A spatio-temporal probability model of cattle and African buffalo (*Syncerus caffer*) contact as a proxy for foot-and-mouth disease risk:

A case study at the wildlife-livestock interface of the Kruger National Park, South Africa

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by

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Declaration

I declare that the thesis, which I hereby submit for the degree *Philosophiae Doctor* at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

OL van Schalkwyk
12 February 2015

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A case study at the wildlife-livestock interface of the Kruger National Park, South Africa

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The work presented here investigates a number of important components in the epidemiology of foot-and-mouth disease (FMD) at the wildlife-livestock interface along the Kruger National Park (KNP) and its adjoining private and provincial nature reserves (APNR). This epidemiological setting is unique and complex, mainly due to the presence of African buffaloes (*Syncerus caffer*) persistently infected with the Southern African Territories (SAT) strains of the FMD virus. Despite a great deal of experimentation and field research, FMD transmission from both persistently- and acutely-infected buffaloes to cattle is still poorly understood, although it is accepted that the two species have to be in close contact for it to occur. And even then, 'close contact' is ill-defined. Comparisons of three intensive study sites in the FMD protection zone, comprising both communally-farmed as well as smallholder cattle rangelands, were conducted to better understand this livestock system and determine livestock distribution patterns. This vast heterogeneous landscape of the FMD protection zone follows a latitudinal gradient of both human density and rainfall (increasing from north to south), which is reflected in similar gradients in cattle densities, the number of households owning cattle, consumption patterns as well as herding practice, whilst inversely associated with cattle sales and calf mortality rates. Distribution studies of the cattle in these study sites revealed a dry season dependence on water, and contraction of home ranges around preferred habitat during the warm wet season. Herding, or the lack thereof, was evident in daily activity budgets of these cattle. Interestingly, seasonal differences in stray buffalo dispersal patterns were the inverse of their domestic counterparts, being condensed along the fence line during the dry season. Stray buffalo events mainly consisted of single animals or very small groups, predominated by adult bulls. Most of these animals were destroyed soon after straying from the FMD infected zone, although some managed to move into areas with unvaccinated cattle, especially along major river courses. Swift removal of stray buffaloes from livestock areas is paramount, since recent outbreaks all share the characteristic of stray buffaloes being reported roaming the outbreak-area over extended periods (months) prior to an outbreak. Combining cattle and stray buffalo habitat suitability estimates revealed areas likely to facilitate contact between these species, which was mostly driven by cattle dispersal into those condensed areas along the fence and rivers more suitable for stray buffaloes during the cool dry season. This is also the season when acute infection with FMD is most likely in buffaloes. Yet, when adjusting cattle habitat suitability to incorporate their density, the concentration of preferred habitat during the warm wet season forms small pockets of high cattle density, amplifying contact risk with stray buffaloes in these areas. Simulation of stray buffalo movements along a least cost path, which incorporates fence permeability, is shown to be a useful visual aid to finding high-risk stray buffalo movement corridors. Contact-risk models performed well in retrospectively identifying high risk areas during recent outbreaks. These risk outputs have value in informing risk-based surveillance and strategic vaccination programs as well as in the delineation of disease control zones.

Keywords: Foot-and-mouth disease; Wildlife-livestock interface; Kruger National Park; Communally-farmed cattle; Cattle demographics; Cattle movement patterns; African buffalo; Distribution modelling; Risk modelling; Disease control.

Chapter 1

Foot-and-mouth disease contextual literature review and project objectives

Chapter summary

Here, a review of foot-and-mouth disease (FMD), which has been well-studied over the past half a century, is presented. The large interest in FMD stems from its economic impact through production losses and trade embargoes, making it the most feared animal disease to enter Europe at present. In southern Africa, a unique situation exists: more than two-thirds of the African buffalo (*Syncerus caffer*) population is presumed to be persistently infected with the Southern African Territories (SAT) type FMD viruses and hence deemed to be the main source of FMD in livestock in the region. In many parts of the subcontinent this has resulted in the isolation of these persistently-infected buffalo herds within fenced-off game reserves, igniting controversy over the ecological consequences. Transmission of FMD virus between buffaloes and cattle is still poorly understood, despite numerous experimental studies attempting to shed light on the processes underlying it. Acutely-infected buffaloes (presumably most prevalent among calves) pose the highest risk of virus transmission, although the risk posed by persistently-infected animals is also considered significant. Other species, such as impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*), have also been implicated in FMD epidemiology in the region. Airborne transmission is unlikely under local climatic conditions. The control of FMD in such an endemic setting comes at extensive cost, both directly through control measures (fencing, vaccination and movement controls) as well as indirectly though exclusion of vaccinated livestock from lucrative export markets and the ecological impact of fencing. Most of these control measures have been imposed by the World Organisation for Animal Health and importing countries to promote 'safe' trade. Current trade regulations focus on the animal, rather than its products, which put a large number of poor rural farmers at a distinct disadvantage, despite being able to produce livestock products that are essentially safe. Currently, however, alternative trade scenarios, with less consideration of the geographic origin of livestock are being considered. A large number of models have been developed to appraise FMD risk, although few assessed the risk of transmission posed by persistently-infected buffaloes to domestic cattle. Within the context of this literature, the project objective of developing a spatio-temporal probability model of FMD risk, based on contact between cattle and African buffaloes, is presented.

Contextual literature review

Foot-and-mouth disease (FMD), a disease characterized by high morbidity and low mortality in livestock, is caused by a virus from the family *Picornaviridae,* which usually affects cloven-hoofed animals and camilids. Seven immunologically distinct types of FMD virus (FMDV) exist, namely A, O, C, Asia 1, South African Territories 1 (SAT-1), SAT-2 and SAT-3[1]. The SAT type viruses are all endemic to African buffaloes (*Syncerus caffer*) of southern Africa[2-4], and even as far north as Uganda[5]. Recently, African buffaloes have been intentionally bred free of the virus, mainly as part of commercial enterprises[6], whilst only a few, isolated, naturally FMD-free buffalo populations exist in South Africa[7]. These latter populations most likely stem from the near-extermination of buffaloes during the mid twentieth century, as part of the tsetse fly control program, leaving only small, isolated populations in the Eastern Cape and Kwazulu-Natal Provinces, likely too small to maintain FMD virus infection (RG Bengis, personal communication, 15 January 2015). SAT type viruses are also unique in that they have discrete geographic areas of distribution and are adapted to persist in a multi-species wildlife environment with significant African buffalo populations[8,9]. During the twentieth century, 48% of FMD outbreaks in cattle in southern Africa were due to SAT-2, 36% due to SAT-1 and 16% due to SAT-3, with the latter also being least frequently associated with outbreaks in cloven hoofed wildlife[1,3]. SAT types of FMDV have a very high mutation rate, causing as much as 20% intratypic variation in the case of SAT-2 in buffaloes[10], a trait which is useful in establishing the geographic origin of FMDV strains during outbreaks[11,12]. Recent advances in molecular-based diagnostics could allow even more detailed investigation of virus dispersal and tracing of outbreaks[13].

Disease epidemiology

Foot-and-mouth disease in cattle

The most likely route by which cattle will acquire infection, is the respiratory route[14], mainly due to their large inspiratory volumes[15,16]. Nevertheless, hours of inhaling infected air is required for transmission to occur[14]. FMD infection in cattle almost invariable causes short-lived pyrexia, coupled with vesicular lesions of the mouth (tongue, dental pad and gingival) and hooves (coronary and inter-digital areas)[1]. Recently, Charleston et al.[17] determined the FMD incubation period in cattle to be 2.9-5.9 days. More importantly, however, they found the infectious period to be only 1.7 days (0.3-4.8 days) in duration and only starting shortly after the development of clinical signs, which is in contrast to the much longer infectious period suggested previously, believed to start before the onset of clinical signs[1]. The practical implications of these findings by Charleston et al. [17] have however been debated by some[18]. Although animals mostly recover fully from these symptoms, secondary infections can be debilitating (also see disease impact section later)[1,19].

The role of small stock

Due to a smaller inspiratory volume, it is more difficult for small stock to become infected with FMDV[20]. Sheep and goats can, however, become carriers of FMDV[21], with some virus types even showing predilection for small stock[22] (although none of the SAT types are mentioned in either study). FMDV exposure was confirmed in goats in Botswana by a high seroprevalence of antibodies to especially SAT-1 virus, with buffaloes being implicated as the primary source of infection[23]. No antibodies were, however, found in sheep during the same study. Nevertheless, the role of these species is not deemed important during outbreaks[24,25] in southern Africa and they are usually only quarantined and not vaccinated when an outbreak occurs. This has been further confirmed by the postulation that indigenous sheep and goats do not contribute to the persistence or spread of FMD (Type A, O, SAT-2)[26].

African buffaloes as host

Condy et al.[27] and Hedger[28] first postulated that African buffaloes are the usual source of SAT type FMD outbreaks in livestock in southern Africa. This has subsequently been generally accepted[9,10,24,29-32], even though the exact mechanism whereby this occurs remains ill-defined[9]. Most knowledge on FMDV transmission by wildlife has been inferred from livestock[9].

Acute infection of African buffaloes

Acutely-infected African buffaloes excrete virus through similar routes and in similar amounts to acutely-infected cattle, but potentially for longer periods, peaking around four weeks following exposure[30,33]. During this period, the highest amounts of FMDV are found in oro-nasal secretions for 1-3 days prior to, and 7-14 days following the development of lesions[1,14,34]. Nevertheless, Gainaru et al.[30] was unable to demonstrate FMDV in the air exhaled by infected buffaloes, while it could be demonstrated in cattle during the same study. In the same study, FMDV was also found circulating in buffaloes' bloodstream six days after exposure during. Only on rare occasions, or under experimental conditions, do buffaloes develop overt FMD[10,28,30,33,35-39].

Persistent infection of African buffaloes

A persistently-infected animal (sometimes referred to as a 'carrier') is defined as an animal from which it is possible to recover infectious FMDV 28 days after infection[40]. Individual buffaloes can remain persistently-infected for up to five years and it has been claimed for one particular buffalo population, on an isolated island in Lake Kariba, Zimbabwe, that they maintained FMDV infection for as long as 24 years[41]. It is interesting to note that no other species were found to be seropositive for FMD on the same island. Hedger et al.[42] also reported a SAT-3 FMDV strain, found in Zimbabwean buffaloes, which had not been seen in cattle for at least 15 years. The physiological mechanism for FMD viral persistence is, however, still poorly understood[43], although recently virus has been located in the germinal centres of lymphoid follicles harvested from persistently-infected buffaloes[44]. Only buffaloes[42] and impalas (*Aepyceros melampus*)[45] are considered to play an important role in the perpetuation of FMDV in the Kruger National Park (KNP), South Africa. About 60% of buffaloes become persistently-infected with FMDV following infection[46] and are able to carry more than one strain of FMDV at the same time[28]. These persistently-infected buffaloes can transmit infection to other animals (of the same or other species) with which they are in close contact, albeit extremely rarely and under unknown circumstances.[9,47]. Thomson[2] reports that 85% of buffaloes older than one year in the KNP have antibodies to all three SAT type viruses. However, the persistently-infected state in this species probably does not last lifelong[31]. The proportion of persistently-infected buffaloes seems to peak in the age group 1-3 years before starting to wane[48], to the point where they can become susceptible again[28]. Furthermore, virus has been isolated from some individual buffaloes more frequently than others[41], which might be of epidemiological importance. Buffaloes are gregarious animals, forming herds with defined home ranges (40-1000km^2), to which they confine themselves for several years depending on environmental pressures, other herds in the vicinity and/or reserve boundaries[49,50]. It is this herd-forming as well as the fragmentation behaviour of buffaloes[49-52] that has been postulated as a mechanism enabling them to maintain FMDV in a population over extended periods of time[28,42]. To date there has been no evidence that buffaloes can become persistently-infected with type A, O or C FMDV[9].

Viral transmission

Circumstantial evidence for transmission from buffaloes to cattle does exist[9,24,35,39,42,53,54], albeit a very erratic[10] and unusual event due to the transient and indirect nature of contact between these species, as well as the potential protection through vaccination[37,55]. Interestingly, in Kenya, Anderson[56] concluded that the viruses in cattle and buffaloes were so different, that transmission between these species seemed unlikely. Whilst questioned by some[42], several authors circumstantially relate FMD outbreaks with stress or disturbance, ranging from lions causing havoc in an area[20,57] to transportation[58] and changing weather[30]. These latter authors[30] further explored this theory by injecting persistently-infected buffaloes with dexamethasone, which did not induce clinical disease or transmission to susceptible cattle. It was later found that treating carrier cattle with dexamethasone, in fact, decreased virus shedding (which returned to normal after cessation of treatment)[59].

Three possible pathways for buffalo infecting other species have been proposed[48,60]:

- acutely-infected buffaloes infecting susceptible animals
- persistently-infected buffaloes infecting susceptible animals
- sexual transmission by male buffaloes mounting female domestic cows

Experimentation to find definitive proof for the former two pathways has had varied results, with only one experiment[30] and one circumstantial event[39] successful in showing transmission from acutely-infected buffaloes to cattle, while four were unsuccessful in doing so[30,36,61,62]. However, it seems most authors still consider this the most feasible mechanism for infection, explicated by the so-called 'childhood infections'[61]. Buffaloes are seasonal breeders with synchronous calving, peaking in January in the KNP[63,64], which is possibly linked to the previous year's vegetation greenness[65]. Nonetheless, some animals do not follow this pattern and may calve year round[28,64]. The majority of calves thus lose their maternal immunity almost synchronously during mid-winter[9,45] during which time, aged 3-12 months[66], they normally become infected with FMDV. This infection does not necessarily come from their dams[67] and probably spreads horizontally between the calves[12], causing sub-clinical epidemics in breeding herds which make them a potent source of infection[2,31,68]. That being said, Bengis et al.[61] were unsuccessful in experimentally establishing such a 'childhood infection', while Hedger[28] attested to high virus titres in 12-36 month old buffaloes, indicating active infection in this age group rather than the proposed 3-12 months age group. The amount of virus excreted by sub-clinically infected buffaloes has also been reported as sufficient to initiate infection[28,30]. The interval between loss of maternal immunity and active infection is shortest for SAT-1 and longest for SAT-3 FMDV[68]. The matter of seasonality of acute infections in buffaloes is further supported, circumstantially, by Bastos et al. [8] and Vosloo et al.[4], reporting 90% of impala outbreaks in KNP between June and November, corresponding with the period associated with loss of maternal immunity in most buffalo calves and impala kids[38]. Vosloo et al. [45] subsequently postulated a seasonal risk of transmission between buffaloes and impalas (contrary to the previous model outputs[68]). It is, however, still unclear whether older/younger/larger/smaller groups of buffaloes are more efficient transmitters of disease[60].

Looking at the second proposed transmission pathway, Condy and Hedger[67] were able to demonstrate (persistently-infected) buffalo-to-buffalo transmission, although the mechanism for this also remains obscure[9]. A number of years later, three experiments had success in demonstrating transmission from persistently-infected buffaloes to cattle[10,30,36,58], while four failed to do so[30,35,47,62], leading to persistent infection being questioned as a mechanism for virus transference by some[35,69]. In the experiment of Dawe et al.[36], no transmission to cattle occurred during the acute stages of infection in buffaloes, notwithstanding large amounts of virus circulating, whilst disease did develop in the cattle five months later, thus contradicting support for transmission from acutely-infected animals rather than persistently-infected ones. Thomson[2] (see also [10,68]) reported that persistently-infected buffaloes transmit infection poorly and probably 'only after prolonged and intimate contact' and that these uncommon transmission events[39,55] are probably only likely when the ratio of susceptible to persistently-infected animals is high (e.g. in unvaccinated herds). Yet, some authors[70] concluded that the risk of transmission from persistently-infected buffaloes to cattle is significant, and that transmission from carrier cattle to susceptible cattle cannot be excluded (referring specifically to SAT-2). While some propose that the period from most recent infection may play a role in the ability of persistently-infected animals to transmit disease[35,39,61], the conjecture of others is that unknown 'trigger factors' may result in higher levels of FMDV being excreted under field conditions, sufficient to cause transmission[69]. In essence, most authors agree that it is under 'unknown natural circumstances' that FMDV transmission occurs[8,54,60]. Not surprisingly, the role of persistently-infected buffaloes in the epidemiology of FMD has been a matter of contention for some time[69]. In a recent review article, the FMDV transmission rate from persistently-infected buffaloes to susceptible cattle was computed to be 0.0256, it being concluded that this should be seen as a 'worst-case estimate'[71]. Furthermore, due to their high variability, antibody levels cannot be used to differentiate between persistently-infected and uninfected animals[70], although serology is more reliable than viral isolation as a diagnostic tool for identifying these persistently-infected animals[9].

The third of the proposed pathways for FMDV transmission, via coitus, is supported by anecdotal and circumstantial evidence and suggests that during most experiments where transmission was successful between buffaloes and cattle, male buffalo were used in conjunction with domestic cows, while with those resulting in unsuccessful transmission, steers were used in the cattle group[72]. The authors affirmed this theory in showing that during previous transmission experiments[10,36], transmission only occurred after the male buffaloes became sexually mature and only during December, coinciding with the start of the buffalo breeding season. Sexual transmission could thus explain the erratic transmission between in-contact persistently-infected buffaloes and cattle, even though it could not be established if virus was only present in acutely-infected animal semen, or also in that of persistently-infected ones[72]. Despite anecdotal mention of buffalo bulls mounting domestic cows, evidence for sexual transmission is still considered tenuous by some[9].

It is disputable whether there is any affinity between buffaloes and cattle that will facilitate FMDV transmission. Some reports give anecdotal evidence in favour[9,73], whilst others provide contradictary views[20]. During one experiment[30], both interspecies avoidance as well as affiliative (grooming) behaviour was observed in two different groups of animals. It has been noted that wildlife (in some cases buffaloes) in arid areas avoided waterholes where livestock was present[74,75].

The role of intermediary hosts in transmission

Anderson et al.[46] postulated FMDV transmission between buffaloes and livestock via an intermediary host species, especially those present in sufficient numbers and density[31,45]. Even though Anderson et al.[46] disregarded the significance of such intermediaries in Zimbabwe, he was later challenged by Hargreaves et al.[57], who suggested that jumping antelope, like kudus (*Tragelaphus strepsiceros*) and impalas, were responsible for an outbreak in livestock during a period where intact double fences made direct contact between buffaloes and livestock highly unlikely.

Despite the seemingly mild reaction to FMDV infection in most wildlife[9], abundant clinical signs[38,39] due to FMD, have been reported in impalas, specifically those of the KNP, the only locality to report clinical signs in this species[9]. FMD outbreaks in impala in the KNP are all presumed to originate from buffaloes[38]. This is substantiated by phylogenetic and geographic clustering of impala and buffalo FMDV strains from these outbreaks[8,50,76]. Impalas also seem to be the wildlife species most susceptible to FMDV in South Africa[48], seemingly due to their higher predisposition to aerosol transmission[45] and smaller quantities of virus required to establish infection[1]. During FMD outbreaks in impalas, infection and attack rates vary, with the latter sometimes much lower than the former, indicating sub-clinical infection[9]. Sub-clinical infection is considered common, unless a highly pathogenic FMDV strain is circulating[45]. As with buffaloes, impalas can also be co-infected by more than one SAT type, a phenomenon that seems to be especially prevalent in the Orpen region of the KNP[45]. FMD appears to spread more slowly in impalas compared to intensively-farmed livestock, and inter-epidemic periods are characterized by low a FMD seroprevalence[38]. Vosloo et al.[45], however, reports impala FMD outbreaks in KNP declining as well as becoming more localised (as opposed to multi-centric) and of shorter duration since 1977. Of note, Gainaru et al.[30] could not induce transmission experimentally by placing susceptible impalas and infected buffaloes in adjoining pens. Impalas are less effective transmitters of FMDV compared to cattle and buffaloes[38], excreting virus only while clinically ill[77]. Vosloo et al.[4], nevertheless, are of the opinion that the excreted virus from acutely-infected impalas is enough to cause infection in susceptible animals, based on experimentally-infected impalas (SAT-1) that spread infection to buffaloes and possibly cattle in adjacent pens of their experiment. They further reported that in KNP, from 1971-1981, five outbreaks of FMD occurred in impalas, of which four could be linked molecularly to outbreaks in cattle (three of which preceded the cattle outbreaks by 5-6 months), while only one outbreak in cattle was found to be directly linked to an isolate from buffaloes during the same period. It was, however, mentioned that multiple wildlife-livestock transmission events involving the same genotype between 1977 and 1979 were likely. Historic evidence also supports the notion of impalas being an intermediary[78,79]. However, impalas do not become persistently-infected with FMDV[37,77], even though it has been postulated that SAT-1 viruses could have circulated in impala herds for as long as 10 years[4,31], which can be explained either by extended epidemics maintained in herds, or repeated transmission events from buffaloes[45].

Seasonality of impala FMD outbreaks[4] has been related to the shared habitats and environmental factors that cause impalas and buffaloes to come in close contact[8]. These authors[4,8], however, agree that FMD tends to occur where the highest densities of impalas are present in conjunction with buffaloes, which would be the KNP in South Africa, a reserve where intensive FMD surveillance in impalas could also have caused biased reporting in this species[38]. Vosloo et al.[45] further reported that FMD seroprevalence in impalas varied between different ecological areas in the KNP and postulated a linear relationship between the impala:buffalo density ratio and the probability of impala becoming infected. This is supported by 90% of FMD outbreaks in the KNP occurring south of the Olifants River, an area with a high impala density[8]. Buffaloes and impalas often congregate around the same water sources, especially in the dry season, while also utilizing some of the same grass species[80], particularly since impala's preference for grazing, as opposed to browsing, peaks during this time[81]. This interspecies contact and mixing is further accentuated by drought, and thus increased contact at especially watering points[20,45,48,82], which could cause disease to spread faster[83]. Even so, less than one tenth of impalas' contact events with other species would be with buffaloes[82]. The majority of impala FMD outbreaks occurring and spreading along watercourses[48,76] during dry periods[4,8,9,38], further supports the postulation of outbreaks associated with shared water sources. Similarly, others also identified watering points as critical contact points for FMD transmission[84-87]. Even though impalas have been reported to come in contact with cattle outside the KNP, this is less common than buffalo-cattle contact[88].

Altough it is rather difficult to estimate the prevalence of FMD in wildlife[45], Bastos et al.[53] attributed the difference in prevalence between the various SAT type viruses in buffaloes and other species to a differential ability of the various SAT type viruses to cross the species barrier. They used the example of clinical outbreaks in impalas between 1985 and 1995 in the KNP, all being of SAT-2 origin, while in buffaloes from the same geographic area, SAT-1 was most prevalent. In concordance, Vosloo et al.[45] attributes the higher SAT-2 seroprevalence recorded in species other than buffaloes to this serotype being inherently more amenable to spread between species. Seropositivity in impalas has also been recorded in Zimbabwe, Botswana and Tanzania[27,46,89,90], while Sutmoller et al.[20] makes reference to reports where 18.4% of antelopes tested seropositive for SAT-2 FMDV in the KNP. Low amounts of antibodies against FMDV found in species in close contact with buffaloes, suggest that they require exposure to high amounts of virus from for example clinically infected animals[28].

The role of kudus in FMD epidemiology remains unclear[4,38], although they are able to carry FMDV for up to 140 days, with a higher and longer antibody response than impalas[28]. In Zimbabwe, prevalence of clinical FMD in kudus has been recorded as being higher than that of impalas, while some FMDV strains isolated from kudus have been related to strains isolated during livestock outbreaks in Botswana – the direction of spread could, however, not be ascertained[4]. While they do get infected with FMDV and develop lesions (especially on their carpal joints and rostrum of the snout) or succumb[9], warthog does not seem to fulfil the same 'amplification' host role[14] as domestic pigs do in FMD (G.R. Thomson, personal communication, 12 November 2008). Giraffes (*Giraffa camelopardalis*) have been reported showing lameness during natural FMD outbreaks in KNP, questioning their potential role in FMD epidemiology[91]. When experimentally infected with SAT-1 and SAT-2 FMDV, they did develop clinical signs, yet failed to become persistently-infected and were consequently deemed to be insignificant in the epidemiology of FMD[91]. Furthermore, it is important to remember that transmission from livestock to wildlife cannot be excluded[46,92].

In South Africa, FMD outbreaks have been caused mainly by buffaloes that moved through compromised game fences[4], although the important role that antelope seem to play in the dissemination of FMDV, warrants their consideration in the control of the disease too[45,57].

Virus survival and fomites

FMDV can survive for days to weeks in the environment if it is kept moist and at a neutral pH. Mechanical transmission is therefore possible, but only if infected material makes direct contact with a susceptible animal[93]. Faeces[30] and viscera[47] from FMDV-infected buffaloes have been dismissed as possible mechanisms for transmission. Alexandersen et al.[70] were successful in experimentally infecting susceptible cattle with the saliva of carrier cattle, yet questioned the likelihood of this under field conditions. Even though Whyte[82] speculated that drinking water might be a possible source of FMDV infection, it had already shown that a higher infective dose is required to initiate infection through ingestion rather than inhalation[34], hence contradicting this theory. Infected bush meat potentially poses a risk of FMDV transmission, but this is only likely if omnivores (such as pigs) ingest the meat; in perspective this is probably not a major risk compared to for example large scale illegal movement of infected livestock[9]. Oxpeckers (*Bupghagus* species)[82] and arthropods[94] have been proposed as mechanical vectors in FMDV transmission, although the role of the latter was negated by van Vuuren et al.[95]. Some authors[20] even suggested mechanical transmission by lions as a potential route for virus transmission.

Airborne transmission

Four criteria for the survival and subsequent airborne spread of FMDV over long distances have been defined[96]:

- High virus outputs
- Light or no wind
- Relative humidity (RH) >60% (or RH>55%[15]; also see [14])
- Cattle should inhale infected air for many hours

It was also shown that FMDV survived well in temperatures of up to 27°C, although the role of temperature is probably much less than that of RH[14]. Sunlight seems to have no effect on the survival of FMDV[97]. Smith[98] further expanded on the requirements for airborne:

- some species are greater emitters of infectious aerosols than others (confirming the findings by other authors[99])
- large herds produce more infectious aerosol than small dispersed units
- larger animals are at greater risk of aerosol infection (due to their large inspiratory volumes)
- greater separation of animals reduce aerosol concentration due to air movement and thus reduces the risk of infection
- intensive farming systems increase risk for aerosol spread of virus

Sørensen et al.[15] argue that, only when commercial pigs are involved, does airborne transmission occur over distances of more than three kilometres. Long distance airborne transmission in the southern African lowveld is unlikely, due to the low domestic pig densities, low cattle stocking densities as well as the warm dry climate[1,57]. Others concur that the local climate is unsuitable for long distance airborne spread[100-102]. Moreover, FMD viruses in cattle that are related to buffalo strains are normally from buffaloes in close proximity to where the virus was found in cattle, therefore making long distance airborne transmission unlikely[53].

Short distance airborne spread, under local conditions, has been shown to occur when SAT-1 virus in experimentally infected impalas infected buffaloes on two separate occasions in nearby pens, without any direct contact between the two species[10]. Gainaru et al.[30] mention that, during their failed SAT-1 transmission experiment, the temperature was very high and RH low, while in the subsequent, successful, SAT-2 transmission experiment, the climatic conditions were more favourable, even though no transmission in the persistently-infected phase or in the acute phase occurred to impalas in adjacent pens. Likewise, Bengis et al.[61] mention that the night time winter climate in the southern African Lowveld is suitable for short distance airborne transmission, hence attributing their failed attempt at natural transmission from buffalo dams to offspring to the severe dry conditions that prevailed. Furthermore, Du Toit[103] speculates that FMDV spread appears to be enhanced by cool, damp spells that arise during winter when south-easterly winds bring moist air to the south-eastern lowveld of Zimbabwe.

During their experiment, Gainaru et al.[30] could detect airborne FMDV in the vicinity of infected buffaloes, but still regarded intimate contact, rather than airborne transmission, as the more likely cause for transmission from buffaloes to cattle. They attribute this to the fact that, under field conditions, it is unlikely that more than a minority of buffaloes will be excreting virus and hence would not cause a sufficiently high virus concentration in the air conducive to transmission. Mokopasetso[102] modelled an effective distance of airborne transmission under local conditions to 91m, thereby insinuating that infection through an intact fence cannot be excluded, although they do caution that airborne transmission is highly dependent on the prevalence of disease. They also postulated that low contact rates can be expected in communal farming areas and that not all in-contact animals are expected to become infected. Hargreaves et al.[57] put forward that the virus circulating in the air due to infected buffaloes was too low to measure, therefore making the possibility of airborne transmission very low (the outbreaks referred to, occurring during winter and with no compromised fences evident).

Impact of foot-and-mouth disease

The impact of FMD occurs at different levels, starting with its clinical effect in livestock, with concomitant losses in milk production and draught power. It is however the exorbitant cost of disease control programmes and loss in export opportunities for countries harbouring the disease that has the greatest impact[60] (Figure 1.1[104]).

Trade impacts and alternative trade strategies

Southern Africa is at a distinct disadvantage when it comes to the export of livestock as well as wildlife commodities to high value markets[4,9], due to the presence of persistently-infected African buffaloes in a number of large conservation areas[1,32,48,105]. Furthermore, the logistical and economical burden that eradication of FMD poses has made those countries that have achieved eradication very wary of re-importing what they currently consider to be their biggest livestock disease threat[106]. As a consequence, trade embargoes are posed on agricultural products from those countries that do not adequately control the disease[1,4]. This, in turn, has the effect that many developing countries harbouring FMD, have to spend great amounts of resources to control the disease in an attempt to gain access to lucrative international agricultural market[29,31].

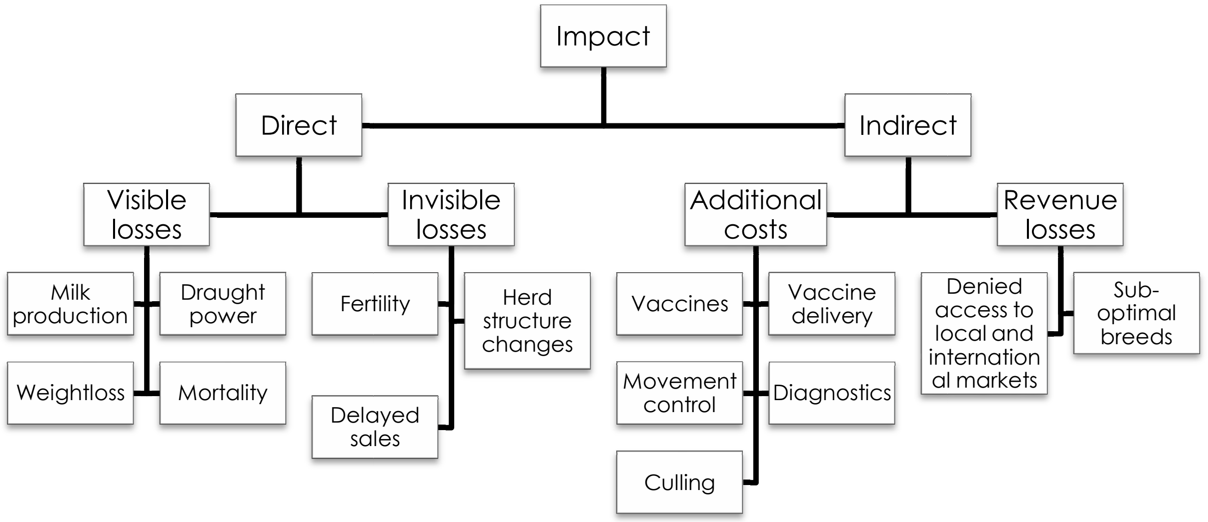

Figure 1.1. The impact of foot-and-mouth disease in livestock (adapted from [104])

Failing to maintain disease-free status can cost the country in the order of millions of dollars in income losses as well as through the cost of control measures[107,108]. Geographically-based disease control measures, although necessarily ineffective, have a number of unintended consequences[109,110]: Firstly, these zones are often demarcated by elaborate fences with multiple undesired ecological consequences (see later) and, secondly, they isolate large numbers of (often poor) livestock farmers from lucrative export markets, especially when their animals are vaccinated[109,111-113]. Interestingly, these 'FMD free' zones are not always recognized by the European Commission, a significant importer of livestock products, further complicating the control and the economic impact of FMD in the subregion[60,110]. For more than a decade alternative trade options have been advocated to counter the prevailing trade restrictions. A number of authors[60,110,114,115] have proposed trade and trade control in commodities (i.e. animal products), rather than live animals, in a bid to overcome the disadvantage at which developing countries with persistently-infected wildlife are put (see also [116]). Commodity-based trade (CBT) is in essence a value chain approach that integrates livestock disease control with food safety[114,117,118]. It has been demonstrated scientifically that certain livestock products originating from FMD prevalent areas, pose a negligible disease risk for importing countries[119]. Even though this philosophy will have significant trade benefits for developing countries[120], it places an even greater responsibility for the control and prevention of FMD on these countries, therefore necessitating effective and efficient identification and management of risk areas[121]. In South Africa especially, the presence of FMD places significant constraints on wildlife farming as well as on the potential integration of wildlife and livestock farming, which is considered to be ecologically and financially desirable, particularly in marginal areas[112]. Hence, FMD considerably influences the development of integrated land-use policy in southern Africa[31,32,112]. A reduction in cattle numbers to reduce the incidence of FMD outbreaks and overcome vaccine inefficiencies has been proposed by some authors[122]. Reduction and/or maintenance of buffalo and antelope populations have also been proposed, in conjunction with vaccination and fences, as a measure to prevent FMD outbreaks[57].

Disease Control

In South Africa, FMD control is essentially based on the separation of endemic host species and susceptible livestock[2,9,20,25,29,66], bi-annual to tri-annual vaccination of cattle[60,123] and frequent inspection as well as movement controls (permit system)[31,124,125]. These disease control measures, including the creation of FMD free zones, are based on the recommendations of the World Organisation for Animal Health (OIE)[126]. When these controls are in place, they have proven to be effective in preventing disease[31,123], but when not, disease can appear quickly[127]. Between 1970 and 2009, 15 outbreaks of FMD in livestock occurred in South Africa, although this did not follow a regular pattern[128]. In the period mid-1984 to early 2000, not a single FMD outbreak in livestock occurred, despite 11 outbreaks recorded in impalas in the KNP during the same period. Coincidentally, this is also the period during which South Africa used a locally produced FMD vaccine (RG Bengis, personal communication, 15 January 2015). Since 2000, however, South Africa experienced a sharp increase in FMD outbreaks[128]. Of concern, is the similar trend noticed in other parts of the sub-region[129].

Emphasis is often placed on sustained FMD control, rather than eradication in those countries harbouring persistently-infected African buffaloes[53]. Moreover, FMD control in African countries varies greatly, with strict controls through vaccination and separation in some, contrasted by countries that lack adequate or any surveillance or FMD control policies (especially in pastoral systems)[31]. During outbreaks, these countries have to utilise very limited resources to bring the disease under control[4,130]. Nevertheless, FMD control was successfully applied in several southern African countries long before FMD was effectively controlled in Europe, despite the latter region benefitting from the absence of endemic host species[60]. Ironically, Vosloo et al.[31] notes that most livestock owners in Africa do not view FMD as a serious disease, since it has little impact on them other than reduced milk production and draught power. Recently, the OIE and several of its worldwide collaborators proposed a global strategy to control FMD[121,131-133] which included a progressive approach for countries to gain disease freedom even if only in defined zones within those countries (Figure 1.2[131]):

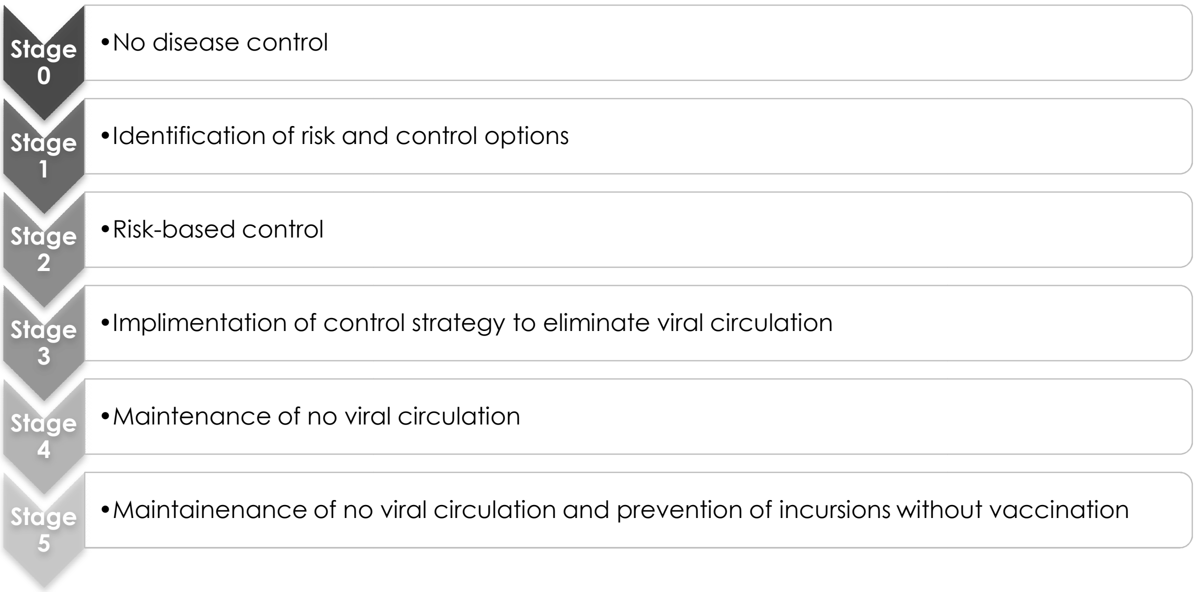

Figure 1.2. Stages of the Progressive Control Pathway for foot-and-mouth disease (adapted from [131])

On the land adjoining the KNP, a diverse array of land uses can be found[29], including commercial and communal crop farming, commercial and communal cattle farming as well as many game ranches, which makes an across-the-board set of control measures, for a disease with a complicated epidemiology, very difficult to enforce. Brückner et al.[29] further point out the difficulties that are experienced in FMD monitoring in communal grazing areas, due to the sharing of management facilities and lack of clearly delineated epidemiological units. The latter is also a complicating factor in modelling disease risk and spread[134].

Vaccination

SAT type FMDV in buffaloes constantly undergo antigenic variation[10,135,136], which makes effective vaccination in proximity to wildlife reserves harbouring these endemic hosts challenging[11,48,136]. It is important that livestock vaccines are appropriate for the prevailing strains maintained in buffaloes in any given locality[9,130]. This was fittingly demonstrated by Dawe et al.[54], who described acute infection of vaccinated cattle after five years of being in contact with buffaloes at watering points. They attribute this lack of vaccine-induced immunity to a 20% antigenic difference between the infective virus and the field strain that was used in the vaccine. Immunity of cattle against FMD due to primary vaccination with alhydrogel/saponin vaccines is short-lived (3-4mths in cattle) and might be more effective when oil-adjuvant vaccines are used. Cattle receiving several inoculations generally have a high immunity when challenged with a homologous virus[9]. A recent study in communal cattle along the KNP showed that the immune response after vaccination was shorter than the four month vaccination interval[137]. Furthermore, at a recent Southern African Development Community (SADC) workshop (of the Programme for the 'Promotion of Regional Integration (PRINT) in the SADC Livestock Sector') it was concluded that the vaccines presently in use in SADC against FMD, does not appear to be as effective as in the past and that they may not be adequate to control disease in future[60] (see also Weaver13). Bastos et al.[53] suggested regional approaches for FMD control through strategic vaccination, due to the geographically distinct lineages of FMDV, as was also suggested for disease control in a heterogeneous landscape, such as the one adjacent to KNP[138]. While it has been shown that vaccinated animals can become disease carriers, no evidence of transmission from these carriers to other vaccinated animals has been found[60,139].

It has been demonstrated that vaccination of wildlife, including buffaloes and impalas, induces a similar serological response as seen in cattle, but of a lower order[140]. Unfortunately, this latter study did not include a challenge of this purported immunity. Another study[9] suggested that buffalo should receive double the recommended cattle dose of oil-adjuvant FMD vaccine, but concluded that protection will be difficult to assess, especially with regard to infection versus clinical disease, while warning that current knowledge regarding FMD vaccines dictates that it is better to avoid vaccination of wildlife altogether.

Fencing

Fencing as a means of separating endemic FMD hosts and susceptible livestock species has been a matter of great controversy. Most criticised, is its high environmental, economic and social costs[103,141-144], while others[25] warned that fencing should only be used to separate wildlife and livestock, and not be used between wildlife and wildlife. Notwithstanding, these fences are also sometimes seen as beneficial to local communities, through protection of their livestock from predators and crops from damage by large animals[145]. In unfenced wildlife-livestock interfaces, disease burdens in livestock are also increased[146]. The most common livestock-wildlife contact recorded by farmers along the western boundary of the KNP has been between cattle and buffaloes[88,147], which has multiple disease implications[148]. An extensive review of the environmental, social and economic impacts of disease control fences in southern Africa was recently compiled and gives an excellent overview of a wide variety of viewpoints[143]. The main argument against fencing as a FMD control measure is that vaccination should be sufficient in protecting livestock from FMDV infection, but, as has been the experience in southern Africa, exclusive reliance on vaccines could be dangerous[9]. It is also argued that fencing does not control indirect mechanisms of transmission, e.g. intermediaries and airborne transmission[25,31,103].

Hargreaves et al.[57] postulated that the risk of FMDV transmitted from wildlife to cattle can be effectively controlled by a fence high and strong enough to be impervious to both antelope and buffaloes. The authors suggested a fence height of 2.4m to be effective in preventing escape of jumping antelopes (see also [20]). Flooding has been implicated as an important cause of fence damage in the KNP that eventually contributed to FMD outbreaks, with buffaloes straying from the Park through broken fences mostly during the rainy season[9,128,147,149]. Fences running along rivers are especially prone to flood damage[103], mainly due to the large number of tributaries these fences have to cross. Furthermore, apart from the sheer power of water, riverbeds provide a very poor substrate upon which to construct a fence[149]. On the other hand, elephants (*Loxodonta africana*) and large ungulates[20,150,151] can also cause damage to a fence in a bid to reach water or food resources on the other side of it[103,152,153]. Although African elephants play an insignificant role in the physical transmission of FMDV[154], they play an important role in the facilitation of buffaloes crossing fences. The human factor in fence integrity[147,155,156] should also not be disregarded, mainly through inadequate maintenance[73,103], but also vandalism and theft[147] (especially of solar panels supplying electricity to the fence). Nonetheless, the likelihood of buffaloes going through an opening in a fence still depends on their stocking density as well as the period that such an opening remains unrepaired[20,157].

Trans-frontier conservation areas

The creation of trans-boundary conservation areas might complicate FMD control further, although this challenge could also be seen as an opportunity for the integration of FMD control policies in southern African countries, which are fundamentally similar[60]. These multi-national conservation initiatives have promising biodiversity and ecotourism benefits, with subsequent economic reward, but they also promote the spread and diversification of pathogens by consolidating previously isolated populations of disease carrying wildlife[146,158-160]. The increase in conservation areas also brings about an increase in the interface they form with various other land-use options, mostly agricultural and often subsistence livestock farming areas[109,161]. The nature of this wildlife-livestock interface can vary greatly, both spatially and temporally, with factors like fences, water availability and reservoir host/susceptible host habitat ranges determining to a great extent the risk of contact and hence transmission of diseases between wildlife and livestock[162]. In the case of FMD, this adds to its already complicated epidemiology and calls for innovative and pro-active disease control measures that benefit all land-use options[158], but that would also be more compatible with biodiversity conservation[112]. This conservation ideology would also require clever integration with the rural livestock sector to ensure its sustainability[109].

Risk modelling

Models allow us to conceive and communicate our ideas accurately about the behaviours of a specific system and are abstractions and simplifications of the real world[163]. Yet, existing biological and veterinary knowledge of FMD are not adequate to encompass all mechanisms of disease transmission and model results of FMD will therefore always be probabilistic[164]. Determining a model's accuracy, spatial limitations and practical application to disease control, rather than just predicting infection risk, is the real challenge in modelling. Hence there is a need for advancement of ecological zone mapping to define the extent of a model's relevance and ensure appropriate targeted surveillance[165]. This is in agreement with a larger scale approach that is advocated globally[121].

To date, most spatio-temporal models for FMD have been aimed at the risk and/or characteristics of disease spread, rather than the risk of outbreaks occurring, mainly because the investigated outbreaks stemmed from imported point sources[93]. This situation is quite different from the endemic scenario in southern Africa. Only a few models have looked at the SAT type FMDV specifically[68,102,157,166]. The model of Thomson et al[68] determined that acute infection of buffalo calves is a potential mechanism to sustain infection in a buffalo population for prolonged periods and suggested that this occurs through cyclic (not seasonal) epidemics, unique for each SAT type. Mokopasetso[102] postulated that transmission from an infected animal is possible within the first seven days of infection, being most likely on day three, and while airborne transmission could not be excluded, it was unlikely. Sutmoller[25] and Sutmoller et al.[20] suggested in a model developed for Zimbabwe that control should aim at preventing antelope from escaping from reserves as well as maintaining a low density of cattle in close proximity to reserves carrying persistently-infected buffaloes. The model presented in the latter publication proposed five possible scenarios for FMDV transmission:

- Infected buffaloes straying from reserves and coming in contact with susceptible cattle ($5x10^{-6}$ probability per year of causing a FMD outbreak in Zimbabwe)
- Cattle straying into reserves and coming in contact with infected buffaloes ($3x10^{-4}$ probability per year of causing a FMD outbreak in Zimbabwe, although it is noted that these cattle are normally detected quickly and immediately destroyed)
- Small stock acting as intermediaries between buffaloes and cattle (although generally no effective contact between buffalo and sheep/goats is achieved)
- Antelope acting as intermediaries between buffaloes and cattle (it was concluded that this scenario had the highest risk of occurring)
- Aerosol transmission.

A recent qualitative risk assessment of FMD at the wildlife-livestock interface of the KNP, identified fence permeability, livestock immunity and movement control efficiency as the most influential factors in that particular epidemiological setting[55]. Yet, this approach lacked a spatial component, limiting its application in risk-based approaches in heterogeneous landscapes. Dion et al.[157], on the other hand, used multi-agent simulation to assess buffalo-cattle contact along the KNP boundary at a very high spatial and temporal resolution. This approach is useful, since it can incorporate not only geographic parameters, but also behavioural characteristics of the animals. Their approach was also expanded to investigate the effect of a number of scenarios on buffalo-cattle contact risk[166].

Landscape, ecological or spatial heterogeneity is seldom considered in conventional risk analyses, with administrative boundaries commonly being the only spatial attribute of such analyses[165]. Capturing spatial heterogeneity has been identified as a major challenge in realistically representing FMDV spread through a landscape[167], with only a few FMD spread models incorporating geographic/topographic features. This shortcoming has also been identified before[163] as one of the aspects inadequately addressed and understood in many FMD models (others mentioned include farm management and biosecurity). Green and Medley[168], however, warn that incorporating spatial complexity in models is more of an art than science, and that introduction of factors such as physical geography is no small task.

In a cellular automata model on the potential for FMD to spread in Australia, Doran and Laffan[169] incorporated ten universally applicable ecological factors into their model that determine the maintenance and transmission of the disease by wild animals: population density and distribution, reproductive status and seasonality, wildlife/livestock interaction, animal response to disturbance, animal movement and distance travelled, habitat requirements, social organisation, age structure & population, home range and barriers to dispersal. They also considered the potential effect of dry and wet seasons on the dynamics of an outbreak in feral pigs, and found it to be significant. Ward et al.[86] further proposed a hypothetical cellular automata model that looked at the role of wild animals as reservoirs of FMDV in the United States of America (USA), and focused only on local transmission of FMDV from wildlife to livestock, i.e. through local interactions (e.g. across fences, windborne, environmental, herd-to-herd contact), thus excluding long distance transmission (e.g. transportation, long distance airborne or mechanical (human) transmission). They utilized land-use data and 'estimated ecological site carrying capacity' to derive feral pig and deer densities, while for livestock they used census data (disaggregated by 1km land cover data), and stocking rates from USDA Ecological Site Descriptions, in conjunction with likely stocking rates derived from expert opinion. They suggested that the factors used for density/distribution calculations needed to be seasonally dynamic (i.e. have temporal dependency), such as the model of Doran and Laffan[169], and include spatial fragmentation. Hence, they speculate that the risk of transmission between wild animals and livestock will vary substantially between regions, species and seasons, although they recognized the home ranges of wild animals as an area of uncertainty in their model. Moreover, it was demonstrated that the number of outbreaks in livestock increased if the density of wildlife was increased and, decreased if the density of livestock decreased, even though a substantial number of model runs failed to develop an outbreak of FMD in the wildlife populations. The role of watering points as important contact points in FMDV transmission, as discussed earlier, was also pointed out by this model. They claim to have explicitly included geographic variations in a simple way in their modelling framework, rather than using exhaustive animal census data or complex mathematical structures, although the model still allowed for uncomplicated incorporation of factors like soil, water availability, vegetation and topography.

Durand and Mahul[170] found geographic density as well as connectivity and size of susceptible herds to be the most important factors in the propagation and maintenance of FMD, while Woolhouse et al.[122] speculated about the environmental conditions and husbandry practices conducive to FMDV transmission. In yet another study, Bessell et al.[171] concluded that rivers and railways played an important role as barriers for the spread of FMD in the United Kingdom (UK), while roads did not seem to play any role.

The issue of spatial scale, including geographic extent and pixel resolution, was highlighted by Hendrickx et al.[172], suggesting that the working scale should be determined by the objectives of the study. They further advised that the advantages and limitations at different scales should be systematically considered to find the best cost to benefit ratio, while remaining pragmatic in one's approach. Furthermore, they suggest a sequential approach, where data and outputs at a lower level contribute to the design of higher levels.

Accurate epidemiological models are useful tools for determining pertinent control measures and are essential for boosting public confidence in the use of models. On the other hand, inaccurate models may be abused for disease control, either resulting in too much or too little control[93,173]. Moreover, the need and value of risk-based surveillance (or targeted surveillance) in identifying surveillance needs, setting priorities and effective/efficient allocation of resources has been emphasized in a global context[174]. In this regard, Brückner[175] alluded to the need for African countries to establish identifiable low risk areas within infected areas to be maintained as disease free compartments, which could then act as a source of disease free animals for export. When used and applied correctly, risk mapping could be a means to assure focused surveillance and cost-effective disease control[165]. This type of FMD control, applied progressively, could eventually contribute to the global effort at reducing the threat of infectious diseases[121,131,176].

From this review, it is clear that effective FMD control in southern Africa will become increasingly important, especially at wildlife-livestock interfaces where persistently-infected African buffaloes occur. Three pertinent reasons for this are that eradication is not currently an option, efficacy of current vaccines is dubious and changes to geographically-based trade regulations seem imminent. Disease control efforts will therefore need to be based on risk assessments that are done at a spatial and temporal scale suited to the heterogeneity of these wildlife-livestock interfaces. Yet, such approaches should be practical and simple enough to facilitate regular updating with current data that would ensure timely adjustment of control measures to mitigate risk under local conditions.

Project overview and objectives[a]

Overall aim

To develop a spatio-temporal probability model of buffalo-cattle contact based on distribution models for cattle and African buffaloes, as well as secondary drivers of contact and/or FMD transmission between these species.

Objectives

- Conduct a spatial and temporal analysis of cattle demography, distribution and movements at the wildlife-livestock interface in South Africa, contributing to the development of a cattle distribution/density model
- Conduct a spatial and temporal analysis of stray buffalo distribution and movements outside the FMD infected zone
- Integrate the findings of the spatial and temporal analyses of cattle and buffalo distribution to construct a probabilistic framework for buffalo-cattle contact as proxy for FMD transmission risk

Structure

The work that follows addresses each of the goals of this study and was written in such a way that each chapter can be read independently. Consequently, a certain amount of repetition is inevitable.

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[a] This work formed part of a much broader research project, 'Remote Sensing tools to study the Epidemiology and Space/Time dynamics of diseases (EPISTIS)', funded by the Belgian Federal Public Planning Service, Science Policy as part of their research program for earth observation 'Stereo II' (contract SR/00/102).

