buffalo in the KNP	Normal Distribution RiskNormal(m, s) m=0.117, s= 0.027	Buffalo census, KNP (1995-2005)
V	Viraemia in days in buffalo infected by 3 SAT types at different periods during year 1	Pert Distribution, RiskPert (min,most_likely,max) min=1, most likely= 3, max=5 3 * Pert (1, 3, 5)	Gainaru <i>et al.</i> 1986 Thomson <i>et al</i> , 1992 Sutmoller <i>et al.</i> , 2000
P_c	Probability for an excreting buffalo becoming a carrier	Pert Distribution, RiskPert (min,most_likely,max) min=0.17, most likely= 0.6, max=0.7	Vosloo et al., 2007
n_{bcf}	Number of buffalo crossing the fence/year	Normal Distribution RiskNormal(m, s) m=86.87, s=33	Department of Agriculture 2002-2007
P_{ycf}	Proportion of young buffalo crossing the KNP fence	Normal Distribution RiskNormal(m, s) m=0.16, s=0.09	Mpumalanga Veterinary Services, 2002-2006
P_{coo}	Probability of contact cattle buffalo in the BVZ	Beta distribution RiskBeta(α_1 , α_2) $\alpha_1 =19$, $\alpha_2=964$	Abu Samra, et al.2012
n_{ch}	Cattle herd size in the BVZ	Lognormal Distribution RiskLognorm(m,s) m=15.548, s=13.94) Truncated(0;60))	Abu Samra, et al.2012
P_{coih}	Probability of contact cattle buffalo inside KNP	Beta distribution RiskBeta(α_1 , α_2) $\alpha_1=372$, $\alpha_2=8390$	Jori et al., 2011
T_c	Time of contact between buffalo and cattle outside the KNP (mns)	Discrete Distribution RiskDiscrete({xi},{pi}) x1=360, x2=720, x3=360 p1=0,3. p2=0,4, p3=0,3	Abu Samra, et al.2012
V_c	Vaccination coverage in cattle from Mpumalanga Province	Normal Distribution RiskNormal(m, s) m=0.754545, s=0.0665	Department of Agriculture 2002-2007, Mpumalanga Veterinary Services (1996-2006).
Tr	Transmission rate for carrier animals infections/carrier/month	Pert Distribution, RiskPert (min,most_likely,max) min=0.004625; most likely=0.0148, maximum0.0341	Tenzin et al., 2008

n_h	Buffalo herd size inside the KNP	Lognormal Distribution RiskLognorm(m,s) m=44.164, s=237.64) Truncated (0;480))	KNP Census Data (1985-2005)
P_{catKNP}	Probability of cattle entering the KNP	Beta distribution RiskBeta(α_1 , α_2) $\alpha_1 = 22543$, $\alpha_2 = 601974$	Abu Samra et al., 2012

Table II: Different outputs of interest calculated with the model showing the mean value and the 90% confidence interval after running 10000 iterations (Latin Hypercube sampling).

Name	Mean	Confidence interval (90%)
Probability for a young buffalo to cross the fence (Pycf)	0.0108	[3 10 ⁻⁴ ; 0.0414]
Probability for an adult buffalo to cross the fence (Pacf)	0.0065	[3 10 ⁻⁴ ; 0.0235]
Probability of contact between a buffalo and a susceptible cattle outside KNP(Pcoo).	0.005	[0.001; 0.013]
Probability of contact between a buffalo and a susceptible cattle inside KNP (Pcoi).	0.007	[0.04-0.03]
Probability for a buffalo to be young, excreting FMDv and to cross the fence (P1)	3.6 10 ⁻⁵	[6.96 10 ⁻⁷ ; 1.4 10 ⁻⁴]
Probability for a buffalo to be young, carrier FMDv and to cross the fence (P2)	2 10 ⁻⁴	[4.4 10 ⁻⁶ ; 7.3 10 ⁻⁴]
Probability for a buffalo to be an adult carrier FMDv and to cross the fence (P3)	0,0022	[1 10 ⁻⁴ ; 0.008]
Probability of transmission between a young excreting FMDv buffalo and susceptible attle outside the park cell (Pt _{ye})	1.4 10 ⁻⁶	[2.7 10 ⁻⁸ ; 5.1 10 ⁻⁶]
Probability of transmission between a young carrier FMDv buffalo and a susceptible cattle outside the KNP (Pt _{yc})	7.5 10 ⁻⁶	[1.6 10 ⁻⁷ ; 2.8 10 ⁻⁵]
Probability of transmission between an adult carrier FMDv buffalo and susceptible cattle (Pt _{ac})	8.6 10 ⁻⁵	[4 10 ⁻⁶ ; 3.2 10 ⁻⁴]
Annual Probability of at least one cattle head to become infected in the KNP (P _A)	0.11	[0.031; 0.24]
Annual Probability of at least one cattle head to become infected in the BZV outside the KNP (P _B)	0.08	[0.002; 0.34]
Annual probability for at least one cattle becoming infected at the KNP wildlife/livestock interface(P(I _{cbz}))	0.18	[0.045; 0.47]