Chapter 2

Communal cattle demographics at the wildlife-livestock interface of the Kruger National Park, South Africa

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Chapter summary

In South Africa, communal livestock farming is the predominant farming system in the foot-and-mouth disease control zone adjacent to the Kruger National Park (KNP) and its adjoining private and provincial nature reserves (APNR), where persistently-infected African buffaloes (*Syncerus caffer*) roam. During routine veterinary inspections of cattle in this area, a large amount of production and demographic parameters are being recorded. These data were collated for a five-year period (2003-2007) in three study sites, to better understand the temporal dynamics and spatial heterogeneity in this system. A latitudinal gradient in both human and cattle population densities was observed, decreasing from south to north. Rainfall and human population density alone could explain 71% of the variation in cattle density. Over the study period, the northern and central study sites showed an overall decrease in total cattle (15.1% and 2.9%, respectively), whereas a 28.6% increase was recorded in the southern study site. In contrast to cattle numbers, the number of cattle owners remained stable during the study period. Only 4.0% of households in the southern study site own cattle, compared to 13.7% and 12.7% in the northern and central study sites, respectively. The overall annual calving rate was 23.8% (as proportion of the entire herd). Annual mortality rates ranged from 2.4% - 3.2%. Spatio-temporal mortality clusters were characterised by significantly lower normalised difference vegetation index (NDVI) and rainfall values in the preceding season, rather than the current one. The northern study site recorded low calf mortality (2.1%) compared to the southern study site (11.6%). Annual offtake in the form of slaughter averaged 0.2%, 11.7%, and 11.0% in the northern, central and southern study sites, respectively. These figures provide valuable baseline data and demonstrate that there is considerable spatial heterogeneity in cattle demography and production at this wildlife-livestock interface. This is important to take into consideration when performing disease risk assessments or designing disease control systems.

Introduction

A large area neighbouring the Kruger National Park (KNP) and its adjoining private and provincial nature reserves (APNR) in South Africa, is used for communal farming of both livestock and crops. Proximity to a wildlife sanctuary, however, has certain consequences. Although South Africa is considered by the World Animal Health Organisation (OIE) to be a FMD-free country where vaccination is practised, the KNP and APNR are considered endemically infected with foot-and-mouth disease (FMD)[29,31,110], due to the presence of the reservoir host of the disease, the African buffalo (*Syncerus caffer*)[4]. To prevent spillover from the reservoir host to livestock, a fence was erected around the KNP in the 1960s[110,177], and within the area directly adjacent to the infected zone (the so-called protection zone with vaccination), compulsory weekly cattle inspections and bi- to tri-annual vaccination against FMD takes place at government livestock inspection points (IPs). Livestock in the remainder of the protection zone (protection zone without vaccination) are inspected every fortnight and are not vaccinated. In addition, strict movement controls, enforced through a movement permit system, enable traceability of animal movements to, from and between IPs inside the protection zone[29,31,110].

In South Africa, the farming sector has a distinct dual nature, primarily as a result of the country's political history. Under the apartheid regime (1948-1994), independent 'homeland states' were established within the borders of the country. Today, farming enterprises in the former South Africa (i.e. excluding these homeland states) produce close to 99% of the country's total farm income, despite comprising only around 14% of the total farming operations in the country. This is mainly due to the fact that 93% of the households that practice farming in the former homeland states do so primarily for subsistence purposes[178]. Land in these areas remains public property and is managed under communal tenure. Communal farming is an inherently different agricultural system to commercial farming enterprises[179,180] and direct comparisons are not advisable[181,182]. Nevertheless, productivity comparisons of these systems have been widely attempted, with the finding that, on a per animal basis, communal farming compares poorly to commercial enterprises, but on a per hectare basis, it performs as well, if not better[183,184].

Close to three quarters of the income of subsistence farming households in South Africa is generated from wages and salaries, often earned through jobs in urban centres, or social grants unrelated to the farming operation, with very little income derived directly from crops or livestock[178,185]. The benefits of livestock, and in particular cattle, are not restricted to their financial value, and include various direct-use benefits such as meat, milk, manure, draught power, transport, and hides[182,183,186,187]. Much of the financial value of cattle is locked up as potential value, such that the animals act as 'a living savings account'[188,189]. These extended benefits of cattle, over for example goats, makes them a good choice of livestock in these communal areas[186]. Livestock have the further advantage over crops that they can be utilized at any time during the year[190]. That being said, the socio-economic foundation to rural livelihoods is still poorly understood[184]. Although a number of studies have been conducted within the communal livestock farming area along the western boundary of the KNP[182,186,191-195], none of these explicitly considered the heterogeneity within the larger area, since they mostly focused on individual communities.

The regular monitoring of cattle at IPs in the FMD protection zone presents a unique opportunity to gain insight into some of the basic production and demographic parameters of the cattle population in this sedentary smallholder and communal livestock farming system, at the interface with a conservation-based land use system. This paper aims at providing quantitative data on the heterogeneity and spatio-temporal trends of the cattle population of roughly 350 000 animals found in this disease control zone. Furthermore, baseline demographic information and population trends can aid disease risk assessments, surveillance and control in the region, activities which currently do not explicitly consider such heterogeneity.

Material and methods

Study sites

The study was conducted retrospectively in three sites along the western boundary of the KNP and APNR. Figure 2.1 shows the location of these sites, which were originally selected based on a combination of areas perceived by local experts to be at high risk of FMD outbreaks (due to African buffaloes straying from game reserves and coming in contact with cattle) as well as the perceived differences between the sites with regard to land use, population density and general environmental conditions.

All three sites are situated in the Lowveld region of north-eastern South Africa, a low altitude area characterised by hot summers, during which the peak rainfall occurs (November to February), and mild, dry winters. Prior to 1994, these sites formed part of the former Venda and Gazankulu homeland states. The three study sites comprised 38 IPs in total (North: 10; Central: 12; South: 16), all of which fall in the FMD protection zone with vaccination.

Census data. Data on the number of people and households were obtained from the 2001 national census[196]. Numbers per IP were derived using the centroids of census polygons falling inside the IP boundaries as determined for density analyses (see below).

Livestock data

Livestock register. During the compulsory weekly inspection of cattle for FMD, cattle population data are collected by animal health technicians of the provincial state veterinary services. These data are kept in a livestock register on a per owner basis and aggregated per month at an IP level. Data for this study was retrieved from the monthly aggregates, which are shown in Table 2.1.

The data were entered into an electronic database from routine monthly aggregate hardcopy reports of the livestock register. This was done on a per IP basis for the period January 2003 to December 2007.

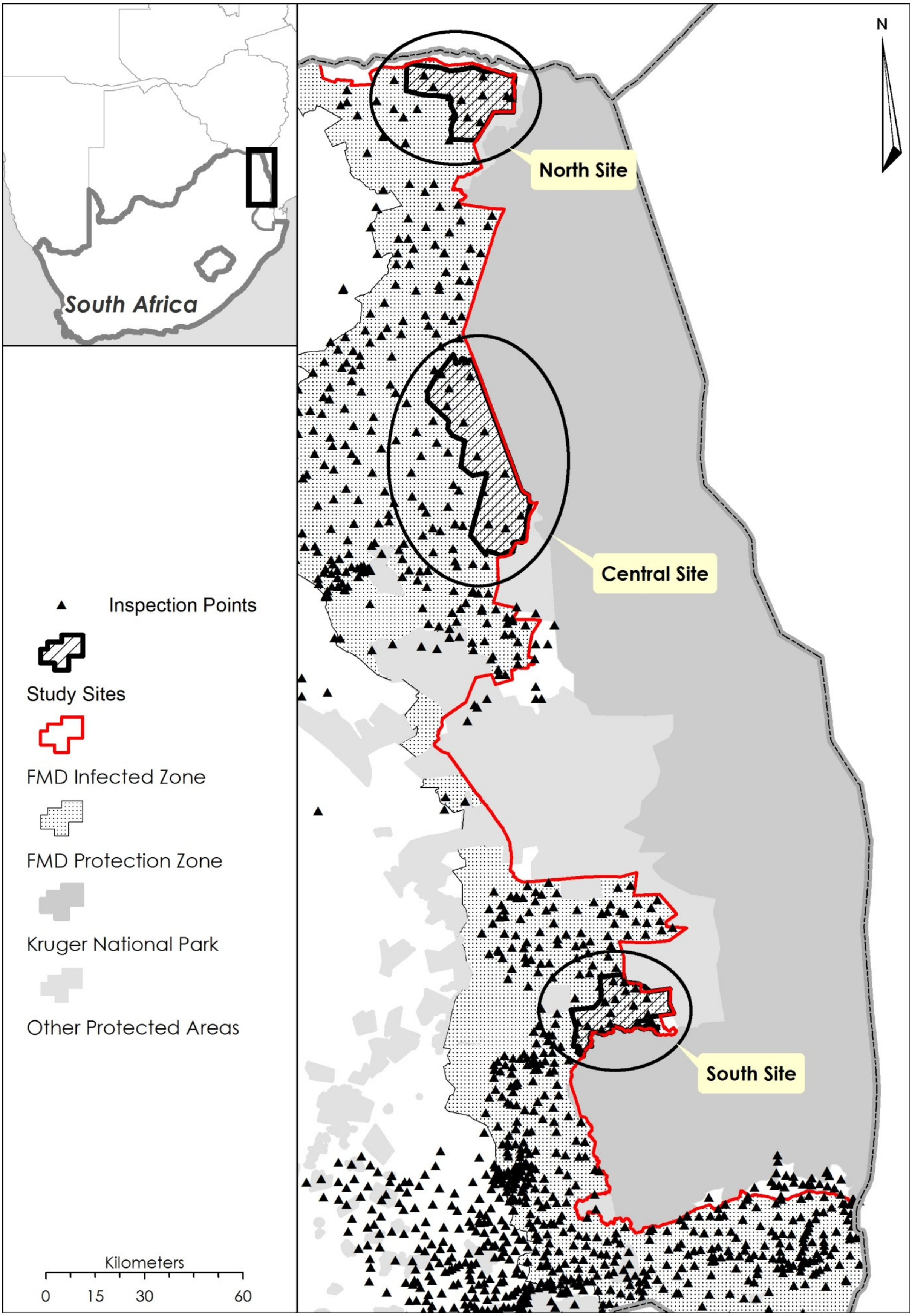

Figure 2.1 Location of the three study sites

Table 2.1 Attributes recorded per livestock inspection point (IP) from the monthly aggregates of the livestock register for each of the study sites

Attribute	Remarks
Number of cattle owned	Number of cattle registered per IP
Number of calves in herd	Estimate of the number of calves up to one year of age at each IP
Number of calves born since last inspection	
Mortality since last inspection	No cause of death recorded. Also includes stock theft
Calf mortality since last inspection	No cause of death recorded. Also includes stock theft
Local sales and animals slaughtered	Home slaughter for own consumption or selling to, and slaughter by, a local butcher within the same IP area, which requires no movement permit
Permits	Could include permits for buying/selling, giving/receiving or borrowing/lending of livestock to/from someone outside the IP area. No registered abattoirs/feedlots exist in any of the study sites, and any commercial sale to abattoirs/feedlots would thus also fall under permit movements, rather than *local sales and slaughtered*.

Derived variables

Calving rate. The livestock register data set did not contain detailed information on the age and gender composition of the cattle population (other than calf numbers) and therefore the calving rate reported is of calves born as a proportion of the total cattle population, rather than just cows, as is the convention.

Conception time series. Based on the calving data, a conception time series was created using a nine month gestation period lag.

Net permit movements. The net movement of animals by means of permits was calculated by subtracting outgoing permits from incoming permits at each IP. Negative permit figures therefore reflect a net movement away from an IP.

Offtake. Since some of the data only contained net permit movements, we could not separate incoming and outgoing permits to work out crude offtake/import rates. Hence, we only calculated net offtake, being the sum of net permit movements and slaughter per year as a proportion of the median number of cattle at a particular IP within the same year.

Own/local consumption. Total number of cattle slaughtered per year as a proportion of the median number of owners at that IP, during the same year

Density. Areas used for the calculation of cattle densities in the South site were based on historic farm boundaries (so-called 'parent farms')[197]. No such farm boundaries exist for the North and Central sites, so areas here were based on Thiessen polygons derived from the location of the IPs. Thiessen polygons define the area around sample points, so that any location within each polygon is closest to its sample point[198]. The choice of area delineation was confirmed by cattle tracking data collected in a related study in all three of these sites (see Chapter 3). Where subdivisions of IPs existed (e.g. where two groups visited the same IP location, but bearing a different IP designation – e.g. Ireagh A and Ireagh B), cattle numbers were aggregated for density calculations.

Cattle:owner ratio. Since these data were aggregated per IP, we did not have numbers at the owner level. The cattle to owner ratio was thus used as a proxy for the mean herd size at a given IP location, even though a large amount of the variability in individual herd sizes will be inherently lost[182,199,200].

Proportion of households keeping cattle. The number of cattle owners divided by the census households in the area of the IP can be used as an indication of the proportion of census households keeping cattle (making the assumption that no more than one cattle owner resides in each household).

Missing data

Respectively, 68.8%, 84.3% and 71.6% of the monthly records in the North, Central and South study sites were complete for the study period (74.9% overall). Missing data points were imputed by linear interpolation and by carrying forward or backward the closest observation where missing values were at the beginning or end of a time series. Missing net permit movements for the current month ($P_{net,t}$) were calculated after interpolation of the total cattle (N_t) in the current month (t) and in the previous month (N_{t-1}), the births in current month (B_t), the mortalities in current month (M_t) and the number of animals locally sold/slaughtered in the current month (S_t) using the following formula:

$$P_{net,t} = N_t + B_t - M_t + S_t - N_{t-1}$$

Linear interpolation had no influence on the variance of the final dataset. Two IPs opened and one closed during the study period; data for the periods when these IPs did not function were not imputed and retained as true missing values.

Environmental data and years

Normalised difference vegetation index (NDVI). NDVI is a ratio of the red and near infrared reflectance as measured by the Moderate Resolution Imaging Spectroradiometer (MODIS) and is generally used to assess the health and density of vegetation[201,202]. NDVI data from 2001 to 2008 with a 16-day interval were obtained from the United States Geological Survey[203] and de-noised using a cubic spline interpolation[204].

Land cover. Landsat 5 derived land cover data at 30m resolution[205] was re-categorized into four categories: 1) areas potentially suitable for grazing (i.e. open woodland, open sparse bushland, open sparse grassland, and bushland and thicket), 2) urban areas, 3) non-wet bare areas which have low potential for grazing and 4) dryland subsistence cultivation areas. In the remainder of the text, these land cover categories are referred to by their abbreviated name: 1) Grazing, 2) Urban, 3) Bare and 4) Subsistence cultivation.

Rainfall data. Rainfall per IP was based on its nearest weather station and aggregated per month from daily data obtained from the South African Weather Service for the period 1998-2008.

Year. A year refers to the 12-month period from 1 July through 30 June. This was used in the analysis of the livestock data (rather than calendar years) to avoid splitting rainy and/or calving seasons, which peak around the beginning/end of the calendar year.

Statistical analysis

General statistical analyses were conducted using the R statistical software[206] and Microsoft Excel 2007 (Microsoft Corporation), while spatial analyses were done using Idrisi Andes[207], ArcInfo[198] and Hawth's Analysis Tools for ArcGIS[208]. Space-time cluster analysis was done using a discrete Poisson space-time scan statistic in the SatScan software package[209]. Figures reported in text refer to the median followed by the interquartile range in square brackets, unless otherwise specified. Comparisons between study sites were conducted using the Kruskal-Wallis rank sum test (p-value reported), unless otherwise specified.

Time series decomposition. This was used to split time series values for livestock data into 1) a trend component (calculated by a moving average considering a symmetric window with equal weights), 2) a repeating pattern component within each year (also known as the seasonal component), which averages each point in the time series over the entire period, after trend removal and 3) the remainder (noise) ('decompose' function of the R 'stats' package).[210]

Gini index. The Gini index measures statistical dispersion in a dataset, and can be seen as a quantitative measure of clustering in data (temporal in this case). A Gini index of zero signifies perfect equality, e.g. all months having equal calving frequencies, compared to one, where all births would occur in a single month[211,212]. Gini index was used to assess seasonality in birth, mortality and offtake.

Cross correlation. The cross correlation function ('ccf') in the R 'stats' package[206] was used to compute the correlation between two univariate time series spanning the same period, but at different lag periods to each other. Where necessary, time series were log transformed. Since we were also interested in correlation of the seasonal components of these time series, seasonal components in the time series were not removed.[210]

Results

Study Sites

Table 2.2 Overview of the biophysical and demographic characteristics of each of the study sites

	Study site		
	North	**Central**	**South**
Area (km^2)	405	965	321
Mean elevation (m)[213]	366	403	413
Mean annual rainfall (range) (mm)[214]	310 (200-400)	520 (400-700)	680 (550-850)
Mean temperature (range) (°C)[214]	23.5 (10.2 - 34.5)	22.2 (8.8 - 32.8)	21.5 (8.1 - 31.5)
Population density (people/km^2)[196]	22.4	62.0	565.7
Household density (households/km^2)[196]	5.5	13.3	122.5

Table 2.2 gives an overview of the biophysical and demographic characteristics of the study sites. A strong latitudinal gradient in human population densities can be observed, with the lowest densities occurring in the North. This gradient is also reflected in the land cover (Table 2.3) of the study sites. The relatively high proportion of subsistence cultivation found in the South was not proportional to the increase in population, with the area of subsistence cultivation per household higher in the North (1.10ha [0.57ha - 2.16ha]) and Central sites (0.90ha [0.54ha - 1.33ha]), than in the South (0.24ha [0.17ha - 0.30ha]). Despite subsistence cultivation areas providing potential seasonal fodder[215,216] and bare areas being lush green with annual grass and herbaceous plants in the early wet season (personal observation), they were not considered as potential grazing areas due to the inconsistent nature of their grazing potential. Less than half (43.9%) of the South site could be regarded as potential grazing area, compared to 91.4% in the North and 78.4% in the Central sites.

Table 2.3 Predominant land cover of the three study sites

Study Site	**Land cover**				
	Grazing	**Urban**	**Bare**	**Subsistence cultivation**	**Other**
North	91.4%	0.8%	3.1%	3.9%	0.8%
Central	78.4%	4.0%	4.8%	11.1%	1.6%
South	43.9%	16.7%	10.3%	24.8%	4.4%

Total cattle

Total cattle numbers for each study site are shown in Figure 2.2, with the dashed line depicting the temporal trend after removal of seasonal fluctuations through time series decomposition of the data.

The North and Central sites, respectively, showed an overall decrease of 15.1% and 2.9% in total cattle over the five-year study period, whereas a 28.6% increase in the number of cattle was recorded in the South, corresponding to an annual growth rate of 5.15%. Notwithstanding, fluctuations of 35-42% were recorded in all three study sites over the study period.

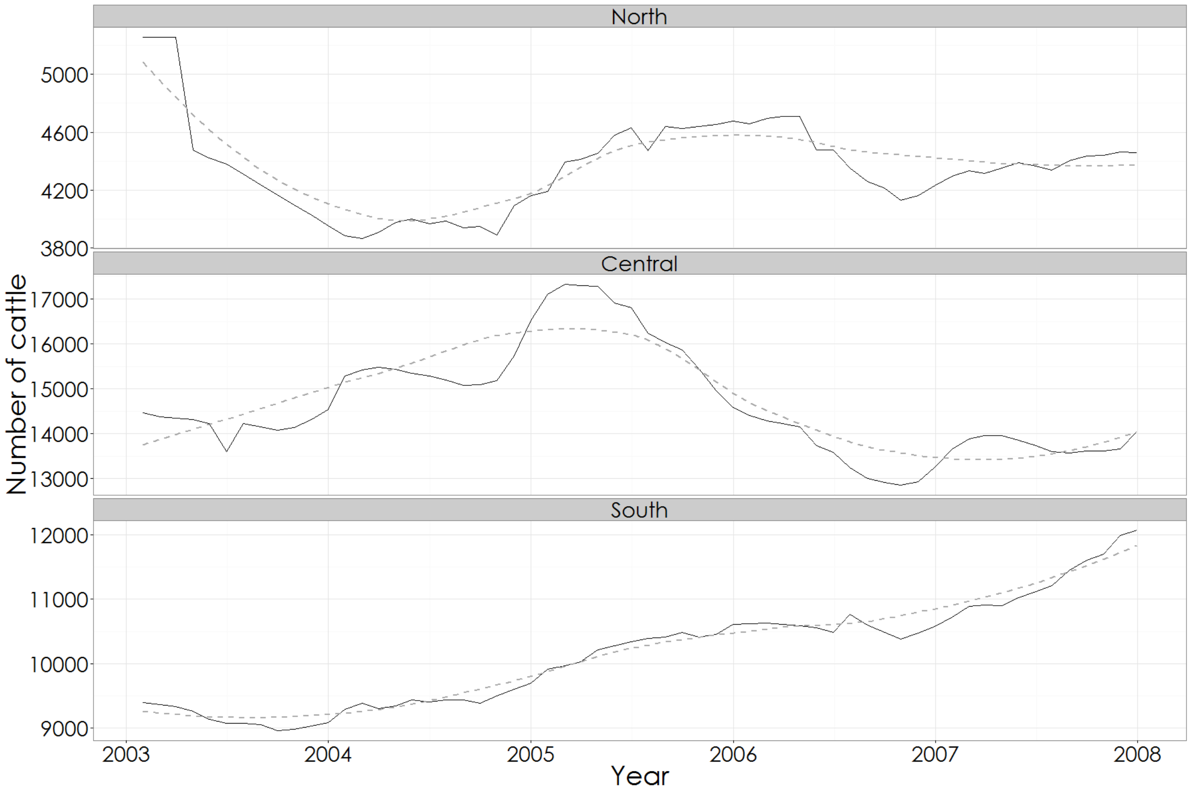

Figure 2.2 Total cattle numbers in each of the study sites (temporal trend shown as a dashed line)

Time series decomposition revealed a seasonal pattern in the cattle numbers of all three study sites. The fluctuation ascribed to seasonal variation evaluated as a percentage of the median number of cattle in the study area, showed that seasonal variation was only responsible for 4-6% of the fluctuation in the North and Central sites, and less than two percent in the South site.

The median proportion of calves in the cattle population differed significantly in the Central site from the other two sites, at 19.37% [14.16% - 23.40%] versus 11.91% [8.21% - 16.98%] and 10.71% [6.95% - 16.53%] in the North and South sites, respectively ($p<0.01$).

Cattle density

The median density of cattle during the study period was 11.6 [9.4 – 14.2], 18.6 [15.1 – 22.4] and 32.7 [27.5 – 37.1] animals per square kilometre for the North, Central and South sites, respectively. A combination of human population density and annual rainfall could explain

71% of variation in cattle density recorded per IP ($R^2=0.71$; $p<0.01$). When considering all IPs across the three study sites, a 68.2% correlation between the cattle density and area of subsistence cultivation per household was evident ($t = 12.56$, $p<0.01$; area of subsistence cultivation per household square root transformed; data normally distributed). Within each study site, however, this correlation was less pronounced, with it only being significant in the North site (33.6%, Pearson's product moment coefficient; $t=2.34$, $p<0.02$).

Ownership and cattle:owner ratio

The median number of cattle owners in each study site was 292 [280 – 295], 1150 [1122 – 1168] and 1282 [1270 – 1290] for the North, Central and South sites, respectively. These numbers remained remarkably stable during the study period in comparison with cattle numbers. The maximum fluctuation in the number of owners reached 20% in the North and Central sites, while the South site was more stable, recording a maximum fluctuation of only six percent. The median cattle:owner ratio was 16.9 [12.7 - 21.9], 12.7 [11.2 - 14.0] and 8.1 [6.8 - 10.3] in the North, Central and South sites, respectively, with a significant difference between the three study sites ($p<0.01$).

A significantly lower percentage of households own cattle in the South at 4.0% [2.4% – 4.6%], compared to 13.7% [10.6% – 33.2%] and 12.7% [9.3% – 15.1%] in the North and Central sites, respectively ($p<0.01$).

Calves and calving patterns

Calving peaked around December/January of each year with more than half (55.4%) the annual calf crop born from November to the end of February (four months). The period between the beginning of June and the end of August (three months) had the lowest calving percentages, only producing 14.5% of the annual crop. This temporal pattern was more pronounced in the Central site, where 62.9% of all calves were born from November to February.

A median annual calving rate per IP of 23.82% [17.19% – 29.91%] was recorded for the entire study area. Although calving rates varied between years, there were no significant differences in annual calving rates between the study sites over the total study period, other than the significantly higher calving rate for the Central site during the 2006/2007 year compared to the other two study sites ($p<0.01$). Table 2.4 shows the calving rate and Gini index per study site for each year. It is noteworthy that the three peak calving months in all study sites over the four calving seasons were the same (January, December and February, in that order).

Table 2.4 Calving rate, median Gini index and top three calving months (in decreasing order)

Site		2003/2004	2004/2005	2005/2006	2006/2007	All years
North	Calving rate	0.21 (0.15-0.28)	0.31 (0.28-0.32)	0.21 (0.15-0.23)	0.23 (0.17-0.28)	0.24 (0.16-0.30)
	Gini Index	0.39	0.51	0.63	0.57	0.53
	Peak months	Mar, Jan, Feb	May, Feb, Jan	Jan, Dec, Feb	Jan, Dec, Nov	Jan, Dec, Feb
Central	Calving rate	0.25 (0.14-0.26)	0.25 (0.23-0.28)	0.18 (0.14-0.23)	0.33 (0.29-0.35)	0.25 (0.20-0.31)
	Gini Index	0.46	0.62	0.55	0.55	0.55
	Peak months	Jan, Nov, Dec	Dec, Jan, Nov	Dec, Feb, Jan	Jan, Dec, Feb	Jan, Dec, Feb
South	Calving rate	0.22 (0.18-0.28)	0.27 (0.20-0.42)	0.21 (0.11-0.27)	0.22 (0.18-0.25)	0.23 (0.17-0.28)
	Gini Index	0.48	0.53	0.34	0.46	0.47
	Peak months	Jan, May, Feb	Jan, Dec, Apr	Dec, Jan, Sep	Dec, Jan, Nov	Jan, Dec, Feb

To assess the influence of rainfall and/or NDVI on conception rates, a cross correlation analysis of the conception rate time series (log transformed) compared to the NDVI (mean) and rainfall (log transformed) time series was conducted. This revealed a significant relationship between conception rate and both these covariates ($p<0.05$), with both covariates leading conception in time, but at different time lags. Table 2.5 shows the lag between peak rainfall/NDVI and peak conceptions.

Table 2.5 Time lag (months) between peak rainfall/NDVI and peak conceptions

Study site	Rainfall		NDVI	
	Lag (months preceeding)	**Correlation coefficient ($p<0.05$)**	**Lag (months preceeding)**	**Correlation coefficient ($p<0.05$)**
North	3	0.44	2	0.60
Central	2	0.65	0	0.64
South	2	0.34	1	0.43

Mortalities (including calf mortalities)

Annual mortality rates recorded per IP during the study period were 2.75% [1.61% - 4.06%], 2.35% [1.70% – 3.54%] and 3.16% [2.31% – 5.08%] for the North, Central and South sites, respectively. This was however highly variable between years, with the Central site, for example, reporting a mortality rate of 14.42% [3.37% – 35.31%] during 2005/2006. A space-time cluster analysis, using a discrete Poisson model, revealed a significant cluster of increased mortality (relative risk: 21.32; p <0.01) in the northernmost six IPs of the Central site for the period October 2005 to April 2006, while a secondary cluster (relative risk: 15.47; p <0.01), spanning exactly the same period and completely overlapping the primary cluster, extended further north to include the entire North site. Surprisingly, none of the concurrent NDVI or rainfall values for the affected IPs were significantly lower than those of the IPs outside either the clusters. However, rainfall and NDVI values from the previous season were significantly lower in these clusters than in the rest of the Central and other study sites (p <0.01) for both clusters.

Another latitudinal gradient was observed in calf mortality, with the North recording significantly lower calf mortality than the other two study sites (p <0.01). Actual numbers aggregated for the entire North site over the four years, gave a remarkably low median calf mortality of 2.1%, while at an IP level, across all years, three quarters of the reported annual calf mortality rates were below 2.9%. This is in stark contrast to the South, where the median calf mortality per IP was 11.6% [5.2 - 21.4%]. In the Central site, very high calf mortalities were reported during 2005/6 (14.6% [6.3 – 21.3%]) compared to the other three years studied (6.3% [3.3 – 9.3%]). The North and South sites did not show any particular temporal pattern in calf mortalities within years, while in the Central site, calf mortalities were most concentrated between January and February (Gini index: 0.28).

While no significant relationship between cattle density and annual mortality (all age groups) was found, calf mortality did show a positive correlation with cattle density, even though it only accounted for 21% of the variation in calf mortality (R^2: 0.21; p<0.01). Adding the negative correlation that calf mortality showed with cattle:owner ratio, explained 30% of the variation in calf mortality (R^2: 0.30; p <0.01), whilst the same combination could explain very little of the variation in annual mortality rates in the total population (R^2: 0.06, p <0.05). This effect was more pronounced in the South compared to the other study sites.

Offtake (slaughter and permit movements)

The number of animals slaughtered as a percentage of the median number of animals per IP during the same time period, showed a significant difference between the North and the other two study sites, with annual slaughter percentages of 0.2% [0-1.4%], 11.7% [9.2-16.5%] and 11.0% [7.6-15.2%] for the North, Central and South sites, respectively (p <0.01). Although no distinct temporal (monthly) pattern was detected in the slaughter behaviour of IPs, the greatest number of animals slaughtered over the entire study period was reported in January (10.3%). The highest Gini index was detected in the North (0.34), where slaughter peaked equally in January and April. Annually, and in relation to the median number of owners per IP, very low local consumption rates were observed in the North (0.04 cattle slaughtered per owner [0 - 0.16]), compared to the Central (1.6 [1.1 - 2.1]) and South (1 [0.6 - 1.1]) sites.

To get a better idea of the net movement of animals, as opposed to own/local consumption, we looked at the per-IP aggregated net permit movements per year, divided by the median number of owners at the same IP during the same period. Figure 2.3 clearly shows the tendency of owners to move cattle away from the IP in the North (-1 [-2.8 – -0.05]) and Central (-0.4 [-1.2 – 0.1]) sites, compared to the South site (0.1 [-0.1 – 0.4]), where owners were slightly more inclined to move animals towards the IP than away from it, i.e. buy or receive animals. In general, these permit movements and own/local consumption data indicate that owners from IPs in the North are 26 times more likely to move an animal away ('sell/give') from the IP than to slaughter it locally. This contrasts with the Central site, where an owner is four times more likely to slaughter an animal than move it away from the IP, and with the South site, where an owner is twelve times more likely to slaughter one of his own animals than to move an animal towards the IP ('buy/receive').

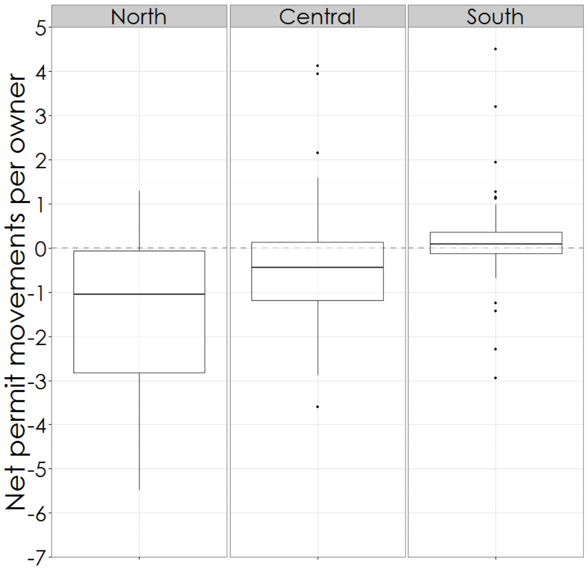

Figure 2.3 Net permit movements at livestock inspection points during the study period in each study site

Significant correlation (p <0.05) was found between slaughter and mortality in the Central and South sites. Cross correlation analysis (Figure 4) showed that in the Central site, slaughter and permit movements lead mortalities by up to five months. In the South, slaughter and mortalities peaked at the same time, or peak mortalities preceded slaughter by one month. What is more, in the Central site, at ten and twelve months after peak mortalities, a significant influx of animals through permits occurs, possibly indicating some level of restocking. The North site only showed a significant correlation at a lag of three and five months, with mortalities leading outgoing permit movements.

The Central site had the highest median net offtake rate at 16.09% [7.75-22.78%], compared to the North at 7.23% [0.66-20.77%] and South at 8.43% [3.96-16.62%]. The median offtake rate across all sites and years was 10.8% [4.35-19.20%]. Some concentration of offtake occurred during the winter months, mostly in the North site (Gini index: 0.31)

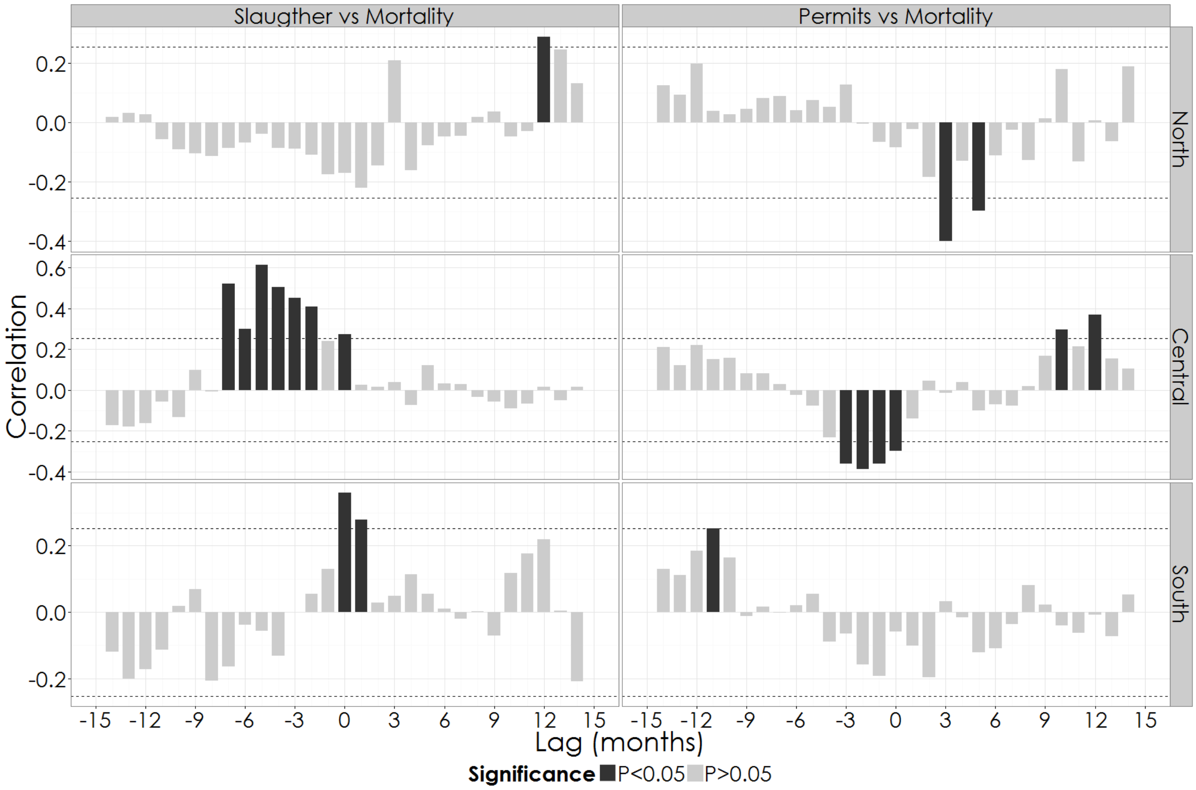

Figure 2.4 Cross correlation between mortality and slaughter as well as net permit movements during the study period. A positive lag signifies mortalities leading slaughter/permit movements. Outgoing permit movements were recorded as negative values and would thus result in negative cross correlation values when outgoing permit movements predominated. Dashed horizontal lines signify the 95% significance level with dark bars falling within this significance threshold.

Discussion

Although it is self-evident that one finds cattle where one finds people[217], the direct relation between these two interdependent species is all but simple. As an example, in the vast network of villages of the Bushbuckridge district (within which the South site is located), in just over a decade after 1993, urban areas increased by 39%, resulting in both expanded as well as denser settlements, with concomitant losses in natural vegetation and restriction of rangelands[215,218,219]. This poses a potential threat to the natural resource base that is crucial not just to subsistence livestock farming, but to many livelihoods dependent on its wide range of natural products[189,191,218]. But, this urban expansion was not necessarily a result of human population increase, since the human population of this district in fact decreased slightly over a similar period[220]. At the same time, the cattle population in the South grew by more than five percent per year during our study period, which was about five times more than the growth in the number of cattle owners during the same period. Satisfying the increased demand that accompanies this level of urban expansion as well as these increases in cattle numbers could be a great challenge under these natural resource constraints[221]. Notwithstanding, an increase of 168% in cattle has been reported previously for a six year period in a specific village in Bushbuckridge (albeit a period immediately after the severe drought of 1992)[186] and, similar to our findings, this was mainly due to an increase in herd size, rather than numbers of livestock owners[184,222]. Herd accumulation in communal systems when optimal conditions prevail, may thus act as a form of insurance against adverse events[223]. While the rate of increase in cattle in the South site might be disconcerting, especially considering the rate of rangeland decrease[218], the realism of establishing a fixed grazing capacity to prevent irreversible damage has also been contested[219,222]. The seemingly large fluctuations in the cattle population which we encountered in all three study sites are therefore not surprising, but rather further proof of the dynamic nature and resilience of these communal herds[184,186,224,225].

The cattle densities we report (11.6 - 32.7 animals per square kilometre) fall within a similar range as reported elsewhere, driven primarily by annual rainfall and human population density[187,217,226]. We also found a positive correlation between cattle density and subsistence cultivation at a broad scale (across all study sites), which has been suggested as an important determinant of cattle distribution[217,226] through provision of post harvest supplementary fodder[215,216,227]. Regardless, no association between mortality or calving rates and the area of subsistence cultivation available[228] could be detected in this study. The actual utilisation of crops as supplementary fodder appears to be low[186,229] and buying of supplementary fodder is not common either, although during severe droughts or disease outbreaks, this does occur more often or is provided/subsidised by Government (J van Rooyen, personal communication, 22 January 2012).

Our approximation of the proportion of households owning cattle was lower than expected, especially in the South, where others have reported a greater proportion of households owning cattle[183,184,186,230]. A possible disparity in the definition of census household and 'cattle owning household' in these publications might be the cause. However, the South site does appear to be less active from an agricultural perspective compared to for example the North site, as evidenced by the lower proportion of cattle-owning households, the smaller cattle to owner ratio, and the less than one third of a hectare of land cultivated per household. While this could be ascribed to other income generating opportunities in these highly populated areas, it does not necessarily equate to a lower dependence on livestock[184,186], especially when considering the much higher local consumption, most likely demand driven, in the South compared to the North site. This heterogeneous demand is also reflected by the general consumption behaviour of the study sites, with the North (and its assumed low demand deduced from the low human population density) more of a net 'exporter' than the South site, where local consumption and net 'imports' dominate. In this regard, the Central site seems to be somewhere in-between, with a fair amount of local consumption, but still showing a dominant net movement of animals away from IPs.

Concentrated or seasonal calving as a consequence of wet season conceptions, similar to what we observed, has been reported previously in cattle where no manipulation of reproduction occurs[216,231]. This stems mostly from the favourable body condition of cows during the wet season when grazing is abundant[231], hence the peak of conceptions that closely follow the NDVI increases. The strong relationship between both the rate and seasonality of calving to rainfall and NDVI of the previous year is a clear indication that environmental conditions play a major role in calving patterns, more so in the drier northern and central regions than in the south. A poor conception year followed by a higher than normal conception year, e.g. in the Central site during 2006/7, is a phenomenon previously described[229]. This is most likely related to the number of cows not pregnant or lactating following a low conception year that are available for mating during the next year. This potentially comes at a cost though, since the highly fertile cows that do conceive during these difficult years often succumb under nutritional strain due to the demands of pregnancy or lactation, effectively selecting against their higher fertility[182,194,225,232,233].

Since our calving rates are based on the entire herd and not just cows, it is difficult to compare these directly to a number of comparable figures published, although studies in similar areas to our study sites suggest the proportion of the herd that is cows, to be approximately half[182,193,195]. If this is indeed the case, our calving rates are very similar to what has been reported by others in communal herds[179,192,216,224,234]. A fifty percent calving rate, suggesting an average of one calf per cow every two years, is quite good in reproductive terms, especially considering the general lack of forced weaning[216] and the low number of farmers that provide supplementary feed[186,229]. We were however unable to quantify embryonic loss, abortion or stillbirths; neither could we directly estimate the role of disease, if any, in reproduction. Studies in the vicinity of the Central and North sites have reported 20-23% calves in the population, with lower proportions observed in drier years[182,195,235], similar to our findings in the Central site.

The annual mortality rates reported in the three study sites were relatively low (0-16%), compared to those reported in the literature (0-30%)[184,187,216]. Even though we did not experience any drought during the study (which can cause very high mortality rates of up to 70%;[182,223,225,228,232], the significant relationship between elevated mortality and the previous season's rainfall/NDVI, rather than that of the concurrent season, was an interesting finding. This is most likely because mortality does not follow a linear relationship with precipitation and NDVI (as proxy for available fodder), but is rather a consequence of these factors pushing the animals to a threshold in their nutritional resilience[224,225]. That being said, our data did not distinguish between nutritional and disease-related mortality. The latter may be especially pertinent during the rainy season, and possibly aggravated by animals in poor condition, since during this period, prevalence of tick borne diseases can be quite high[236]. Generally, however, the majority of mortalities can be attributed to poor nutrition, especially during dry periods[184,216,225]. Since we could not quantify stock theft (which is also recorded as 'mortalities'), it is important to keep it in mind as a confounder of our reported mortality figures, especially in the more densely populated areas, where it seems to be increasing[184,216,237] and animals are penned every night in an effort to prevent it[186,238].

A similar positive correlation between cattle as well as human density and calf mortality found in this study has been reported before[239]. Lybbert et al.[239] further reported a negative correlation between herd size and calf mortality, which we did not measure directly at the herd level, even though our data showed a similar pattern at an IP level. These phenomena could stem from competition for milk, both with other calves and with humans[240,241]. We also did not measure milk consumption (by people), but if this was to follow a similar pattern as local/own consumption through slaughter, being much higher in densely populated areas, it could put additional nutritional strain on calves. This, as well as the limited available grazing areas in densely populated regions, such as the South, could also affect nutrition of lactating cows, with subsequent lower milk production.

Offtake rates recorded during our study are slightly elevated when compared with other studies[182,184,187,195,216,228,235]. The offtake strategy as well as the response of owners to perceived adverse conditions, such as increased or imminent mortalities, varied between the three study sites. In the South site, with apparent high local demand, slaughter rates were correspondingly high; however, these offtake rates were often more than natural production could replace, hence the net import of animals to IPs observed here. This high offtake rate is further exacerbated by small herd sizes and high calf mortalities in the same area. The high proportion of own consumption by owners of small herds in densely populated areas, which is not unexpected[228], might be regarded as increased integration of livestock into the local markets, which would be encouraging[242]. In the North site, offtake was dominated by movement of animals away from the IP, with local slaughter rates very low and peaking close to the Christmas/New Year and Easter holidays. This might indicate some level of market intelligence, should there be a lag of reporting slaughtered animals over Christmas holidays, or could just be related to the start of the school terms and the need for cash to pay school fees. This behaviour also corresponds with that of the Batswana owners of larger herds to sell rather than slaughter cattle[199]. In the Central site, on the other hand, local consumption was only slightly lower than in the South site, but low enough in relation to natural production to allow movements away from IPs as an additional offtake strategy. The Central site had the highest offtake rate of the three study sites, confirming that overall offtake rates are not necessarily highest in areas with the largest herds[234,243]. The negative association between herd size and slaughter, and the positive association between herd size and movement that we observed, differed from the findings of Lybbert et al.[239], who found a negative association between herd size and movement/sales and a positive association between herd size and slaughter. Our findings are most likely explained by the general lack of local markets, in combination with the inverse relation between herd size and human density, limiting local opportunities to sell or slaughter for those owners with bigger herds. However, our findings of a general inverse association between movements/sales (i.e. not local/own consumption) and rainfall zone, does concur with the findings of others[184].

A great variety of responses of livestock owners to adverse conditions, such as increased slaughter, both increased and decreased sales, increased movements, reduction in herd size and even complete destocking have been reported in a number of communal areas in the past[184,229,244]. What is noteworthy in this study is the apparent proactive risk aversion strategy of owners in the Central site, which occurred both through slaughter and movements away from IPs a number of months before mortalities started peaking during an extended dry period as well as ostensible restocking through increased importation of animals in the more favourable months that followed. In the South site, on the other hand, the timing of the response to increased mortalities seemed to be more a case of salvage (or distress) slaughter than risk aversion, possibly because the smaller herd sizes in this study site do not allow large scale pre-emptive sales/slaughter without complete, or near-complete, destocking.

Surprisingly, the North site seems almost indifferent towards anticipated mortalities, opting for a subdued reactive response rather than proactively avoiding losses, which might be as a consequence of their larger herds that could buffer such losses, as well as the low demand for meat from local slaughter.

Offtake through (non-local) sales is not a simple matter in these study sites, especially considering the lack of commercial abattoirs or feedlots in these areas as well as the distances involved in travelling to sell cattle, often for only a few animals[243]. This problem is, however, frequently overcome through speculators and auctions, although very low levels of competition often leads to poor prices; hence the tendency to sell locally, when demand allows it[245].

While Behnke[199] observed remarkable stability in the communal farming system during the second half of the twentieth century, Jones and Thornton[242] predicted significant changes in cropping and livestock keeping patterns in Africa for the first half of this century, especially in poor communities. Many expect changes in the system as a consequence of changes in rainfall patterns, especially extreme events[221,246], with marginal areas potentially starting to put more emphasis on livestock, rather than crop farming[247]. This is mainly based on livestock's comparative resilience to variable climate patterns, with goats (and other browsers) becoming an increasingly prominent option as vegetation and other changes occur. Such change in livestock species composition bears further significant consequences for disease risk and control[247].

From a disease risk perspective, the cattle density gradient from north to south is notable, especially where direct contact diseases like FMD are considered, both from a likelihood of interaction with buffaloes as well as a cattle to cattle spread viewpoint. Also, the seasonality of calving is useful in prospectively determining the period at which most young animals would be losing their maternal immunity and be most susceptible to disease. This is helpful in the spatio-temporal risk profiling as well as the implementation of vaccination programmes, especially in the case of FMD, where buffaloes and cattle tend to show very similar seasonality in their calving patterns[65], with possible linkages between young animals and infectivity[2,48,61]. Furthermore, offtake strategies could influence disease spread, especially over larger distances, while local consumption patterns could influence especially zoonotic disease risk.

Considering the general lack of good livestock demographic data in communal farming areas in Africa, the disease control livestock registers maintained within the FMD protection zone of South Africa offer a wealth of long term cattle demographic information. Whilst some information remain dubious or lacking, such as stock theft, disease versus nutritional mortalities as well as herding strategies, these require minor adaptations to the current system to be included. Furthermore, migrating to a central online data repository could allow for near real-time analyses and responses, both from a veterinary and agricultural production point of view.

Conclusion

The findings we present here, clearly show that a great deal of heterogeneity exists in the communal livestock component of the KNP and APNR wildlife-livestock-human interface, not only in its physical attributes, but also in the way people and animals respond to and interact with these attributes and each other. These attributes and interactions are important to consider, especially in disease control strategies and disease risk assessments, where they are often oversimplified or unknowingly ignored due to their indirect nature. While a number of these findings could be further broken down, they already increase our insight into how this unique system operates, and enable us to employ risk assessment and control strategies that not only are more effective from a disease prevention point of view, but also have the least possible negative impact on the system itself.

Chapter 3

Cattle movement and distribution patterns in the areas adjacent to the Kruger National Park, South Africa

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Chapter summary

Communal livestock farming makes an important contribution to the livelihoods of a large number of households in South Africa. Current knowledge suggests that there is very little organisation of grazing in these farming areas, with only a few studies that have looked at cattle movement and distribution patterns of these cattle herds. This study investigates the grazing patterns, home ranges and habitat suitability of communally-farmed and smallholder cattle in four study sites along the foot-and-mouth (FMD) infected zone in South Africa, utilising Global Position System (GPS) data from handheld devices and animal collars. Home range was determined with the time-based local convex hull (T-LoCoH) method, whilst habitat suitability was determined through maximum entropy modelling. Daily activity budgets showed walking peaks in the mornings and afternoons, with grazing occurring mostly from late morning to early afternoon. The grazing pattern was also bimodal in sites where no herding of cattle occurred. More grazing occurred during the warm wet season in the northern site and on smallholder farms. Grazing trajectories in the south (where cattle were kraaled daily) were the shortest and significantly longer in the northern site and smallholder farms where animals were often left to roam free. The maximum grazing radius was attained around midday in the communal areas (median ranging from 2-3km). A more pronounced positive relation between a trajectory's grazing radius and its maximum distance from water in the cool dry season, especially in the central site, suggests dependence on water as an important driver of grazing patterns. Utilisation of cultivated fields was significantly elevated during the early dry season. Home range estimates (95%) were larger in the cool dry season, suggesting concentration of animals in specific areas during the warm wet season. Habitat suitability, determined through maximum entropy modelling, echoed this apparent contraction of preferred grazing areas during the warm wet season. The results presented here gives valuable insight into communally-farmed and smallholder livestock movement patterns in the area adjacent to the FMD infected zone, which could serve as inputs to spatio-temporal disease risk models.

Introduction

Communally-farmed cattle make up forty percent of the national cattle herd in South Africa.[248] Although the communal livestock sector only contributes about one percent of the country's agricultural revenue[178], it plays an important role in the livelihoods of a large number of people as a source of food, wealth, security and derived products and services (e.g. manure, draught power)[182,183,186,187,193] (also see Chapter 2). Apart from land tenure[249], communal livestock farming areas in South Africa are differentiated from commercial livestock ranches in that they have multiple managers, contain more than one livestock species, employ continuous grazing across the diverse landscape, and production is aimed at a large range of products, primarily for personal use[250]. Very little organisation of grazing, such as rotational grazing, occurs in these communal rangelands, which are often considered to be overgrazed[249,251]. Moreover, animal performance (including reproduction and immunity) is highly dependent on forage quantity and quality, which are limited throughout the year in most of these areas[251]. Yet, the communal farming system in South Africa is still considered to be rather poorly understood[222,251,252] (also see Chapter 2).

In southern Africa, most African buffaloes (*Syncerus caffer*) are considered to be persistently-infected with foot-and-mouth disease (FMD) virus, particularly the three Southern African Territories serotypes (SAT 1, 2 and 3)[28,41]. For this reason, and to allow the larger part of South Africa unrestricted access to agricultural export markets, game reserves containing buffaloes persistently-infected with FMD virus are fenced off with game-proof fences (forming the so-called FMD infected zone), and areas surrounding these persistently-infected buffalo sanctuaries are divided into a FMD protection and FMD inspection zone according to international recommendations[125]. An estimated 350 000 cattle are kept in the FMD protection zone. The protection zone is further divided into a vaccination zone closest to the reserves (with weekly inspection of cattle for signs of FMD and bi- to tri-annual vaccination against the disease), and a zone without vaccination (with fortnightly inspection of cattle), lying adjacent to the vaccination zone (also see Chapter 4). So, while their commercial activity might already be considered low (also see Chapter 2), the communal and smallholder[b] areas adjacent to the FMD infected zone are further affected by regulatory livestock movement restrictions between these control zones[1,4,29]. More than three quarters of the western and southern boundary of the Kruger National Park (KNP) and the private and provincial nature reserves adjoining it (APNR), forming the main component of the FMD infected zone, lie adjacent to vast communal or smallholder farmlands. Only a few clustered

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[b] Smallholder farms differ from communal areas in that they normally have a single owner, are fenced off and hold one herd of cattle. Commercial activity is however very low, and more subsistent.

areas adjacent to the central and southern parts of this boundary are used as commercial livestock and/or crop farms, or game farms/reserves.

Modern-day global positioning system (GPS) technology makes it possible to collect positional data of animals at a relatively high frequency and over extended periods of time. Such data can be used to investigate animal behaviour and habitat selection with very little intrusion and at various levels of interest. At the same time, sensors fitted to the GPS units, as well as access to large amounts of relatively high resolution spatio-temporal biophysical data, enables us to record a plethora of related landscape and physiological information[253], probably only limited by battery life and/or internal memory of the device[254]. Despite these numerous advantages brought about by the use of GPS telemetry, it comes with the risk that more and more data interpretation will occur without an adequate field-based understanding of animal ecology[255].

In his seminal works on cattle behaviour and movement studies, Bailey[256] defined optimal livestock habitat as those areas where uniformity and sustainability of livestock grazing can be maintained, whilst at the same time, sufficient animal performance and economic sustainability can be achieved. Bailey et al.[257] also showed that large herbivore foraging can be considered at six broad spatio-temporal scales, depending on the frequency of decision making and area of affect: Bite (1-2 seconds), feeding station (5-100 seconds), patch (1-30 minutes), feeding site (1-4 hours), camp (kraal, 1-4 weeks), home range (1 month – 2 years). During each day, the grazing itinerary is mainly divided into walking, grazing (or browsing), drinking and resting, with some workers preferring an even more detailed subdivision of activities[258]. Feeding site selection of cattle along a path is a combination of biotic, abiotic and social factors, as well as active animal decisions[256]. The speed at which the animal moves along this generally straight foraging path is negatively correlated to the abundance of fodder encountered, and as soon as the feeding patch is depleted, the animal moves quickly to the next feeding patch[257,259]. In their detailed review of the behavioural processes driving habitat selection, Launchbaugh[260] attributed site selection to a combination of inherited behaviour and own experience.

At the next of Bailey's scales, the camp (or kraal in the local context), abiotic factors such as slope and distance to water are generally the primary constraints of grazing distribution, within which feeding site selection then has to occur[256]. Such constraints come at a cost, however, especially to larger herbivores, which may be forced to select lower quality diets to maintain adequate intake while travelling over larger distances[257], which could also affect milk production and body condition[261]. Across the highly heterogeneous savannah landscape, especially across its diverse seasons, adaptable or even opportunistic foraging strategies are a prerequisite for livestock to survive[262,263]. In South Africa, the main limiting factor in communal livestock systems has been deemed the local dry season, during which forage is characterised by low protein, low energy and high fibre[251].

Two broad approaches to the analysis of animal movement data exist[264]: Lagrangian and Eulerian. The former involves analysis of discrete distance and time segments, mainly covering aspects of feeding site selection and grazing itineraries, which have been discussed so far, while the latter involves the analysis of space use, such as home range and distribution.

In his famous work, Burt[265] simply defines the home range (HR) concept as the '…area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.' It is likely that an animal's home range is determined not only by the immediate environment, but also to some extent by periodically updated 'cognitive maps' of the environment (a kind of 'memory')[257,266,267]. Statistically, HR is most commonly considered as the intensity of an animal's use of the landscape[267] which is often expressed as a probability of occurrence at any location in the landscape, or the 'utilisation distribution' (UD)[268]. Hence, HR is often quantified as the 95% UD[269], with the 50% UD considered less sensitive to differences in the shape of the area (i.e. the ratio of perimeter to area) than the 95% UD[270]. The 50% UD could therefore be considered as a 'core' of the HR, which is considered more informative than the 95% UD by some[271]. A wide range of techniques are available for the calculation of UD, with the classic hull methods (a minimum enclosing polygon)[272] and kernel density estimators (KDE)[273] still applied widely. The hull methods are non-parametric, and of these, the minimum convex polygon (MCP)[274] is probably best known and most used[275]. MCP, however, does not take into consideration point density or time, and can be very sensitive to outliers[276]. KDE, on the other hand, is a parametric method, and is suited more towards concave analysis that takes into consideration the density of points[276]. A major assumption with these classic techniques, however, is the independence of individual points in both time and space, which is very often breached in studies where high frequency GPS data is used[277]. To this end, another approach in estimating UD is to consider the segment between two consecutive points, rather than the points themselves, which in effect then looks at the 'movement' component of a trajectory. The first of these techniques was based on a combination of Brownian movement and KDE, and called the 'Brownian bridge' technique[278-280]. Recent modifications of the Brownian bridge include integration with biased correlated random walks to create the 'biased random bridge' approach[281], while Kranstauber et al.[282,283] relaxed the Brownian bridge model to make it more realistic by adding parallel and orthogonal directional components. Huck et al.[284], however, is concerned that the Brownian bridge technique does not perform well in species with a small home range size in comparison to the speed that they move. The movement-based UD techniques are better suited to high frequency GPS telemetry data, for which they were developed, compared to the classic methods which stem from observation, capture, or low frequency radio telemetry data[285]. For the hull methods, a nearest neighbour modification of the MCP was later developed, termed the 'local convex hull' (LoCoH), which was able to estimate home range within 12% (underestimate) of its true value[286]. Getz et al.[287] argued that the parametric kernel techniques did not adequately identify hard boundaries (e.g. fences) or areas of avoidance/inaccessibility in the landscape, and proposed further improvements to the LoCoH technique. They applied this modified LoCoH to African buffalo GPS telemetry data and adjudged it to outperform the KDE methods[287]. Huck et al.[284], similarly found LoCoH to perform better than MCP, KDE and Brownian bridges when applied to badgers, with LoCoH consistently giving the smallest home range of the four techniques[286,288]. Despite these differences in HR size reported between the hull and kernel methods, it would seem as though their representation of use of the landscape is still correlated[288]. More recently, a time-based LoCoH method (T-LoCoH) has been proposed by Lyons et al.[276]. T-LoCoH allows for the construction of local hulls specific in both space and time. The addition of a time component to the construction of hulls allows for the inclusion of metrics such as revisitation and residence time, since T-LoCoH assesses time difference between all point pairs and not only in a sequential fashion[276]. Furthermore, T-LoCoH is very effective at identifying spatial edges of landscape features and temporal segmentation of UD due to temporal partitioning in movement patterns. For illustration, the difference in HR/core area estimation between two of the classic techniques (MCP and KDE) and T-LoCoH is shown in Figure 3.1 (based on a single herd followed during this study). Despite the extensive debate regarding spatial and/or temporal autocorrelation in high frequency GPS telemetry[254], it has been shown that serial autocorrelation had no negative influence on home range estimation with KDE, and in some cases even improved it[289]. As long as a constant recording frequency is employed, the effect of autocorrelated data on home range analysis could even be positive, rather than negative, especially since biological significance might be sacrificed when sub-sampling high frequency data to achieve statistical independence[290].

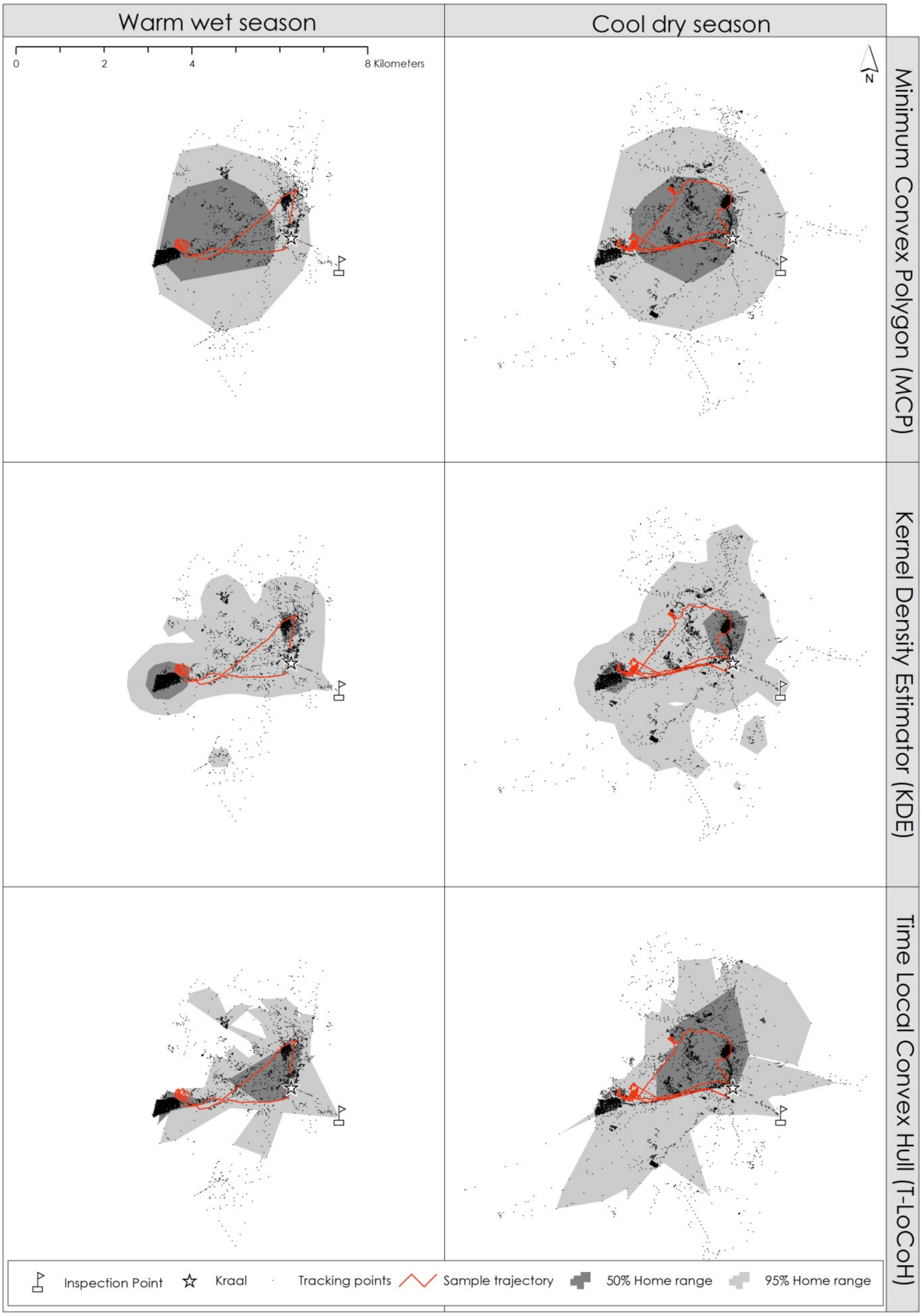

Figure 3.1 Comparison of two classic methods (minimum convex polygon and kernel density estimator) to time-based local convex hull method for home range estimation on the same dataset

Over the past fifteen years a large degree of development occurred in the field of species distribution modelling (SDM, also referred to as habitat suitability models)[291,292], with a variety of different techniques gaining popularity, and their statistical application being scrutinized[293-297]. Habitat suitability models are in many respects similar to the resource selection function (RSF)[291,298]. It is important to differentiate the rather general term SDM into those models that strictly predict the species distribution[291,299], and those that predict the ecological niche (ENM) of the species[300], despite an ongoing debate on semantics[292,299]. To start, ENM consists of four major components: the *fundamental niche* (i.e. all conditions in the environment of a species that determines its survival, including biotic, abiotic and mobility factors), the *realised niche* (i.e. the subset of the fundamental niche that the species actually occupies)[301], and the *potential niche* (i.e. the subset of the environment that the fundamental niche occupies)[299]. The realised niche can also be limited by historical, abiotic, biotic or anthropogenic elements, which then results in the fourth component, the *occupied niche*[302], which is the actual distribution of the species. It is very important to interpret any ENM in the context of which niche it produces as an output[299]. Adding true absence data to a SDM model produces the occupied niche, probably best defining a SDM in the strict sense of the word, although very few studies on mammals have true absence data available. On the other hand, using incomplete absence data, various pseudo-absence datasets or just presence-only data generally produces the realised niche[299]. This realised niche should however always be interpreted with caution and only within the context of the study area and predictor variables used[292]. When a study area is well-chosen and the quality of predictor variables good, the realised niche starts to approximate the fundamental niche[294]. Habitat suitability, based on ENM, is therefore actually a subjective interpretation of the ENM[299], and can only be considered a SDM when it includes some steps to transform the potential or realised niche into the occupied niche, such as incorporation of areas of exclusion[292]. Fundamental assumptions of presence-only models, such as maximum entropy modelling (maxent), are that either a random or representative sample is taken and that the detection probability is constant across the landscape[297]. Furthermore, presence data is dependent on three probabilities: the probability of a site being sampled, the probability that the species occupied the site at the time of sampling, and the probability that the species was actually seen during the sampling[297]. It is therefore important to correct for any possible sampling bias, by selecting background data (pseudo-absence), for example, with the same sampling bias as the presence data[303]. The attraction of SDMs lies in their outputs being continuous in space, hence making them more useful for visualisation and management applications[304]. ENMs are however prone to overfitting[305], which could be countered by proper pre-selection of predictor variables or by removing redundant correlated information (although this could also come at the cost of under-informing the model)[292]. Nevertheless, environmental variables should be chosen through sound ecological reasoning, rather than purely on technical merit[306,307]. When interpreting a predictor variable's importance, it is crucial to keep in mind that the true influence of that variable might fall outside the scale/extent of the model and/or that its variability at the scale/extent of the model might not be a true reflection of its variability at a larger scale[308,309]. Perhaps Yackulic et al.[297] sum it up best: '*All maps are partial truths*…'.

Livestock biomass across large scales has been found to have strong associations with rainfall, human population and cultivation[217,226,310]. Yet, most livestock distribution studies to date have been at a rather course resolution (~25km^2) for continental-scale applications[217,311], with no distribution studies at a finer resolution (i.e. <1km^2) to allow localised spatial risk modelling. A number of studies on the mobility of pastoral and communal cattle has been done in Africa, mostly in west and east Africa[261,262,312-322], with only a few in southern Africa[263,288,323,324].

In this chapter we investigate the movement patterns and home range of a number of communal and smallholder cattle herds in the vicinity of the KNP and APNR, and assess the influence of both man-made and natural factors on their distribution patterns and habitat suitability. A better understanding of these attributes and reliable distribution models could be invaluable as a basis for spatio-temporal risk modelling in this very important agricultural zone at the wildlife-livestock interface in South Africa.

Materials and Methods

Study area

The study was conducted in four study sites along the western boundary of the Kruger National Park (KNP) in South Africa (*Figure 3.2*). These sites have been described in more detail elsewhere (Chapter 2). Smallholder sites were located inside the central study site.

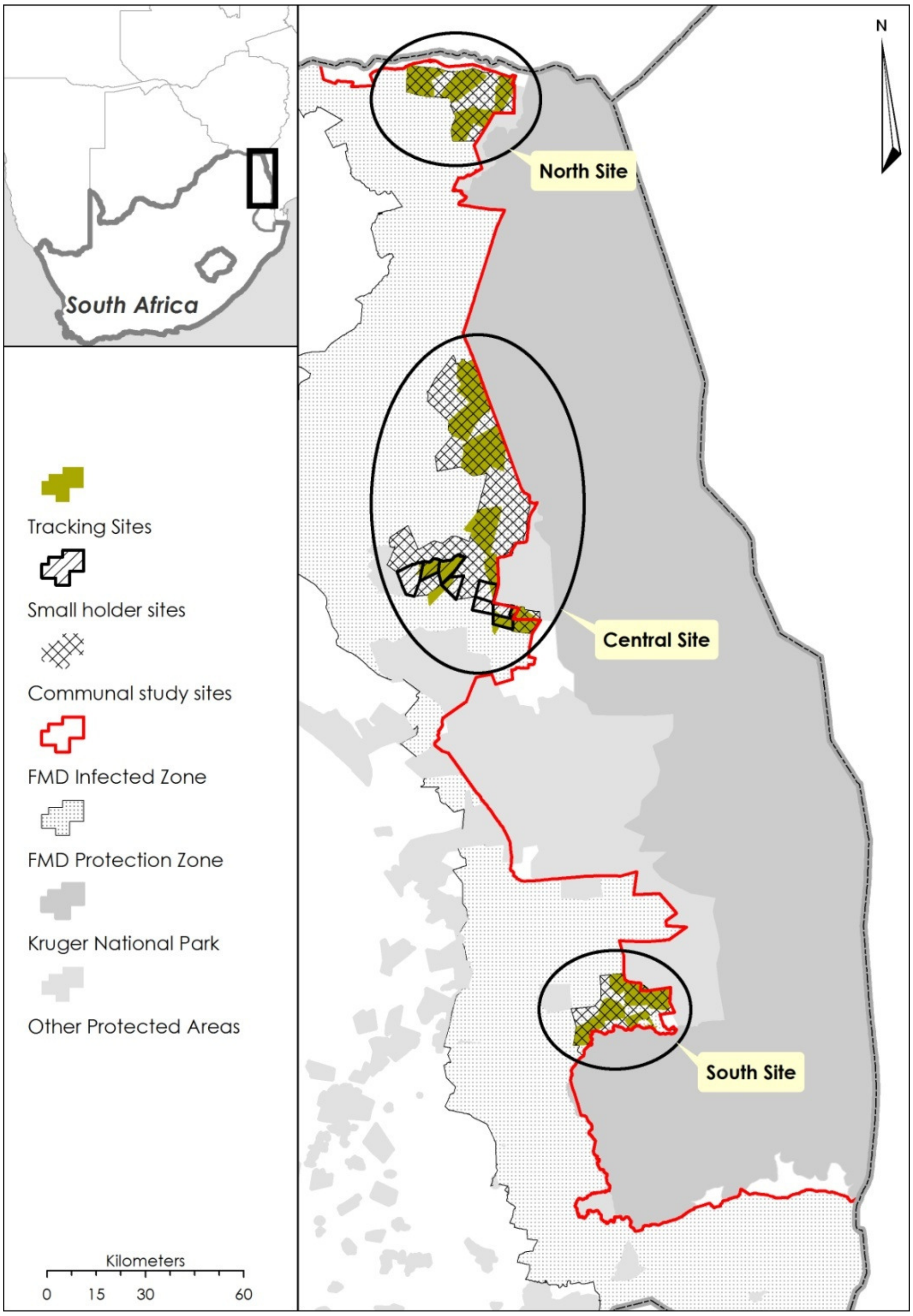

Figure 3.2. Study sites in relation to the Kruger National Park and adjoining private and provincial nature reserves. Areas where cattle tracking occurred are shown in solid green (see Chapter 2)

Selection of cattle tracking inspection points

To record a representative sample of cattle movement data across each of the study areas, we conducted a hierarchical cluster analysis on dissimilarities structure ('hclust' function of the R 'stats' package)[206] on a subset of attribute data of FMD inspection points (IPs) in the four study sites using Ward's agglomeration method[325]. This was used as a guideline to select IPs, while logistical constraints also had to be taken into consideration. These attributes considered were:

- proximity to
    - perennial rivers[197]
    - non-perennial rivers[197]
    - surface water[197]
    - game reserves[326]
- the proportion of land cover[205] surrounding each IP that was considered
    - to have high grazing potential,
    - low grazing potential or
    - that was under subsistence cultivation (see Chapter 2 for aggregation and reclassification of land cover data),
- the number of cattle at the IP (see Chapter 2)
- the number of cattle owners at the IP (see Chapter 2)
- the farm management system at the IP (smallholder versus communal).

Collection of cattle movement data

In the southern study area (South site), handheld Global Positioning System (GPS) devices (eTrex H, Garmin, Kansas City, United States of America, www.garmin.com) were carried by herdsmen of the selected IPs while tending to their cattle. Each GPS was set to record an automatic track log of points with a frequency of five minutes. After consultation with the whole group of farmers/herdsmen at each of the six selected IPs, herdsmen to participate in the study were selected on a voluntary basis. The aim at each IP was to use herdsmen that generally did not graze their cattle in the same areas. Each herdsman was given a practical demonstration of the GPS to ensure they could record a track (only required to switch GPS on and off) and change the batteries daily (rechargeable; Figure 3.3).

Each GPS was shared by three herdsmen, with it being rotated between them on a weekly basis. Depending on the number of owners at each IP, one or two devices were deployed per IP (i.e. 3-6 herdsmen per IP). During the fourth week of every month, the GPSs were retrieved and their track logs downloaded[327]. Herdsmen were asked to track their grazing movements at least three days per week, i.e. for each herdsman a minimum of three grazing tracks were recorded per month. In this study area, all cattle were kraaled every night and therefore tracks were recorded from the moment the cattle left the kraal until they returned. A total of 29 herdsmen took part in the study that was conducted between 24 June 2008 and 30 September 2009 (463 days).

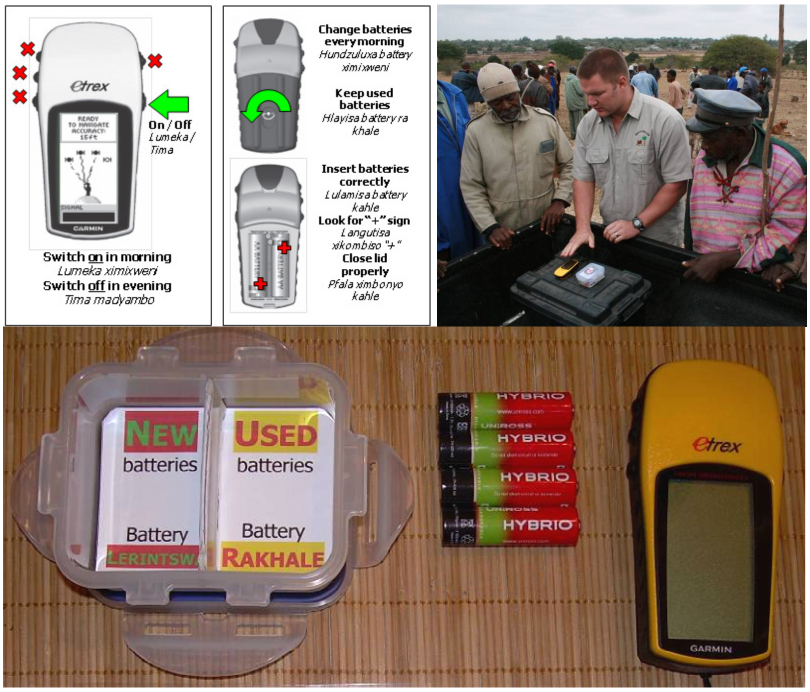

Figure 3.3 Equipment and instructions provided in the South site for handheld GPS tracking

Data derived from these GPSs required systematic cleaning to remove human (e.g. forgetting to switch off the GPS upon returning home in the evening, accidentally switching it on at night, switching it on while in a car, etc.) and GPS error (e.g erroneous dates or projection). This was achieved by filtering out:

- tracks with dates falling outside the study period,
- tracks outside the study area,
- points recorded between one hour after sunset and one hour before sunrise (to remove points when the GPS was accidentally left on during the night),
- points where more than twenty consecutive points fell within a six metre radius (i.e. static) in an urban area[205] - this was generally due to a GPS left switched on after returning home (during the day), and
- points exceeding twenty kilometres per hour.

For the habitat suitability analysis, handheld GPS data were filtered to 15 minute frequency, in order to match the data from the other study areas and avoid introducing sampling effort bias.

In the northern (North site) and central study areas (Central site), the latter including some smallholder farms (Smallholder site), 14 GPS/GSM collars (HOTStock-M4-4H-7b-Primary collar, HOTGROUP, Pretoria, South Africa, www.hotgroup.co.za) were fitted to cattle (Figure 3.4). The collars automatically downloaded data via the cellular network to a web-accessible data repository from where the data was manually retrieved in Microsoft Excel format (Microsoft Corporation, 2007).

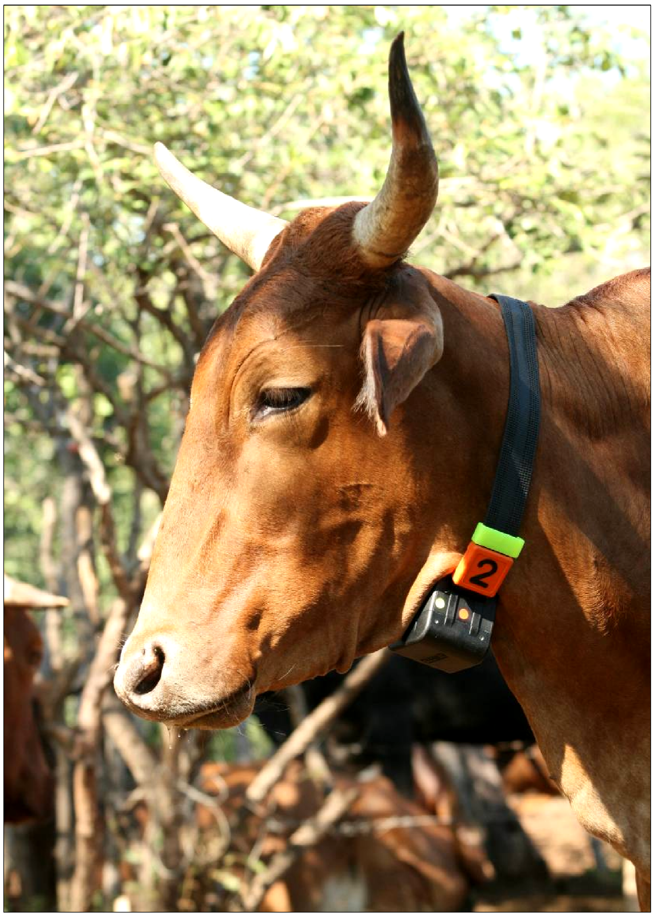

Figure 3.4 A cow with one of the GPS/GSM collars used during the study

Herdsmen at each pre-selected IP were chosen to partake in the study in a similar fashion to the handheld GPS study in the South (see earlier, North=4, Central=6, Smallholder=4). With prior consent from the owner, a collar was placed on one animal in each herd, since it has been shown that the individual's grazing behaviour is generally a good representation of the herd average (within 15%)[328], although some between-individual variation could be sacrificed[329]. Collars had a very simple mechanism for attachment and adjustment around the neck, which included a mechanism for self-release if the collar got stuck onto something (e.g. bush, fence, animal's front leg). Each owner and/or herdsman was given a practical demonstration of the collar mechanism to ensure they could fix minor problems that might cause discomfort to the animal and to prevent loss of the collar. Mature animals that were likely to graze with the larger herd were preferred, which involved input from the herdsman.

The majority of the animals selected were mature cows, preferably with horns to further secure the collar to the animal.

In the event of collar failure or loss, collars were replaced. Each collar was set to record a location every 15 minutes and download data to the web server after every five attempts at location fixes. When a location fix could not be attained, which is a well-documented phenomenon[313,330-333], it was recorded as such by the collar. The maximum GPS inaccuracy allowed was set to 255m. In the event of no cellular network coverage, collars stored the data internally. At the above settings, collars were able to store up to 52 days' data. Data recorded by the collars included: date and time (with time zone information), location (latitude/longtitude), whether a location fix was attained, altitude, heading, the time it took to locate satellites, the number of satellites used in calculating the position, GPS accuracy, activity (measured through a single captive-ball tilt sensor and reported at an arbitrary scale between 0 and 31, zero being no activity). The study occurred between 25 March 2009 and 14 July 2010 (476 days).

Two main seasons were defined[334,335], each subdivided where higher temporal resolution was required (e.g. utilisation of cultivated land): cool dry season (April – September), sub-divided to the early dry season (April – June) and late dry season (July – September) as well as the warm wet season (October – March), sub-divided to the early wet season (October – December) and late wet season (January – March).

Preparation of individual trajectories

Individual herdsmen's kraal locations for each of the collars and GPSs were accurately recorded. For each tracking point, the distance to its associated kraal was calculated and any tracking points within fifty meters of the kraal were deemed to be 'kraal-associated'.

Since all cattle returned to the kraal on a daily basis in the South site, each day's tracking data per GPS was classified as a unique trajectory. With the GPS collars, however, unique trajectories had to be derived from the animals' movements. For each collar, sequential points were analysed and a new trajectory was defined when 1) two tracking points were more than three hours apart, or 2) the animal visited the kraal (<50m) for at least two hours, or 3) the trajectory reached seven days in length without a kraal visit (<50m). The latter was especially to deal with smallholder cattle and cattle in the North site, where these animals were often left to graze without kraaling for extended periods. However, all the study sites fell inside the FMD inspection zone where weekly inspection of cattle occurred, so it was therefore known that the animals were collected at least once per week (hence the cut-off).

For collars, missing points in trajectories (determined by time frequency) were linearly interpolated. Individual collar trajectories with more than 50% interpolated points were discarded. Since the handheld GPSs were switched on and off manually and produced a negligible amount of no location fixes, no interpolation of missing location data was done for them. Spurious trajectories of less than one hour in duration were also discarded.

For each unique trajectory as defined above, the 'as.ltraj' function in the 'adehabitatLT' package[306] of the R statistical software[206] was used to calculate its movement parameters between consecutive points[336] for more detail on the 'ltraj' data class. This included 1) displacement from previous point, 2) speed, 3) displacement from the origin, as well as 4) absolute and 5) relative (to previous point) direction of movement.

Behavioural state classification

The behavioural mode of each GPS fix was determined by using a k-means cluster analysis[337-339]. The three most likely clusters of the combination: speed, relative direction of movement (absolute value and normalised) and activity (according to the activity sensor; log-transformed and normalised) were determined for data from GPS/GSM collars (i.e. the South site was excluded from this analysis). Furthermore, only non-interpolated data with a location fix were used in this analysis. The clusters were renamed as 'Resting', 'Grazing' and 'Walking' after visual inspection of classified points, especially those that were kraal-associated and most likely belonging to the 'Resting' class, whilst 'Walking' very often occurred along roads.

Trajectory analysis

For each retained trajectory, the following variables were derived (again, excluding kraal-associated data):

- start time
- end time
- duration of trajectory (h; end time minus start time)
- total length (km) of the trajectory
- maximum distance from the kraal (km)
- maximum distance from an urban area (km)
- maximum distance from any known water source
- proportion of time spent in subsistence cultivation areas

Home range analysis

The T-LoCoH method was chosen to conduct HR analyses[340] in this study, and implemented through the R package 'tlocoh'[276]. The time-scaled distance metric (s) term was inspected with the help of the 'lxy.plot.sfinder' function (using 3, 4, 8, 12 and 24h alternatives), and fixed at 0.01. The minimum adaptive (*a*) parameter was automatically calculated with the 'auto.a' function for the 16 nearest neighbours of 95% of the points. The adaptive method is particularly useful when data contains very dense and very sparse areas, and avoids overestimation of utilisation distributions because of these sparse areas. The 0.50 (50% home range / core) and 0.95 (95% home range / home range) isopleths were then calculated for each unique kraal and the area of its enclosing polygon calculated.

Statistical representations and comparisons

Due to the large number of outliers in the data set, central tendency is reported as the median, followed by the inter-quartile range in square brackets, unless otherwise specified. Likewise, comparison between two groups (e.g seasons) was done with the Mann-Whitney-Wilcoxon rank sum (MWW) test, for which the W statistic and p-value are reported. In the case of comparison between more than two groups (e.g. comparison between study sites), the Kruskal-Wallis rank sum test (KW) was used, for which the Chi-squared statistic (χ^2), degrees of freedom (df) and p-value are reported. A KW post-hoc multiple comparison test (KWMC) at the 0.01, 0.05 and 0.10 significance levels using 'kruskalmc' function from the 'pgirmess' R package[341] was also done for pair-wise comparisons between multiple groups, and the p-value reported. P-values are given directly, except when smaller than 0.001. In the case of KWMC, since the test is done for specific significance levels (0.1, 0.05 and 0.01), the lowest p-value is reported in the case of a difference between pairs.

Where box-and-whisker plots are used ('ggplot2' package in R)[342], the midline represents the median, the upper and lower margins of the 'box' represents the quartiles, whilst the 'arms' represent the upper and lower ends of the 95% distribution and the dots are outliers.

Habitat suitability

Maximum entropy modelling (maxent) was used to estimate habitat suitability from the cattle tracking data[295,301]. Maxent is considered one of the best-performing SDM techniques[343,344] and is equivalent to Poisson regression[345]. Modelling was implemented using the 'maxent' function of the 'dismo' package in R[346], using ten-fold cross-validation[347], and allowing it to iterate up to 500 times to approach convergence with the 'auto features' setting selected. As presence data, all tracking points that were not kraal-associated were used as inputs. The context of presence data is very important in defining habitat selection or preference. For example, one might make the mistake of interpreting a presence location as a site being 'selected' by the animal, whilst in fact it might just be 'in transit' through that particular site[348]. In this study, the interest lies in probability of a pixel being suitable for cattle, regardless of why it is there, since we would eventually like to model the presence of cattle in conjunction with other species (buffaloes in this case). The assumption that occupancy equates to selection or habitat quality is therefore not made here.

The boundaries of the three study sites were used as a sampling bias mask for the selection of random background points[295,303,349]. To avoid low prevalence estimates and possible misinterpretation of model performance[350], equal numbers of random background points to tracking points for each study site were created and assigned random dates within the date range of that study site's tracking data. These dates were used to obtain actual NDVI and LST data in a similar fashion as for the tracking data. Available predictor variables are listed in (Table 3.1) and were prepared as described in Chapter 3 at the same resolution as the MODIS-derived data (269.63m x 269.63m). It is recommended that the resolution for maxent analyses is kept as fine as possible when a large amount of presence data is used[351].

A multivariate environmental similarity surface (MESS)[352] based on the presence data (see above) was created for each potential predictor across the broader study region where cattle could be found[348]. For each potential predictor's MESS layer, the percentage of area that had positive MESS values was calculated. Only predictors with more than 85% of their pixels containing positive MESS values (arbitrary), were retained for modelling. Despite maxent being more adept at handling correlation between predictor variables than other models (e.g. stepwise regression)[295], multicollinearity (measured by variance inflation factor or VIF)[353] was tested between all the predictor variables, using the 'vif' function of the 'usdm' R package[354]. This function determines the coefficient of determination (R^2) by regressing each predictor variable against all the others. A R^2 value of 0 equates to a VIF of 1. As R^2 approaches 1, VIF approaches infinity. When the VIF is more than 10, multicollinearity is considered undesirably high, and removal of the variable should be considered[353].

Outputs of habitat suitability modelling were mapped using ArcGIS 10.0[355].

Table 3.1 Predictor variables submitted to multivariate environmental similarity surface (MESS) evaluation. Variables in bold were retained for modelling. A column showing the variance inflation factor (VIF) for each variable is added, as well as a column with VIF after variable selection (VIF-2).

Predictor	**MESS>0**	**VIF**	**VIF-2**	**Description**	Reference
LandCoverRecl	100%	NA	NA	Reclassification of LandCover (MESS not applicable to factors - Calculated as area under land cover classes represented in presence data)	205,263
AllPermWaterDist	99.85%	7.86	1.04	Euclidean distance (m) from any perennial water source (rivers/dams/etc.)	197,256,263
NDVI	99.47%	Inf	4.45	Normalised difference vegetation index - Actual values at most recent date in dataset	203,356
urband	98.83%	1.88	1.26	Euclidean distance from urban areas derived from LandCover	205,357
Slope	93.73%	2.01	1.67	Slope (degrees) calculated from DEM	213,256
NDVIMean	90.82%	9.88	15.73	10 year mean NDVI for period 2001-2010	203,356
Isothermality	89.07%	33.84	1.21	Mean diurnal range divided by the annual temperature range	214,256
LST	88.65%	6.49	3.25	Land Surface Temperature (Celsius) - Actual values at most recent date in dataset	203,256
NDVIMax	88.03%	6.42	10.18	10 year maximum NDVI for period 2001-2010	203,356
AllSeasWaterDist	85.66%	4.36	1.76	Euclidean distance (m) from any non-perennial water source (rivers)	197,256,263
PrecipSeasonality	84.54%	29.86		Also called the coefficient of variation - standard deviation of monthly precipitation estimates expressed as a percentage of the annual mean precipitation	214,358
MeanTempColdQ	80.29%	5576.32		Mean temperature of the coldest quarter of the year (Celsius x 10)	214,256
PrecipDryQ	80.25%	25.80		Total precipitation of the driest quarter of the year (mm)	214,358
LandCover	74.02%	NA		(MESS not applicable to factors - Calculated as area under land cover classes represented in presence data)	197,263
MeanTemp	73.23%	3796.15		Annual mean temperature (Celsius x 10)	214,256
MeanTempWarmtQ	68.42%	2551.33		Mean temperature of the warmest quarter of the year (Celsius x 10)	214,256
MeanDiurnalRange	65.79%	19.50		Mean diurnal temperature range (the difference between the monthly maximum and minimum temperatures) (Celsius x 10)	214,256
Precipitation	65.46%	432.03		Annual total precipitation (mm)	214,358
DEM	58.30%	3.6		Elevation (m) derived from 30m Digital Elevation Model	213,217,256
PrecipWetQ	55.79%	345.50		Total precipitation of the wettest quarter of the year (mm)	214,358
TempSeasonality	54.42%	522.55		Temperature coefficient of variation - standard deviation of the monthly mean temperatures expressed as a percentage of the annual mean. Degrees Kelvin is used to avoid dividing by zero.	256

The receiver operating curve (ROC) was determined, and the area under the curve (AUC) used to assess model performance[295], with values above 0.7 considered acceptable by some[359]. It is however important to note that the maxent ROC curve is not based on the classification of presence vs. absence values, as is the norm, but rather presence vs. background (which could be absence or not), and that proper quality thresholds have not been estimated for this particular case of AUC[297]. Maxent outputs can be reported as an actual raw value (approximation of detection density per pixel) or as a logistic value on a continuous scale from zero to one, one being the highest probability of presence according to the model[344]. However, this logistic occurrence probability is not an absolute value, but rather a relative one in the case of maxent, since the constant of proportionality is unknown and is automatically set to 0.5 by maxent, which is a critical assumption to keep in consideration[295,360]. Although there has been criticism of maxent's logistic output[297], we report it here, since it gives an approximation of conditional probability of occurrence, which is important for further use of these outputs in contact risk mapping (see Chapter 5)

A model was run for the entire study period (i.e. whole year's conditions considered), as well as a model for each of the two main seasons, sub-setting tracking and background data accordingly. AUC, variable contribution and jackknife values for the influence of each variable on the model AUC are reported, as well as response curves of the variables.

Results

Selection of tracking areas

Figure 3.5 shows the IPs selected for tracking after considering both the hierarchical cluster analysis and logistical constraints. Ten groups were retained in the selected IPs.

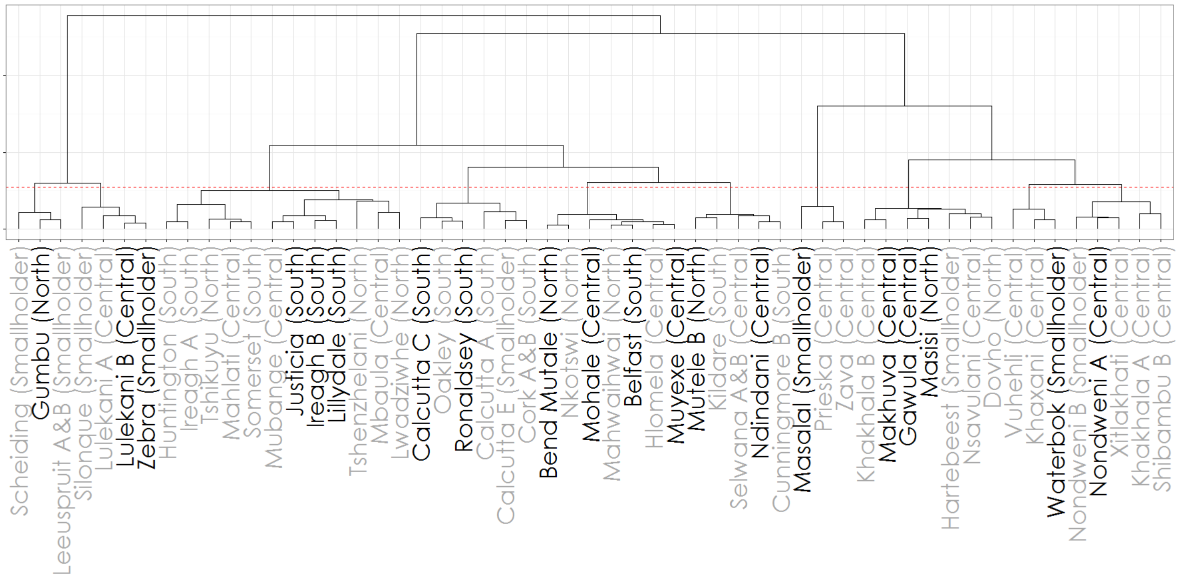

Figure 3.5 Dendrogram of hierarchical cluster analysis to select inspection points (IPs) for tracking. Names in black indicate selected IPs, with their respective study sites in brackets.

Telemetry

Five handheld GPS units were replaced during the study due to malfunctioning (n=3), being lost in the field (n=1) or as a result of theft (n=1). Thirteen replacements of GPS/GSM collars were made during the study due to hardware failure (mainly battery, n=11), collar loss (fell off animal, n=1) and stock theft (n=1). Overall GPS accuracy attained, was 4m [3 – 7m].

Apart from the Smallholder site, which is by definition not associated with urban areas, kraals used during this tracking study mostly fell inside a village or within 1km from it (mean: 206m; 95% within 1km from a village).

Table 3.2 summarises the grazing trajectories recorded during the study.

Table 3.2. Summary of grazing trajectories recorded during the study.

Study site	IPs	Kraals	Start	End	Number of trajectories recorded	GPS fix rate	Total hours recorded* (h)	Total distance covered* (km)
North	4	4	2009-05-05	2010-03-12	378	83.8%	8247.5	3897.7
Central	6	6	2009-03-27	2010-07-14	1294	88.9%	18270.3	12688.45
South	6	29	2008-06-24	2009-09-30	736	NA	4939.7	5816.1
Smallholder	4	4	2009-03-25	2010-02-17	298	89.8%	12387.3	3828.5

*kraal-associated portions of trajectories not included

Behavioural states and daily activity budgets

Tracking data classified as resting, grazing and walking through clustering of speed, relative direction of travel and activity, revealed the daily activity patterns of cattle in the North, Central and Smallholder sites. Figure 3.6 indicates the contribution of three variables to the classification of activities. Speed for each of the states were as follows: walking 1.96km/h [1.48-2.6km/h], grazing 0.18km/h [0.05-0.41km/h] and resting 0.03km/h [0.02-0.07km/h] and for later comparisons, the means were 2.07 km/h, 0.28 km/h, 0.09km/h, respectively. The high relative turning angles seen with resting is explained by the GPS inaccuracy while being stationary, causing spurious turning angles within the radius of this inaccuracy (see earlier GPS inaccuracy measures)[361].

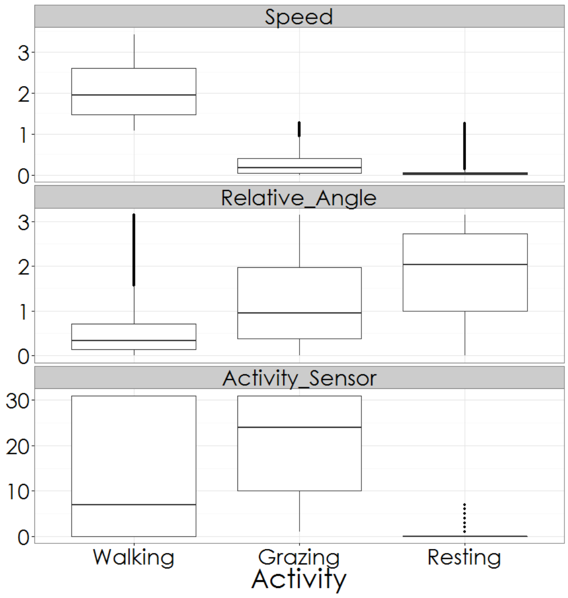

Figure 3.6 Values of the three parameters used to assess the behavioural state of the GPS collared animals after k-means cluster classification

Figure 3.7 depicts the density of the various activities as a function of the time of day, and clearly shows the tendency to become active in the early morning and late afternoon, with virtually no walking during the midday. Grazing was most intense from mid-morning to mid-afternoon, with decreased intensity over the midday, when resting increased. During the cool dry season in the North site, grazing was more intense during the afternoons than the mornings. In the Central site, on the other hand, the animals appear to spend more time grazing in the morning, likely away from the kraal, followed by a more intense walking period in the late afternoon, probably returning to the kraal (also see Figure 3.10). As expected, most resting occurs during the night and over midday.

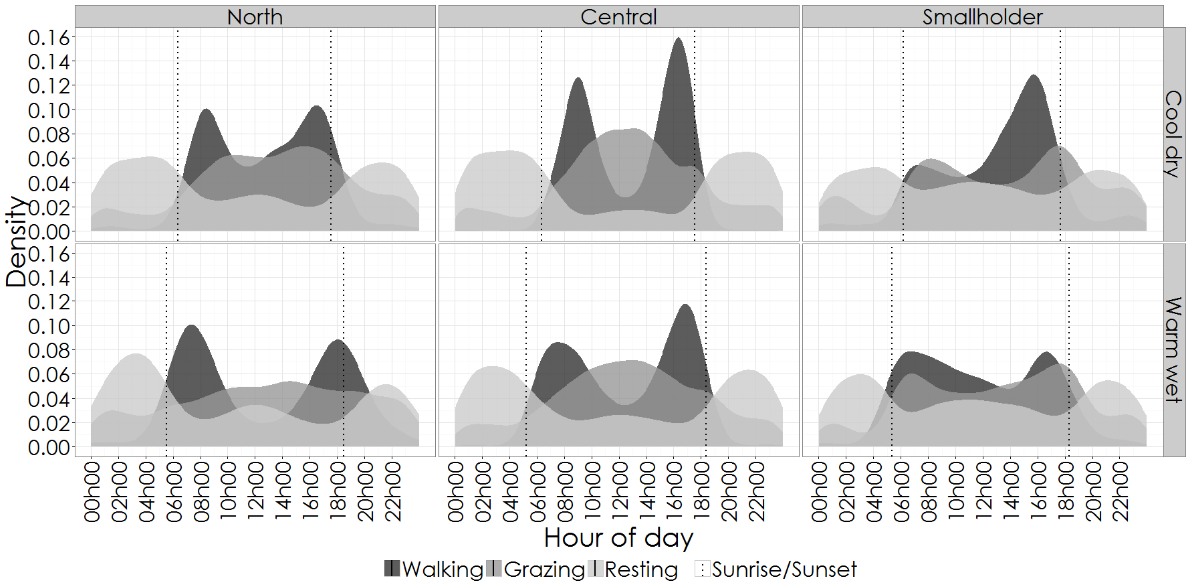

Figure 3.7 Daily activity patters of cattle in the North, Central and Smallholder sites in relation to sunrise and sunset

Median daily activity budgets for GPS collared cattle are shown in Table 3.3. These figures exclude kraal-associated data.

Table 3.3 Activity budgets for the various study sites and seasons (note that the median and inter-quartile range is used, so the figures might not sum to 100%). Kraal-associated data is excluded.

Study Area	**Season**	**Walking**	**Grazing**	**Resting**
North	Cool dry	16.54% [9.09-24.21%]	56.48% [33.33-75.00%]	18.72% [0.00-46.00%]
	Warm wet	11.58% [4.88-17.17%]	72.58% [61.11-82.24%]	10.98% [4.88-23.88%]
Central	Cool dry	19.35% [10.53-33.33%]	64.19% [26.09-80.65%]	7.69% [0.00-37.12%]
	Warm wet	18.18% [8.53-33.33%]	44.44% [0.00-75.38%]	19.56% [4.79-72.47%]
Smallholder	Cool dry	11.11% [6.67-16.67%]	2.86% [0.00-67.48%]	75.00% [14.29-89.65%]
	Warm wet	8.38% [3.49-11.68%]	54.31% [1.27-69.78%]	36.25% [21.24-85.10%]

Trajectory duration and length

Table 3.4 summarises the time at which trajectories started from their respective kraals and ended (upon return to the kraal). Grazing trajectory start and end times varied considerably in the North and Smallholder sites, where kraaling did not occur every night, whilst it was more concentrated in the South and Central sites. In the Central site, where the routine was most consistent, grazing trajectories normally started around 1.5h after sunrise and ended close to sunset, compared to the South site, where herding started about 2h after sunrise in the cool dry season, and only 3.5h after sunrise in the warm wet season, on average. In the North and Smallholder sites there seemed to be no consistent routine, most likely due to the longer trajectory durations (>1 day, see below).

Table 3.4. Summary of grazing trajectory start and end times in relation to sunrise/sunset.

Study site	Season	Start	Sunrise	End	Sunset
North	Cool dry	08h48 [07h34-11h06]	06h23	16h34 [11h04-17h49]	17h32
	Warm wet	07h02 [06h17-10h26]	05h31	17h32 [06h51-18h55]	18h28
Central	Cool dry	07h53 [07h08-08h34]	06h20	17h23 [16h40-17h53]	17h33
	Warm wet	06h53 [05h28-08h01]	05h12	18h07 [17h13-18h38]	18h23
South	Cool dry	08h17 [07h10-11h13]	06h18	17h08 [16h24-17h34]	17h33
	Warm wet	08h44 [06h51-12h56]	05h19	17h39 [15h39-18h23]	18h25
Smallholder	Cool dry	11h48 [06h48-14h55]	06h11	13h19 [08h03-19h17]	17h41
	Warm wet	09h42 [05h33-17h18]	05h20	17h03 [09h28-21h08]	18h20

The duration of trajectories differed significantly between study sites (χ^2=363.04, df=3, p<0.001). The general pattern was however similar between the North (11.0h [7.5 - 30.5h]) and Smallholder study areas (12.3h [5.8 - 48.0h]), and likewise for the Central (9.8h [8.5 - 11.4h]) and South sites (7.1h [3.2 - 9.5h]), although the latter two sites still differed significantly (KWMC: p=0.01). Figure 3.8 depicts trajectory duration between study sites and seasons. During the warm wet season, 75% of trajectories in the Smallholder site were longer than 3.5 days in duration and a similar fraction of the trajectories in the North site were longer than 1.5 days (Figure 3.8). In the Central site however, less than 5% of trajectories were longer than one day (by definition, trajectories in the South site were never longer than 24h). Across seasons, trajectory duration differed significantly too (W=883760, p<0.001). These differences were significant for all study sites (North and Central: p<0.001; Smallholder: p=0.032), except the South.

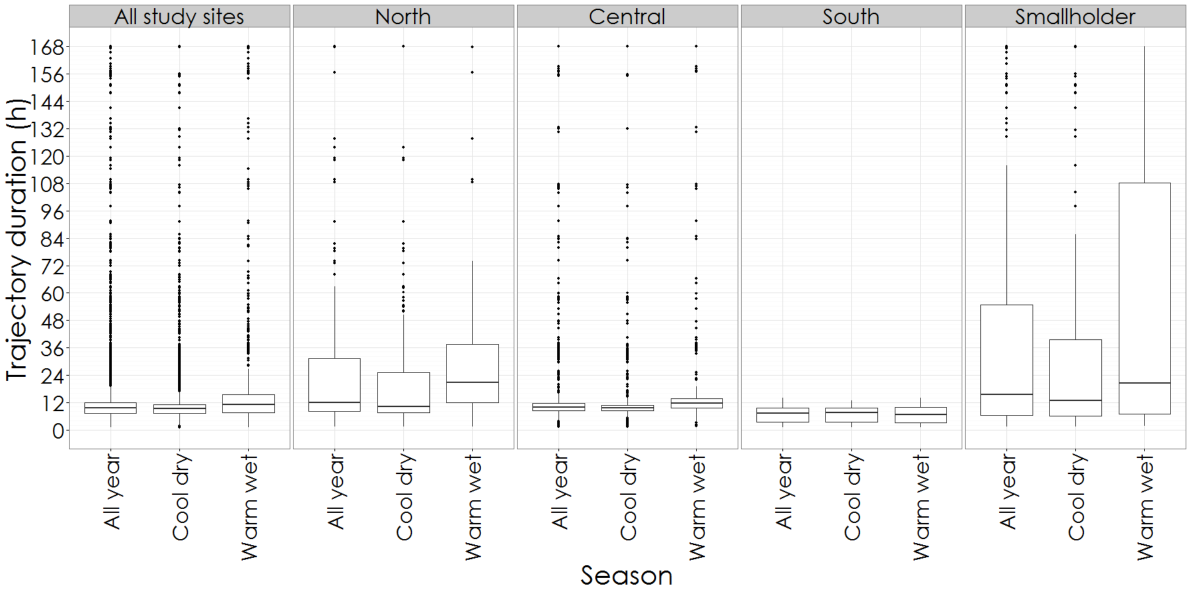

Figure 3.8. Comparison of trajectory duration per study site and season

Similar to trajectory duration, trajectory length (or distance, Figure 3.9) also differed across seasons (W=809417, p<0.001). This was however only signifiant in the North and Central sites. In the North trajectory length was significantly further in the warm wet season (11.20km [4.70 - 18.56km]) compared to the cool dry season (6.53km [3.88 - 10.68km]; W=18395.0, p<0.001). Although significant, the same pattern was much less prominent in the Central area (8.98km [5.72-14.36km] vs. 8.38km [5.22-11.62km]; W=179241.0, p=0.003). Trajectory length also differed across study sites (χ^2=57.600, df=3, p<0.001). During the warm wet season the North (11.20km [4.70 - 18.56km]), Central (8.38km [5.22 - 11.62km]) and Smallholder (5.40km [2.65 - 27.06km]) sites had similar trajectory lengths (KWMC), whilst trajectory lengths in the North and Central sites were significantly longer than in the South (6.99km [3.97 - 10.92km]) (KWMC: p=0.01). During the cool dry season, only the North and South sites had similar trajectory lengths 6.85km [4.22 - 11.15km] and 7.20km [4.57 - 10.35km], respectively), whilst the other sites all differed significantly from each other, here listed in the order of longest to shortest median track lengths: Central (8.54km [5.42 - 11.73km]), South, North and Smallholder (4.80km [1.37 - 13.47km]; KWMC: p=0.01).

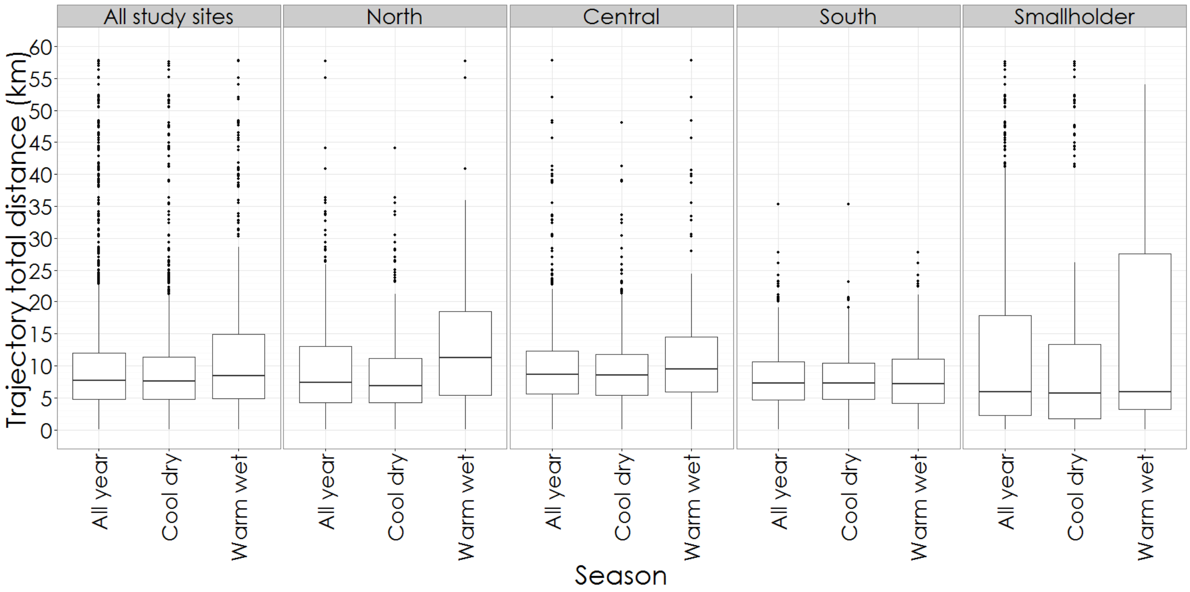

Figure 3.9. Comparison of trajectory length (distance) per study site and season

Grazing radius

Figure 3.10 depicts the average distance cattle were displaced from the kraal during the day. It can be seen that most trajectories started from the kraal.

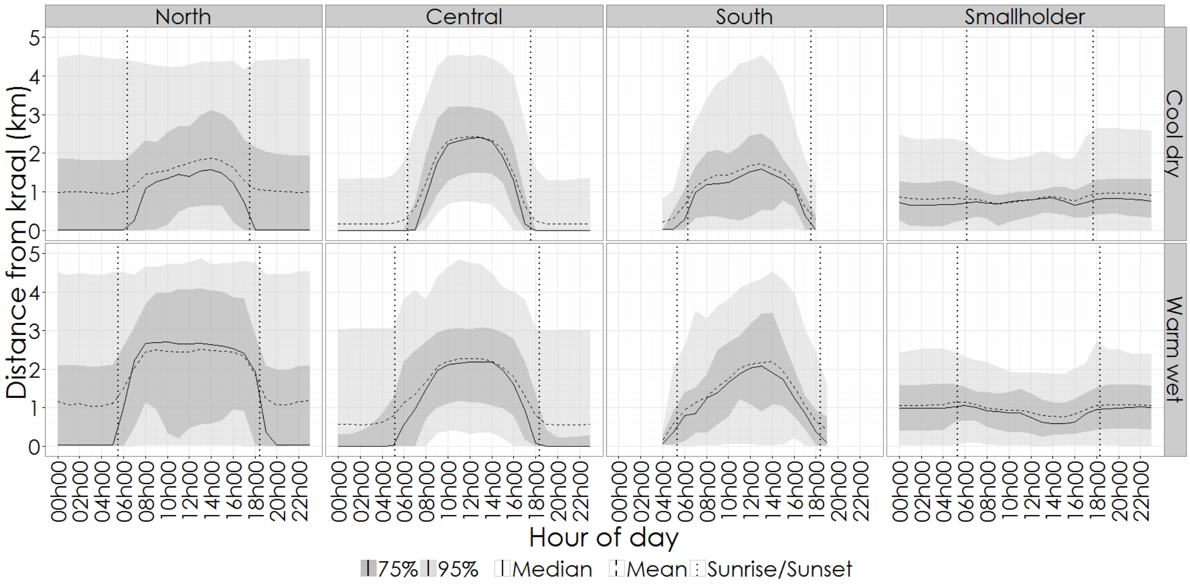

Figure 3.10 Daily patterns of distance from the kraal

The maximum displacement from the kraal that trajectories reached (also called grazing radius), were significantly different across study sites (χ2=351.039, df=3, p<0.001) and are depicted in Figure 3.11, which also compares the grazing radius to the maximum distance the animals were from any urban area during the same grazing trajectory. Only in the North (2.68km [1.70 - 4.64km] vs. 5.53km [3.31 - 6.45km]; W=20748, p<0.001) and Smallholder sites

(1.55km [0.75 - 2.28km] vs. 1.91km [1.30 - 2.23km]; W=11944, p=0.010) did the grazing radius differ between seasons, being further in the warm wet season. Across all seasons, the North and Central sites had similar maximum displacement from the kraal, whilst differences between all other sites were significant (KWMC: p=0.01) and are listed here in descending order: North (3.28km [1.91 - 5.52km]), Central (3.18km [2.02 - 4.85km]), South (2.05km [1.54 - 3.06km]), Smallholder (1.73km [0.93 - 2.27km]).

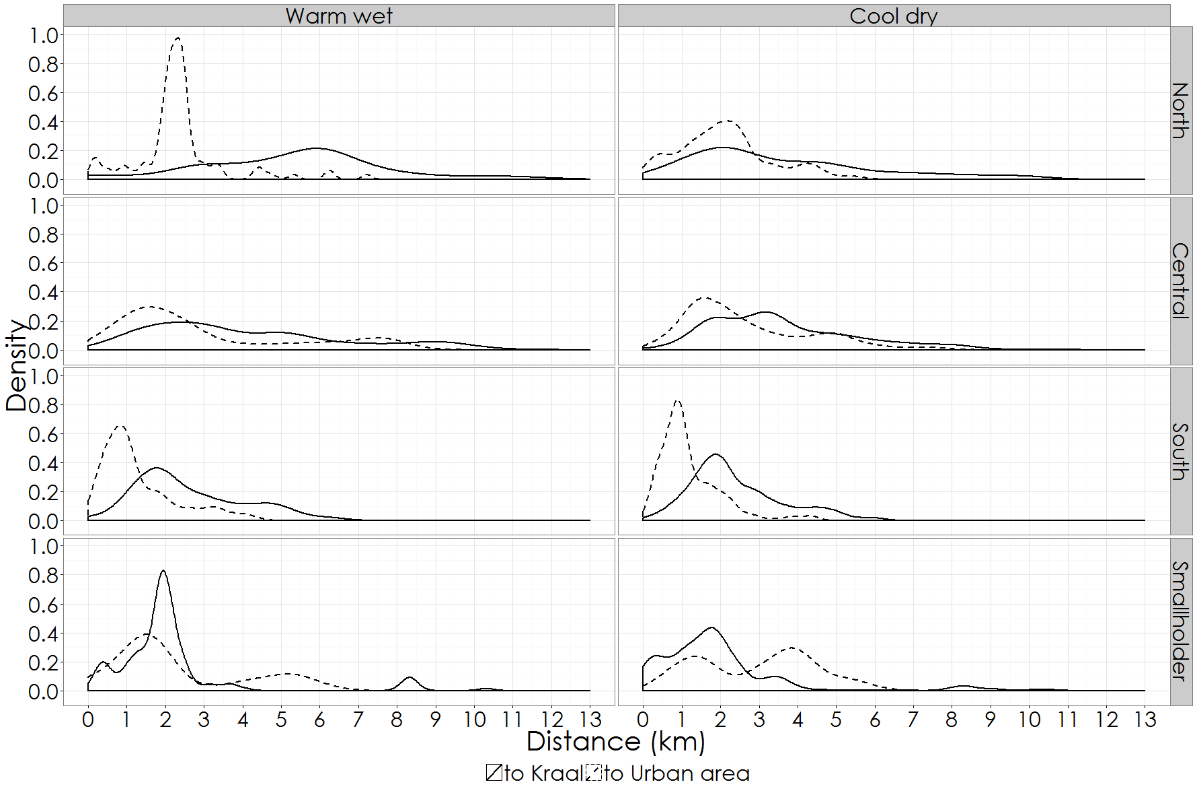

Figure 3.11. Grazing radius (solid line); and nearest urban area (dashed line).

Utilisation of cultivated fields

Since cultivated fields are often used post-harvest as supplementary feed, and since this window can be a few months only, utilisation patterns of cultivated fields were measured against subdivided seasons (see earlier) and are shown in Figure 3.12. Overall, utilisation of cultivated fields during the early dry season was significantly more than any of the other seasons ($\chi^2=41.610$, df=3, p<0.001), being most pronounced in the Central site ($\chi^2=81.094$, df=3, p<0.001). In the South and Smallholder sites, peak use of the cultivated fields only occurred towards the late dry season.

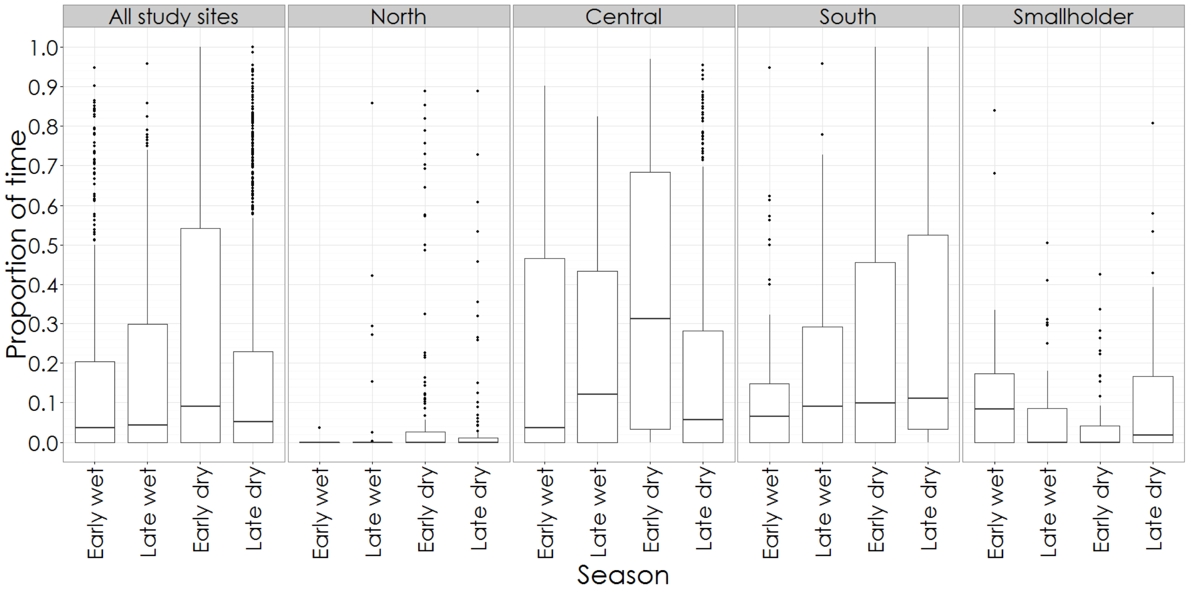

Figure 3.12 Utilisation of cultivated fields during the year

Proximity to water

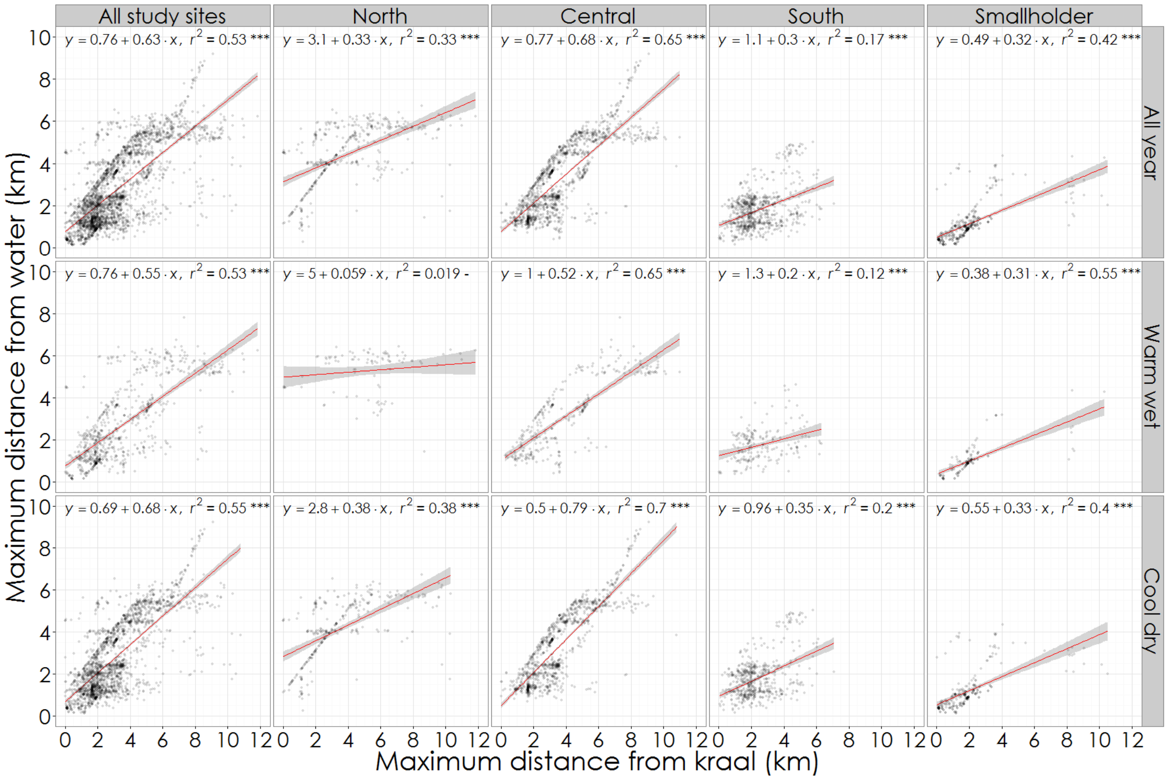

Figure 3.13 Relation between grazing radius and maximum distance from water. Red lines depict the linear model as reported in the top of each graph (grey shading: 95% confidence interval; '***' means $p<0.01$ and '-' means $p>0.1$)

In Figure 3.13 the relationship between the grazing radius and maximum distance from water during a trajectory is depicted as linear functions. All but the warm wet season in the North site had significant correlations between grazing radius and proximity to water.

Table 3.5 Proximity to water for all tracking data (excluding kraal-associated data)

Study site	**Season**	
	Warm wet	**Cool dry**
North	4.24km [3.21 - 5.14km]	3.29km [2.14 - 4.05km]
Central	2.14km [0.99 - 3.16km]	1.63km [0.88 - 3.09km]
South	0.91km [0.47 - 1.46km]	0.89km [0.45 - 1.53km]
Smallholder	0.33km [0.11 - 0.80km]	0.44km [0.22 - 0.82km]

Home range

The T-LoCoH 95% HR across study sites and seasons are depicted in Figure 3.14. Despite the generally larger HR noticeable in the cool dry season, none of these differences were significant within study sites, most likely as a result of the very small sample size. Across study sites, however, home range was smaller in the warm wet season (5.25km^2 [3.59 - 8.35km^2]) compared to the cool dry season (8.12km^2 [4.57 - 12.17km^2]) (W=1238, p=0.013). However, during the cool dry season, the Central site's HR (13.83km^2 [12.14 - 26.29km^2]) were significantly larger than the South (6.95km^2 [4.33 - 9.50km^2]) (KWMC: p=0.05).

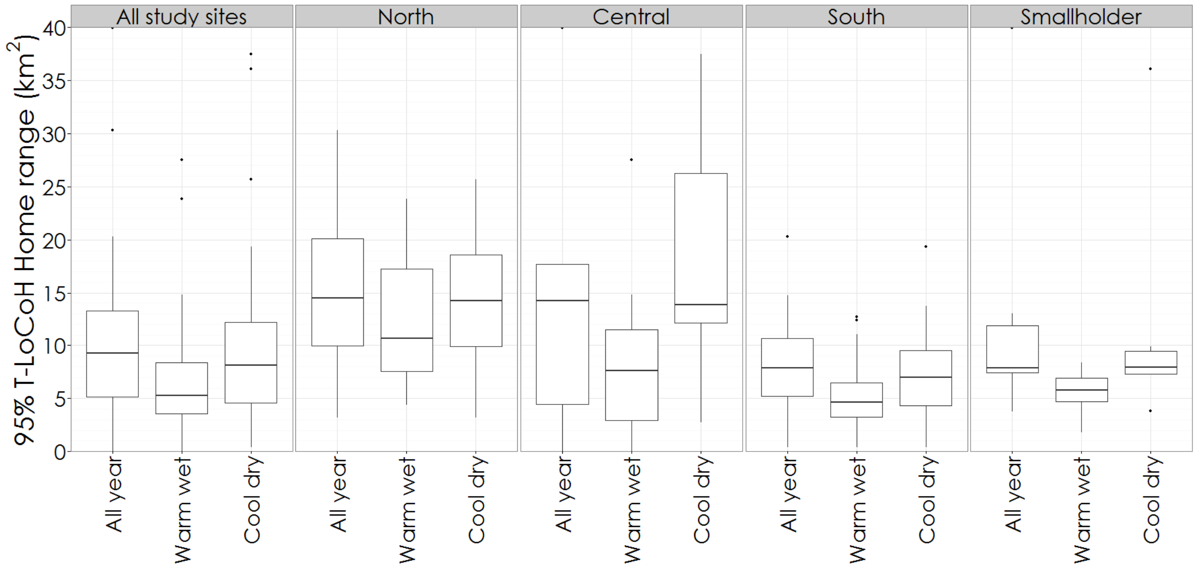

Figure 3.14 The 95% T-LoCoH home range for the various study areas and seasons

Core (50%) HRs for all study sites combined was 2.44km^2 [1.42 – 3.60km2] and there was no significant difference in seasonal core HR across the entire study region or in any one of the study sites (Figure 3.15), although it would seem as if a trend of smaller core HR in the wet season exists in the communal areas. There was also no difference in core HR between study sites.

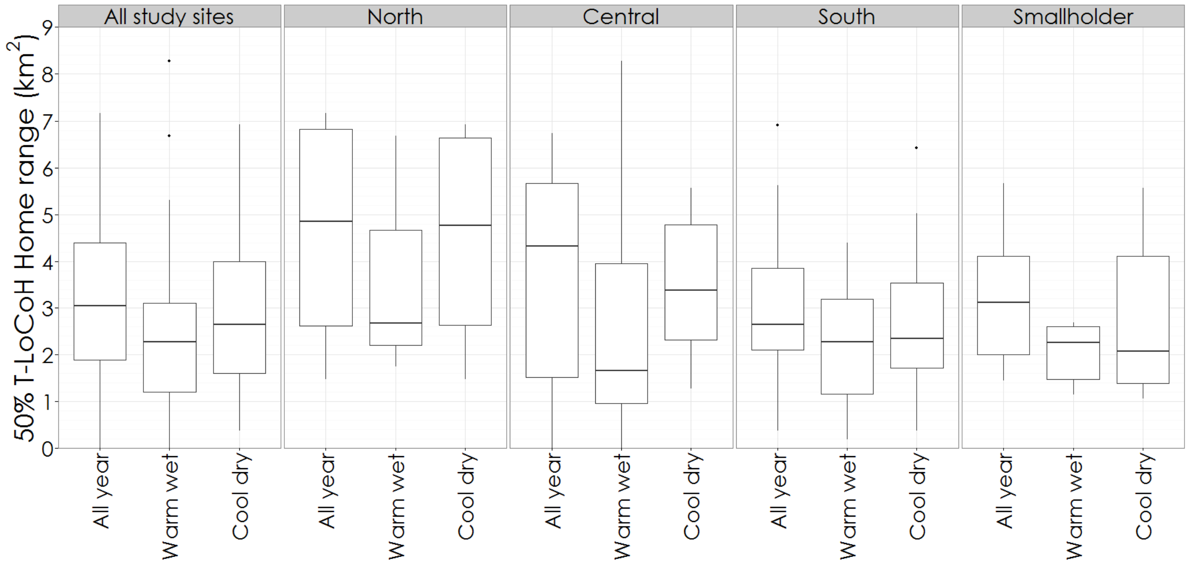

Figure 3.15 The 50% T-LoCoH home range across study sites and seasons

Suitability mapping

Table 3.1 shows the adapted MESS and VIF values for the predictor variables considered for maxent suitability mapping.

The ROC curve for each of the three models run (all year, warm wet and cool dry) can be seen in Figure 3.16. For each, the mean AUC with its standard deviation is annotated on the graph. All three AUC values were above 0.7, being acceptable (Swets88).

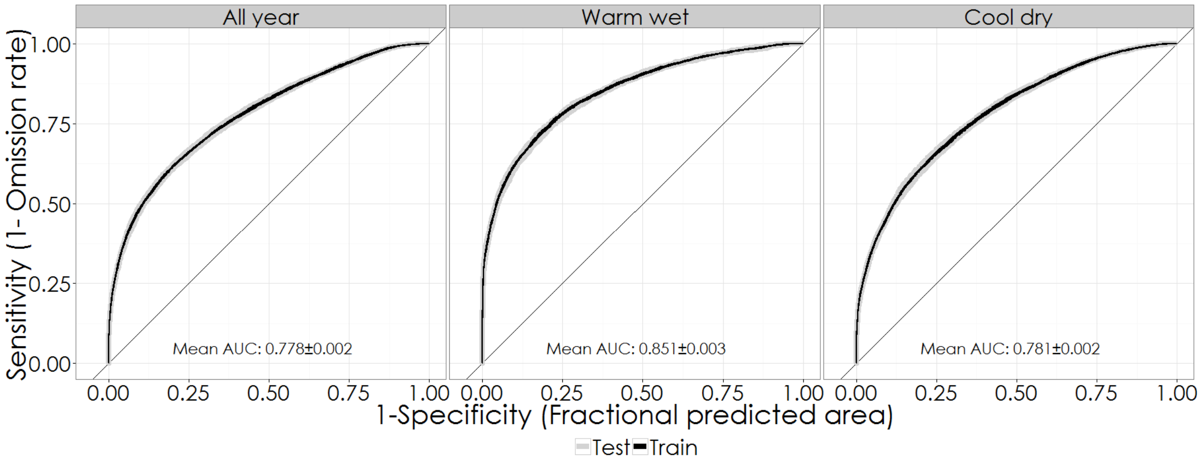

Figure 3.16 Receiver operating curves (ROC) for the three maxent models, as well as their respective AUCs. Mean values are in black and range in grey.

Table 3.6 summarizes the contribution and permutation importance of each predictor variable to the various models.

Table 3.6 Predictor variable contribution and permutation importance for each of the three maxent models

Predictor variable	**All year**		**Warm wet**		**Cool dry**	
	Contribution	**Importance**	**Contribution**	**Importance**	**Contribution**	**Importance**
AllPermWaterDist	31.07%	26.03%	25.67%	15.87%	33.1%	44.04%
	(±4.03)	(±0.37)	(±3.55)	(±0.25)	(±3.55)	(±0.19)
AllSeasWaterDist	26.47%	20.16%	25.03%	17.77%	20.96%	16.41%
	(±4.00)	(±0.38)	(±3.5)	(±0.48)	(±3.88)	(±0.42)
Isothermality	12.4%	12.88%	10.97%	10.02%	14.4%	14.97%
	(±3.55)	(±0.21)	(±2.71)	(±0.28)	(±3.32)	(±0.2)
LST	1.27%	0.84%	2.75%	1.90%	1.11%	0.77%
	(±0.38)	(±0.05)	(±0.75)	(±0.14)	(±0.25)	(±0.09)
LandCoverRecl	4.12%	2.73%	6.72%	3.12%	1.16%	1.01%
	(±1.51)	(±0.18)	(±2.69)	(±0.14)	(±0.47)	(±0.1)
NDVI	0.58%	0.46%	1.99%	1.85%	4.97%	2.29%
	(±0.15)	(±0.03)	(±0.33)	(±0.27)	(±0.51)	(±0.15)
NDVIMax	4.39%	8.35%	6.06%	12.74%	4.86%	4.06%
	(±1.10)	(±0.26)	(±1.35)	(±0.23)	(±1.46)	(±0.21)
NDVIMean	7.57%	13.66%	7.74%	20.59%	7.44%	5.45%
	(±2.34)	(±0.57)	(±1.95)	(±0.51)	(±1.55)	(±0.47)
Slope	3.69%	2.37%	4.32%	2.28%	2.98%	2.66%
	(±0.99)	(±0.11)	(±1.01)	(±0.12)	(±0.64)	(±0.1)
urband	8.45%	12.52%	8.75%	13.86%	9.02%	8.34%
	(±1.11)	(±0.34)	(±1.70)	(±0.3)	(±0.57)	(±0.34)

In Figure 3.17 the jackknife test results, based on the AUC values, are shown for each variable across the models. For each variable, the AUC of the model is calculated with only that variable used to run the model, and thereafter running the model with all the variables except that one. The AUC for each of these sub-models are then calculated to show the influence of inclusion or exclusion of the variable in the model, represented by the two bars in the graph.

Habitat suitability maps for the three study sites are shown in Appendix A.

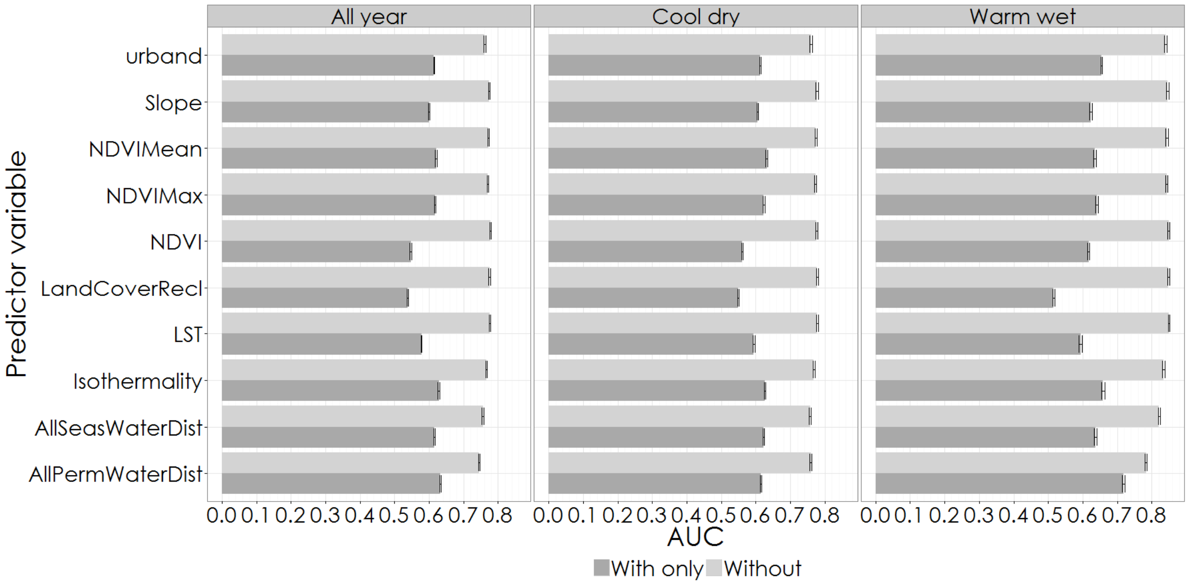

Figure 3.17 Results of the jackknife tests on the AUC of the three maxent models

The response curves for each of the predictor variables used in the three maxent models are shown in Figure 3.18 and Figure 3.19.

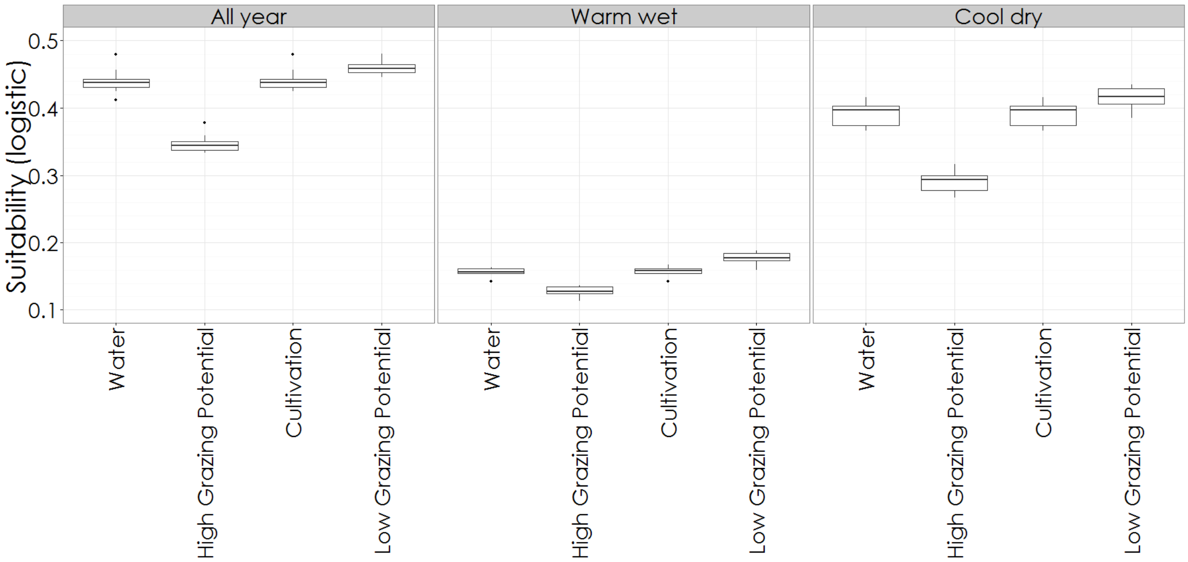

Figure 3.18 Box-and-whisker plots for the classes of the categorical variable LandCoverRecl during the ten model replicates.

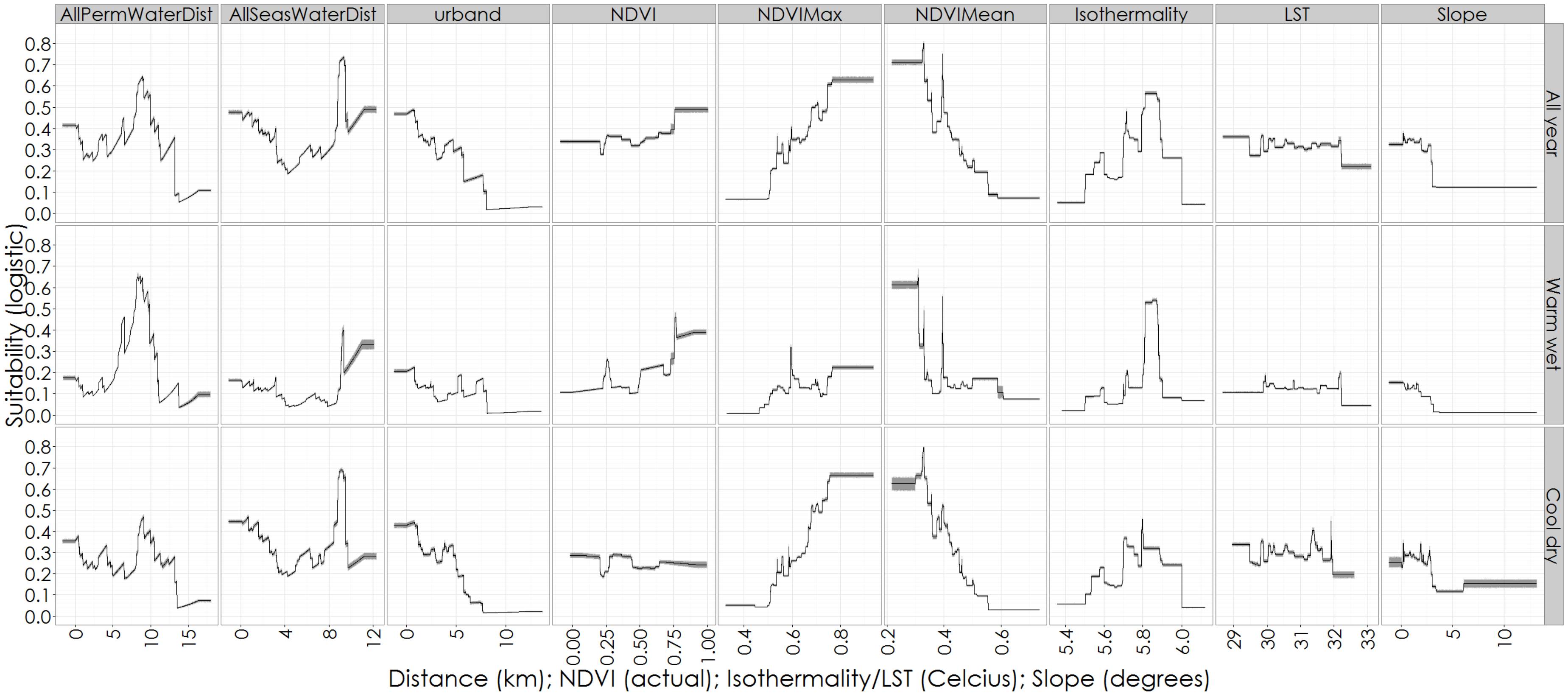

Figure 3.19 Response curves for the nine continuous predictor variables for each of the maxent models. Grey shading indicates variation across the ten model replicates

Discussion

The findings presented here constitute the first of their kind for the FMD protection zone in South Africa and are of importance, since cattle movement and distribution are the primary denominator when considering risk of disease transmission through direct contact, especially with other species.

The use of two different GPS telemetry options in this study is probably not ideal, but also provides an opportunity to compare the two systems in practice (Table 3.7):

Table 3.7 Comparison between handheld GPS and GPS/GSM collar tracking

	Handheld GPS	**GPS/GSM Collar**	**Related references**
Cost	Cheap	Expensive	
Frequency of field visits by researcher required	Frequent (days-weeks)	Infrequent (weeks-months)	
Human dependence	Only herded animals No night grazing recorded	All movement/activity recorded	316
Human bias	Yes (herdsman)	No (unless herded)	316
Precision	Dependent on herdsman movements (15-45m)	Accurate (1-10m)	362
Battery life	Approximately 1 day, easy to exchange with rechargeable batteries	Approximately 1 year, requires complete replacement of unit	This study
Data download	Difficult (requires travel, manual download and special software)	Easy (GSM/Internet download, generic format)	363
Additional interpretive data	Can be added by user (e.g. behaviour state such as drinking)	Only activity sensor, needs calibration	316
Re-use	Easy to transfer between herds	Requires handling of animals to transfer between herds	

Perhaps an optimal solution for livestock is to use a handheld GPS, but to fit it to a custom-made collar for the animal, as was done in a few recent studies[364,365].

Classification of animal behavioural (or movement) states is subject to a great deal of variation, especially when working with an animal that can constantly adapt to prevailing conditions[366]. Some authors advocate more complex approaches for the classification of behavioural states from telemetry data than we present here[367]. We categorised three behavioural states retrospectively in this study (walking, grazing, resting), by considering only three attributes of movement (speed, relative angle and activity), which has been used with success before (92% accuracy)[313]. Differentiating between resting and grazing has been shown to be the most difficult to achieve, often leading to underestimation of the grazing category[318,368], which could be the case in this study too, since no field validation of behavioural states occurred, and resting seemed unnaturally elevated in certain instances (Smallholder site during cool dry season, for example). Even considering only speed, Putfarken et al.[369] classified walking (>1.2km/h), grazing (0.072 - 1.2km/h) and resting (<0.072km/h) close to 95% accurate in cattle at pasture, even though the use of speed alone is not recommended[362]. These findings however correlate well with the speeds linked to the behavioural states in this study walking 1.96km/h [1.48-2.6km/h], grazing 0.18km/h [0.05-0.41km/h] and resting 0.03km/h [0.02-0.07km/h]). Even classification of the distantly related African buffalo's behavioural states in an area very close to our study sites agreed well with the findings presented here (walking 1.66±0.22 km/h, grazing 0.33±0.06 km/h and resting 0.02±0.00 km/h)[370].

The choice of fifteen minute location recording frequency in this study was based on the intention to do the eventual analyses on pixel-based (raster) surfaces. Apart from the BIOCLIM rasters[214], which were interpolated, the directly measured MODIS imagery (NDVI and LST) had the coarsest resolution at 269.63m by 269.63m (7.27ha). Reliable assessment of movement behaviour can be done at observation/recording frequencies of less than one hour[371,372]. For herbivore patch selection and movement studies, it has been found that a one hour recording frequency would provide only 30% accuracy at one hectare resolution, whilst a 10 minute frequency would push this up to 70%[373]. A fifteen minute frequency at 7.27ha therefore seems appropriate. The major argument against high recording frequency, is that of spatial and/or temporal autocorrelation (STAC)[374,375], since it violates the assumption of data independence. However, it has also been advocated to integrate STAC in analysis of movement and home range assessments, rather than remove it[290,376]. Moreover, GPS accuracy should be considered when selecting the recording frequency of a study. Five to fifteen minute recording frequencies have been deemed appropriate for the GPS inaccuracy encountered during this study[377]. The straight line displacement between locations (step length) should also be appropriate to the resolution of modelling[378], which seems to be the case here, with more than 95% of 'grazing' steps being less than 269.63m long, whilst more than 95% of 'walking' steps were longer than 269.63m.

As would be expected, resting was the dominant behaviour for cattle at night (non-kraal-associated), although a low, secondary resting peak also occurred around midday, more so during the warm wet season, which is most likely to avoid some of the midday heat. For the

Central site, grazing peaked around late morning to midday, between two pronounced walking periods in the early morning and late afternoon, most likely as a result of active herding from and to the kraal. This midday grazing peak is also the time associated with the animals reaching their maximum grazing radius[364]. In the Eastern Cape Province of South Africa, a similar midday grazing pattern was seen[323], which is made possible by the relative heat tolerance of zebu type cattle[379]. In the Smallholder site, and to some extent also the herds in the North site, grazing followed a more bimodal pattern[364], similar to their walking pattern, which could be due to the reduced herding in these sites. This pattern is similar to what was noted during experimental free grazing studies in Zambia[380], as well as in pastoral cattle of the Sahel[321]. Interestingly, this bimodal pattern was also surprisingly similar to what was reported for buffaloes in the nearby KNP[370]. Whilst only the North and Smallholder sites had noteworthy periods of night time grazing, it consistently peaked around 01h00, and was very low compared to day grazing. This has also been recorded by others[258,321,380]. Most rumination also occurs during the night, with zebu cattle spending less time ruminating in relation to grazing time than the European breeds[258]. The time that cattle spend in each of the behavioural states (so-called activity budgets) has been the subject of many a research project over the years and is probably best compared to our results through a table summarising other studies on zebu cattle in Africa (Table 3.8; also see Table 3.3 in the results section). Most of these studies are based on direct observation, however, and comparison with our retrospectively classified results probably comes with some risk of misinterpretation. Note the great variation between these studies. Whether this is true variation or perhaps due to differences in classification of behavioural states, is difficult to ascertain. Nevertheless, our findings do fall within the range of these studies combined, albeit at the lower end of the grazing and walking ranges. It is very important to interpret our daily activity budget findings in the context of the trajectory duration, to assure a true reflection of the time spent in each behavioural state.

We noted a relatively high grazing effort in the North and Smallholder sites during the wet season, compared to the cool dry season. This trend was reversed in the Central site. In Zambia[381] and Zimbabwe[263], dry season grazing was also found to be lower than in the wet season, which was attributed to possible energy conservation and night-time feeding on crop residues[263]. Also, no loss in condition could be related to a decrease in grazing efforts during the dry season[380]. Of note perhaps, is the increase in browsing as the dry season progresses, mentioned by some authors[263,319]. In Nigeria on the other hand, lower grazing periods were recorded during the wet season, offset by higher resting periods, although this was attributed to rain preventing the animals from going out to graze.

Table 3.8 Activity budgets of zebu cattle noted during other studies throughout Africa

Season	Walking	Grazing	Resting	Reference (Country)
All year	8%	70%	22%	[323] (South Africa)
Wet season / Dry season	21% / 24%	62% / 66%	17% / 10%	[364] (Kenya)
Wet season / Dry season	16% / 20%	67% / 58%	17% / 22%	[318] (Niger)
Wet season / Dry season		27% / 42 %		[380] (Zambia)
All year	24%	70%	5%	[379] (Nigeria)
All year	20%	68%	12%	[368] (Senegal)
All year	9%	72%	19%	[381] (Zambia)
All year		12-55%		[263] (Zimbabwe)
All year	3%	39%	57%	[258] (Uganda)
All year	21%	60-70%		[382] (Tanzania)
Median	**19%**	**65%**	**19%**	
All year (African buffaloes)	9%	47%	44%	[370] (South Africa)

The very high resting percentage (especially if compared to grazing) that was recorded in the Smallholder cattle during the cool dry season is surprising and counterintuitive, especially when viewed in conjunction with trajectory duration and distance. To some extent it could be explained by possible supplementary feeding at the kraal, a factor that was not recorded during the study. More likely, it could be as a result of misclassification between resting and grazing behaviours[313,318,362]. Walking effort was lower during the warm wet season, likely attributable to the shorter distance between feeding patches[364], although herder decisions might not always follow this logic[383]. In the North and Smallholder sites, where less herding occurred, walking and grazing were inversely related[364]. Increased walking has been found to negatively affect feed intake ($R^2=0.53$, $p<0.02$)[383], although similar to our Central site, their study also noted higher grazing times to offset this added travel time. Even though other factors, such as human and cattle density, could also affect walking time[384], it did not seem to have any effect between our demographically diverse study sites (also see Chapter 2).

We found grazing trajectories to be consistently longer in duration during the wet season (except in the South site), as was the case elsewhere and within a very similar time range to what we found[319,381]. In the Central site, one explanation for this could be as simple as routine and day length, since departure and arrival times were consistent in relation to sunset and sunrise throughout the year. Some have attributed shorter dry season grazing times to herdsmen starting later to avoid the cold of winter[381], or to first finish their work in the cultivated fields before herding their cattle[379]. However, in the North and Smallholder sites, where very little daily routine was noted, these longer grazing trajectories could be related to the abundance of forage and water in the field during the wet season, negating the need to return to the kraal. Season and herd management strategies play a very important role in the duration of grazing trajectories[319,383]. Also, some of the decisions made by herdsmen might be repetitive, rather than planned, and made before they leave for the day's grazing in the morning[362,383].

When foraging, animals often follow the natural path that the landscape provide (e.g. open vegetation, footpaths) or the herding path, the latter being driven by the human desire to not only minimize walking time and maximize grazing, but also to vary the type of fodder, to avoid livestock mixing or getting lost, or to encourage or avoid social interaction[385]. Overall, the trajectory distances recorded in this study were relatively short compared to other studies[316,319,364,368,382]. Although our tracking data was similarly skewed towards urban areas, as has been shown by Coppolillo[261] ($R^2=0.89$, also see Ogutu et al.[75]), the influence of human density on trajectory distances was not significant. Seasonal differences were however significant, and only in Senegal[368] were longer wet season and shorter dry season foraging trajectories seen, as in our study. A number of other studies noticed the opposite[319,364], however, which is also the pattern noticed in wild savannah herbivores[371]. Also contrary to our findings, a positive correlation between grazing radius and progression of the dry season has been reported[317,364]. The distance which cattle travel for high quality forage, however, has to be balanced with the energy costs associated with such travel[386]. So, when forage is severely limited, which is likely the case in the overgrazed communal rangelands[251], it could lead to a reduction in trajectory distance to attain a favourable energy balance, unless overridden by the herdsman's decision making. Schlecht et al.[319], for example, noticed an almost 40% reduction in trajectory distance in free grazing herds during the late dry season, compared to herded animals. Trajectory distance could also be constrained by water availability[263], but is probably a complex combination of water availability, settlement density, herd size and availability of herding labour [261].

Although kraaling and herding has its origins more in preventing livestock losses from predators and to prevent damage to crops during the growing season[387,388], today it is also done to avoid stock theft[249]. Regularly returning to the kraal, converts these herded cattle into classical central-place foraging animals, which is important to bear in mind when interpreting for example resource selection by these animals[357,389]. It has been shown that cattle alter their grazing behaviour when kraaled, grazing more intensively during the period of day outside the kraal than non-kraaled animals would do, and resting more during the night[390,391]. This seems to have very little impact on their production[379], which is mostly manifested as weight loss due to limited feed intake during the dry season or limited grazing duration (<7h) during the wet season[390]. This anthropological influence is also manifest in the 1-3km range that animals preferred around urban areas in this study (see Figure 3.11 and

Figure 3.19). In fact, the influence of herdsmen on cattle grazing is considered even more dynamic than what is proposed by optimal foraging theory[383].

Water is an important limiting factor of habitat selection by cattle[256], although in more arid areas, forage availability could become an even more limiting factor[392]. The influence of water availability has also been shown under local and regional conditions, especially during the dry season, when water availability is the major determinant of grazing patterns, even in wildlife[370]. This is also the likely explanation for the correlation between the distance to available water and distance travelled during a grazing trajectory that is often noticed[261,263]. We found a strong association between the maximum distance to water and maximum distance from the kraal recorded during each grazing trajectory, especially during the dry season of the more arid central and northern parts of the study region. To this end, the peak grazing radius was also observed around the midday to early afternoon[364], being the time most associated with drinking[288,393,394]. Similar to findings by others[75,250,395,396], we found cattle to be grazing in relative close proximity to water (1.24km [0.48-2.90km]), which fits the classic piosphere model of increased herbivore densities as you approach water points, kraals and settlements[397,398]. Kraals are also associated with relatively short distances to water, since water is also a determinant of human settlement[75]. Likewise, 81% of the variation in dry season grazing radius could be explained by the proximity of perennial water in an east African study[261], despite the relatively high rainfall in that study area. Kraaling does however dampen this piosphere effect[261].

At a continental scale, it has been shown that subsistence cultivation and cattle distribution are related[217], largely due to the synergies between these land use options: during the early dry season, crop residues of the cattle owner can be used as supplementary fodder for his livestock[261,263,388], whilst livestock manure can act as fertilizer for the next crop to be planted, whether from grazing the cultivated fields or through collection at the kraal[381]. In fact, during this study, the question of how herdsman knew where to take cattle for grazing was often met with laughter, because 'the cattle are not stupid, they know what to eat, we just need to keep them out of the crops'. Accordingly, we found significant preference for cultivated fields during the early dry season in particular, especially in the Central site, but even during the late dry season in the South and Smallholder sites.

In free-ranging wild herbivores, home ranges become larger as resource distribution becomes patchier and more unpredictable[371]. This theory concurs with the overall findings presented here, where home ranges were consistently smaller during the warm wet season compared to the cool dry season. The home ranges reported here are overall considerably larger than those reported by others in the region[251,288,324], which is likely due to the fact that we used more animals over more extensive study sites and/or study periods. What is interesting though in our findings, is the apparent inverse relation between home range and grazing trajectory distance. This could be as a result of the trajectory following a zigzag shape during the warm wet season between the abundant feeding patches. Some support for this might lie in decreased walking (as compared to grazing) behaviour noticed during the warm wet season. It might also point at more repetition in grazing trajectories during the wet season[362] versus more variation between grazing trajectories in the cool dry season. Bailey[394] showed experimentally that animals revisit the same foraging patches more often in heterogeneous landscapes than homogeneous ones, even though they might move between these patches frequently. Also of interest, is that larger segregation of habitat selection by cattle has been noted in the dry season by others too[262].

As was noted already in the introduction, slope and proximity of water has a strong influence on resource selection by free-ranging cattle[256,399]. Since our study areas fell in a relatively flat landscape (slope <10%)[256], slope's minor role in habitat suitability was expected, whilst proximity to water, as expected, was the variable contributing most to habitat suitability, in both seasons. Often, these water sources are also in low-lying habitat types that generally have plentiful herbaceous fodder throughout the year, adding to their attraction, especially when the normal grazing becomes limited in the cool dry season[250,263]. It can be expected that cattle would actively select areas of high quality forage, whilst avoiding low quality forage[394], although such positive selection could also decline over time if food is abundant[386]. NDVI can be a useful indicator of forage nitrogen content[356], hence our inclusion of NDVI and its derivatives as predictor variables in the maxent model. Surprisingly, actual NDVI values contributed very little to habitat suitability, and its mean and maximum values only slightly more. Aarts et al.[400], however, warns that habitat availability does not necessarily equate to habitat use, which could explain the low importance of NDVI partly, although the higher importance of especially the mean NDVI could also indicate some form of revisitation or 'memory'[257,264,394,401]. Again, the influence of the herdsman is difficult to separate from the animals' own choices. NDVI can also act as proxy for precipitation, especially in semi-arid areas[402,403], albeit at a one to two month lag[404]. Precipitation was dropped from the maxent predictor variables due to poor coverage and high correlation with NDVI, although its contribution should be captured in the NDVI contribution. Since cattle aim to maximise nutrient intake at the patch level[257,405], not including a biomass proxy (e.g. through NDVI derivative) in our model, might be of some concern. Maxent and the resource selection function are rather alike[400], since both are applied to evaluate habitat use in relation to the availability of those habitats. However, maxent is prone to produce rather conservative predictions, and especially areas considered to be unsuitable habitat should be considered with caution[406], since an overabundance of suitable habitat could lead to spurious negative coefficients, appearing as avoidance[407]. This tendency is partly as a result of maxent's sensitivity to background prevalence[296].

There are a number of weaknesses in our study. We could have incorporated herd size more explicitly in the various analyses, such as home range. The lack of behavioural state validation and its complete omission from the South site, mainly due to an oversight in planning and use of different technologies in the study sites, caused an unfortunate gap in our outputs. As has been recommended by others[271,408], a further improvement in the study could have been to switch collars between different herds, rather than leaving them with a single herd for the duration of the study. However, due to practical and financial constraints, the number of herds tracked in this study (as compared to the number of samples per herd) was relatively low, running the risk of not being fully representative of the population[255]. This is more so for the GPS/GSM collars than handheld GPSs, which was frequently switched between herds. A minimum of twenty animals with at least fifty observations per animal has been suggested as a ballpark figure[409]. All the work presented here could be subject to bias brought about by violating the assumption of data independence through spatial and/or temporal autocorrelation, which has been proven to cause erroneous KDE and MCP estimates[375], although it has been argued that such 'erroneous' estimates might be more realistic[290]. To quote Rooney et al.[277] on spatial autocorrelation in telemetry studies of mammals: 'the correct strategy for the best possible estimation of range size and use from telemetry would be the repeated use of as short a sampling interval as is possible over an extended period of time.'

This cattle tracking data set has proved to be a valuable source of information, and more could still be done with it. For example, intensity of use in the form of residence times as well as recursion analysis, i.e. adding the time component more explicitly to analysis[336,410-412], could perhaps shed some light on the disparities found between home range and trajectory distances. Various techniques also exist to further analyse movement behaviour and optimal foraging[413]. Linkages between the individual and population level (consider the findings of Chapter 2) could also add a great deal of value to this data[414], especially when considering that cattle numbers in southern Africa could decline in the near future due to an expected reduction in annual rainfall[415]. Having a good understanding of the drivers of habitat selection by cattle and the effect that climate change will have on these components are important, since it could lead to, or even necessitate, changes in the livestock management system[416] or species composition (especially in African developing countries)[417].

Conclusion

Here we have presented a large body of work on the movement and distribution attributes of communal and smallholder cattle in the FMD protection zone in South Africa. Of note is the amount of heterogeneity in movement patterns between seasons as well as study sites, especially due to the influence of management practices such as herding and cropping. In the context of disease risk, consider for example the effect that kraaling (and herding), or the lack thereof, has on the period that these animals are exposed to potential contact with buffaloes. Distribution patterns on the other hand seems to be less heterogeneous across seasons and this study region, although findings such as the particular influence of water proximity and slight contraction of home ranges during the wet season could be of importance when considered in the context of disease risk due to contact with buffaloes. Whilst a great deal more could be achieved with this data set, it lays a good foundation as denominator data for spatio-temporal risk modelling of a contagious disease spread through direct contact.

Chapter 4

*Description of events where African buffaloes (*Syncerus caffer*) strayed from the endemic foot-and-mouth disease zone in South Africa, 1998-2008*[c]

Chapter summary

African buffaloes (*Syncerus caffer*) are reservoir hosts of the Southern African Territories (SAT) foot-and-mouth disease (FMD) virus strains. In South Africa, infected buffaloes are found in the FMD-infected zone comprising the Kruger National Park and its adjoining reserves. When these buffaloes stray into livestock areas, they pose a risk of FMD transmission to livestock. We assessed 645 records of stray buffalo events (3124 animals) from the FMD infected zone during 1998-2008 for (i) their temporal distribution, (ii) group size, (iii) age and gender composition, (iv) distance from the infected zone fence, and (v) outcome reported for each event. A maximum entropy model was developed to evaluate spatial predictors of stray buffalo events and assess current disease control zones. Out of all buffaloes recorded straying, 38.5% escaped from the FMD infected zone during 2000/2001, following floods that caused extensive damage to wildlife fences. Escape patterns were not apparently influenced by season. The median size of stray groups was a single animal (IQR [1 – 2]). Adult animals predominated, comprising 90.4% (620/686) of the animals for which age was recorded. Of the 315 events with accurate spatial information, 204 (64.8%) were recorded within one kilometre from the FMD infected zone. During late winter/spring (June-October), stray buffaloes were found significantly closer to the FMD infected zone (median= 0.3km, IQR [0.1 – 0.6]). Less than 13% (40/315) of stray groups reached the FMD protection zone without vaccination, posing a higher risk of spreading FMD to these more susceptible livestock. Model outputs suggest that distance from the FMD infected zone, urban areas and permanent water sources contributed almost 85% to the spatial probability of stray buffalo events. Areas with a high probability for stray buffalo events were well covered by current disease control zones, although FMD risk mitigation could be improved by expanding the vaccination zone in certain areas.

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[c] In large part, the work presented here has been accepted for publication in *Transboundary and Emerging Diseases*. doi:10.1111/tbed.12280

Introduction

Foot-and-mouth disease (FMD) is caused by a highly contagious virus from the family *Picornaviridae* which usually affects cloven-hoofed animals and camelids. The disease is characterized by low mortality, but high morbidity in unvaccinated livestock and major production losses due to export restrictions. The logistical and economic burden that eradication of this disease poses means those countries that have achieved eradication are very wary of re-importing it. This has resulted in trade embargoes on agricultural products from countries in which the disease is not adequately controlled[1,4]. The control and prevention of FMD is considered a global public good, protecting the livestock sector of FMD-free areas, as well as the livelihoods of livestock keepers in FMD-endemic areas through progressive reduction in the risk of outbreaks[121].

Globally, seven serotypes of FMD virus occur (A, O, C, Asia-1, SAT 1, SAT2, SAT3), of which the three Southern African Territories types (SAT 1, 2 and 3) are all endemic to certain areas of southern Africa[418]. In these endemic areas, the wildlife reservoir of the SAT viruses, the African buffalo (*Syncerus caffer*), is widespread[4,28,115]. Nearly sixty percent of free-living buffaloes in southern Africa, mainly those up to three years of age, are persistently-infected with one or more of the SAT-type viruses[28]. Viral persistence in this species can last up to five years in a single animal and 24 years in an isolated herd[41]. It is estimated that 85% of buffaloes over the age of one year have been exposed to all three SAT-type FMD viruses[2]. Under normal circumstances, buffaloes do not show any overt clinical signs of the disease, even in its acute stages. Only a few, isolated, naturally FMD-free buffalo populations exist in South Africa[7], while in some cases animals have been intentionally bred free of the virus, mainly as part of commercial enterprises[6].

The main refuge for persistently-infected buffaloes in South Africa is the Kruger National Park (KNP) and the adjacent private and provincial nature reserves (APNR) along its western and southern boundary. To the east, the KNP is contiguous with its international neighbour, Limpopo National Park in Mozambique. This area, altogether comprising more than 30 000km^2, forms the main body of the Great Limpopo Transfrontier Park (GLTP), which also includes Gonarezhou National Park in Zimbabwe. Current estimates of the GLTP buffalo population are close to 45 000 animals (C. Greaver, personal communication, 12 January 2009), following a steady increase in the population since a collapse to 12 000 animals in the KNP section of the GLTP during the 1991/1992 drought in the region (South African National Parks annual census data).

Eradication of FMD from the region would require the destruction of all endemic hosts, an option untenable for more than just ethical and ecological reasons[1]. Prevention of transmission of FMD virus to livestock in endemic areas is achieved mainly through physical (fence) and biological (vaccination) separation of livestock and wildlife, especially buffaloes. To this end, a 'disease control' fence was erected around the KNP in the 1960s in response to severe FMD outbreaks in livestock in 1958[55,177]. In 1993 this boundary was extended westward through incorporation of the APNR into the KNP. To further enable South Africa to export agricultural products, the country has been divided into a FMD infected zone (where endemically infected buffaloes occur), a FMD protection zone and a FMD free zone[125]. Regular surveillance and strict control of livestock movements are implemented in the entire protection zone, while compulsory bi- to tri-annual vaccination is only applied in a defined part of the protection zone immediately adjacent to the infected zone ('protection zone with vaccination')[55,125].

Infection with FMD virus in buffaloes is postulated to occur in calves when they lose their maternally-acquired immunity at the age of between three and twelve months[2,47]. Since buffaloes calve synchronously in the wet season (peaking in January in South Africa)[65], these calf infections have the potential to cause small 'epidemics' in herds[61] as the calves become susceptible and subsequently infected almost concurrently during the dry season (April-September). Acutely-infected buffaloes are considered to excrete FMD virus at the same rate and quantities as acutely-infected cattle[30,33], and thus pose a considerable risk to other species susceptible to the disease[61]. Persistently-infected buffaloes also pose a significant transmission risk to livestock[70]. However, the exact circumstances under which persistently-infected African buffaloes transmit FMD virus to cattle are still poorly understood. Although other species such as impala (*Aepyceros melampus*)[45] and kudu (*Tragelaphus strepsiceros*)[57], have also been implicated in the transmission of FMD to livestock when clinically diseased, persistently-infected buffaloes remain the most important endemic host in the region.

Conditions in southern Africa are not conducive to long distance aerosol transmission of FMD virus, and therefore control of the disease is mainly focused on preventing direct contact of infected buffaloes with livestock through physical barriers, with vaccination added as an additional (biological) barrier where fences fail. Buffaloes frequently escape their wild refuge into farming areas, posing a risk not only to the health of livestock, but also to the local and national economy. Very little information exists in literature about the characteristics of these stray buffalo events. No outbreaks of FMD occurred between 1983 and 2000 in South Africa, whereas six FMD outbreaks in livestock occurred between 2000 and 2008. Five of these outbreaks have been attributed to contact between buffaloes and cattle, when the former strayed into livestock areas. To this end, the efficacy of fencing and vaccination has been called into question in recent years[55,110]. In this paper, we analyse stray buffalo events from the FMD infected zone reported between 1998 and 2008, since basic descriptive data on such events does not currently exist. We also make use of this stray buffalo data set to model suitable areas for stray buffaloes outside the infected zone, to assess the adequacy of current FMD control zones. It is expected that the temporal and spatial analysis of stray buffalo events will allow identification of potential patterns in this process, so that preventive efforts and resources may be applied more efficiently.

Materials and methods

Study area

This study included all areas adjacent to the KNP and APNR in South Africa (Figure 4.1). The area falls in the Lowveld region of north-eastern South Africa, a low altitude area (<1000m), characterised by hot summers, during which the peak rainfall occurs (November to February), and mild, dry winters. Annual rainfall varies from 500-700mm in the south to 300-500mm in the drier north. Vegetation consists mainly of subtropical savannah, underlain by soft basaltic sediments towards the east and coarser granite soils and hills in the west, interspersed by gabbro intrusions. Six major rivers, namely the Limpopo, Levuvhu, Letaba, Olifants, Sabie and Crocodile flow through this area towards the Indian Ocean, crossing through the KNP and APNR.

The KNP and APNR also form the FMD infected (endemic) zone in South Africa and cover an area of approximately 20 000km^2, with a boundary of just over 700km long (excluding international boundaries). The adjoining protection zone covers approximately 16 000km^2. Cattle within a portion of the protection zone directly adjacent to the infected zone (approximately 5 000km^2), are vaccinated bi- to tri-annually against FMD (SAT viruses).

Stray buffalo data

Due to both the danger to people and the risk of disease transmission to livestock that stray buffaloes pose, environmental and veterinary departments are involved in the control of buffaloes straying from conservation areas into livestock areas. Local offices of the Department of Agriculture, Forestry and Fisheries (Directorate Animal Health), Mpumalanga Department of Agriculture, Rural Development and Land Administration (Chief Directorate Veterinary Services), Mpumalanga Tourism and Parks Agency, Limpopo Department of Agriculture (Veterinary Services) and Limpopo Department of Economic Development, Environment and Tourism were contacted during 2009 to obtain any records of stray buffaloes reported between January 1998 and December 2008. Since no standard reporting system for such events existed, records were made available in many different formats, such as official monthly and quarterly reports of local and regional offices (hard copy and electronic), personal data bases (electronic) as well as diaries and notes kept by officials (hard copy and electronic). These records were consolidated into a single electronic database. Duplicated records were removed as far as discernible.

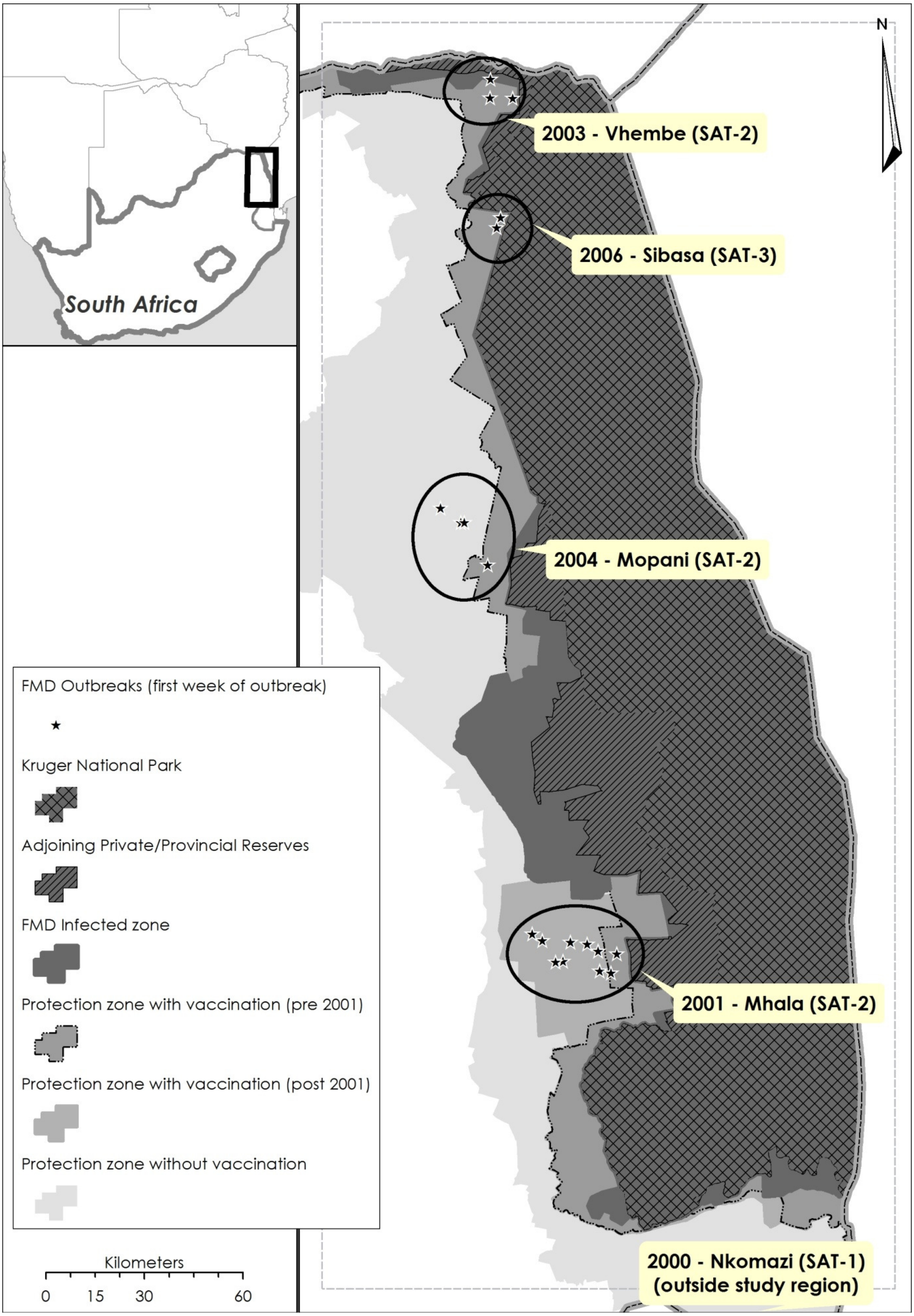


Figure 4.1 Map of the study area

From these records, we extracted information on five basic characteristics of stray buffalo events: (i) the temporal distribution of these events (by month, season and year), (ii) the number of animals involved in each event, (iii) the age/gender composition of stray buffalo groups, (iv) the distance from the FMD infected zone fence that these events were recorded/resolved and (v) the resolution or outcome reported for each event. Only events stating at least the group size and containing the year (temporal analysis) or an accurate location (spatial analysis) were retained. The date and location of an event were taken as the date and location at which the resolution took place (i.e. end of the event), or the last sighting of the animal(s) in cases where no further action was taken.

Some of the official reports however contained very limited information on stray buffalo events, for example not specifying the group composition or size, lacking exact dates and/or only making reference to a district or area name, rather than a more precise location. To obtain more accurate data, eight workshops were arranged during 2009 with those officials involved in the actual control of stray buffaloes. Since there are only a few of these officials in the entire area, the workshops were small (one to six participants, apart from the facilitator). Participants were asked to bring along any personal (e.g. diaries) or official records (e.g. reports, data sheets) they had of stray buffalo events to supplement and improve on the records already assimilated. They then pointed out the places where buffalo control events occurred on a digital map[355] that included roads, rivers, villages/towns and major[197], overlaid on high resolution satellite imagery (SPOT 4 Imagery, Southern Africa, 10m resolution and EarthSat NaturalVue, Landsat derived, 25m resolution). Where internet bandwidth was adequate, Google Earth™ was also used. The aim was not to obtain an exhaustive data set, but rather a collection of spatio-temporally accurate stray buffalo events. Events were only included for spatial analysis if the official was absolutely sure he could link his written records accurately with a point on the map where the control action or last sighting occurred. No attempt was made to establish the point of exit from the infected zone or the path that the animal followed after escape from the infected zone, since this would have been speculative at best in most cases. Age classes were defined as follows: Adult (older than three years; sub-adult (one to three years of age) and calves (less than one year old). Seasons were defined as ‘cool dry’ from April through September, and as ‘warm wet’ from October through March[65].

Ancillary data and statistical analysis

Daily rainfall data were obtained from the South African Weather Service for three of the weather stations in the KNP (Skukuza, Phalaborwa and Punda Maria). These data were aggregated and averaged per year for the study period (Table 4.1).

R Statistical Software[206] was used for data analyses. Central tendency was reported as the median, followed by the interquartile range (IQR) in square brackets, unless otherwise specified, since data did not follow a Gaussian distribution and contained many outlier values. Differences in characteristics between seasons were tested using an unpaired, two-sided Mann-Whitney U Test, with the test statistic reported as 'U'. Scaled Euler diagrams to depict group composition were created using the 'venneuler' package in R[419]. Distance of events from the KNP and APNR fence as well as from urban areas (land cover class), was calculated as the shortest distance from the point event to the feature (Euclidean distance).

Maximum entropy model

In a second step, we produced a suitability model for stray buffalo events, based on a number of predictor variables and those events with accurate spatial information (presence records). We used the maximum entropy algorithm (maxent) to construct the suitability model for stray buffaloes[301], since it has been rated among the top species distribution modelling algorithms[343] and is suited to non-exhaustive, presence-only data. Maxent is mathematically equivalent to Poisson regression, but scale dependent[345], although considered lenient towards spatial sampling error[420]. Only stray buffalo events after 1999 could be considered in this suitability model, since no normalised difference vegetation index (NDVI) data was available for 1998 and 1999. The predictor variables were derived from disease control zones, such as the distance from the FMD infected zone fence in km (*fenced*)[421], or from topographic maps, such as distance in km from permanent (*AllPermWaterDist*) or seasonal water sources (*AllSeasWaterDist*)[197], long term climatic data on temperature and precipitation[214], as well as land cover (Landsat derived)[205], including distance from urban areas (*urband*). Vegetation biomass was derived using NDVI, obtained from the MODIS sensor[203]. NDVI data were downloaded from the earliest available date in 2000 to the end of 2008, and long-term averages and maximum values were extracted, following Scharlemann et al.[204]. All predictor variables were resampled to a resolution of 269m by 269m, which was the resolution of the coarsest directly measured predictor variable (NDVI). We created 10000 random background points outside the infected zone as pseudo-absences. All models were implemented using the 'dismo' package in R ('maxent' function)[346], each with ten-fold cross-validation to estimate errors of fitted functions and with each fold allowed to iterate up to 500 times to approach convergence. The algorithm was run using its linear, quadratic, product, threshold and hinge features, which ensures that different transformations of the predictor variables are tested within each model. The regularization multiplier was left at the default setting of one. Each model's performance was evaluated using the area under the curve (AUC) of the receiver operating characteristic, which is a ranked approach to assess model fit, by determining the probability that a presence location is ranked higher than a random background location[295,301]. AUC values above 0.9 are considered very good, 0.7-0.9 good and below 0.7 is considered uninformative[359]. It is important to note that the maxent ROC curve is not based on the classification of presence vs. absence values, as is the norm, but rather presence vs. background (which could be absence or not), and that proper quality thresholds have not been estimated for this particular case of AUC[297]. Two models were developed: The first model (model 1) included 18 predictor variables. After confirming that model 1 performed adequately using AUC, the top-ranked predictor variables whose cumulative contribution to model 1 was 95%, were selected to run the final model (model 2)[422]. Outputs of model 2 were used to predict the suitability of each pixel for stray buffaloes, which is reported as a logistic value on a continuous scale from 0 to 1 by maxent. We then categorized this continuous suitability value into a binary output by using a threshold at which the true skill statistic reaches a maximum (sensitivity + specificity – 1)[423]. This binary output was used to assess the fraction of each disease control zone area being considered as suitable or unsuitable to stray buffaloes.

Results

A total of 645 out of 678 (95.1%) records were retained after selection of those containing at least group size information as well as the year of occurrence or accurate spatial information. These 645 events comprised 3124 buffaloes straying from the KNP and APNR between January 1998 and December 2008. Only 87.1% (562/645) of records mentioned the month of occurrence. Accurate spatial information was obtained for 315 (48.8%) of the 645 events.

Table 4.1 Number of stray buffaloes and stray buffalo events recorded per season of each year, including the average rainfall for that year in the KNP (Average of Skukuza, Phalaborwa and Punda Maria)

Year	**Events**			**Animals**			**Average rainfall (mm)**
	Season		**Total***	**Season**		**Total***	
	Warm wet	**Cool dry**		**Warm wet**	**Cool dry**		
1998	7	29	38	13	126	147	434
1999	11	12	29	24	40	89	573
2000	39	76	120	82	564	655	1008
2001	14	34	51	52	463	543	712
2002	16	25	50	30	71	364	297
2003	29	18	49	75	37	166	272
2004	24	26	67	39	51	169	723
2005	12	10	31	25	16	68	368
2006	24	37	73	126	179	557	637
2007	34	28	80	120	49	242	510
2008	40	17	57	83	41	124	372
Total	**250**	**312**	**645**	**669**	**1637**	**3124**	

*The total for each year includes events/animals for which the month was not recorded and hence was not attributed to a season

Temporal distribution

During the study period, 18.6% of all stray buffalo events (120/645), consisting of 21.0% (655/3124) of the total number of buffaloes recorded to stray, occurred in 2000, the same year in which exceptionally high rainfall was registered (Table 4.1). When combined with the subsequent year (2001), when the extensive flood damage to the disease-control fences of the infected zone was still evident in many areas, this two-year period comprised 26.5% (171/645) of all stray buffalo events and 38.3% (1198/3124) of the total number of stray buffaloes recorded during the entire study period (Table 4.1). The relation between stray buffalo events and annual rainfall was however not linear, since the years with the lowest number of stray buffalo events (29 in 1999 and 31 in 2005) were not characterised by low rainfall. During the years with below-average rainfall (297mm in 2002, and 272 mm in 2003), the number of stray buffalo events were not lower than average (50 in 2002, 49 in 2003), nor was the number of stray buffaloes (respectively 364 and 166).

During 2000 and 2001, following the extensive fence damage caused by flooding, 88.5% (1027/1161) of the animals escaped during the cool dry season. No significant difference between the cool dry and the warm wet season could however be detected for the number of animals that escaped (U=74.5, p=0.375) or the number of events recorded (U=70.5, p=0.532) over the entire study period. Table 4.2 gives an overview of the number of events per month over the entire study period, with medians ranging from one to six events per month. February, April and July are the months during which most stray buffalo events occurred. All interquartile ranges are overlapping however. Median values increased in the periods March-April, August-September and November-December.

Table 4.2 Temporal (monthly) patterns of stray buffalo events (median [interquartile range]), 1998-2008

Month	Number of events	Group size	Distance from fence (km)
Jan	3.0 [1.0-5.0]	1.0 [1.0-2.0]	0.68 [0.11-3.75]
Feb	5.0 [3.3-7.8]	1.0 [1.0-2.0]	0.34 [0.15-5.84]
Mar	4.0 [1.0-6.0]	2.0 [1.0-3.0]	0.28 [0.15-6.00]
Apr	5.0 [4.0-6.0]	2.0 [1.0-4.0]	1.24 [0.36-6.77]
May	3.0 [2.5-5.5]	1.0 [1.0-2.0]	1.36 [0.31-12.05]
Jun	4.0 [3.0-7.0]	1.0 [1.0-2.0]	0.25 [0.14-0.84]
Jul	6.0 [4.3-7.8]	1.0 [1.0-3.0]	0.28 [0.07-1.18]
Aug	3.5 [1.0-6.0]	2.0 [1.0-3.0]	0.33 [0.08-0.37]
Sep	1.0 [1.0-6.5]	2.0 [1.0-3.5]	0.26 [0.10-0.66]
Oct	3.0 [1.5-4.5]	1.0 [1.0-3.0]	0.24 [0.11-0.35]
Nov	2.0 [2.0-3.5]	2.0 [1.0-3.0]	0.59 [0.25-6.59]
Dec	2.0 [1.3-3.0]	2.0 [1.0-3.0]	0.43 [0.14-5.76]

Group size

Events consisting of only a single animal predominated at 46.5% (300/645), with only ten percent of the groups consisting of more than five animals. The median group size and interquartile range for 2000 and 2001, following the flood damage of 2000, were the same as for the other years (1 [1 – 2]). However, about half of the 1198 animals escaping during 2000 and 2001 were recorded in only three groups (100, 200 and 285 animals respectively). Only four other groups larger than fifty animals were recorded during the rest of the entire study period; these were also cool dry season events. Nevertheless, season had no significant influence on group size, with (U=37254, p=0.534) or without (U=29427, p=0.642) the influence of the 2000/2001 events. Table 4.2 gives an overview of group sizes on a per month basis. Compared to herd sizes recorded in the KNP[326], the stray groups containing adult bulls (1 [1 –

2]) were only slightly, yet significantly, smaller than bachelor groups inside the park (3 [2 – 6]; U=690004, p<2.2x10-16). Conversely, mixed age/gender buffalo groups found straying were significantly smaller (2 [1 – 3]) than the mixed buffalo herds inside the park (130 [44 – 292]; U=255107, p<2.2x10-16).

Group composition

The age and gender composition of the group was noted for 367 (56.9%) of the 645 events with the median group size of this subset being (1 [1 – 2]), similar to the overall group size reported above, but with a maximum group size of only 16 animals. For the events where group composition was unknown, group size was slightly, yet significantly, larger (2 [1 – 4]; U=61698, $p=2.9\times10^{-9}$), including 26/278 (9.3%) events consisting of more than 16 animals. More than half of the events where group composition was reported (55.6%, 204/367) consisted only of adult bulls (so-called 'bachelor groups'), 71.6% (146/204) of which were single animals. Sub-adults or calves, respectively, were only present in 9.5% (35/367) and 3.0% (11/367) of events where age/gender were reported. Of the total number of animals reported straying, adult bulls, adults cows, sub-adults and calves, respectively, represented 55.1% (378/686), 35.3% (242/686), 7.3% (50/686) and 2.3% (16/686) of these animals. A graphic depiction (proportional) of seasonal variation in group composition can be seen in Figure 4.2.

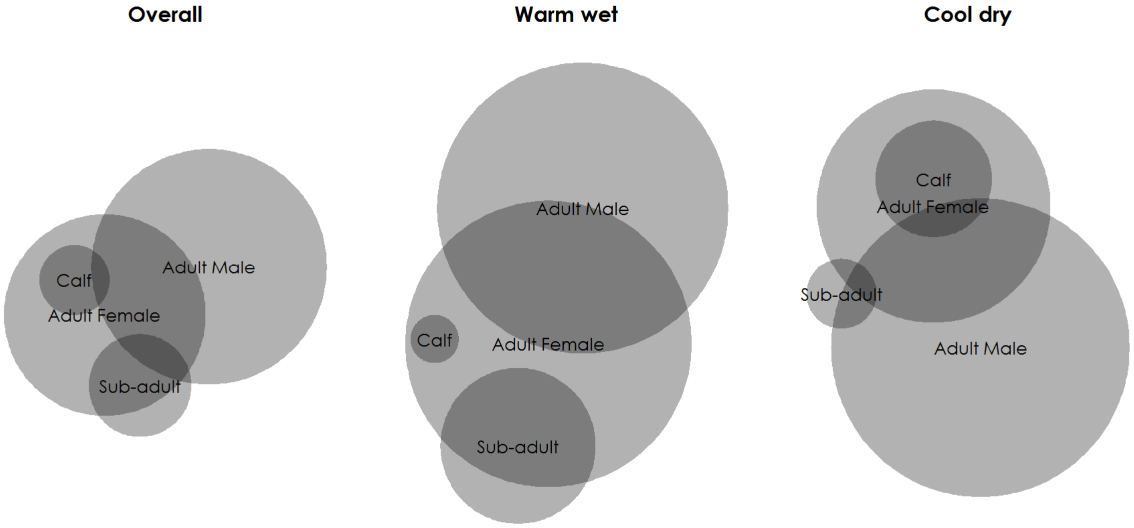


Figure 4.2 Euler diagrams depicting overall as well as seasonal group composition of stray buffalo events. The size of circles and their overlapping areas are relative to the age/gender composition of the average event. The Euler diagram for the 'Overall' study period represents 367 events, while the diagrams for the 'Warm wet' and 'Cool dry' seasons represent 159 and 180 events, respectively

Of the 315 events recorded with accurate spatial information, 64.8% (204/315) were recorded within one kilometre of the park fence and 76.2% (240/315) occurred within five kilometres of it. When looking at the temporal pattern in the distance to the fence (Table

4.2), high values (1.36 [0.31 - 12.05]) were found in May whilst below-average values were observed in the months from August to October. During the five month period of June-October aggregated over the entire study period, stray buffaloes were found significantly closer to the fence (0.3km [0.1 – 0.6]; U=14118; $p=1.8\times10^{-5}$), with only 5.2% (6/115) of events recorded further than ten kilometres from the park fence, in comparison with 18.0% (37/206) of events recorded further than ten kilometres from the fence during the other months (0.6km [0.2 – 6.8]; Table 4.2). Furthermore, only 3.8% (12/315) of the stray buffalo events were reported further than five kilometres from urban areas, as defined by the urban land cover class (1.2km [0.4 – 2.2]).

In 12.7% (40/315) of events did the stray animals (105/705) manage to pass through the protection zone with vaccination into the protection zone without vaccination (as delineated at the time of the event), 32.5% (13/40 events comprising 40/105 animals) of which were recorded during 2000/2001. Almost half (10/22) of the mixed age/gender groups that moved into the protection zone without vaccination (24/61 animals), did so during 2000/2001.

Resolution of events

In 76.6% of the events for which an outcome was recorded (467/610), resolution of the event included culling of all or some of the animals in the group. Culling was mainly employed for small groups (1 [1 – 2]). This is in contrast to the 6.2% of events where animals were chased back into the park (38/610), which was the preferred method for larger groups (10 [4 – 30]), especially when the animals were found relatively close to the fence (1.2km [0.1 – 3.8]). Translocation (2.2% of events; 13/610), on the other hand, was the main resolution in medium sized groups (3 [1 – 4]), especially when the animals were found relatively far from the park (9.9km [5.0 – 19.6]). In 5.1% of the events (31/610) it was reported that animals returned to the park by themselves. Of concern, however, is the fact that in 9.3% (57/610) of events animals could not be found after being reported, in some instances after other animals in the same group were removed or destroyed. For 5.4% (35/645) of all reported events, neither an outcome nor a follow-up report could be found on the fate of some of these buffaloes.

Suitability model and evaluation of disease control zones

Model performance, percentage contribution by each predictor variable and permutation importance of each variable are reported in Table 4.3. Both the full variable (model 1) and reduced variable model (model 2) performed well with AUC's of 0.954 (standard deviation= 0.011) and 0.955 (standard deviation= 0.014), respectively. Predictor variables and their relative contribution to each of the two models are shown in Table 4.3.

Seven predictor variables were retained in model 2, with the response curves for the four top ranked variables of model 2 shown in Figure 3. These curves show that the probability to encounter stray buffaloes is higher near urban areas (with a clear limit <10 km), closer to the FMD infected zone fence and permanent water sources (<10km). The mean threshold at which the true skill statistic of the model 2 was maximised for the binary classification of the suitability prediction, was 0.143 (0.017), with a minimum threshold of 0.121 achieved during one of the ten model replicates. Using this binary classification, 46.7% of the current protection zone with vaccination was deemed suitable for stray buffaloes, with 16.7% of the current non-vaccinated part of the protection zone being classified as suitable. The part of the inspection zone covered by our study area, had 1.7% of its area considered suitable for stray buffaloes. No suitable areas were found in the small portion of the FMD free zone covered by our analysis.

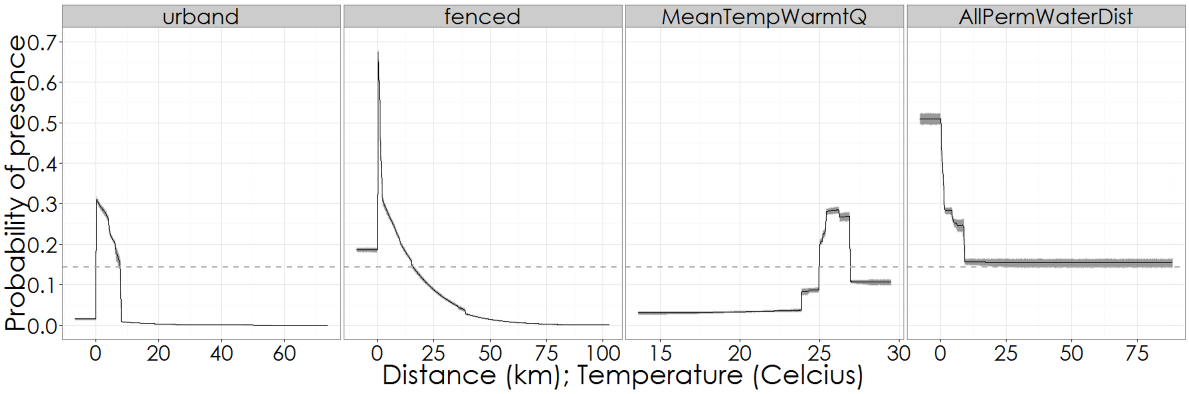


Figure 4.3 Response curves of the four highest ranking predictor variables used in the final maximum entropy model (model 2). Shaded areas represent the 95% confidence intervals of the ten model replicates. The dashed line represents the threshold for the binary su

In addition, a summary of all FMD outbreaks associated with stray buffaloes in South Africa between 1998 and 2008, are reported in Table 4.4.

Table 4.3 Predictor variables used for constructing the maximum entropy model and their relative contribution and permutation importance to the full variable (Model 1) and final, reduced variable (Model 2) models

		Model 1		**Model 2**		
Variable	**Description**	**Variable contribution (%)**	**Permutation importance (%)**	**Variable contribution (%)**	**Permutation importance (%)**	**Source**
urband	Distance from nearest urban area	37.9	62.4	38.2	60.2	2
fenced	Distance from FMD infected zone fence	36.3	25.9	38.2	27.9	1
AllPermWaterDist	Distance from permanent water source	8.4	1.5	8.5	1.6	2
MeanTempWarmtQ	Mean temperature of the warmest quarter	7.1	1.3	9.3	6.6	4
Isothermality	Isothermality	1.6	0.8	2.4	0.5	4
lcc	Land Cover	1.5	0.6	1.5	0.7	5
PrecipSeasonality	Precipitation seasonality (Coefficient of Variation)	1.5	1.4	1.8	2.5	4
MeanDiurnalRange	Mean diurnal range	1.2	0.9			4
PrecipDryQ	Precipitation of the driest quarter	1	0.4			4
Precipitation	Mean precipitation	0.9	1			4
MeanTempColdQ	Mean temperature of the coldest quarter	0.5	0.2			4
NDVIMax	Maximum normalised difference vegetation index (NDVI)	0.4	0.4			6
MeanTemp	Mean temperature	0.4	0			4
NDVIMean	Mean NDVI	0.3	0.4			6
AllSeasWaterDist	Distance from seasonal water source	0.3	0.3			2
PrecipWetQ	Precipitation of the wettest quarter	0.3	1.3			4
TempSeasonality	Temperature seasonality (Standard Deviation x 100)	0.3	0.9			4
Slope	Slope	0.1	0.2			3

Table 4.4 Summary of FMD outbreaks in livestock related to stray buffaloes in South Africa, 1998-2008

Outbreak district	**Nkomazi**	**Mhala**	**Vhembe**	**Mopani**	**Sibasa**
Index Case	2000/12/15	2001/02/01	2003/08/08	2004/06/26	2006/07/31
Last Case	2001/02/27	2001/05/30	2003/08/18	2004/11/19	2006/08/23
Season	Warm wet	Warm wet	Cool dry	Cool dry	Cool dry
Outbreak virus	SAT-1 (SAR/38/00)	SAT-2 (SAR/1-11/01)	SAT-2 (SAR/1/03)	SAT-2 (SAR/2/04)	SAT-3 (SAR/1-4/06)
Related buffalo viruses	KNP/22/96 (Lower Sabie) KNP/20/89 (Numbi Gate)	KNP/19/89 (Ripape) KNP/18/95 (Mondzweni) KNP/31/95 (Mondzweni)	KNP/5/91 (Satara)	KNP/19/89 (Letaba) KNP/06/03 (Shangoni)	KNP/01/02 (Nwarihlangari)
Distance from fence (Cases: day 1-7) median (minimum-maximum)	28.3km (28.3-28.3)	17km (4.0-26.7)	2km (1.5-6.2)	18.1km (6.7-26.1)	2.2km (2.0-2.3)
Period stray buffalo reported prior to outbreak (months)	9	2	~6	1-2	~6
Number of stray buffaloes reported	numerous	2 bulls	numerous	numerous	numerous
Cause of fence damage	Floods	Floods	Elephants	Elephants	Fence construction/ poor maintenance
Source	4,31	31,424,425	128,426,427	153	428,429

Discussion

In countries where FMD virus is harboured in wildlife hosts, as is the case in southern Africa, control of the disease is largely dependent on the ability to prevent these hosts from coming into contact with susceptible livestock, in conjunction with effective vaccination programs. This study presents data on African buffaloes straying from the KNP and APNR during an eleven year period (1998-2008) and gives insight into the group composition, especially age, spatial and temporal characteristics of these stray buffalo events and relates them to current disease control zones.

Officials interviewed during the study agreed that buffaloes are generally deterred by physical barriers such as fences and concurred with published reports that they mainly pass through gaps in the fence created by people, elephants (*Loxodonta africana*) or rivers[9,128,147,149]. Since 1995, when a general moratorium on the culling of elephants was instituted, the elephant population in the KNP has more than doubled and this increased density has been linked to increased fence damage[152]. Whilst a reasonably simple fence would contain buffaloes, elaborate fences are often required to prevent elephants from damaging the fence to such an extent that buffaloes can escape[149]. Of further critical importance is the maintenance of these fences, a lack of which can have a direct impact on disease risk[55,147,157]. Fencing is a contentious issue in areas with abundant wildlife[142], although the ecological impact of the KNP fence has been considered relatively small compared to disease control fences in, for example, Botswana[430]. The ecological impact of the KNP fence was mainly seen in specific subpopulations of blue wildebeest (*Connochaetes taurinus*), elephant and to some extent in zebra (*Equus quagga burchellii*) whose southeast/northwest migratory routes were impeded by the newly erected KNP fence. General abundance of natural and artificial water, compared to Botswana for example, might also have reduced the ecological impact of the KNP fence, as well as the dropping of fences between the KNP and APNR in 1993. Communal farmers are definitely aware of the role that the fence plays in disease control, and its benefits with regards to prevention of predation and crop damage by wild animals[145], but some also see it as an impediment to potential income generation through utilization of natural resources in conservation areas, despite the dire consequences when a lapse in maintenance of the fence occurs[431].

The substantial impact of the extreme rainfall that occurred in 2000 is noteworthy. This was the most severe flooding in at least a hundred years[432]. The damage that this flooding did to fences and the subsequent increased number of reports of buffaloes straying from the park is evident not only in the data presented here, but were also noted by a number of other authors, especially for the direct role it played in the first buffalo-related FMD outbreak in cattle in the KNP vicinity since 1983[9,29,31,128]. Even in years of normal rainfall, fence crossings of water courses are problematic, since proper construction is impeded by a poor substrate to anchor the fence and repairs are often delayed by the slowly receding water after seasonal rains[149]. So, while the number and the size of stray buffalo events could obviously be influenced by rainfall, this relationship is neither linear nor straightforward, as rainfall influences a number of different factors leading to buffaloes escaping from the park. On the one hand, large rainfall events will cause flooding, leading to fence degradation and thus providing buffalo the opportunity to escape from the park. Low rainfall on the other hand, will reduce the amount of vegetation, possibly tempting the buffalo to leave the park hoping to find better grazing. Moreover, fence crossings at rivers are easier to pass through during the dry season as a result of the dry riverbed.

Groups of buffaloes that strayed from the park were generally small compared to herds inside the KNP, especially the mixed age/gender groups. This is most likely due to smaller groups splintering off larger herds, either passively[51] or through circumstance, e.g. predators chasing herds into the fence, with some ending up on the outside[147]. It would therefore seem to be more of a ‘push’ rather than a ‘pull’ factor that causes these animals to egress. In the latter case, one would expect the whole herd to move out of the park, especially in a gregarious species like the buffalo[49].

Group composition is an important characteristic of stray buffaloes to consider, since current knowledge suggests that the ability to transmit FMD virus differs between buffalo age classes[28,61]. Adult bulls and mixed age/gender groups formed two very distinct categories among the reports collated, with the former predominating. Calves are considered to pose a very high FMD transmission risk[68,138], especially when these animals become acutely-infected with FMD during the period when they lose their maternally-acquired immunity[2,61]. This is typically occurs during the cool dry season[9,138] . Free-living buffalo herds consist of about 15% calves[49] (I.J. Whyte and P.C. Cross, personal communication, 2006), so the low percentage of calves reported among all the stray buffaloes where age/gender was recorded in this study (2.3% and present in only 3% of these events), could be considered a positive finding from a FMD risk point of view. Hedger[28] also implicated sub-adult animals as an age group with a likely elevated potential for shedding FMD virus. As with calves, this age class was underrepresented (more than four-fold) in the reports when compared to their expected fraction in buffalo herds (32%, I.J. Whyte and P.C. Cross, personal communication, 2006). Adult buffaloes can become persistently-infected with FMD virus[41] and these carrier animals can transmit infection to susceptible species, although it is considered a ‘rare’ event[28], under circumstances not yet exactly understood[9,28,41] and at a magnitude of risk much lower than that posed by acutely-infected animals[30,71]. This is also evident in the close proximity of persistently-infected buffaloes and various susceptible cloven-hoofed species in the KNP and APNR, without continuous outbreaks of clinical FMD or evidence of constant exposure in these species[45].While considered tenuous by some authors[9], FMD transmission through sexual intercourse between buffalo bulls and domestic cows has also been postulated[72].

In the case of transmission between buffaloes and impala, it is fundamentally density dependent[45], although this is yet to be properly defined and/or quantified in buffalo-cattle transmission. In all of the five FMD outbreaks that occurred between 1998 and 2008, associated with buffaloes from the KNP and APNR, buffaloes were reported to be roaming the area for extended periods, months rather than hours, days or weeks (Table 4.4), which could have provided the opportunity for 'prolonged and intimate contact' required for transmission as proposed by Thomson[2]. Most anecdotal evidence however indicates that when contact does occur, it is probably of a very brief nature (in the order of hours)[28,55]. As a further example, in a FMD transmission experiment, both interspecies (buffalo and cattle) grooming and avoidance behaviour were noted[30], making it difficult to predict 'affinity' between these species. Under natural conditions it is hypothesised that especially young buffaloes join cattle herds for 'companionship', while bulls are less likely to do so[55].

One possible explanation for the high concentration of stray buffaloes found very close to the fence could be that the reporting and resolution of these events were very efficient, such that buffaloes did not have time to wander large distances away from the park. Many of the officials interviewed, however, believe that the animals often tend to move along the fence, since they try to get back into the park soon after straying from it, even though only 5.2% of reports actually mention buffaloes being successful in achieving this. While the number of animals straying through the fence did not show any temporal pattern, the distance that they moved away from the park was significantly further during the months of November to May. This might be explained by the dense vegetation predominating during this period, which greatly reduces the chances of stray animals being sighted, especially along water courses and drainage lines where they often prefer to roam. Notably, the period when buffaloes move the shortest distance from the fence (June to October), coincides with the period of highest risk of acute infection in buffalo calves[61], which could be seen as a fortunate coincidence from a disease risk perspective. Of obvious concern are buffaloes that manage to move through the vaccinated into the non-vaccinated part of the protection zone, especially since mixed age/gender groups (including calves in some instances) predominated in achieving this. This presents a substantial risk to the fully susceptible livestock in these areas. The extreme rainfall during 2000/2001 further exacerbated this type of event.

The resolution of stray buffalo events is most often a pragmatic choice based on the size of the group, distance from the park, terrain, availability of equipment/vehicles/aircraft and the skill of those involved in the control action. We found that small buffalo groups, relatively far from the park, are generally translocated, while larger groups, if close to the park, are mostly chased back with the aid of a helicopter. In most instances culling of the stray animals is the most rapid and certain way of mitigating the risk that these buffaloes pose to both people and livestock.

The data presented here should be considered with caution since it is non-exhaustive and could potentially contain recollection and/or reporting bias. Reporting bias could arise due to the density and/or proximity of people (both residents and fence workers/rangers)[88,147]. This could have been exacerbated by an ostensibly successful incentive for rural residents to report stray buffaloes to authorities, in return for which the meat of any animals that are shot, is distributed among the immediate community (after being slaughtered and cooked under supervision of veterinary officials to ensure hygiene and safety for consumption as well as to mitigate any FMD transmission risk through offal and by-products). In this light, it is especially interesting to note that the distance at which buffaloes were reported from urban areas in this study by both the descriptive analysis (1.2km [0.4 – 2.2]), as well as model outputs, corresponded very closely to the distance at which communal farmers herded their cattle from urban areas (1.1km [0.4 – 2.3], also with less than 5% further than 5km; Chapter 3). Events at distances further than five kilometres from urban areas, or further than local farmers graze their cattle, are therefore most likely underreported. This bias might be further compounded by buffaloes' likely natural avoidance of urban areas and the lack of any information regarding the precise duration of time that the buffaloes spent outside the park. However, this reporting bias is probably only of concern in areas where cattle are not constantly accompanied by herdsmen or where animals are not kraaled (penned) every night. Caution should also be exercised in the interpretation of age/gender analyses, since lack of age/gender information in the events consisting of more than 16 animals could have caused false overrepresentation of especially bulls, which naturally occur in smaller groups.

Distance from the park fence and urban areas were also affirmed as important predictors by their large contribution to the final suitability model outputs. The role that distance from permanent water sources played as a predictor for stray buffalo events is noteworthy, especially when considering that the index cases (first week of outbreak) of the five stray buffalo associated FMD outbreaks during the study period occurred along five of the six major rivers (or one of their main tributaries) draining the infected zone. Based on these suitability predictions, it would seem that the current FMD protection zone is adequately established to detect stray buffaloes, although expansion of the vaccinated portion in certain areas would reduce the risk of FMD spread to unvaccinated livestock. In particular, these suitable areas for stray buffaloes in the non-vaccinated portion of the protection zone seem to occur as intrusions along the major watercourses draining the study area, especially its central and northern parts (Limpopo Province). However, the recent upgrading of the dilapidated electric fence along these northern parts of the infected zone to a high impact fence (albeit after the study period) should reduce stray buffalo events[151]. Caution should be practiced when interpreting these binary outputs since, from a practical point of view, a single buffalo could be enough to cause a FMD outbreak in livestock and such an animal could be an outlier in a dataset/model such as is presented here. Moreover, threshold selection in the binary consideration of suitability for a species has many limitations and should be carefully considered before implementation[433]. In this analysis, we did not directly consider factors such as fence type, permeability of fence river crossings, elephant density, buffalo density, fence maintenance, flooding events, etc. all of which could have a significant impact on the probability of stray buffalo events, since it fell outside the main aim of this study and requires a much more sophisticated modelling approach.

Although we derived useful information from this set of data, a central and standardised record keeping system to monitor stray buffalo events would greatly benefit disease control efforts in South Africa. This should preferably be done in close conjunction with a fence monitoring system that has been proposed by others[147], since no direct link between stray buffalo events and fence breaches is currently recorded. Such a data recording system should include at least detailed information on the time, location, group composition and resolution of stray buffalo events in a standardised format. In addition, information on the cause of the stray buffalo event and the area covered by the animal(s) while moving outside the park would provide authorities with a much better platform from which to make scientifically informed policy decisions, such as delineation of disease control zones. It would also improve communication and data sharing between the various official departments involved in the control of stray wild animals, which is not limited to buffaloes.

Conclusion

Although a relatively large number of buffaloes strayed from the endemic FMD zone in South Africa between 1998 and 2008, these animals seldom managed to cross through the vaccinated part of the FMD protection zone to where livestock were completely susceptible to the disease. Moreover, current knowledge suggests that young buffaloes are the animals at highest risk of transmitting FMD virus to livestock, although this age group represented less than 10% of the animals straying from the endemic FMD zone, which should decrease the apparent risk posed by these seemingly large numbers of stray buffaloes recorded. Current FMD control zones in South Africa seem adequate to detect stray buffaloes, but expansion of the vaccination zone in some areas could further reduce the risk of FMD spread that these animals pose.

Chapter 5

*A spatio-temporal probabilistic approach for predicting contact between African buffaloes (*Syncerus caffer*) and communal cattle adjacent to the foot-and-mouth disease infected zone of South Africa*

Chapter summary

In this chapter, knowledge gained in the former chapters is integrated to produce relative probabilities of stray buffalo and cattle contact adjacent to the foot-and-mouth disease (FMD) infected zone. This used to evaluate potential contact for the entire year, as well as each of the two seasons considered. Firstly, the habitat suitability of cattle derived via maximum entropy modelling in Chapter 3 is used evaluate overlap with areas suitable for stray buffaloes (developed in Chapter 4 and further refined here). In a next step, cattle density (Chapter 2) is incorporated in cattle suitability maps to further improve contact estimates Finally, permeability of the fence is estimated through incorporation of various factors affecting fence integrity, and this is included in a cost surface to simulate movement of stray buffaloes from the FMD infected zone to livestock areas along the least cost path. The habitat suitability approach estimated the highest risk of buffalo-cattle contact during the cool dry season, when cattle dispersal is greatest, hence overlapping with the constricted stray buffalo dispersal patterns detected during the same season. Incorporation of cattle density with their suitability to estimate abundance, switched the probability of buffalo-cattle to being highest in the warm wet season, mainly as a result of the concentration of high cattle numbers in preferred grazing areas and wider dispersal of stray buffaloes during this season. The least cost path approximations in combination with cattle abundance provide useful insight into possible 'hotspots' for buffalo-cattle contact along their movement paths. Finally, these model outputs are tested against past FMD outbreaks, four of which the suitability and abundance type risk models could correctly distinguish. The least cost path method was only able to estimate contact risk higher in outbreak areas versus non-outbreak areas in two of the outbreaks, and only considering the data outliers. The three methods proposed here can be applied practically to set up strategic vaccination programs as well as to identify potential corridors frequently used by stray buffaloes that could direct fence maintenance priorities.

Introduction

In South Africa, foot-and-mouth disease virus (FMDV) is endemically maintained through viral persistence of the three Southern African Territories (SAT 1,2 and 3) FMDV strains in about 60% of the free-living African buffaloes (*Syncerus caffer*)[3,28] occurring in the Kruger National Park (KNP) and adjoining private and provincial nature reserves (APNR). The significance of FMDV maintenance in wildlife lies in its potential transmission to livestock and the presence of the disease, rather than its direct clinical effect. Outbreaks of foot-and-mouth disease (FMD) in livestock have serious economic consequences for the country, with especially trade embargoes costing the national economy in the order of millions of dollars[60,107,108] . Since elimination of the virus would entail eradication of the host, this is not a viable option for FMD control in the region. Separation of wildlife reservoir hosts and susceptible livestock species through physical barriers and vaccination forms the cornerstone of FMD control in RSA. According to the prescriptions of the World Organisation for Animal Health (OIE), RSA has been divided into (i) a FMD infected zone (where FMDV is endemic in persistently-infected buffaloes), (ii) a protection zone along the outside of the FMD infected zone and (iii) a free zone[125,126]. The FMD infected zone is cordoned off by a wildlife fence, nearly 800km long, while cattle in the protection zone directly adjacent to the FMD infected zone (the so-called 'FMD protection zone with vaccination') are vaccinated bi- to tri-annually against the SAT strains of FMDV. Fencing, as a means to isolate wildlife populations, remains an effective yet controversial control measure[144,434].

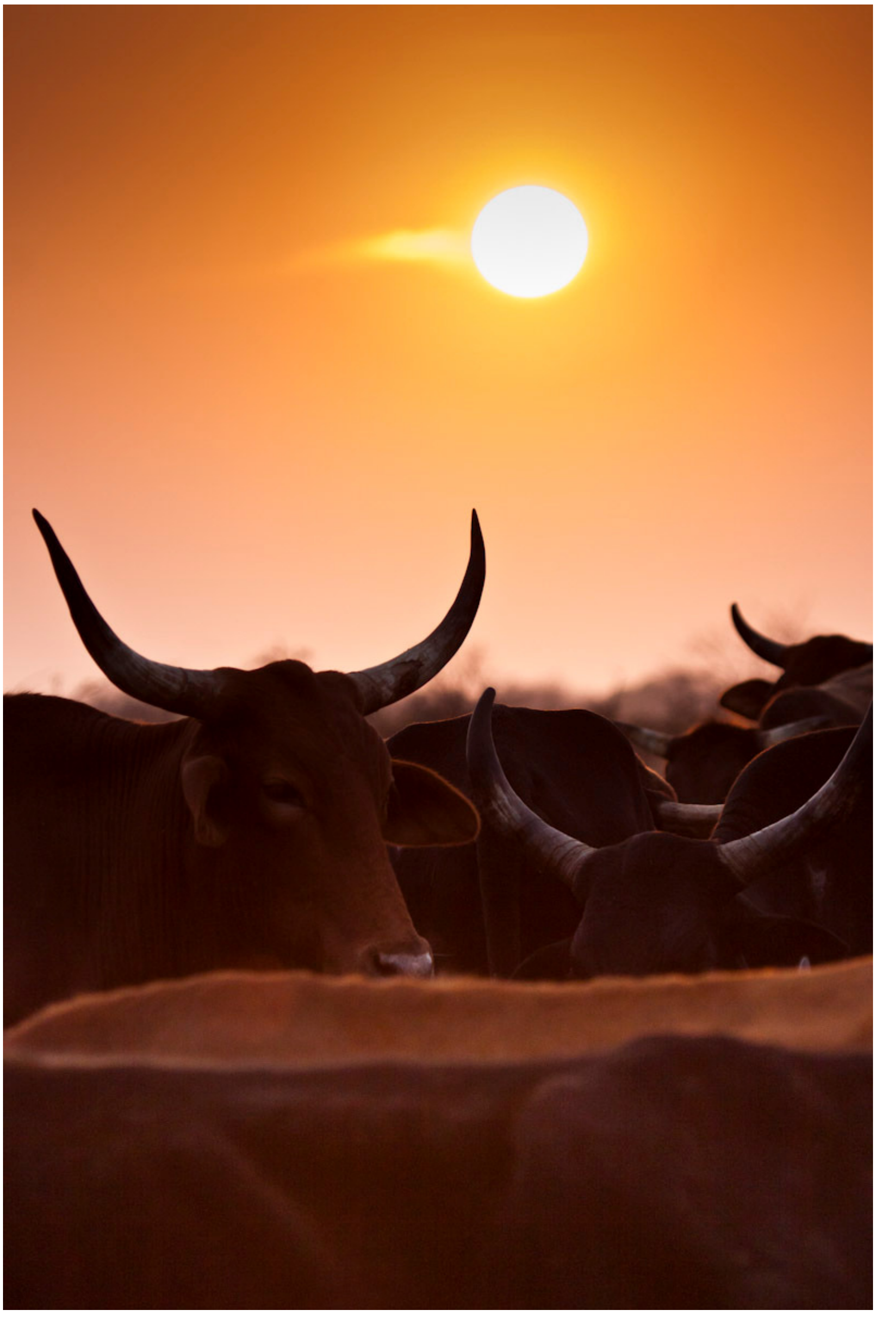
Neither fencing nor vaccination is a perfect means of FMD control, and between 1998 and 2008, more than 3000 buffaloes managed to escape from the KNP and APNR, with five outbreaks of FMD occurring in livestock during the same period that were associated with buffaloes moving through compromised game fences (see Chapter 4 for more detail). Whilst long distance airborne transmission is unlikely in southern Africa due to environmental conditions[4,15,57], two close-contact pathways of transmission have been suggested: (1) through contact between acutely or persistently-infected buffaloes and cattle or (2) through sexual transmission when buffalo bulls mount domestic cows. Acutely-infected buffaloes excrete virus through similar routes and in similar amounts to acutely-infected cattle, but potentially for longer periods [30,33]. Although transmission from persistently-infected buffaloes to cattle has been demonstrated[2,10,36,58], Thomson[2] reported that these persistently-infected buffaloes transmit infection poorly and probably 'only after prolonged and intimate contact', with transmission probably only likely when the ratio of susceptible to persistently-infected is high (e.g. in unvaccinated herds). Prolonged contact was also alluded to in the recent buffalo associated FMD outbreaks in RSA (Chapter 4). Anecdotal evidence, however, suggests that in most cases contact between buffaloes and cattle is rare[87], and of a very brief nature[28,55]. That being said, the principal requirement for transmission between buffalo and cattle in this region remains contact between these species, which is our main departure point for estimating FMD risk. The probability of such 'contact', even if only a relative measure, can then be adjusted for a number of reservoir host, susceptible host and pathogen parameters *post hoc* to seek more accurate estimates of transmission risk.

Habitat overlap has been implicated in disease spread between different species before[285,435-437]. Having already constructed habitat suitability models for cattle (Chapter 3) and stray buffaloes (Chapter 4) in the FMD protection zone, suitable habitat overlap can be interpreted here as a proxy for probability of contact. Furthermore, cattle density, proven to be heterogeneous between the three intensive study sites as evaluated in Chapter 2, could be incorporated into these suitability models to adjust the relative probability of contact according to cattle density. In the absence of data on the movement of stray buffaloes, other than their point of destruction or removal, use of simulated movement paths of stray buffaloes could also be considered for evaluating potential contact between cattle and buffaloes. Permeability of the disease control fence around the FMD infected zone was not explicitly considered in Chapter 4, and should be incorporated in the simulation of stray buffalo dispersal. The fence around the KNP was originally constructed as a disease control barrier between cattle and buffaloes in the early 1960s, when it was realised that buffaloes are the maintenance host of FMDV and the cause of severe outbreaks in the cattle population adjacent to the Park[55,177]. During the past four decades, however, the KNP fence has undergone several structural changes as fence technologies as well as knowledge of disease transmission pathways and host behaviour has increased (e.g. implication of jumping species such as kudu, *Tragelaphus strepsiceros,* in FMD outbreaks led to the standard height of fences being increased from 1.8m to 2.3m in Zimbabwe[57]). The latest fence type to be constructed along 'problem areas' of the KNP boundary since 2007, is 2.4m high and consists of I-beam steel posts, thick cable and barbed wire to withstand severe challenge, especially from elephants. Yet, this fence is without electricity to avoid the high maintenance burden and associated problems in supply of electrical current[147,149] (D.F. Keet personal communication, 12 January 2009). By the end of 2013, approximately 140km of the KNP fence was replaced by this type of fence, mainly along the northern parts of the FMD infected zone, with construction continuing and upgrades also planned for the southern part of the FMD infected zone. While apparently highly effective, the cost of such an elaborate fence is prohibitive (US$12000/km)[144,149]. People are considered to play a major role in fence breaches by buffaloes[147]. The human factor is however a complex one, involving more than just vandalism and theft[149]. Probably the most important factor in fence integrity is its maintenance[73,103], especially speediness of repairs[20,157]. Another major influence on fence permeability is elephants, often leaving a gap in the fence after breaching it in search of water[152], food, maroela fruits[143], or just for the sake of exploration[103,147]. The weaker structure of fence river crossings (aptly termed 'sacrificial' fences), is another common cause of fence breaches, especially after heavy rains in flood-prone areas[149]. Nevertheless, the reason for buffalo egress from game reserves into livestock farming areas remains obscure (Chapter 4), even though evidence exists to show that they prefer the habitat inside reserves to communal land[438]. Hence, a better understanding of the underlying mechanisms of buffaloes' dispersal outside their normal refuge is critical to be able to predict where they might share space with livestock susceptible to the diseases where buffaloes are implicated[148].

From an ecological perspective, barriers and corridors are seen as the two extremes of landscape connectivity[439,440], posing an interesting dichotomy to the probability of contact between cattle and their wild relatives. On the one hand, you may expect considerable overlap in habitat choice (Chapter 3 and Chapter 4)[370], whilst on the other hand, the disease control fence forms an almost impermeable barrier keeping these species apart. The corridor/barrier concept is well established in conservation biology, and has been widely applied to conservation planning through landscape connectivity assessments[441,442]. One of the methods commonly used to identify corridors, is the 'least cost path' (LCP) method (also known as 'cost-distance')[443]. LCP identifies the path along which the total cost (or resistance) in the landscape is the least from origin to destination[443]. The combination of LCP with maxent suitability models has performed well as a method to identify wildlife movement corridors[444,445]. LCP, however, makes the underlying assumptions that there is no distance constraint, that the animal has perfect knowledge of the entire landscape and that the LCP is the most likely path the animal would have taken[443]. Other methods such as circuit-based theory[446] and flow connectivity[447,448] have also been used to assess landscape connectivity. While some have implicated corridors in disease transmission[435,436], others have cleverly exploited the corridor/barrier concept to control disease[449]. Also, more intensive use of corridors occurs in the landscape where barriers become permeable ('bottle-neck' effect), which is of pertinence here[439].

Over the past 15-20 years, advocacy for more amenable international sanitary standards applicable to commodity based trade (CBT) has increased[114,450,451]. This is opposed to currently preferred trade restrictions based on rigid geographic disease control zones, which come at massive financial and logistical cost to governments aiming to export livestock derived products[452]. Although this alternative perspective on trade would give rural communities access to markets they could not consider before[109,111], it would likely require a substantial improvement in disease surveillance and control to minimise disease outbreaks. This could entail increased frequency of surveillance in high risk areas (as determined by prevailing conditions) to ensure early detection of outbreaks, supported by strategic vaccination campaigns, with the aim to reduce outbreaks to an acceptable minimum for those affected. Disease eradication when the maintenance host is an iconic wildlife species is unlikely, and finding practical solutions to ensure co-existence between these species is important[32,112]. Improved knowledge of buffalo-cattle contact will not only inform surveillance for FMD, but also a number of other diseases implicating buffaloes as the host (bovine tuberculosis, brucellosis, theileriosis, anthrax, to mention a few)[148].

Here a probabilistic approach to identify areas and periods of buffalo-cattle contact is proposed, with application in the planning of strategic disease control programmes. The approach is also tested against recent FMD outbreaks in the study region.



Materials and Methods

Study area and temporal window

The study area considered here is the same as the study region and three intensive study sites described in Chapter 3. In the larger study region, two zones were considered: Firstly, the FMD infected zone as source of persistently- or perhaps acutely-infected buffaloes, and secondly, the area adjacent to the FMD infected zone where cattle can be found, mostly inside the FMD protection zone. Since only buffalo-to-cattle transmission is considered here (and not cattle-to-buffalo or to/from other species), areas not currently utilised for cattle farming were not included.

The definition of seasons is similar to former chapters, being 'warm wet' (April – September) and 'cool dry' (October – March). Three temporal windows are considered, being each of these seasons and the entire year ('all year').

Maxent modelling environment

Maxent has been described and discussed in detail in Chapter 3 and Chapter 4 where habitat suitability models were created for stray buffaloes and cattle (Appendix A). Here, maxent is again employed to expand Chapter 4's stray buffalo model, as well as to add habitat suitability models for buffaloes inside the FMD infected zone. As before, the 'maxent' function of the 'dismo' package[453] of the R Statistical software[206] was used.

All models and any derived layers were projected onto a standard template of 269.63m x 269.63m, spanning the study region, and originally based on a MODIS image[201], being the coarsest resolution of the directly measured predictor variables used. Even though WorldClim[214] data had a coarser resolution (1km), these data were interpolated and not directly measured at the pixel level. Hence, WorldClim data were resampled to a higher resolution without interpolation (i.e. 'nearest neighbour' resampling).

Stray buffaloes

Two modifications were made to the final stray buffalo suitability model developed in Chapter 4, to enable better integration with the cattle (see Chapter 3) and FMD infected zone buffalo suitability models (see later). Firstly, the 10 000 random background points were restricted to the areas outside the FMD infected zone where cattle occur, rather than the entire region. Secondly, the presence data were categorized according to season, and a model was developed for each season in addition to the whole-year one. All other settings and predictor variables remain the same as the final model described in Chapter 4, including the use of tenfold cross-validation. Stray buffalo habitat suitability output maps (Appendix B) were created using ArcGIS 10.0[355].

Buffaloes inside the FMD infected zone

For buffaloes inside the FMD infected zone, sightings of buffaloes recorded by ranger staff of KNP were used as presence points[326]. These sightings are routinely recorded during foot and vehicle patrols using handheld, GPS-enabled, digital recording devices and the freely-available CyberTracker software (http://www.cybertracker.org/)[454]. Spatial accuracy and observer offset of these data were not available, but are assumed to be within the limits of the pixel resolution employed for analyses. Sightings recorded between 1 January 2008 and 31 December 2009 (two years) were used. These data suffer from two main sources of bias: firstly, the recording effort in each of the 22 ranger sections in KNP differed, and secondly, most of these sightings were recorded from tourist and management roads, although some were also recorded during foot patrols. Hence, to counter these biases, a bias correction grid[303] was created by combining a rescaled (0-1)[d] layer reflecting the effort of each ranger section (based on the total number of sightings during the period) and a normalised (0-1), inverse distance-from-roads layer. An equal number of background points to the number of presence points were then randomly chosen, weighted against these biases (using the probability weights setting of the 'randomPoints' function of the 'dismo' package). As with the other maxent models (Chapter 3 and Chapter 4), ten-fold cross-validation was used[347] and the model was allowed to iterate up to 500 times to approach convergence with the 'auto features' setting selected. For the two seasonal models, the regularization parameter was set to five, to avoid over-fitting[455], whilst the all-year model's regularization was left at one. For each model, the receiver operating curve (ROC) was determined, and the area under the curve (AUC) was used to assess model performance[295]. Predictor variables were selected in the same way as described for cattle distribution in Chapter 3, using a multivariate environmental similarity surface (MESS)[352] and the variance inflation factor[456]. In Table 5.1 these predictors are listed with the percentage of the FMD infected zone for which they could be used for meaningful prediction (positive MESS values). VIF values should preferably be less than ten. The VIF values after variable selection are also shown to confirm proper reduction in correlated variables.

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[d] 'Rescaled (0-1)' here refers to feature rescaling on a continuous scale between zero (minimum) and one (maximum). Its definition and use is consistent throughout this chapter

Table 5.1. Predictor variables considered for the buffalo maximum entropy modelling. VIF-2 shows the variance inflation factor after variable selection.

Predictor	MESS	VIF	VIF-2	Description	Comment	Source
AllPermWaterDist	99.62%	1.37	1.20	Perennial rivers, pans, dams, boreholes for animal consumption, drinking troughs and waterholes (in use during 2009)		197,326
AllSeasWaterDist	99.50%	1.23	1.10	Non-perennial rivers, pans, marshes/vleis, springs		197,326
DEM	100.00%	11.19	2.87	Elevation (m) derived from 30m Digital Elevation Model		213
Isothermality	99.94%	25.54	-	Mean diurnal range divided by the annual temperature range	Dropped in favour of (Difo) MeanDiurnalRanage	214
LandCover	100.00%	NA	NA	(MESS not applicable to factors) Area under land cover classes represented in presence data)		205
LandCoverRecl	100.00%	NA	NA	Reclassification of LandCover (MESS not applicable to factors)		205
LST	99.93%	2.02	1.96	Land Surface Temperature (Celsius) - Actual values at most recent date in dataset		201
MeanDiurnalRange	100.00%	21.14	3.44	Mean diurnal temperature range (the difference between the monthly maximum and minimum temperatures)(Celsius x 10)		214
MeanTemp	99.99%	480.49	-	Annual mean temperature (Celsius x 10)	Difo LST/MeanDiurnalRanage	214
MeanTempColdQ	99.98%	706.02	-	Mean temperature of the coldest quarter of the year (Celsius x 10)	Difo TempSeasonality	214
MeanTempWarmtQ	100.00%	251.98	-	Mean temperature of the warmest quarter of the year (Celsius x 10)	Difo TempSeasonality	214
NDVI	100.00%	2.73	2.42	normalised difference vegetation index - Actual values at most recent date in dataset		201
NDVIMax	99.96%	6.11	5.08	10 year maximum NDVI for period 2001-2010		201
NDVIMean	99.98%	7.32	6.71	10 year mean NDVI for period 2001-2010		201
PrecipDryQ	99.92%	44.73	-	Total precipitation of the driest quarter of the year (mm)	Difo PrecipSeasonality	214
Precipitation	100.00%	326.41	-	Annual total precipitation (mm)	Difo NDVI	214
PrecipSeasonality	99.67%	86.64	2.76	Also called the coefficient of variation - standard deviation of monthly precipitation estimates expressed as a percentage of the annual mean precipitation		214
PrecipWetQ	100.00%	166.75	-	Total precipitation of the wettest quarter of the year (mm)	Difo PrecipSeasonality	214
Slope	99.99%	1.29	1.20	Slope (degrees) calculated from DEM		213
TempSeasonality	99.97%	275.00	2.89	Temperature coefficient of variation - standard deviation of the monthly mean temperatures expressed as a percentage of the annual mean. Degrees Kelvin is used to avoid dividing by zero		214

Fence permeability

A static layer to represent fence permeability (*FP*) at the beginning of 2009 was created by taking a number of factors into consideration. Fence location and structural design were derived from a structural survey of the FMD infected zone fence conducted by the Department of Agriculture, Forestry and Fisheries during 2007[421] and updated to 2009. Additional information was also obtained from Jori et al.[147]. International boundaries were not considered in this study, and where international boundaries intersected the study region, their permeability was set to zero (being completely impermeable). Three main fence types (*FT*) were categorised (Figure 5.1):

- 'I-beam and cable' - being a very robust 2.45m high fence constructed from I-beam steel straining posts, five strands of 13mm cable and barbed wire[149].
- 'Railway and cable fence' – being an old 1.8m fence that has been heightened in some places to 2.4 metres. It is constructed of steel railway track straining posts and four 13mm cable strands with barbed wire and wire mesh.
- 'Game fence' – being mostly 1.8-2.4m high and constructed from a variety of fencing materials, the most common version having 130mm steel straining poles, interspersed with steel Y-standards and having 22-wire strands. Most of these fences are electrified, or at least are supposed to be electrified.

Figure 5.1. The three fence types considered (from left to right): I-beam and cable; Railway line and cable and Game fence.

For each of these fence types, their vulnerability to damage caused by elephants (*EV*), their likelihood to be vandalised through material theft by people (*HV*) and their dependence on maintenance (*MD*) was estimated in broad classes based on expert knowledge and field observations (Table 5.2; personal observation and [88,147,149,457]).

Table 5.2. Vulnerability of different fence types for fence permeability modelling

	I-beam & Cable	Cable & Railway	Game fence
Human vulnerability (*HV*)	0.2	0.5	0.5
Elephant vulnerability (*EV*)	0.1	0.2	0.5
Maintenance dependence (*MD*)	0.1	0.4	0.6

Elephant pressure (*EP*) on the fence was estimated through averaging the annual density of elephants between 2001 and 2010, using annual census data[326]. Density was calculated for each year using the kernel-based 'density.ppp' function with edge correction enabled (R 'spatstat' package[458]) and bandwidth was set at 10km, based on daily walking distances reported for elephants[459]. Edge correction is an important step, since the values at the edge are precisely what are of interest here. A mean of the ten density rasters was created and rescaled (0-1; 1 being the highest relative elephant density).

Potential human 'pressure' on the fence (*HP*) was approximated through a rescaled (0-1), inverse distance from urban areas layer[197] (zero being furthest from urban areas and hence low human pressure).

Maintenance effort (*ME*) of different portions of the fence was subjectively determined on a scale between 0-1 (1 being perfectly maintained). The timing of fence repairs is a critical component of fence integrity to consider[147,157,166], although it was outside the scope of this study to simulate and/or quantify timing and efficiency of fence repairs, other than through consideration of what is inherently incorporated in *ME* or derived from available information[147,149].

Fence sections with/without electrification were categorised as 0/1 (EL). When working properly (>7kV), electric fencing is deemed highly efficient against elephants[149]. However, since electric fencing is highly dependent on *ME*, efficiency of electrified fence portions were adjusted for the *ME* of that portion and rescaled (0-1; 1 being perfectly maintained electrification).

Even though the height of the fence was recorded, it was not considered, since the only host species of concern in this study was buffaloes, for which relatively low fences (1.0-1.2m) are effective[156]. Fence height would however have been of importance if jumping species were considered[20,25,57]. Apart from a few very small portions of fence lower than 1.8m (mostly adjacent to land without cattle), fences were generally higher than 1.8m.

All fence river crossings (*RC,* Figure 5.2) were classified according to the nine hydrological index categories derived at a quaternary catchment level[460] (1-9; with the higher categories being more inclined to flash flooding). These values were then rescaled (0-1).

Figure 5.2. Three examples of fence river crossings: A net across a large river (Letaba) and two sacrificial fences with varying degrees of reinforcement

Even though this *FP* model did not account for daily rainfall or even actual flooding events, these *RC* are notoriously weak due to the poor substrate in which they are built as well as their often delayed repairs due to flowing water and poor maintenance efforts. *RC* was set to override all other fence permeability parameters. Final *FP* was calculated as follows:

$$FP = (1-HV*HP + 1-EV*EP) * (1-MD*ME) + (0.5*EL) \text{ overlaid by } RC = HI*ME$$

FP was then rescaled (0-1), with zero being completely permeable and 1 being completely impermeable. Currently, only a single fence permeability layer is employed for all seasons.

Cattle abundance

To create a more realistic distribution of cattle, cattle suitability maps (Chapter 3 and Appendix A) were converted to cattle abundance maps (Appendix C). In this step, the assumption is made that habitat suitability and cattle density are linearly correlated. Although this is not always the case[305], it is considered realistic for its application in the given context. December 2008 cattle densities and numbers, based on Thiessen polygon[198] boundaries of each livestock inspection point (IP) were used to calculate abundance (see Chapter 2). To determine the scale factor for each IP polygon, the number of cattle occupying that polygon was divided by the sum of the logistic habitat suitability values in the polygon. This was done for each of the ten model replicates of each of the three temporal windows. This scale factor was then multiplied with its corresponding cattle suitability layer to create an abundance layer, giving the potential number of cattle per pixel, before being rescaled (0-1). Cattle abundance maps (Appendix C) were created using ArcGIS 10.0[355].

Stray buffalo–cattle contact probability and least cost path simulations

To simulate the relative probability of contact between stray buffaloes and cattle, three approaches were used. In all of these approaches the central assumption was that suitability is related to probability of presence. The first approach ('suitability contact risk', SCR) simply multiplies the suitability for stray buffaloes (as derived from the stray buffalo habitat suitability model) by the cattle suitability layers of the corresponding temporal window. This was done for each of the ten model replicates of both species (cattle and stray buffaloes). In the second approach ('abundance-corrected contact risk', ACR), the cattle suitability layers were replaced by the rescaled cattle abundance layers, before being multiplied by the stray buffalo suitability layers for each of the temporal windows. These first two approaches do not take the permeability of the fence into consideration, other than what is inherently included in the stray buffalo suitability models, even though the stray buffalo suitability model made no assumptions about the point of exit from the FMD infected zone or the path that stray buffaloes followed before being located (also see Chapter 4).

In the third approach ('least cost path contact risk', LCPR), aimed at complementing the first two approaches, the permeability of the fence and the potential paths that stray buffaloes could follow out of the FMD infected zone were incorporated. For each of the ten model replicates of stray buffalo suitability (*StrayBuff*), 1000 points were randomly selected from the areas where cattle can occur, weighted according to *StrayBuff* ('randomPoints' function, R 'dismo' package[453]). These points were considered to be 'destination' points, where stray buffaloes hypothetically ended up outside the FMD infected zone. These 'destination' points were not constrained in their distance from the FMD infected zone, since this was already a predictor of *StrayBuff*. Similarly, 1000 points were chosen inside the FMD infected zone, weighted according to the buffalo habitat suitability layer (*ParkBuff*). These points acted as hypothetical 'origins' for stray buffalo events. Each 'destination' point was then paired with an 'origin' point, but due to the vast area covered by the study region, pairing of 'destinations' and 'origins' had to be constrained to be more realistic. So, for each 'destination', it's ten nearest 'origin' neighbours were identified ('nncross' function of the R 'spatstat' package[458]). One of these ten neighbours was then randomly selected as the 'origin' to be paired with the 'destination'. Next, a cost surface was created by combining the *ParkBuff*, *StrayBuff* (ten replicates each) and the fence permeability (*FP*) layer. Since all these layers were scaled from 0-1, they were combined as follows to convert the fence into a more realistic barrier in the landscape:

$3*(1-\mathit{ParkBuff}) + 3*(1-\mathit{StrayBuff}) + (2+\mathit{FP})$

These cost layers were created by applying the mean 'transition' function of the R 'gdistance' package[461] in eight directions, before being geo-corrected ('geoCorrection' function in 'gdistance'[461]) specifically for cost path analysis ('c' type). This resulted in ten cost surfaces for each model type and each of its temporal windows. For each origin-destination pair the LCP was then calculated, i.e. the path between the two points for which the sum of cost layer pixels (in eight possible directions per step) along this path were the least out of all the possible paths. This resulted in 1000 LCPs for each of the ten model combinations of each temporal window. The results were produced in the form of sets of ten raster images, each pixel representing the number of times that pixel was used as part of the 1000 LCPs of that model replicate. These ten raster images were then rescaled and used to calculate a mean and standard deviation of possible LCPs for stray buffaloes. To derive the probability of contact with cattle, the rescaled LCP layers were multiplied by the rescaled cattle abundance layers to produce a relative probability of contact between 0-1.

Contact probability evaluation and application

Maps of each modelling approach's outputs during each of the three temporal windows were constructed (mean probability of contact and associated standard deviation)[355]. These were cropped to each of the three intensive study sites, since too much detail was lost when mapping the entire study region. Since these outputs were left-skewed (containing a large number of very low values), mapped outputs were coloured according to data deciles, which allows for the best visual interpretation.

Comparisons between the SCR and ACR estimates of the cool dry and warm wet season of the entire study region as well as the three intensive study sites (North, Central and South) were compiled. A two-sided Mann-Whitney-Wilcoxon rank sum test, for which the W statistic and p-value are reported, was used to compare the two seasons of each risk model.

For each of the IPs located inside the three intensive study sites (Chapter 2 and Chapter 3), with their boundaries defined as for the calculation of cattle densities (Chapter 2), the pixel-based probability values of all ten model replicates from the SCR and ACR estimations were summarised per temporal window by box-and-whisker plots for each IPs area. In this first plot, outliers were left out to enhance the interpretation of the box-and-whisker plots. Even though central tendency is the main basis for assessing the probability of contact at each IP, important clusters of high risk could be 'hidden' in the outliers, so in addition to the first graph, an additional box-and-whisker plot was constructed from only the pixel values in the 95th percentile (i.e. the 'outliers'). This 95th percentile method was also preferred to assess the LCPR outputs, since these formed narrow routes through the IP areas, and they would have provided very little information through central tendency alone.

Evaluation of risk prediction for past FMD outbreaks

Data from five recent FMD outbreaks in cattle (2001-2009) that were associated with stray buffaloes and fell within the study region (Chapter 4, as well as Nsikazi outbreak[462]) were plotted against the contact probability outputs from the three model types. Since compulsory inspections at IPs occur at a weekly frequency in the FMD protection zone with vaccination, FMD cases presented at these IPs during the first eight days of each outbreak were plotted (see Appendix E)[355]. Note that actual normalised difference vegetation index (NDVI) and land surface temperature (LST) values of the cattle suitability models were not updated for the exact dates of these outbreaks; since they contributed very little to the suitability predictions (Chapter 3). An important assumption underlying this analysis is that vaccination coverage is homogenous throughout the area studied, mainly due to a lack of accurate vaccination data for each outbreak. Furthermore, lesion ages were not available in all the case data, and therefore the assumption that the earliest recorded case is the index case, might be tenuous, hence the eight day period to cover at least two rounds of inspection during the first 'wave' of infection. Yet another caveat is that actual buffalo-cattle contacts were not recorded during these outbreaks, even though buffaloes were present in these outbreak areas for up to six months before outbreaks occurred (Chapter 4). Thiessen polygons for all IPs around the FMD infected zone (similar to those mentioned earlier and in Chapter 2) were used to extract pixel values for IP areas where clinical FMD cases were reported ('outbreak' IPs), as well as for IPs within a 10km radius of these 'outbreak' IP areas ('non-outbreak' IPs). For each outbreak (named after the district in which it occurred), the probability values were compared between 'outbreak' and 'non-outbreak' IP areas. Since a normal distribution of values could not be attained through data transformation, due to the large number of outliers, a one-sided Wilcoxon-Mann-Whitney rank sum test was used. The test statistic (W) and p-value is reported. For the LCPR comparisons, important differences were expected to lie in the extreme values, so in addition to the area-wide comparison, the 95th percentile values of these 'outbreak' and 'non-outbreak' IP areas were also compared using the same statistical test.

Software

Apart from the specific R packages and functions already mentioned, the R 'raster'[463], 'rgdal'[464], 'sp'[465,466], 'maptools'[467], 'SDMTools'[468] and 'ggplot2'[342] packages were all extensively used for elementary data management tasks, analyses and creation of figures. Maps were constructed using ArcGIS ArcMap 10.0[355].

Results

Stray buffalo suitability

Variable selection for the stray buffalo suitability model was done elsewhere (Chapter 4), and the variance inflation factors (VIF) of those variables that were retained, were all smaller than two (less than ten is desired). For the cool dry season, 150 presence points were available and for the warm wet season, 159. All three of the temporal windows' models performed well, with AUC values of 0.921±0.03, 0.929±0.046 and 0.924±0.042 for the whole year, cool dry and warm wet season, respectively. Habitat suitability maps are shown in Appendix B. Figure 5.3 gives an overview of the variable contributions and importance, with the warmest quarter's mean temperature, precipitation seasonality and fence distance being the most important predictor variables throughout. Figure 5.4 depicts the jackknife assessments of the same variables (based on AUC-influence).

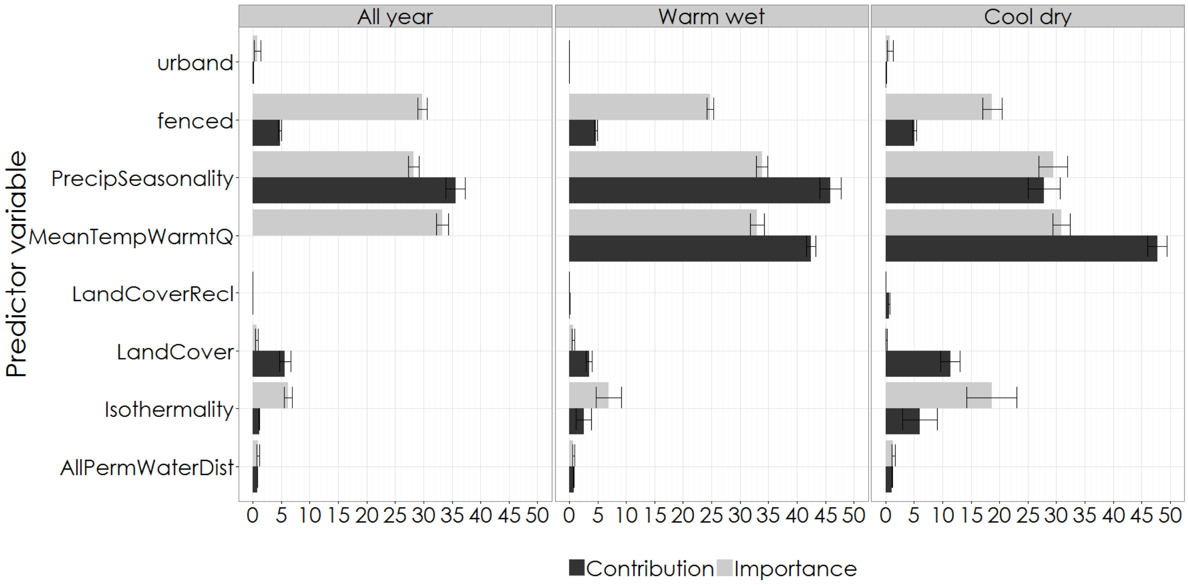

Figure 5.3. Stray buffalo suitability model variable contribution and importance

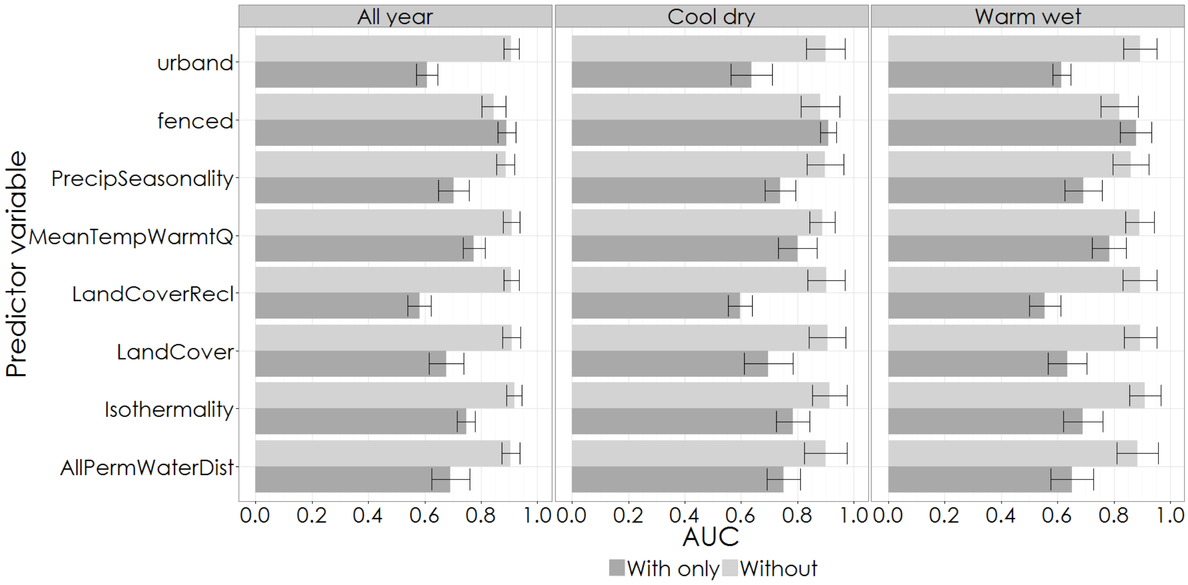

Figure 5.4. Predictor variable influence on stray buffalo habitat suitability model AUC

FMD Infected Zone buffalo suitability

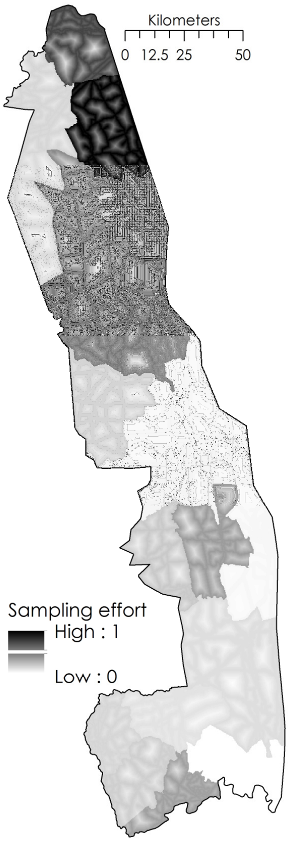

Figure 5.5. Bias grid for buffalo background points

The suitability model for buffaloes inside the FMD infected zone were based on 13 872 sightings recorded throughout the KNP (cool dry season: 7 699; warm wet season: 6 173). The bias grid used for equal background point selection is shown in Figure 5.5)

Variable selection was based on VIF only, since all predictors had good MESS coverage across the FMD infected zone (Table 5.1).

Model performance was very good for habitat suitability of buffaloes inside the FMD infected zone, with seasonal AUC values above 0.90 (hence the regularization) and the whole-year model performing only satisfactorily, despite regularization, at 0.72 (Figure 5.6).

Variable contribution and importance (Figure 5.7) for these models showed a marked difference between the whole-year model and the seasonal ones, with the seasonal models being informed almost exclusively by NDVI and LST, whilst distance to water, land cover and temperature were the higher ranking variables for the whole-year model.

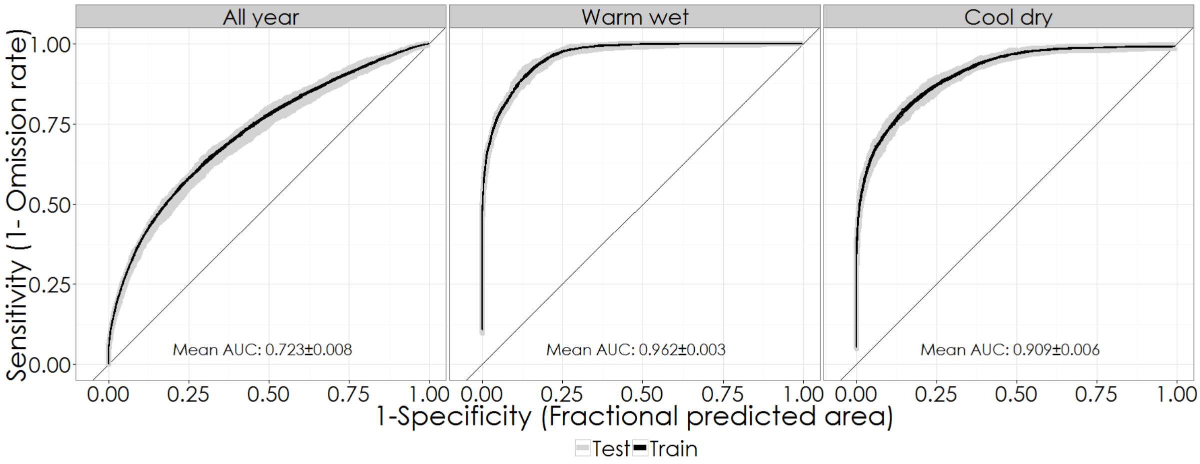

Figure 5.6. Buffalo maxent model ROC curves and associated AUC values (grey band depicts range)

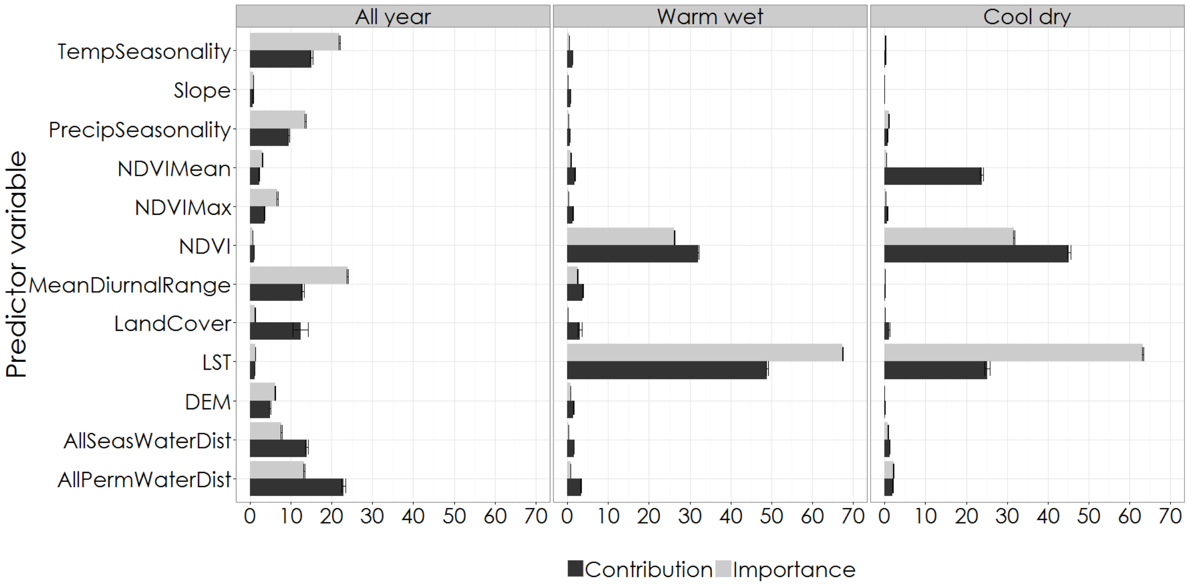

Figure 5.7. Buffalo maxent model variable contribution and importance

Fence permeability layer

A single pixel wide layer of fence permeability for the entire boundary of the FMD infected zone inside the RSA was constructed. At the start of 2009, the length of this fence was approximately 760km, with only 38km of the fence consisting of the 'I-beam and cable' type, 48km of 'railway and cable', and the rest of the fence being one of a great variety of 'game fences'. Fifty-four river crossings were considered to have adequate flooding potential to allow buffaloes to escape, and were overlaid on the permeability layer. Approximately 690km of the fence was classified as electrified, although this was heavily dependent on maintenance effort, which was virtually non-existent in some areas.

Contact probability estimations

Considering the analysis resolution and vast study region, map outputs are best viewed in a geographic information system where one can scrutinize smaller areas. In Appendix D, for each kind of probability model, outputs of the three temporal windows are assembled (i.e. SCR, ACR and LCPR).

In Table 5.3 buffalo-cattle contact probabilities according to the SCR and ACR methods are compared between seasons as well as between the three intensive study sites. Median values are extremely low, due to the positive skew in the data. All SCR cool dry season models showed significantly higher risk than their wet season counterparts. This pattern is switched for ACR models, with the highest risk prevailing in the warm wet season.

The 'risk profile' of IPs in each of the three intensive study sites according to the SCR is shown in Figure 5.8 (outliers deliberately omitted) and in Figure 5.9 (outliers depicted separately). In these graphs, the x-axis (IPs) is sorted according to the median of the whole-year probabilities. Similarly, ACR is depicted in Figure 5.10 and Figure 5.11. Only the outliers of LCPR are reported, since this dataset inherently contains only extreme values (Figure 5.12). Notice the general pattern of high LCPR outlier values during the cool dry season in all study sites, except the South, where this pattern is switched. Also note the IPs that are pushed up the order with LCPR compared to ACR in especially the Central site.

Table 5.3. Comparison of buffalo-cattle contact probabilities across seasons and study sites (median with interquartile range in square brackets is reported)

Model Type	**Area**	**All year**	**Warm wet**	**Cool dry**	**'High risk' season**	**W**	**p**
SCR	Entire area	0.00086 [0.00001-0.00829]	0.00038 [0.00001-0.00829]	0.00001 [0.00001-0.00829]	Warm wet	27659644963	***
	North	0.00076 [0-0.00967]	0.00007 [0-0.00967]	0.00017 [0-0.00967]	Cool dry	1582473828	***
	Central	0.01619 [0.00772-0.03306]	0.006 [0.00772-0.03306]	0.00639 [0.00772-0.03306]	Cool dry	17130716594	***
	South	0.00294 [0.00092-0.00955]	0.00061 [0.00092-0.00955]	0.00111 [0.00092-0.00955]	Cool dry	890523970	***
ACR	Entire area	0.00024 [0.00001-0.00272]	0.00021 [0.00001-0.00272]	0 [0.00001-0.00272]	Warm wet	26964103982	***
	North	0.00026 [0-0.00336]	0.00005 [0-0.00336]	0.00005 [0-0.00336]	Warm wet	1690987258	***
	Central	0.00548 [0.00258-0.01118]	0.00379 [0.00258-0.01118]	0.00185 [0.00258-0.01118]	Warm wet	21352136435	***
	South	0.00154 [0.00048-0.0049]	0.00087 [0.00048-0.0049]	0.00043 [0.00048-0.0049]	Warm wet	1187194326	***

***: <0.001

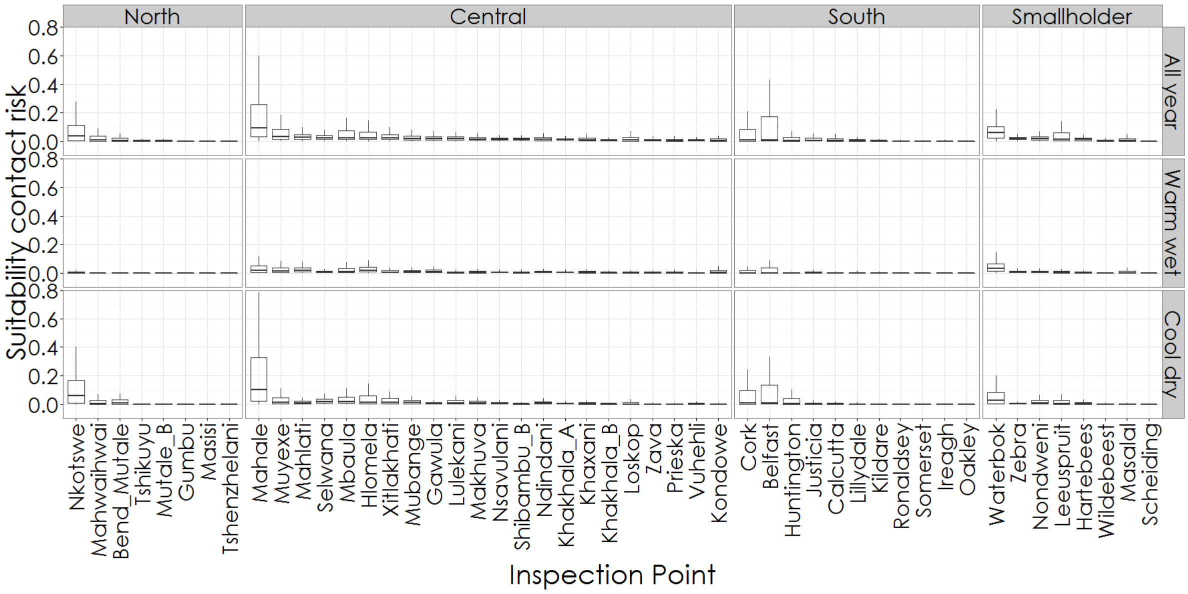

Figure 5.8. Buffalo-cattle contact probabilities according to the ‘suitability contact risk’ approach (outliers omitted)

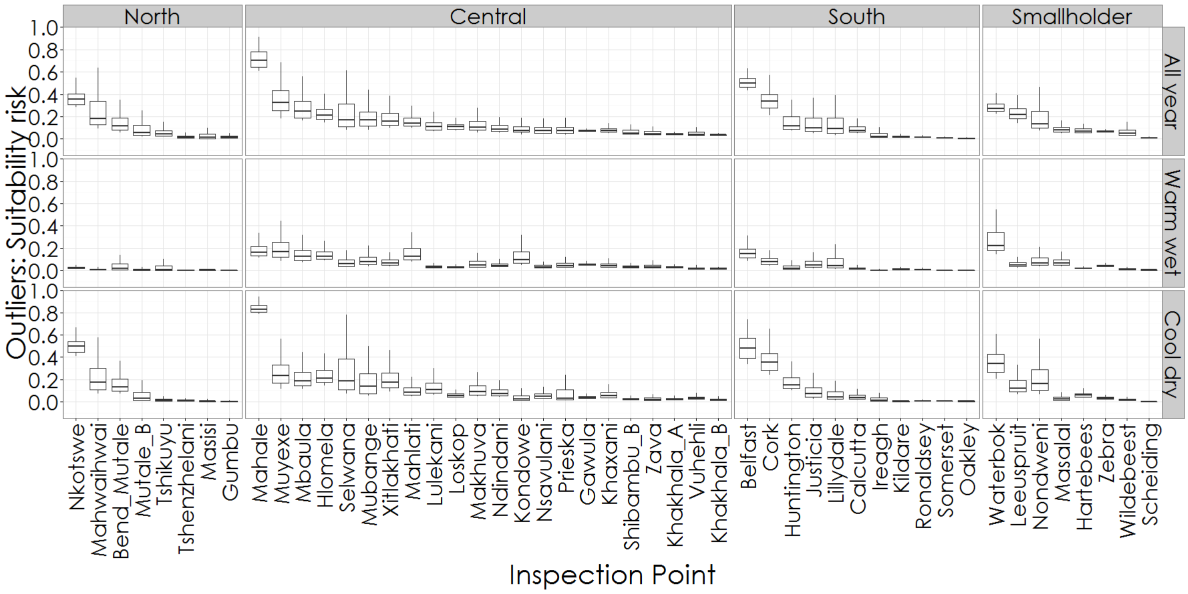

Figure 5.9. Buffalo-cattle contact probability outliers (95th percentile) according to the ‘suitability contact risk’

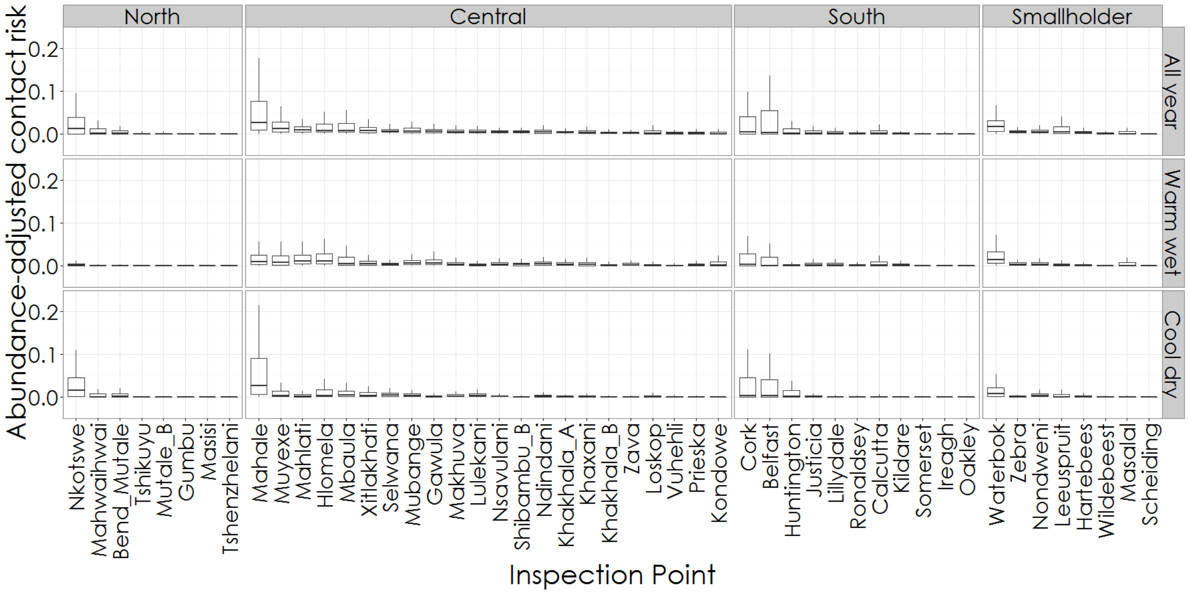

Figure 5.10. Buffalo-cattle contact probabilities according to the 'abundance-adjusted contact risk' approach (outliers omitted)

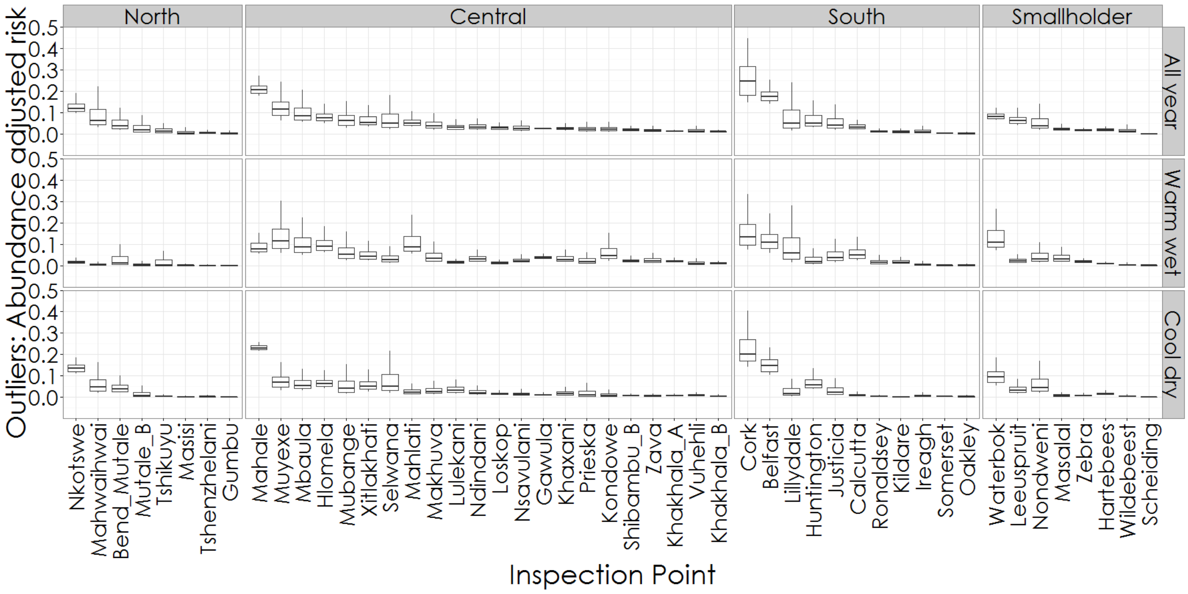

Figure 5.11. Buffalo-cattle contact probability outliers (95th percentile) according to the 'abundance-adjusted contact risk'

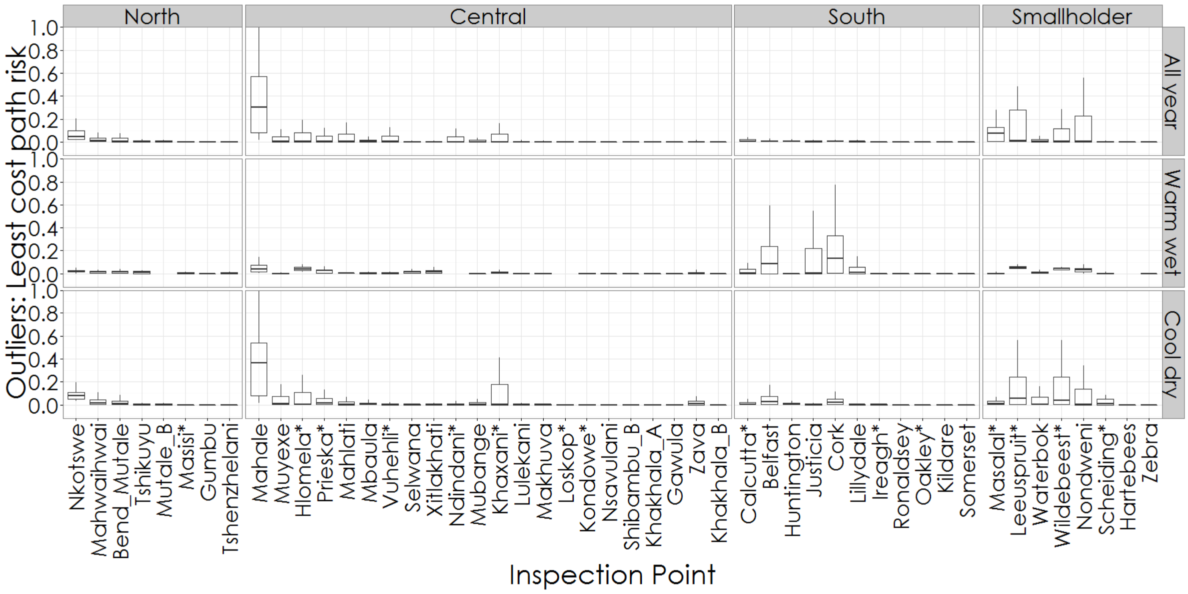

Figure 5.12. Buffalo-cattle contact probability outliers (95th percentile) according to the 'least cost path contact risk'. IPs with an asterisk (*) moved up the ranks compared to 'abundance-adjusted risk'.

Risk evaluation of past outbreaks

Maps of the five areas where recent FMD outbreaks occurred are compiled in Appendix E. The ability of the three types of models to discriminate between 'outbreak' and 'non-outbreak' IP areas, during both the season that the outbreak occurred as well as the whole-year model, is summarized in Table 5.4. The SCR and ACR had significantly higher contact probabilities in four of the five outbreaks considered, with both these model types failing to indicate a higher probability in 'outbreak' IPs of the Sibasa outbreak. Based on all pixels, LCPR failed to identify any of the 'outbreak' IP areas as having a higher probability of buffalo-cattle contact. When comparing the probability values in the 95th percentile of the data, though, the LCPR model was able to identify the Mhala (W=3019303, p=0.004) and Mopani (W=1522586, p<0.001) 'outbreak' IP areas as higher probability areas.

Table 5.4. Comparison of 'outbreak' and 'non-outbreak' inspection point areas to assess ability of different modelling approaches to identify high risk areas

	Outbreak season							
	Suitability contact risk		Abundance adjusted risk		Least cost path risk		Least cost path risk (95th percentile)	
Outbreak	**W**	**p**	**W**	**p**	**W**	**p**	**W**	**p**
Mhala	1215534409	***	1237668988	***	1143674010	-	3019303	**
Sibasa	51667717	-	51190230	-	57790281	-	57790281	-
Mopani	576220436	***	576575003	***	494610337	-	1522586	***
Vhembe	198663414	***	198537773	***	162935643	-	151599	-
Nsikazi	1213276505	***	1186195675	***	1128444802	-	1701961	-

	Whole-year model							
	Suitability contact risk		Abundance adjusted risk		Least cost path risk		Least cost path risk (95th percentile)	
Outbreak	**W**	**p**	**W**	**p**	**W**	**p**	**W**	**p**
Mhala	1276944793	***	1259782049	***	1130907323	-	1130907323	-
Sibasa	55018713	-	54460666	-	55049880	-	23726	-
Mopani	595816550	***	596346447	***	492971694	-	1473843.5	***
Vhembe	196791892	***	196758706	***	166346527	-	162423.5	-
Nsikazi	1362691291	***	1352864322	***	1135978022	-	110386476.5	***

***: $p<0.001$

Discussion

In the area adjacent to the FMD infected zone in RSA, direct contact between FMD infected buffaloes and susceptible cattle is the minimum requirement for the transmission of the virus between these species. Despite the exact circumstances surrounding actual viral transmission being largely unknown[9,47] (Chapter 4), control measures are aimed at either preventing contact, or ensuring immunity of potentially in-contact cattle. Hence, a good understanding of potential high risk areas and/or periods of contact between these species is critical to ensure efficient application of surveillance and control measures.

In the work presented here, habitat suitability (as estimated by maximum entropy modelling) is considered as a basis for determining the probability of contact between buffalo and cattle in three different ways. The first two approaches are very similar, both combining cattle and stray buffalo habitat suitability directly as a proxy for contact between these species, with the only difference being the adjustment of cattle habitat suitability for local cattle density in the second of these approaches. Herein, two major assumptions are made: that suitability equates to occupancy and that suitability and abundance are linearly related. Both these assumptions have been contested[296,469], although they probably hold true within the application of this study. The distribution and density of cattle have been related to FMD incidence in other parts of the world[470]. Also, the incorporation of cattle density is motivated by earlier work that suggested cattle density reduction to mitigate FMD transmission risk[20,25,122]. In concordance, a high susceptible:host density ratio has also been put forward as an important risk factor in the case of buffalo-to-impala (*Aepyceros melampus*) FMDV transmission in KNP[45]. Even though host density may be a critical factor in disease transmission[471,472] , it was not considered here since it was shown that most stray buffalo events consisted of a single animal (Chapter 4) and that the simulated number of buffalo-cattle contacts was not influenced by the number of stray buffaloes[166]. In the third approach presented here, LCPs between realistic ‘origin’ (in the FMD infected zone) and ‘destination’ points (in the livestock areas) are constructed to identify potential movement corridors for stray buffaloes.

Cattle distribution patterns derived in Chapter 3 showed concentration of suitable habitat (and confirmed through home range contraction) during the warm wet season, with the relative increase in cattle dispersal during the cool dry season probably being due to the increased foraging effort required to meet energy demands. In contrast to this, stray buffalo habitat suitability patterns were concentrated close to the FMD infected zone fence (see also [157]) in the cool dry season, and showed increased dispersal into the livestock areas and away from the FMD infected zone in the warm wet season. This is despite increased dispersal by buffaloes shown during resource poor periods in studies conducted inside the KNP[473].

Hence, the higher contact probability indicated by SCR during the cool dry season is likely attributable to the more extensive suitable areas for cattle, extending into areas along the fence where buffaloes are likely to occur. With ACR, on the on the other hand, increased dispersal of stray buffaloes into livestock areas during the warm wet season, combined with concentration of suitable cattle habitat and home ranges, being amplified by adjustment for cattle numbers in these areas, explains the higher contact probabilities during this season. This is supported by the high cattle-buffalo contacts recently reported during the warm wet season[88] as well as wet season dispersal events of more than 100km by buffaloes reported inside protected areas[52]. Vegetation greenness (as measured by the NDVI) has also been implicated in increased cattle-wildlife contact[474]. Further support lies in elephants being more likely to damage fences during the wet season[475], which could lead to increased buffalo egress. Notwithstanding, higher wet season contact probability contradicts the findings by some[87,166]. The cool dry season, on the other hand, is perhaps of greater epidemiological importance, since this is the period in which buffalo calves lose their maternal immunity[38], possibly leading to small, sub-clinical epidemics among them[2,61,67] and subsequent increase in viral circulation in the environment[30,33]. Corroborating this, most FMD outbreaks in impalas also occurred during the cool dry season[45] and most likely originated from buffaloes[8]. High contact probabilities were noticed near water sources (dams, rivers and associated riparian areas), similar to what has been suggested by others studying wildlife-livestock contact related to disease transmission[87,157,389,476,477]. Shared water sources were also implicated in FMD transmission between buffaloes and impalas in the KNP[45]. Dion and Lambin[166], however, suggests that forage, rather than water, drives stray buffalo dispersal, while, Ogutu et al.[389] also mention buffaloes and cattle avoiding each other, either naturally, or through disturbance by herdsmen or their dogs. The latter effect of management practices is perhaps an important factor to consider when interpreting the results presented here (see also herding practice findings in Chapter 3). Stray buffalo avoidance of settlements has also been proposed through multi-agent simulation modelling[166], which might be related to the repellent effect that cultivated fields seem to have on stray buffalo dispersal[438].

The habitat suitability model for buffaloes inside the FMD infected zone performed well enough for further use in the LCPR approach, although a more complex model for application and management inside the KNP/APNR could probably be constructed. Better model performance with fewer variables compared to the whole-year model presented here have been achieved in Zimbabwe (0.78)[438], although not outperforming the regularized seasonal models of the FMD infected zone. Buffaloes prefer high-quality foraging areas, often in relatively small 'hotspots'[478], which would partly explain seasonal buffalo suitability models being almost solely driven by NDVI and LST. The importance of NDVI in buffalo habitat selection is however questioned by some authors[473], which might be due to analysis across seasons rather than within, since the whole-year model constructed here was also much less influenced by NDVI, compared to the seasonal models. Buffalo distribution has also been linked to water sources before (rivers in particular)[98], as was also noted in the whole-year model, and which concurs with the findings for cattle (Chapter 3). Despite the seasonal buffalo models possibly suffering from some degree of over-fitting, they were deemed adequate for their purpose in the stratified random selection of stray buffalo 'origin' points in the LCPR approach. Take note, however, of the fact that buffalo dispersal outside the FMD infected zone was inherently constrained through translocation or destruction of these animals as soon as they were found, although this was considered partially in the stray buffalo models (fence distance, Chapter 4), and should therefore be reflected in the 'destination' selection of the LCP.

Visual assessment of LCPR outputs is probably more informative than comparison of central tendency measures, since LCPR rather estimates the 'concentration' of paths along corridors that overlap with high cattle density areas. Binary classification and/or interpretation of corridors are, however, not advisable[442]. Visual assessment of dry season LCPR outputs in this study (see Appendix D), especially in the North and Central sites, concurs with higher landscape connectivity proposed for poor quality, fragmented landscapes[440]. Similar approaches to LCPR have been used for estimating large mammal dispersal routes before[479,480]. LCP is most often used as a complementary approach to other, more diffuse methods, which do not always identify optimal routes between landscape patches as well as LCP[446,481]; this is the case here with ACR and LCPR. Visual assessment of the LCPR outputs was also more informative and plausible than quantitative assessment when used to identify high/low risk areas in outbreak districts (see also use of LCP visual assessment by Williams[436]). The most critical step of LCP analysis is the construction of the cost surface through the appropriate assignment of weights to cost layers, being mindful of non-landscape factors influencing animals' choice of path as well as of 'legacy effects' in models (i.e. where landscape features or barriers might have changed during or soon after the creation of the cost surface)[440]. For the former, consider for example indirect anthropological influences such as harassment of buffaloes by dogs in rural areas[389], whilst the latter aspect might be pertinent to the fence permeability layer used here. The single most influential component of buffalo-cattle contact probability is fence integrity[157]. The FMD infected zone fence's permeability is constantly changing due to deterioration, repair or upgrades, often related to human influence through simple issues such as access gates being left open or maintenance efforts that might change abruptly (due to for example changes in personnel or motivation). Obviously, a more dynamic fence permeability layer would be preferred. The fence permeability layer used here was based specifically on the fence status at the beginning of

2009, and LCPR performance should therefore be judged with caution outside this period, especially with the retrospective investigation of FMD outbreaks. Dion et al.[157] however cautions that the exact location of fence breakages might not necessarily play such an important role in predicting the exact location of buffalo-cattle contacts. Furthermore, improved variations of LCP are starting to emerge which could better evaluate variations in path selection than the single optimal path method used here[482]. Perhaps even superior to the LCP approach, is circuit-based theory[446], which produces more diffuse cost-path outputs, since it only considers one movement step (or cell) at a time[443], and is therefore less 'directed' than LCP. In the review by Chetkiewicz et al.[442], more emphasis on the behavioural component of path selection is called for, such as the step selection function[483], although this might be difficult in the case of stray buffaloes, since very little empirical evidence exists about the paths that they follow once outside the FMD infected zone. Nevertheless, more detailed investigation of landscape connectivity with regard to buffalo-cattle contact is probably warranted.

Other approaches have been used to assess risk in the study region. Buffalo-cattle contact risk estimation was applied previously in the South site[157], forming part of the same multidisciplinary project as this one. In their approach, Dion et al.[157] employed a multi-agent simulation platform at a very high spatial (1ha) and temporal (4.8h) resolution. Although it provided plausible outputs, the drawback of this approach was its computational demand, limiting it to a relatively small area. As with the work presented here, lack of field data (of fence breakages and stray buffalo movements especially) made external validation of the model difficult. A conventional qualitative risk assessment for the study region was also done previously[55], although its lack of explicit consideration of spatial heterogeneity only allows for generalised application of its findings to surveillance and control. A host of other techniques have been employed to simulate direct contact between species in space and time. Cellular automata[86,484] could be equally considered for simulating stray buffalo dispersal patterns and could perhaps be directly integrated with cattle dispersal. Small area Bayesian approaches, considering IP area polygons for example, might perhaps be more appropriate at the decision making level[485].

Although refinement of contact probability as a 'transmission risk proxy' through incorporation of accurate transmission parameters (see for example [71]) would improve the work presented here, such accurate values are unlikely to have drastically different surveillance and control implications. That being said, risk interpretation at the population level, as opposed to the individual level, could be deceptive, due to some individuals that could pose a much higher transmission risk than others[486]. At the extreme, a single outlier event in these results could be sufficient to cause an outbreak. Other than the buffalo ‘childhood epidemics’[61] and sub adults[28] mentioned earlier, host age and gender differences in FMD infectivity has not been reported (in contrast to seropositivity[2,60]). Yet, adult bulls represented the largest proportion of buffaloes that egressed from the FMD infected zone (~65%, Chapter 4). Adult bulls also tend to form ‘bachelor’ groups that roam separately from buffalo herds[487,488], possibly in an attempt to avoid predation[489] and consequently occupy slightly different habitat ranges, which could in part explain the disproportionate number of adult bulls among stray buffaloes. Considering bulls and herds separately, would be similar to considering more than one species as the host, which could thus be extended even further to include impalas[45] and perhaps kudus (*Tragelaphus strepsiceros*)[57]. Similarly, multiple susceptible species could also be considered[490], especially domestic goats. Very little is known about their role in the transmission of FMD in the region, and their numbers might increase in the years to come due to changes in vegetation[417]. Furthermore, herd demographics have also been implicated in FMD outbreak density, albeit cattle-cattle transmission[491]; data presented in the preceding chapters could be used for this in future refinements of the risk model.

There are a number of weaknesses in this work that needs to be addressed in future work. The first would be a much better study of fence permeability that would result in a spatially and temporally accurate dataset. Secondly, validation of the approaches presented here is hampered by the low number of outbreaks or recorded buffalo-cattle contacts. Given better data availability, temporal resolution could also be much improved, at least to four seasons or even monthly intervals. This however calls for much improved data management at an institutional level, which would also allow for some level of automation and integration of livestock-wildlife data, as well as practical information dissemination among regulatory officials. Other omissions to this work include the probability of cattle entering the FMD infected zone, involvement of other species in FMD transmission[45,57] and fomite-derived transmission events.

Despite these shortcomings, the outputs presented here lend themselves to the identification of priority areas where disease control efforts, such as vaccination, should be focused. An important next step would be to include cattle immunity (through vaccination), which could be as simple as modifying the cattle density used here (ACR) to a ‘susceptible’ density (i.e. corrected for the number animals not considered to be immune at that point in time), which can be updated regularly (e.g. weekly/monthly). If done iteratively, this could be a useful aide to vaccination programmes. Also, this type of approach could become especially important if formally delineated geographic disease control zones were to be dropped in favour of compartmentalisation and CBT type approaches. In such cases, surveillance efforts will probably have to be risk orientated and more adaptable to prevailing conditions.

More strategic/dynamic disease control approaches have been proposed before[112,138], especially at a regional scale. Such strategic approaches might even incorporate geographical distinction between FMD lineages[53], which calls for possible involvement of another emerging discipline (which has a lot in common with landscape connectivity), that of landscape genetics[492].

Conclusion

Even though the probability outputs presented here are only relative values for contact between buffaloes and cattle outside the FMD infected zone, they provide a very useful tool to identify high probability areas for interspecific contact at a relatively fine spatial resolution. Whilst models presented here were constructed mainly with purposely collected data, the concept and application of habitat suitability modelling to inform interspecific contact could be achieved with less data and could also be transferred to other similar areas (in especially southern Africa) quite easily. Proper application of this concept might also lead to more strategic risk mitigation. Such approaches might even encourage cross-border harmonization of disease control efforts for a number of diseases, which could greatly benefit the region.

Conclusion

The aim of this work was to develop a spatio-temporal probability model of foot-and-mouth disease (FMD) risk, based on distribution models for cattle and African buffaloes (*Syncerus caffer*), as well as secondary drivers of contact and/or transmission between these species. It was also specifically intended for the unique epidemiological setting of the Kruger National Park (KNP) and its adjoining private and provincial reserves (APNR) in South Africa, where FMD virus is present in the majority of African buffaloes. Adjacent to these reserves (which form the FMD infected zone) lies vast communally-farmed livestock rangelands, which few have studied in an epidemiological context. Current knowledge suggests that under local conditions, FMD virus transmission requires close contact between host (buffalo) and susceptible (cattle) species. Therefore, understanding the factors that influence distribution patterns of both these species is paramount in identifying those areas where contact is likely to occur and where surveillance and control efforts should be focused.

The data from the study region investigated here show a large amount of heterogeneity in this wildlife-livestock interface. Deliberation of such heterogeneity is important to improve our knowledge of the already complex epidemiology of FMD in South Africa. At a larger scale, the southward-increasing cattle density has bearing on the probability of contact with, and hence the risk of virus transmission from, buffaloes. This could be exacerbated by the steep rise noticed in the cattle population in the southern study site over the study period. The effect of density was further emphasised at a local scale through the concentration of cattle in their preferred habitat during the warm wet season, also increasing the probability of contact with stray buffaloes, albeit the period during which buffaloes are less likely to shed FMD virus. On the other hand, herding and kraaling practices, being more prevalent in the southern and central parts of the region, decrease the probability of contact between cattle and buffaloes, through the direct and indirect deterrent effect that people have on buffaloes as well as by effectively decreasing the potential in-contact period between these animals. Although buffaloes do not stray very far from the FMD infected zone in the cool dry season, this is the season during which buffaloes are deemed to be most infectious, and during which cattle graze in a more dispersed fashion, causing overlap with stray buffalo ranges, particularly near water sources and along rivers. Of importance however, is that buffaloes stray from the FMD infected zone in small groups or individually, with low representation of the age groups considered to be more infectious. The two habitat suitability-based approaches to assess cattle-buffalo contact used here provide valuable temporal and spatial information on the probability of these events, allowing for risk interpretation with and without considering animal abundance. Complementary to these approaches, identification of movement corridors for stray buffaloes has value in assessing potential 'hotspots' where risk of cattle-buffalo contact is elevated, despite the general suitability-based risk estimates being low. The corridor approach can also assist in prioritisation of fence maintenance and upgrades. The data presented here also contributes substantially to current knowledge on livestock management as well as the epidemiological setting of the FMD protection zone of South Africa. In a resource limited environment, as occurs throughout most of Africa, prioritisation of surveillance and control efforts is paramount, especially considering the effect anticipated shifts in trade prescripts might have on disease control approaches. The methods put forward in this work, combined with increased knowledge of the local epidemiological setting, could aid in informing such strategic surveillance and control efforts.

Any accurate spatio-temporal risk assessment is dependent on reliable and current data. An important realisation during this study was that no integrated data repository exists in South Africa for either livestock or wildlife data related to disease control. Despite valiant efforts by some local offices and departments to practice good information management, the majority of data ended up in hard copy filing cabinets or storerooms, only to be retrieved through projects such as these. With currently available technology, centralising these data in an easily-accessible format should be achievable within reasonable cost and must be promoted by Government. Considering the costs of disease control, the costs associated with creating such a system would be well justified through the benefits arising from its routine use to inform surveillance and control programs. This would also improve communication between different role players and provinces involved in the same disease control efforts.

It is important to note that this work only focuses on buffalo-to-cattle transmission outside the FMD infected zone and omits a number of alternative pathways for FMD virus to spread from buffaloes to cattle. These include buffalo-to-cattle transmission when cattle stray into the FMD infected zone, transmission from intermediary hosts (especially impalas) to cattle, mechanical transmission (fomites), transmission due to unauthorised movements of infected animals and long distance airborne transmission.

The complex and dynamic epidemiological setting of FMD in South Africa requires innovative approaches to risk assessment, focused on the endemicity of the disease, rather than borrowing from epidemic approaches or simply following convention. These should be used to guide more sustainable surveillance and control efforts which should benefit, rather than penalise, people whose livelihoods are dependent on livestock production in these areas. Such approaches will help to achieve a much-needed balance between livestock production and wildlife conservation in southern Africa's transfrontier conservation areas.

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Appendix A

Cattle habitat suitability

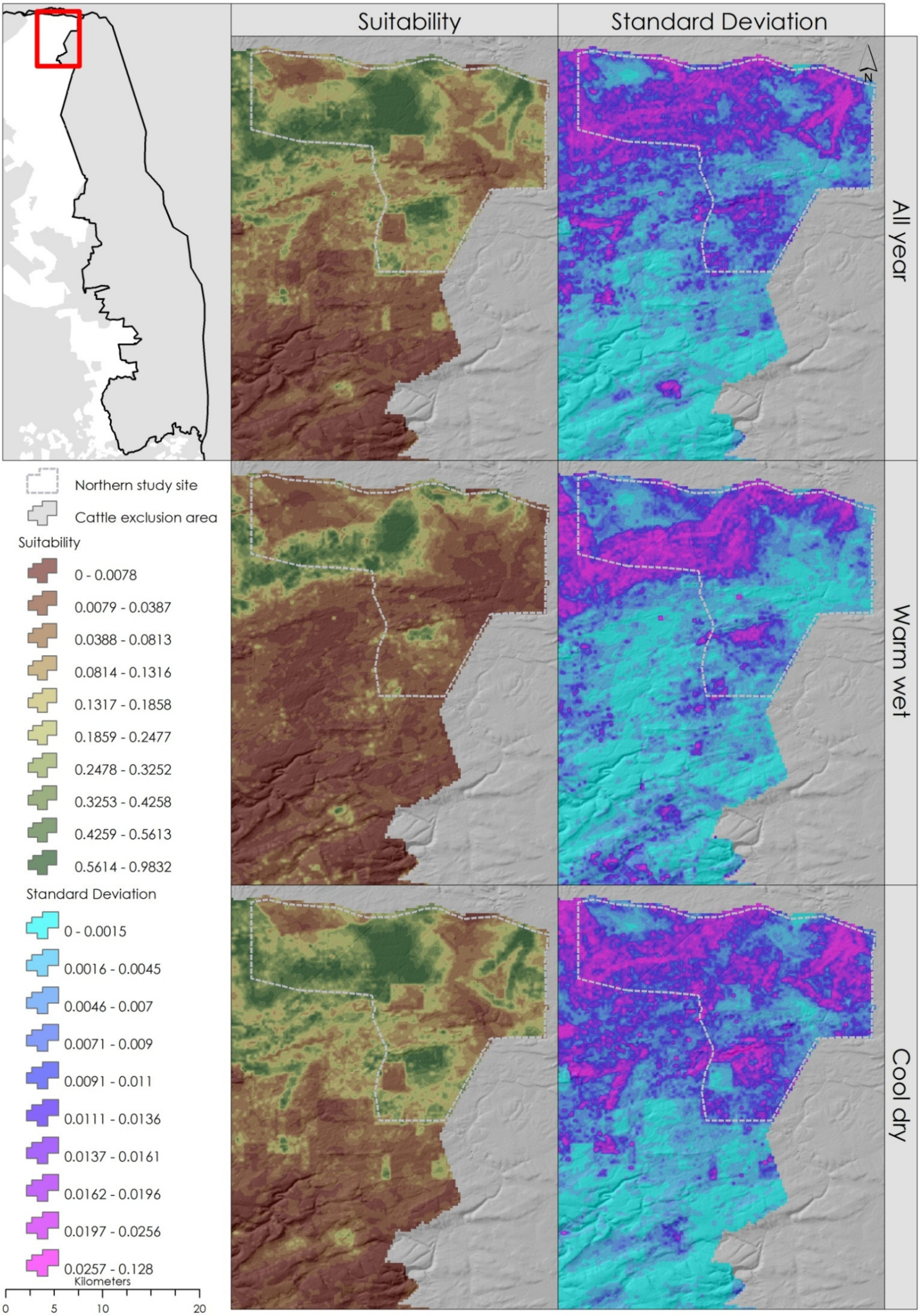

Figure 5.13. Cattle habitat suitability - Northern study site

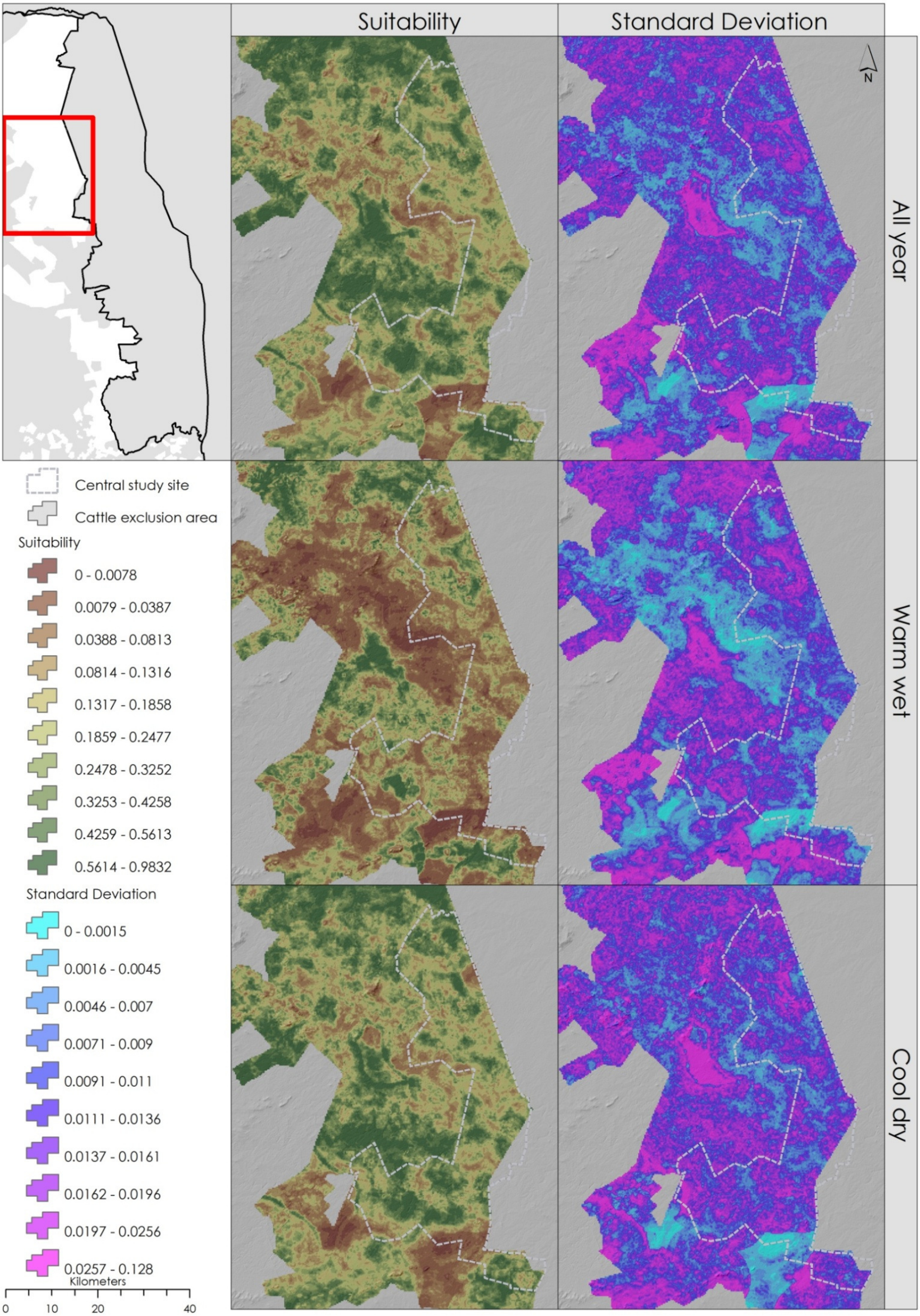

Figure 5.14. Cattle habitat suitability - Central study site

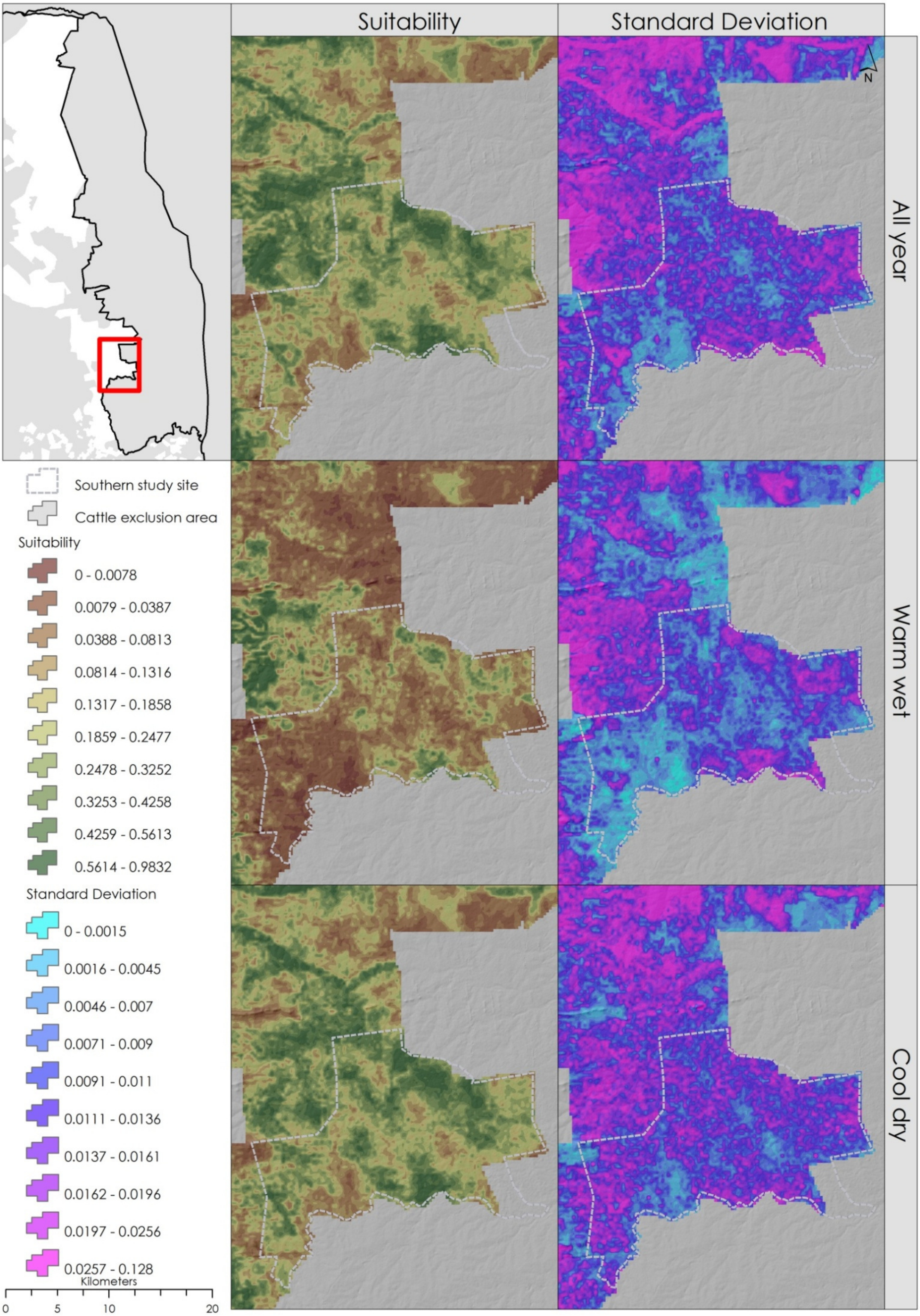

Figure 5.15. Cattle habitat suitability - Southern study site

Appendix B

Stray buffalo habitat suitability

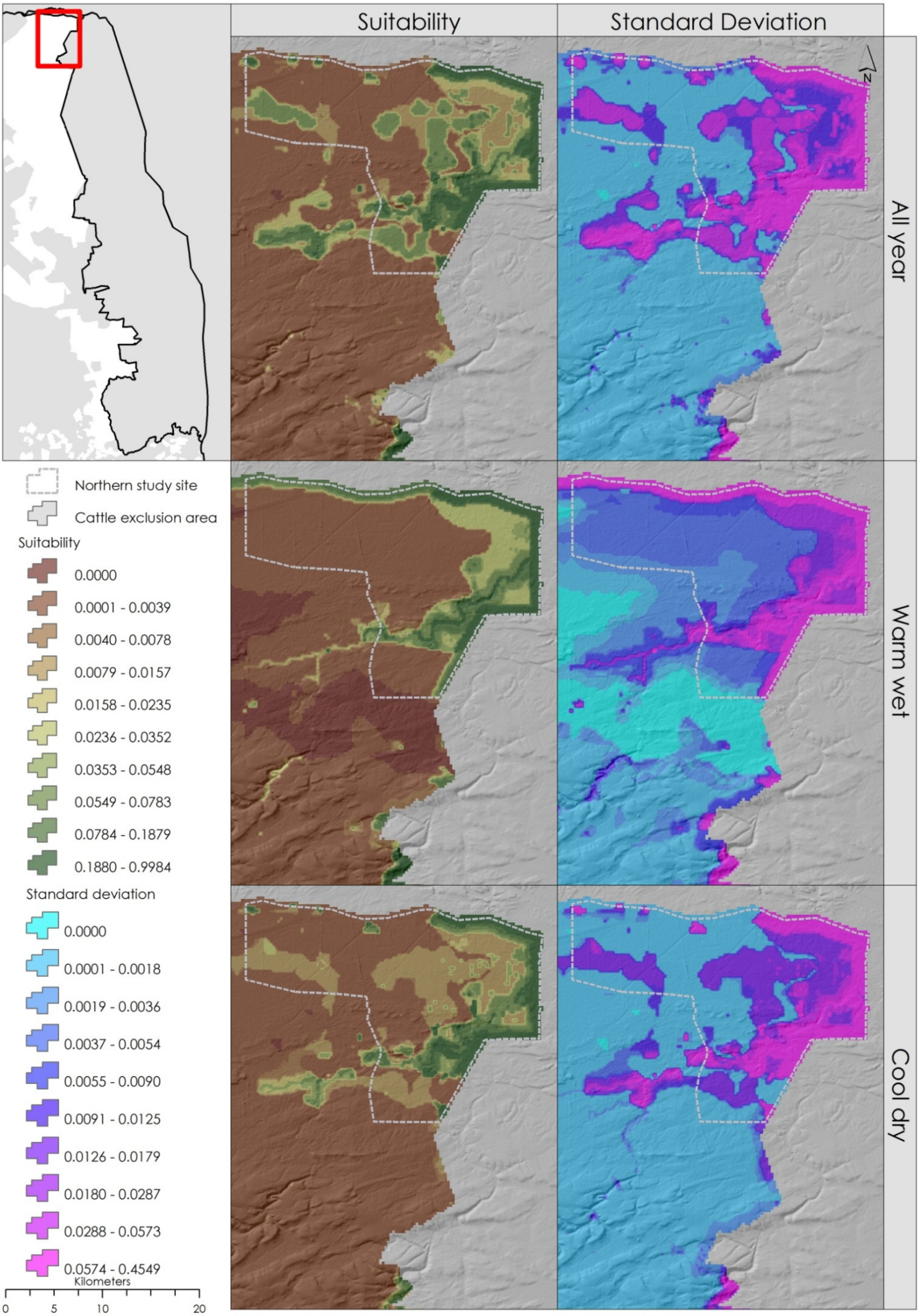

Figure 5.16. Stray buffalo habitat suitability - Northern study site

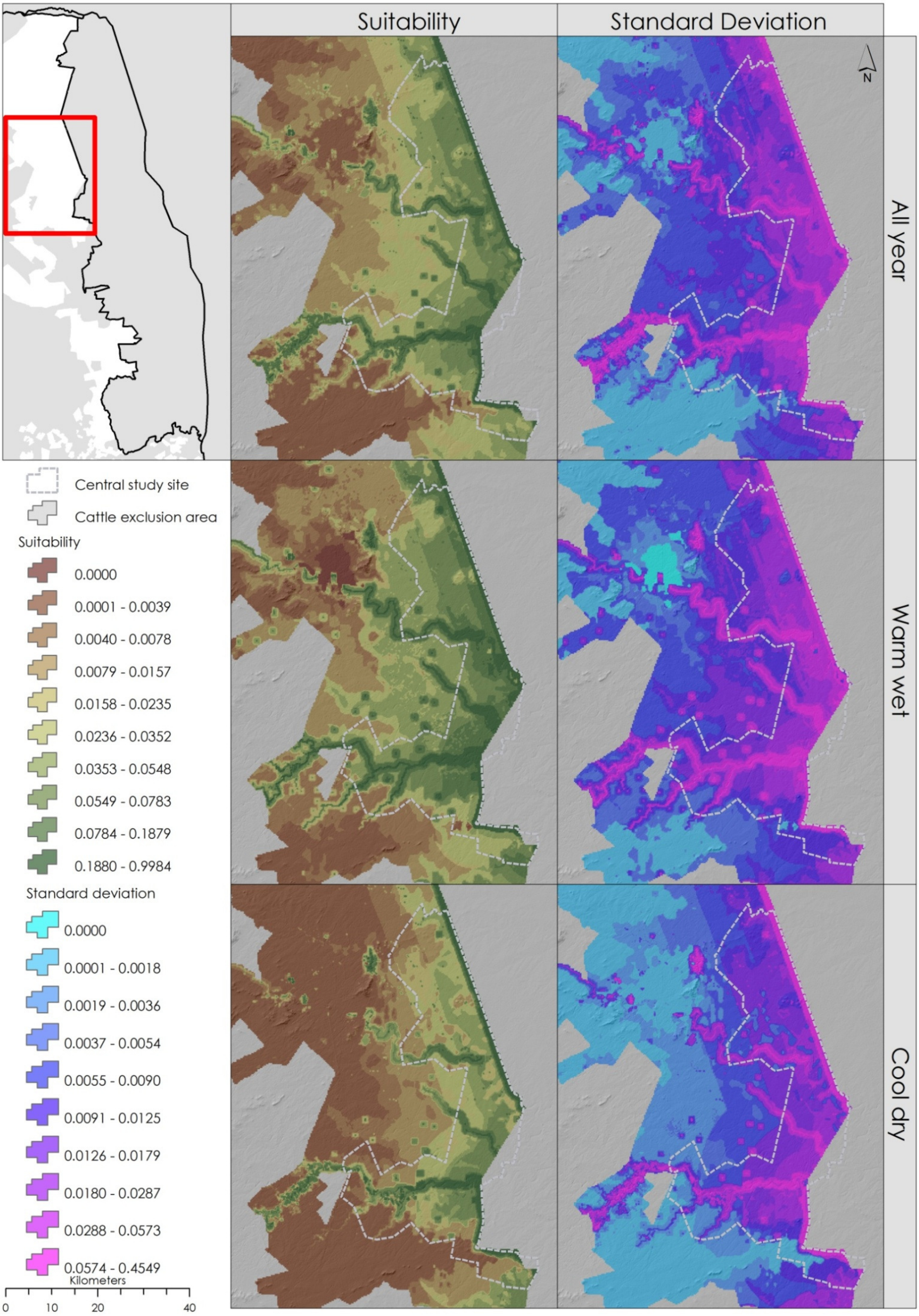

Figure 5.17. Stray buffalo habitat suitability - Central study site

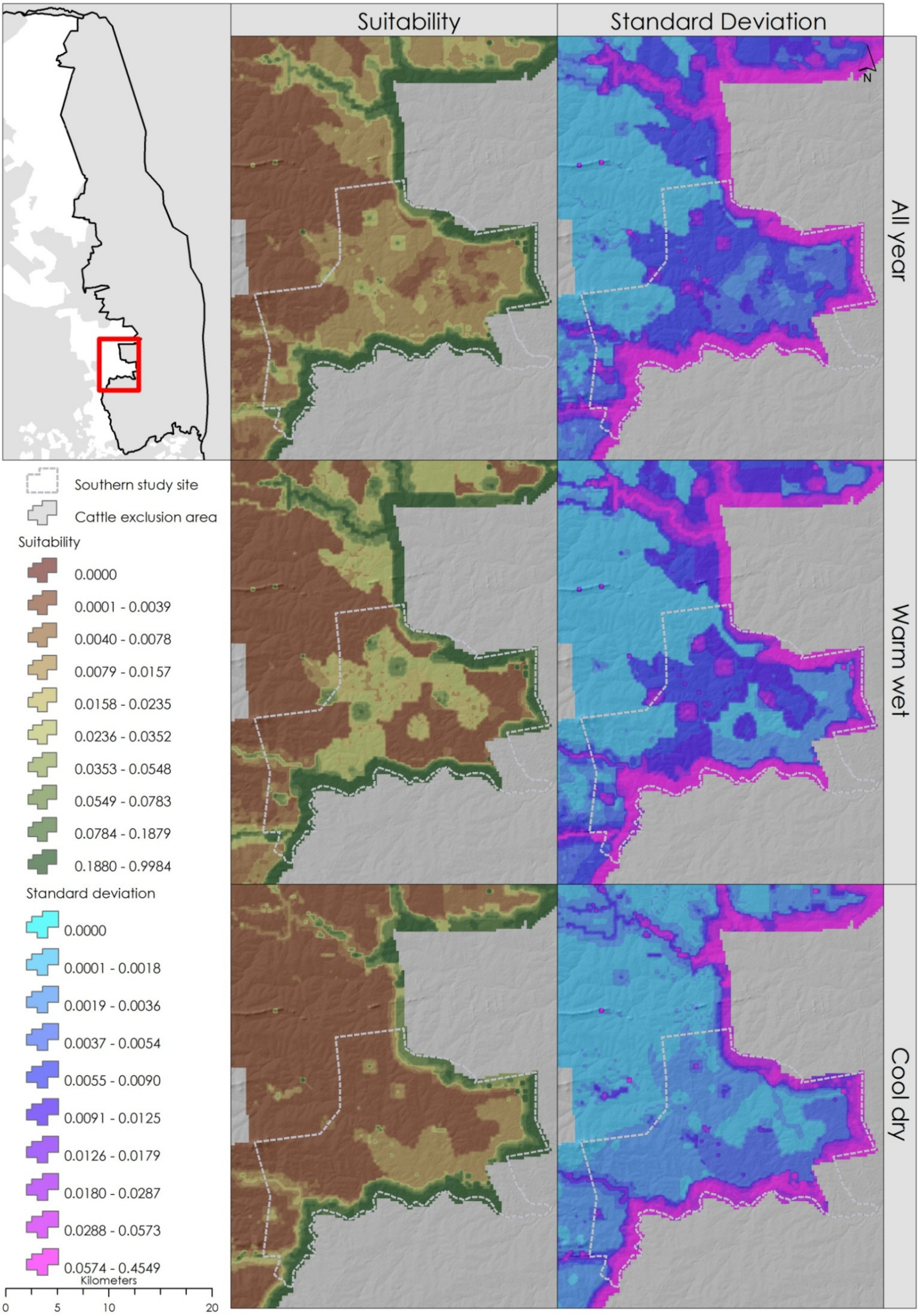

Figure 5.18. Stray buffalo habitat suitability - Southern study site

Appendix C

Cattle abundance

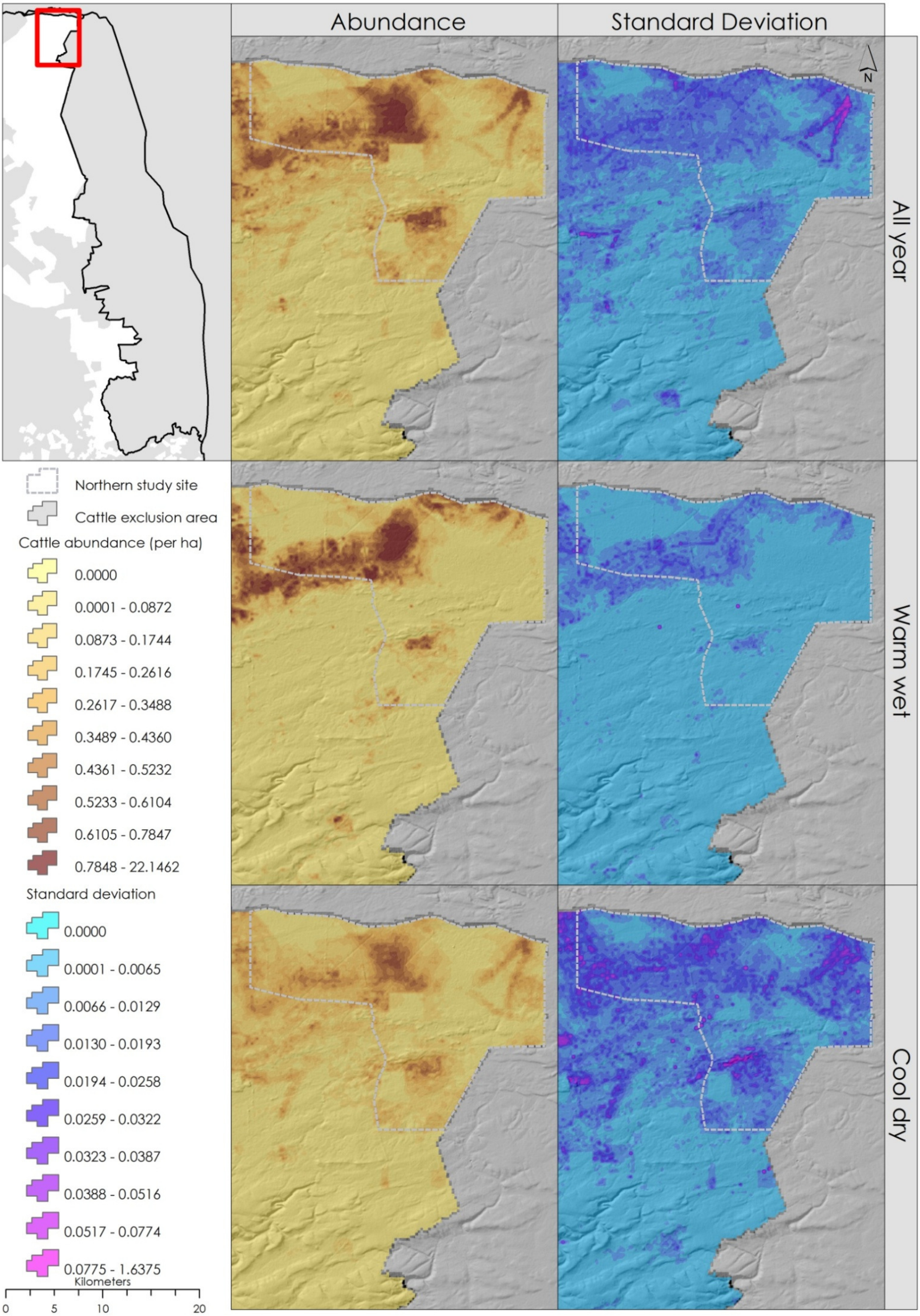

Figure 5.19. Cattle abundance - Northern study site

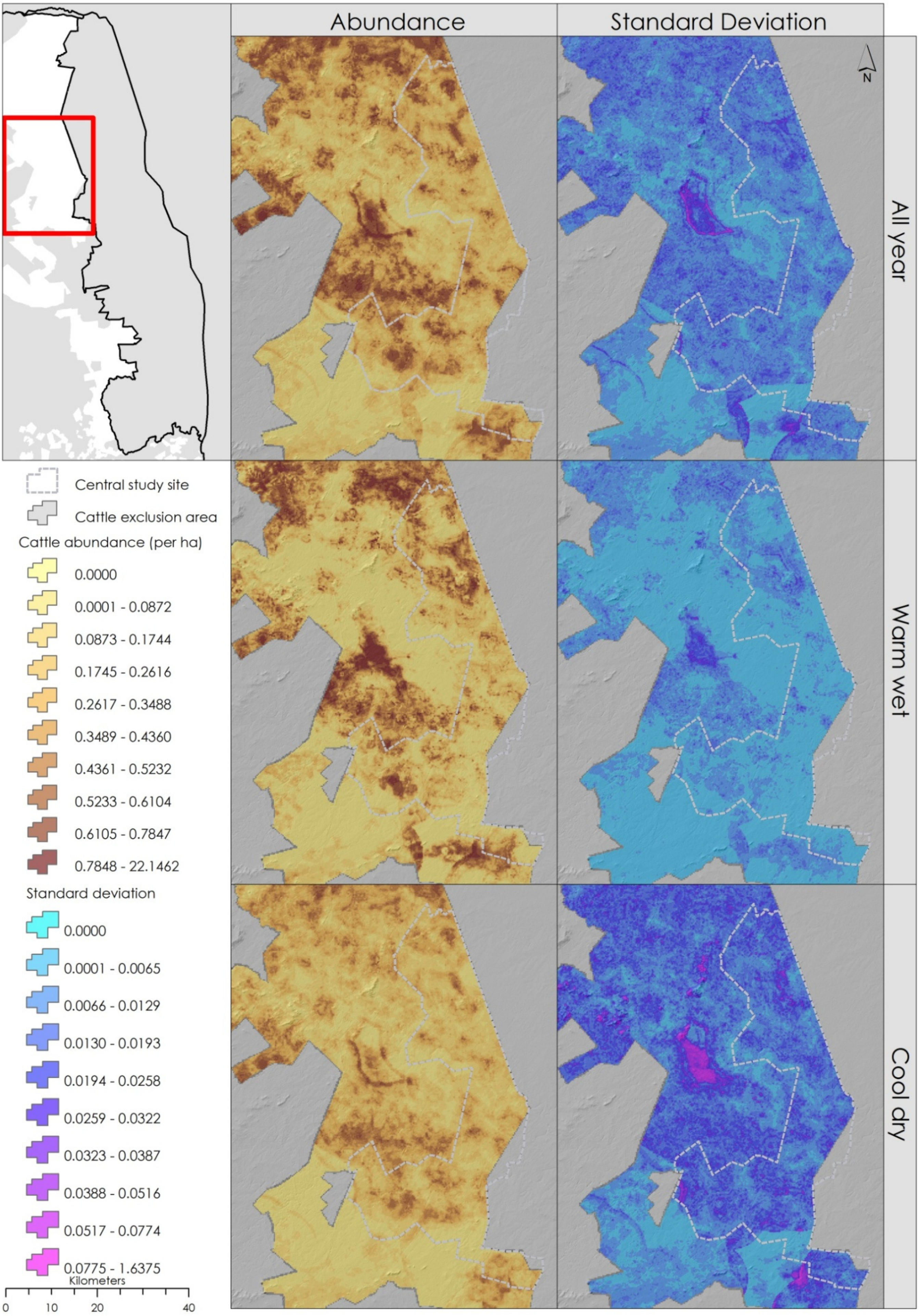

Figure 5.20. Cattle abundance - Central study site

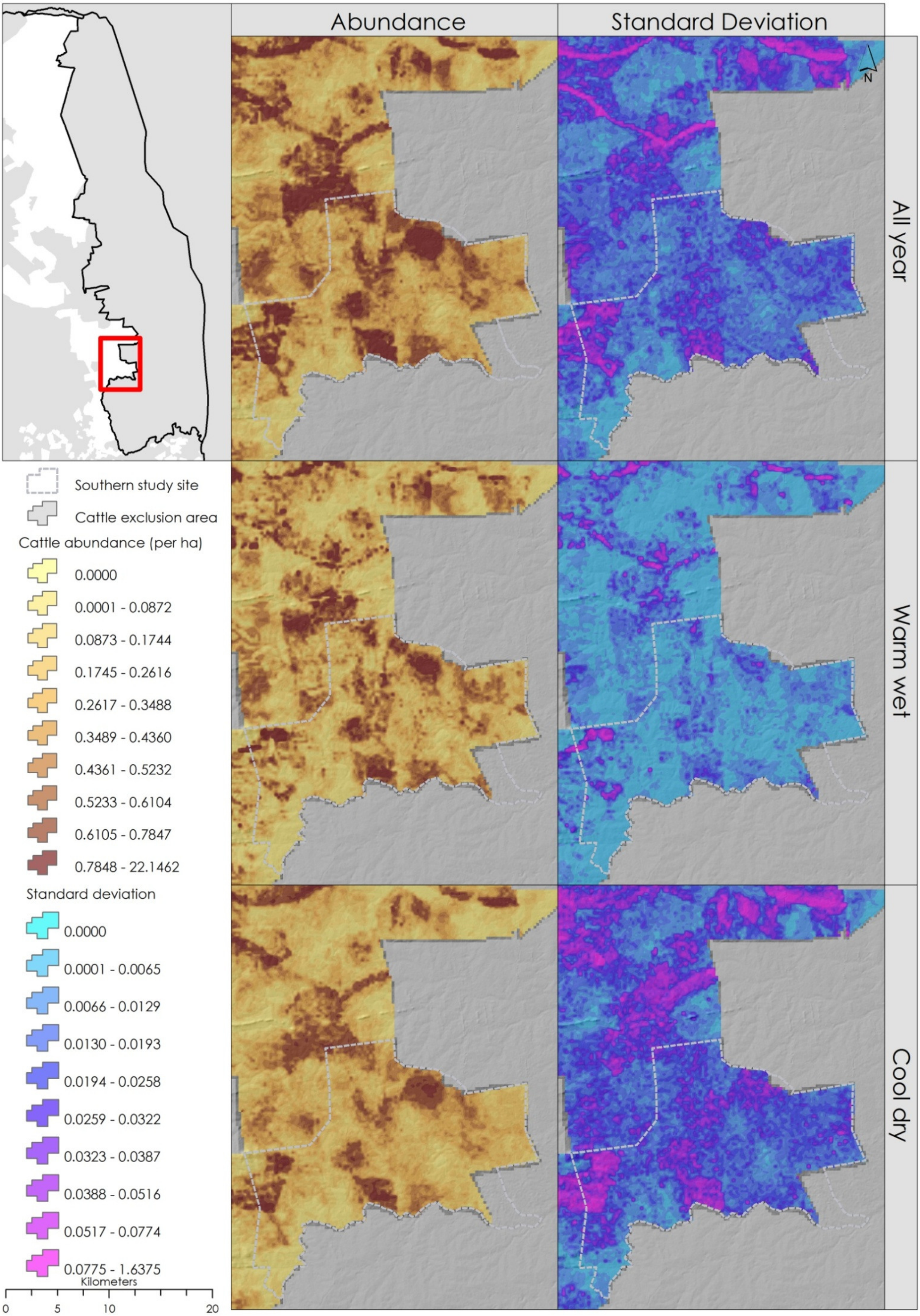

Figure 5.21. Cattle abundance - Southern study site

Appendix D

Outputs of risk models

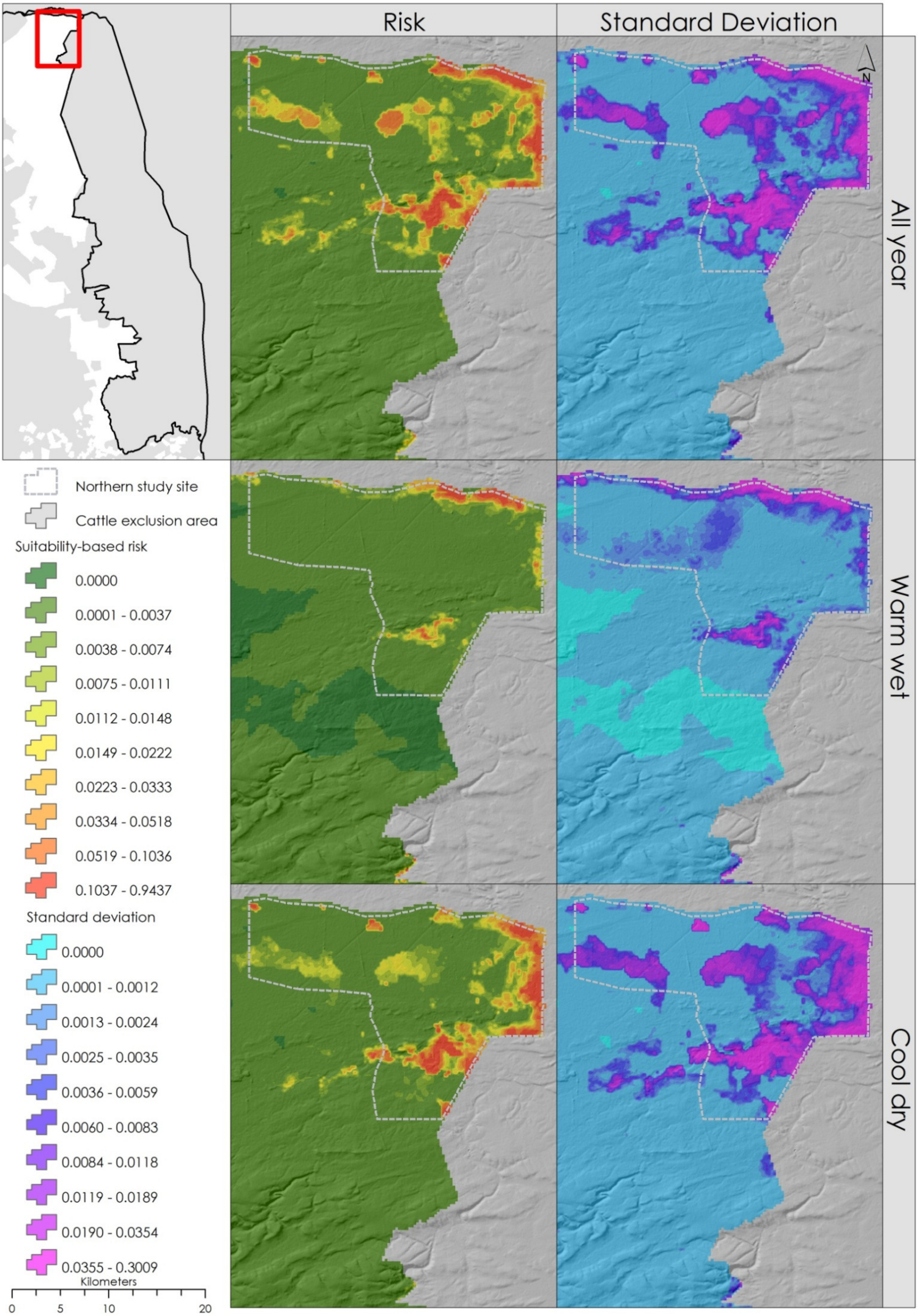

Figure 5.22. Suitability contact risk - Northern study site

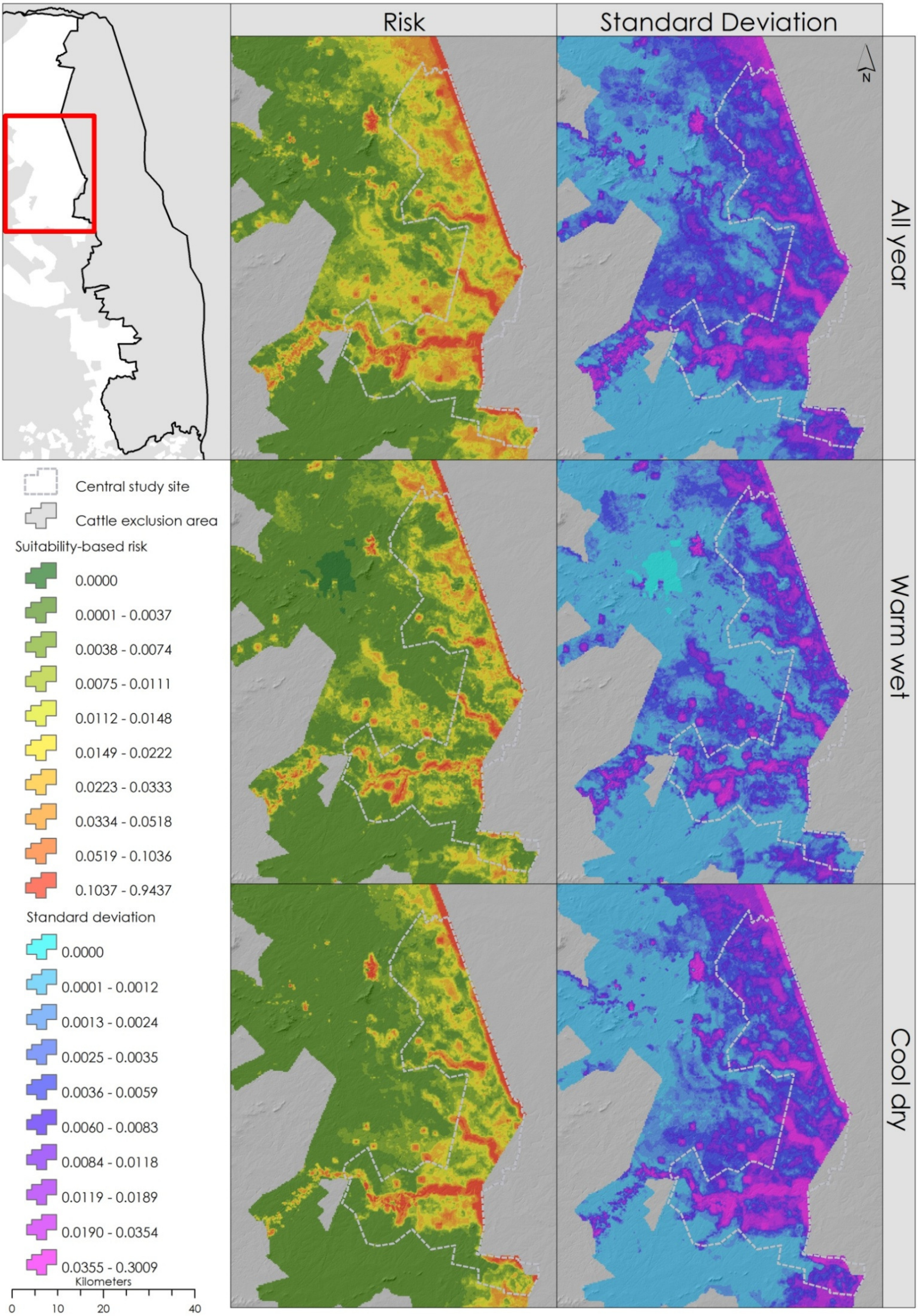

Figure 5.23. Suitability contact risk - Central study site

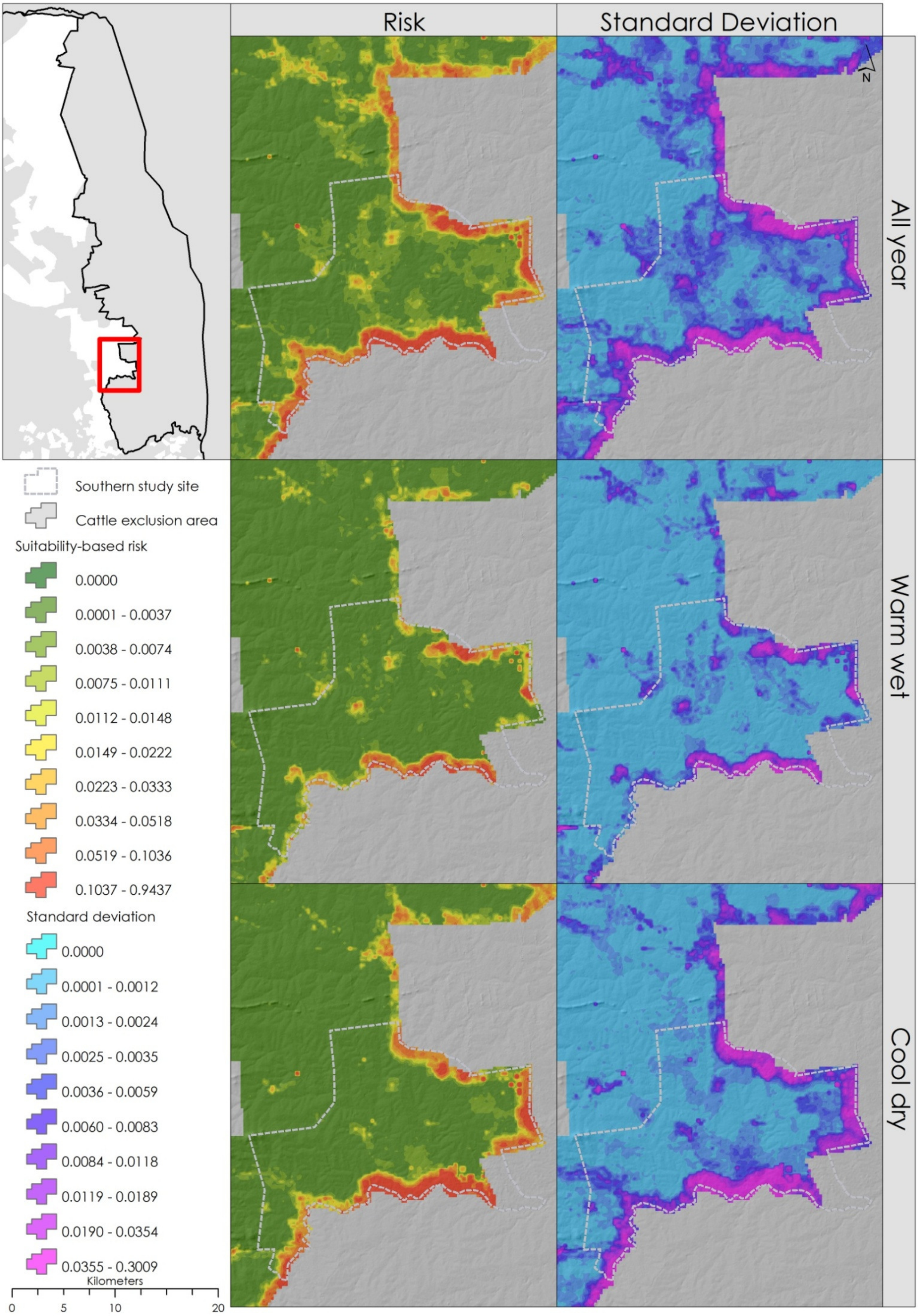

Figure 5.24. Suitability contact risk - Southern study site

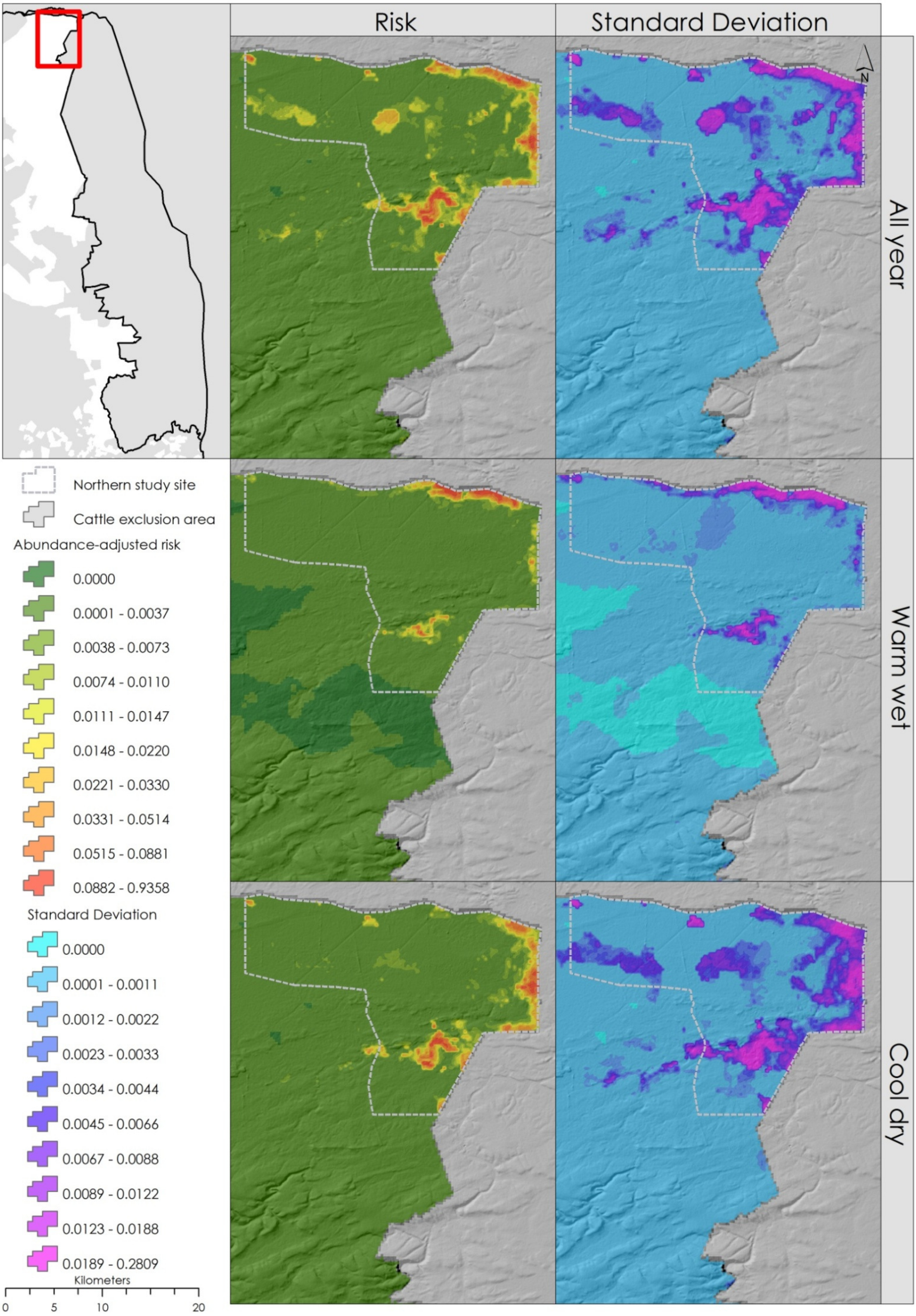

Figure 5.25. Cattle abundance adjusted contact risk - Northern study site

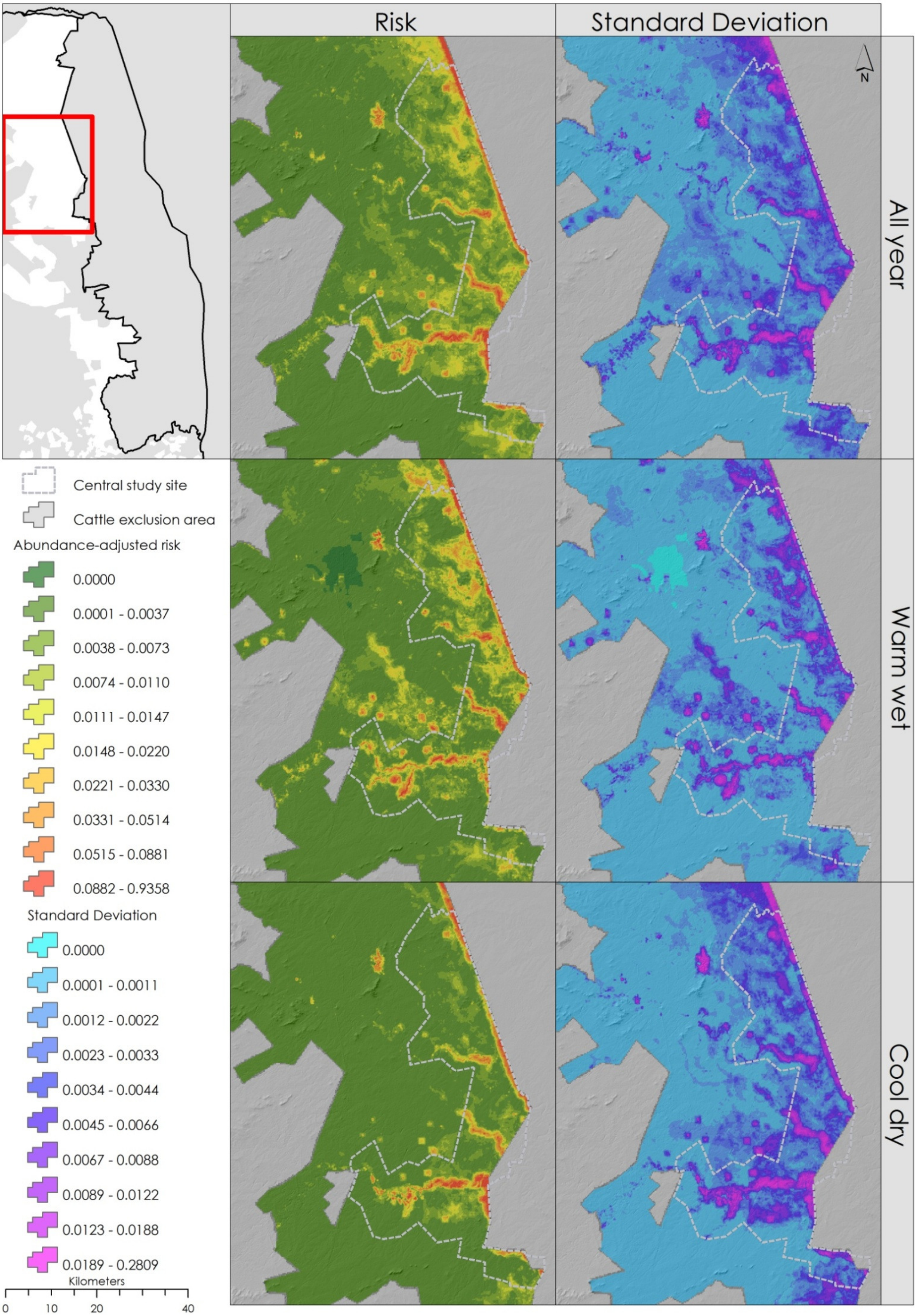

Figure 5.26. Cattle abundance adjusted contact risk - Central study site

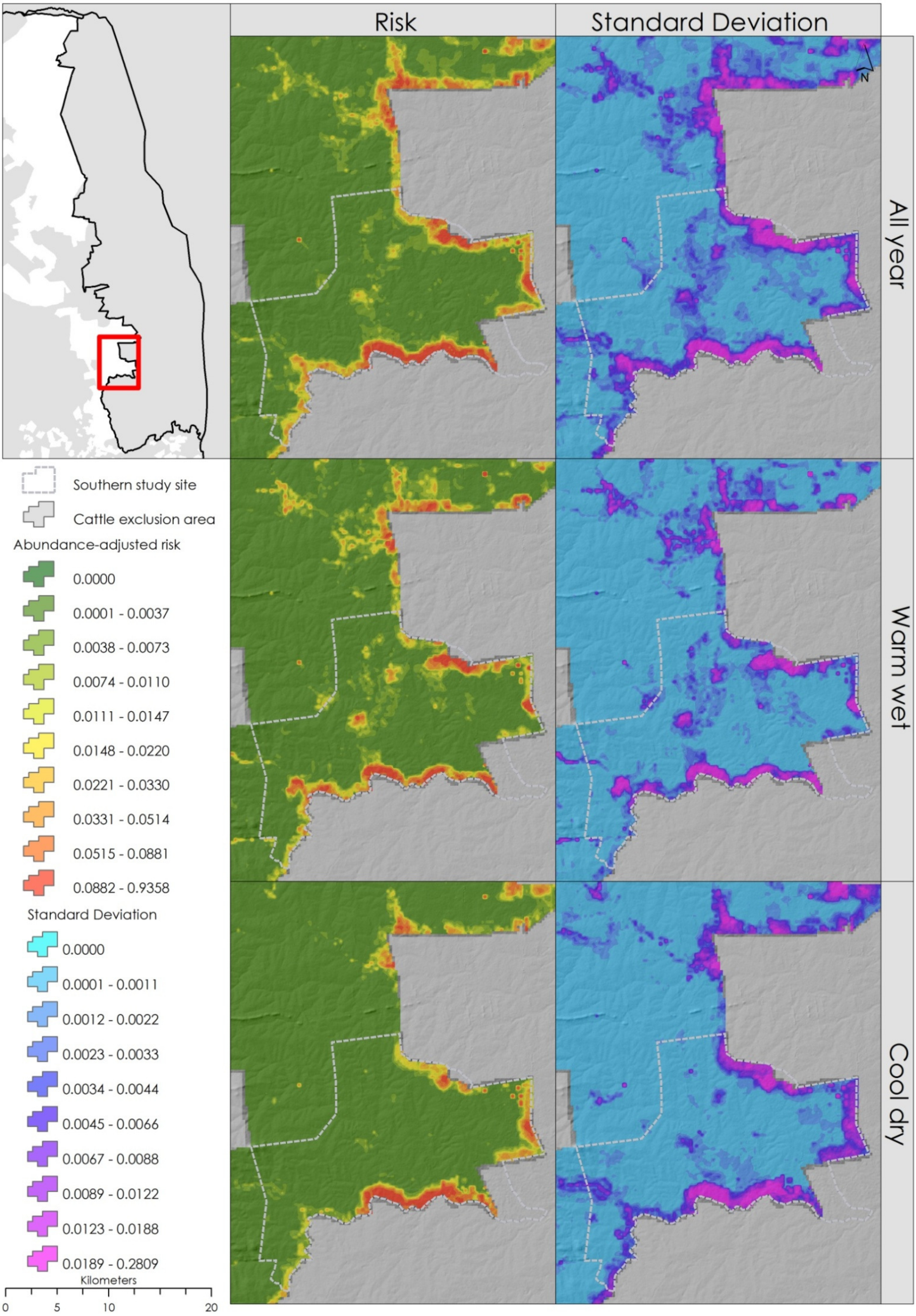

Figure 5.27. Cattle abundance adjusted contact risk - Southern study site

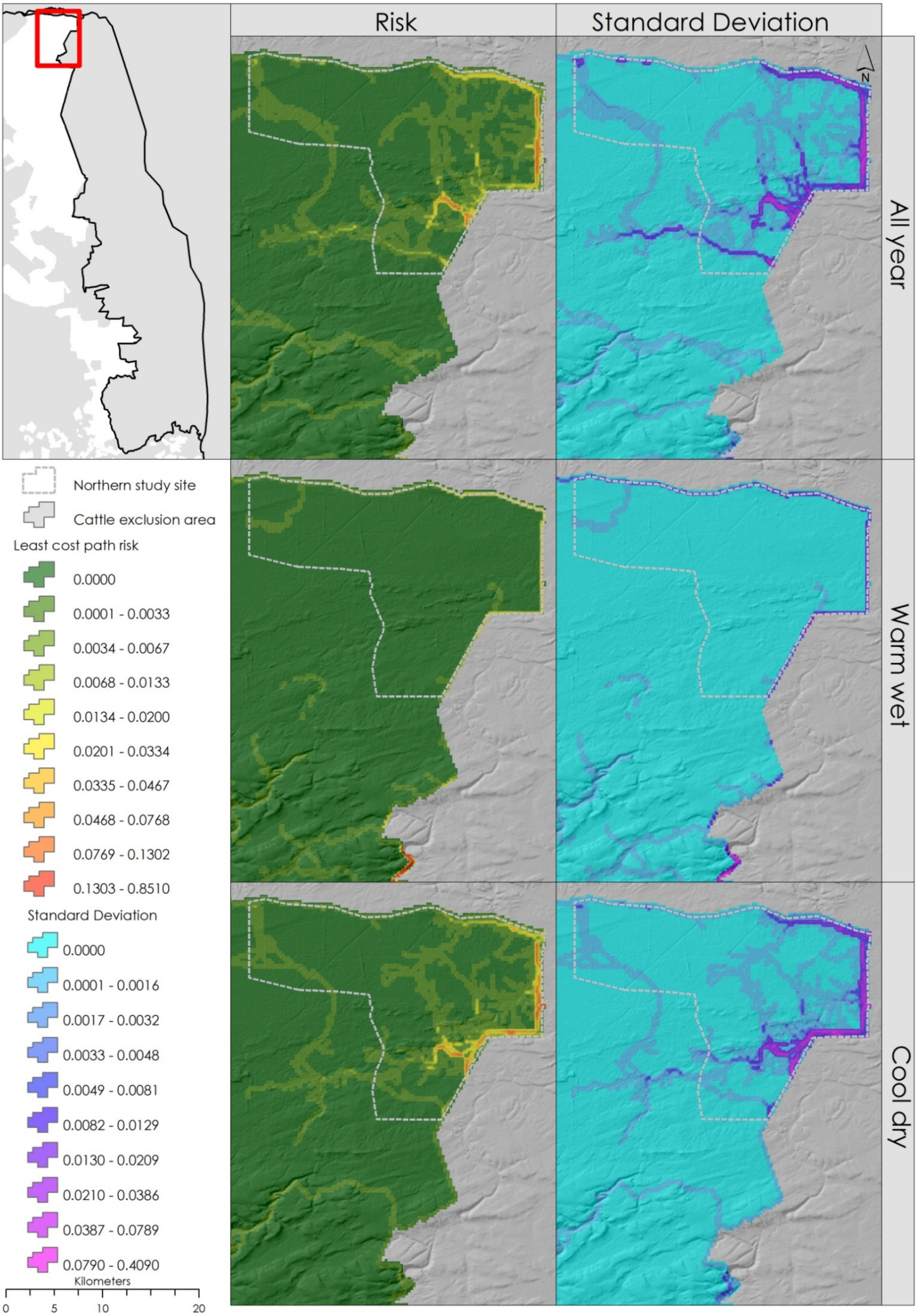

Figure 5.28. Buffalo least cost path contact risk - Northern study site

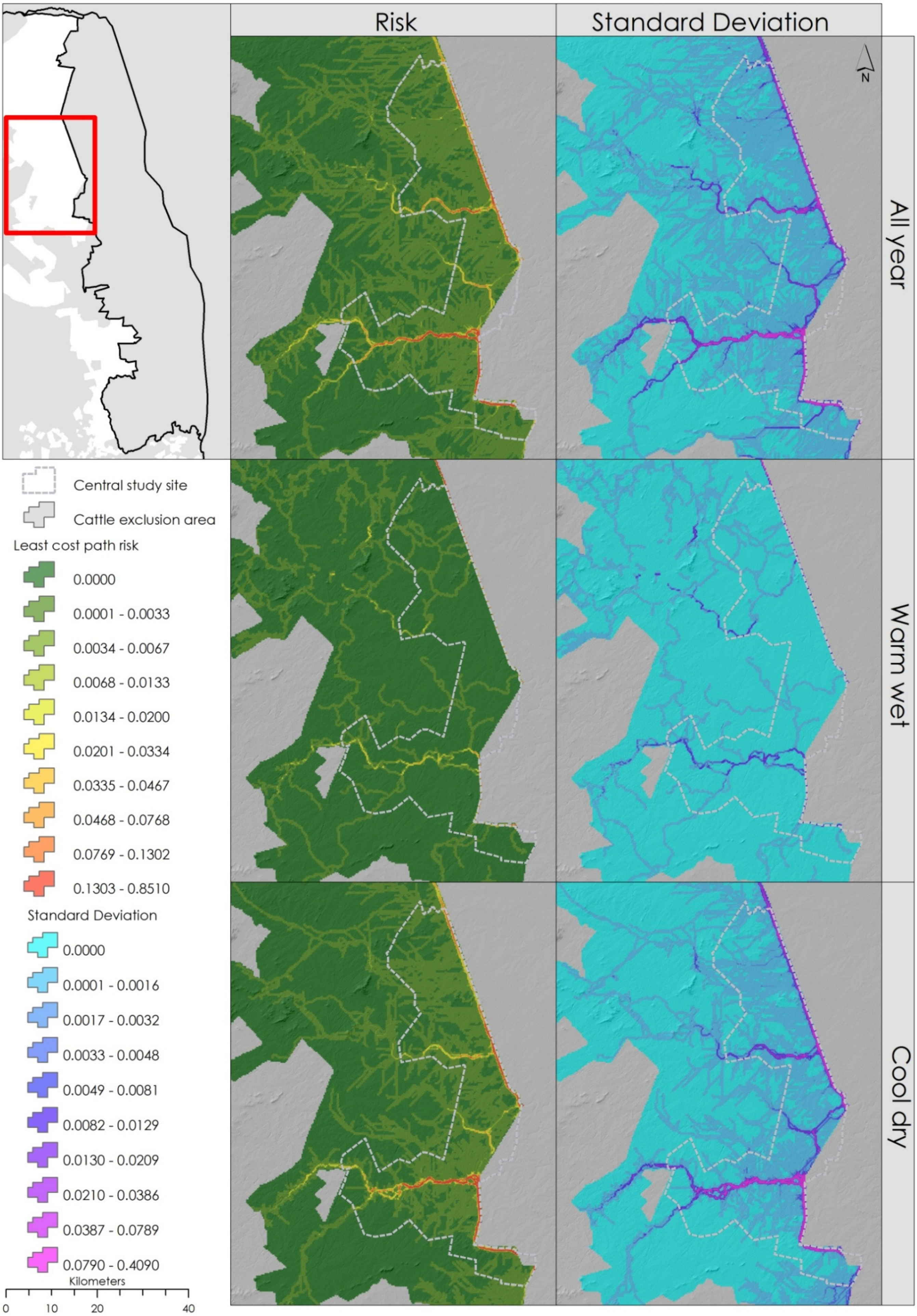

Figure 5.29. Buffalo least cost path contact risk - Central study site

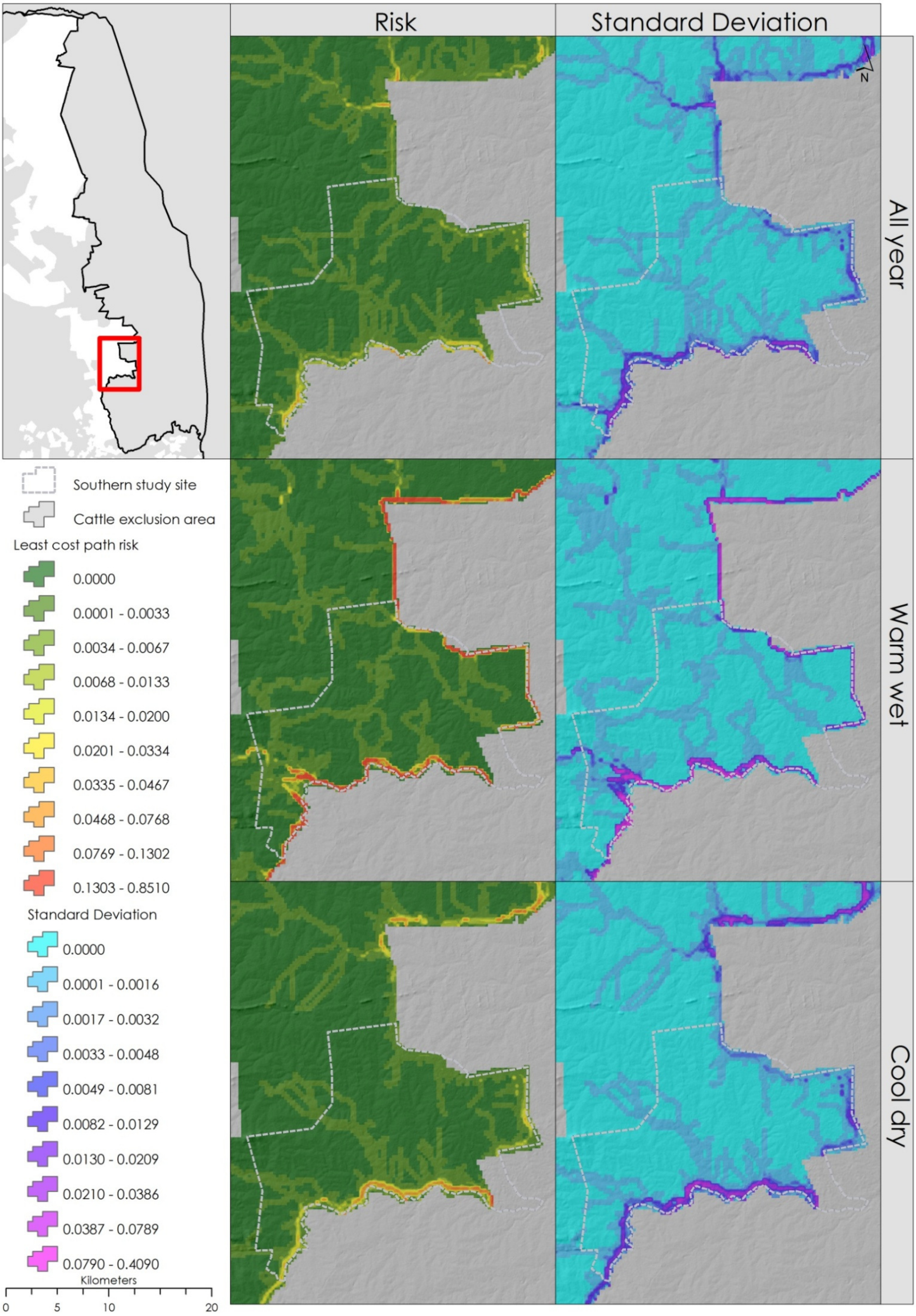

Figure 5.30. Buffalo least cost path contact risk - Southern study site

Appendix E

Evaluation of risk models against recent FMD outbreaks

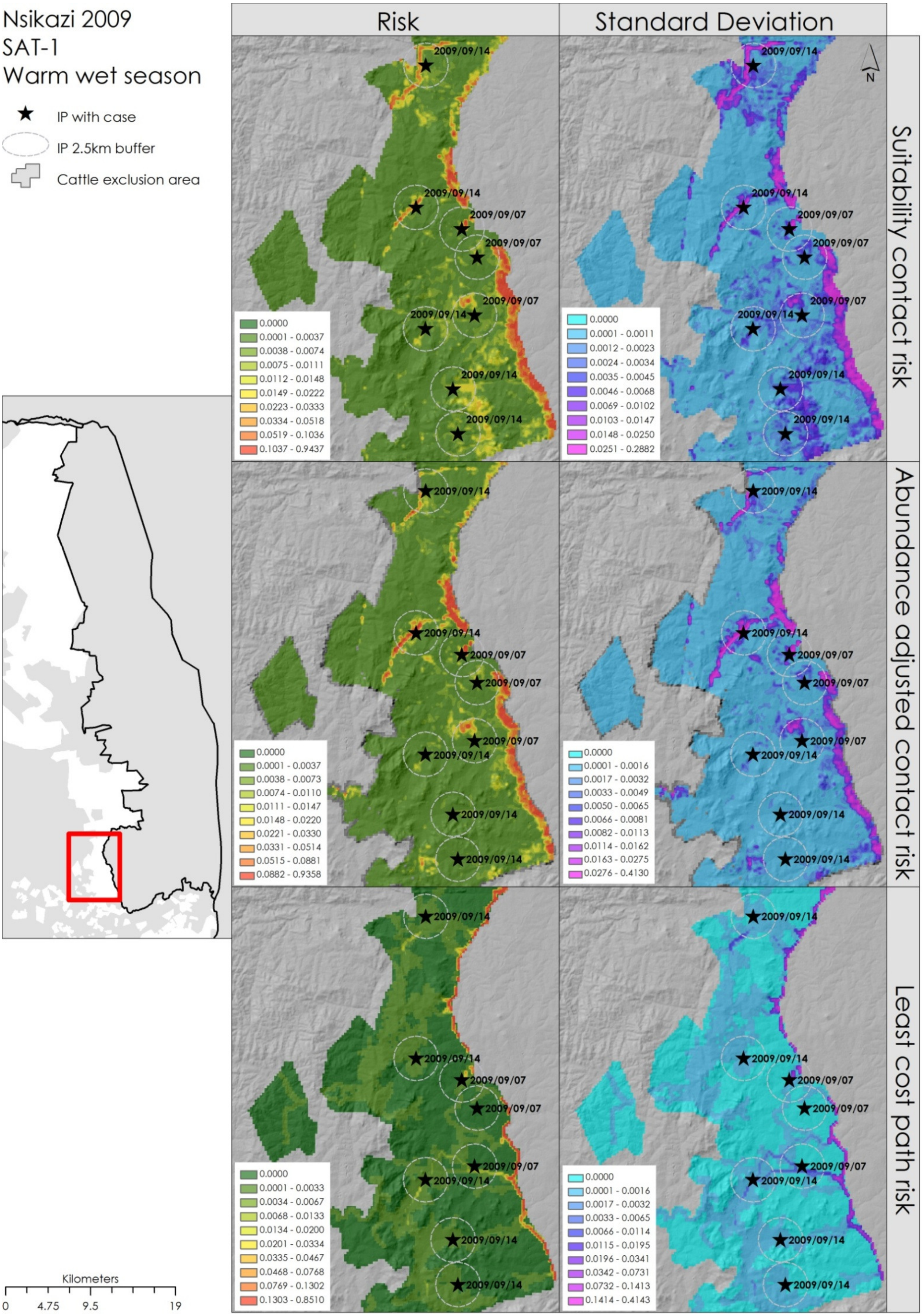

Figure 5.31. Nsikazi outbreak - Warm wet season 2009

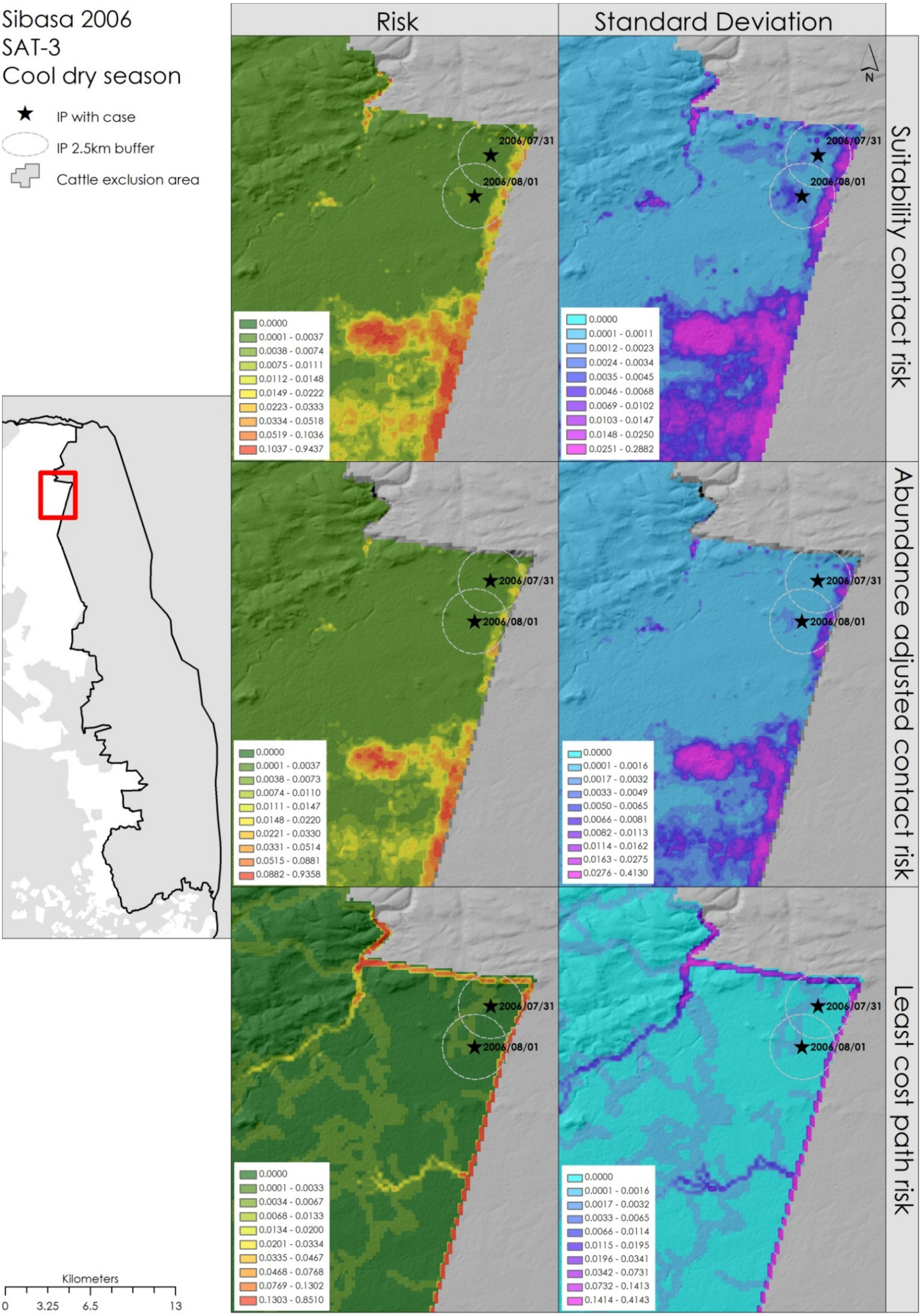

Figure 5.32. Sibasa outbreak - Cool dry season 2006

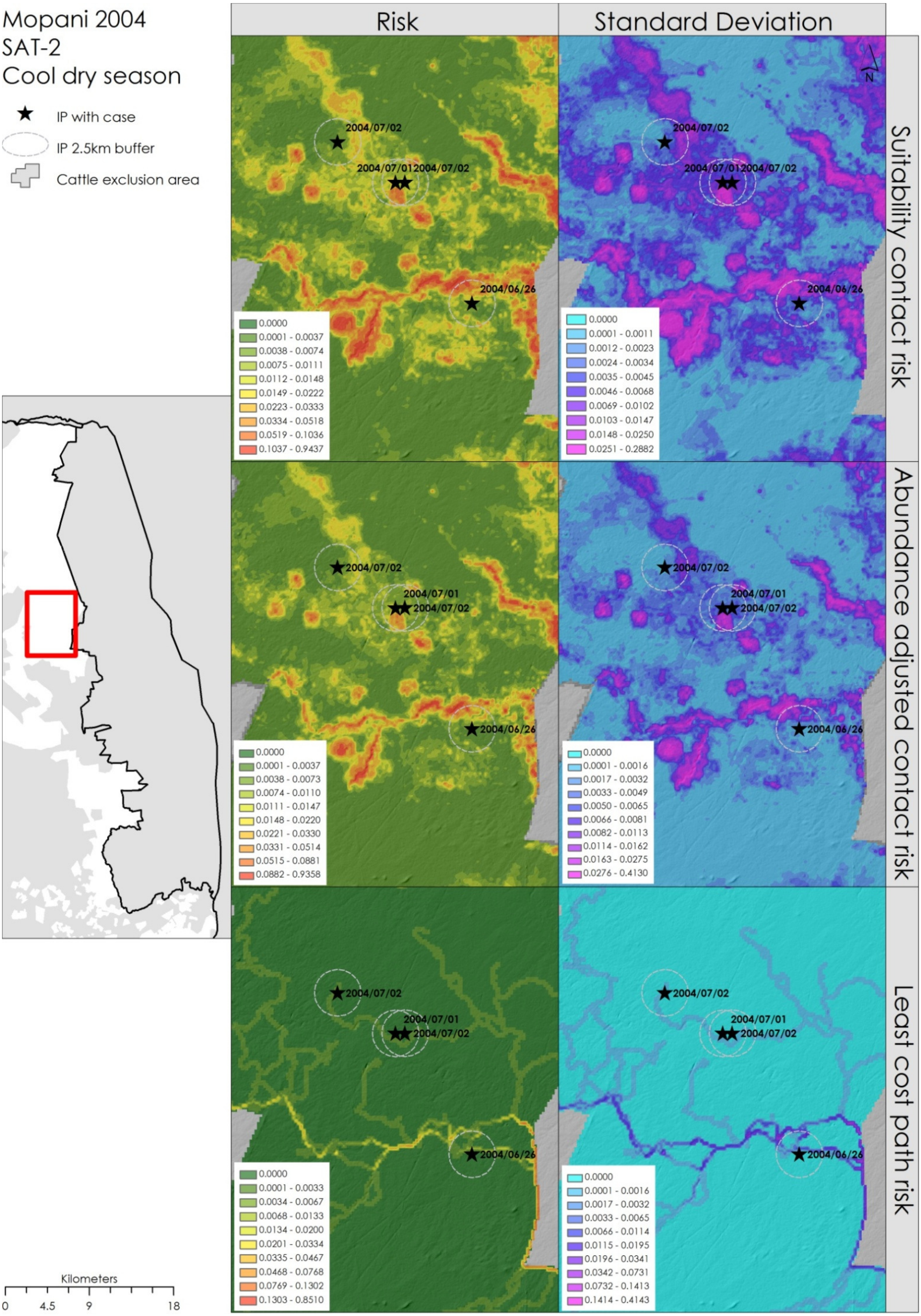

Figure 5.33. Mopani outbreak - Cool dry season 2004

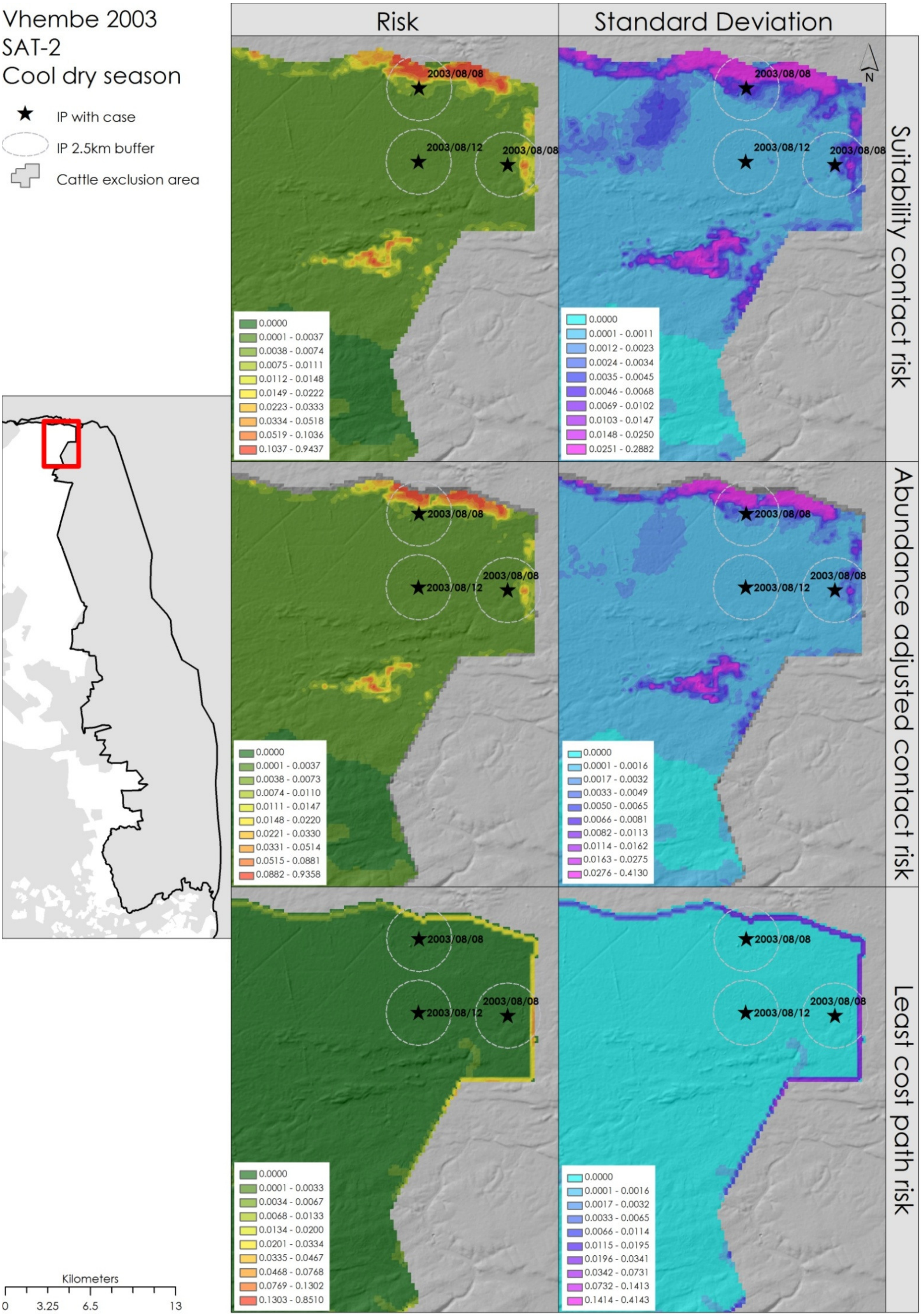

Figure 5.34. Vhembe outbreak - Cool dry season 2003

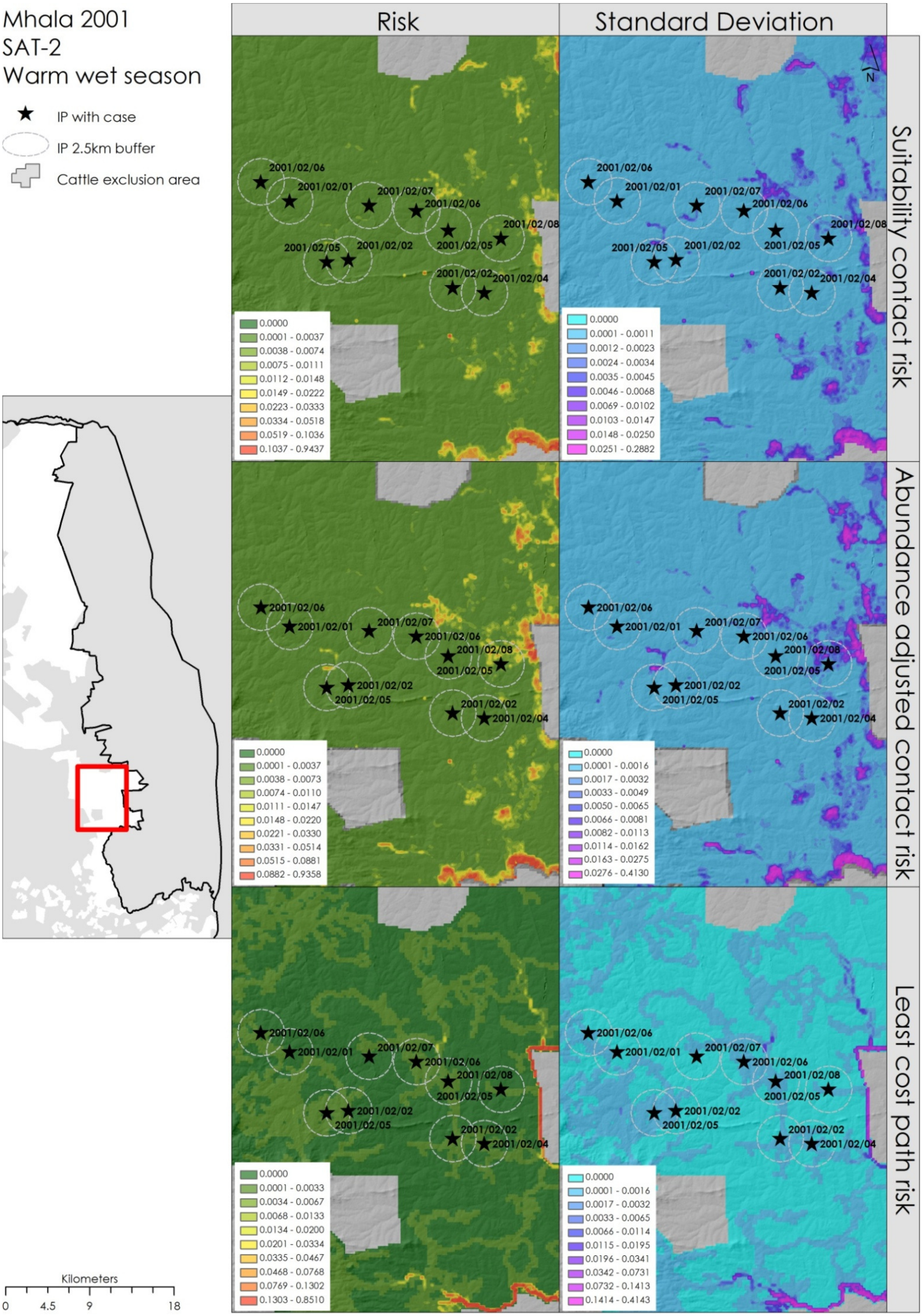

Figure 5.35. Mhala outbreak - Warm wet season 2001