Evidence of increasing intra and inter-species transmission of *Mycobacterium bovis* in South Africa: Are we losing the battle?

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Abstract

Tuberculosis caused by *Mycobacterium bovis* is recognized worldwide as a significant health risk in domestic cattle, farmed and wild animal species as well as in humans. We carried out spoligotyping and variable number of tandem repeat (VNTR) typing methods to characterize 490 *M. bovis* isolates from livestock (cattle, n=230; pig n=1) and wildlife species (n=259) originating from different farms and regions in South Africa, with the aim to further establish the genetic diversity of the isolates, study the population structure of *M. bovis* and elucidate the extent of interspecies transmission of bovine tuberculosis. A total of ten spoligotype patterns were identified, two of which were novel (SB2199 and SB2200) and reported for the first time in the literature, while VNTR typing revealed a total of 97 VNTR profiles. Our results showed

evidence of clonal expansion for some ancestral strains as well as co-infections with two or three *M. bovis* strains on some of the cattle and game farms, which suggested independent introductions of infected animals from epidemiologically unrelated sources. Five spoligotypes and nine VNTR profiles were shared between cattle and wildlife. Our findings showed that besides cattle, at least 16 different animal species in South Africa are infected with bovine tuberculosis, and highlight a strong evidence of inter and intra- species transmission of *M. bovis*. Infection of the blue wildebeest (*Connochaetes taurinus*) with *M. bovis* is described for the first time in this report. This update in epidemiological information raises concerns that bovine tuberculosis has increased its spatial distribution in South Africa and is also affecting an increasing number of wildlife species compared to ten years ago.

Keywords: Bovine tuberculosis, wildlife, spoligotyping, VNTR typing, South Africa

Introduction

Bovine tuberculosis (BTB) is still recognized worldwide as a significant animal health risk, primarily in domestic cattle and wildlife. The causative agent, *Mycobacterium bovis*, has a wide host range which includes farmed and wild animals as well as humans (Neill et al. 2005). *M. bovis* is a member of the *Mycobacterium tuberculosis* complex, which includes mycobacterial species that cause tuberculosis in animals and humans (Brosch et al. 2002; Huard et al. 2006). In South Africa, tuberculosis in cattle and free ranging wildlife species caused by *M. bovis* is well documented (Bengis et al. 2001; Michel et al. 2008 and 2009; Hlokwe et al. 2011). The prevalence of the disease in commercial cattle was reported to be less than 1% in 1995, owing to the implementation of national BTB control and eradication scheme in 1969. The prevalence of the disease in communal cattle is currently unknown. Bovine tuberculosis in wildlife in the

Kruger National Park (KNP) is endemic, with the highest disease prevalence in buffalo herds in the southern zone of the park. A single *M. bovis* strain was responsible for the epidemic and has subsequently spread progressively moving in a northern direction. It has infected at least 12 other wildlife species (Michel and Bengis, 2012) and has undergone evolutionary changes as described (Michel et al. 2009; Hlokwe et al. 2013). More recently, an epidemiological link between the KNP and the Gonarezhou National Park was confirmed, which has negative implications for the Greater Limpopo Transfrontier National Park (GLTFNP), De Garine-Wichatitsky et al. 2010; Hlokwe et al. 2013).

Bovine TB in the Hluhluwe-iMfolozi Park (HiP), which is geographically and epidemiologically distinct from KNP, is caused by at least three distinct *M. bovis* strains (Hlokwe et al. 2011). The prevalence of the disease in free ranging wildlife not associated with KNP or HiP, i.e. in private game reserves and game farms is currently unknown. Bovine tuberculosis in KNP and HiP was introduced by cattle from nearby communal farms and the persistence of the disease in these conservation areas as well as in communal farms pose a risk for ongoing transmission of the disease between wildlife and livestock. The situation may worsen if BTB prevalence in these ecosystems rises, since the disease in wildlife is generally not easy to control (Corner, 2006). Of further concern is that bovine tuberculosis poses a zoonotic risk, particularly in high HIV endemic communities surrounding the conservation areas (Thoen et al. 2006; Michel et al. 2010). An important factor for successful bovine tuberculosis control and eradication programs is contact tracing and point source identification as unregulated and illegal movement of infected animals is considered the major constraint in such control strategies (Aranaz et al. 2004).

Molecular methods have become very tightly integrated with traditional epidemiological tracing of tuberculosis and provide a paradigm for such integration at both local and international levels

(Achtman, 2001). In addition to traditional methods, typing methods such as IS*6110* restriction fragment length polymorphism (RFLP) and Polymorphic G-C Rich Sequences RFLP, spoligotyping and variable number of tandem repeat typing (VNTR) analyses are applied to characterize *M. bovis* isolates (Durr, 2000). Previous studies conducted in the KNP have shown that spoligotyping could not differentiate the parent C8 strain from its variants strains (Michel et.al. 2009; Hlokwe et al. 2013) because of the slow evolutionary rate of the direct repeat region targeted. In addition, it generally has a lower discriminatory power for South African isolates as compared to other typing methods i.e. IS*6110* typing, PGRS typing (Michel et.al. 2008). Very recently, VNTR loci were assessed for their discriminatory power on isolates from South Africa. The results of this study led to a selection of a 13 locus VNTR panel for isolates from this region (Hlokwe et al. 2013).

The aim of the current study was to use spoligotyping and VNTR typing as described to characterize *M. bovis* isolated from livestock and wildlife species in South Africa to further establish their genetic diversity and assess the extent of intra- and inter-species transmission of bovine tuberculosis. The study also aimed to utilize the typing data to elucidate the population structure of *M. bovis* and generate a database to form the basis of back and forward tracing of sources of infection for improved surveillance and control of the disease in the country.

Materials and Methods

Sample collection

The samples used in this study were received between 2002 and 2013 in the Tuberculosis Laboratory of the Onderstepoort Veterinary Institute for routine mycobacterial culture. Samples were collected from animals on livestock farms throughout South Africa and from different

wildlife species from the KNP, HiP as well as private game ranches. They included tissue samples from lymph nodes, organs, and bronchial fluids. The majority of the samples were collected from: (i) tuberculin skin test and gamma interferon test positive animals at slaughter, (ii)gamma interferon test was conducted together with skin test in buffaloes from game farms/reserves. In some cases, buffaloes testing positive in the gamma interferon assay but negative in the skin test were slaughtered and samples collected for culture, (iii) lesions detected in healthy cattle during routine slaughter from abattoir tuberculosis suspect animals, (iv) as part of passive TB surveillance which was based on necropsy of all wild animals found dead in game parks/reserves and the collection of tissues showing pathological changes for specific testing. If tuberculous like lesions were found, the specimens were sent for tuberculosis culture. Bovine tuberculosis has been documented in all provinces of South Africa with a sporadic occurrence, irrespective of the size or density of the cattle population. Routine submissions formed part of the State Veterinary Service's strategy for confirming *M. bovis* infection in either skin test positive reactor cattle or slaughter cattle with suspect tuberculous lesions. All samples were accompanied by sample submission forms with information relating to the animal, owner and precise location. In case where additional information was required, the responsible state veterinarian assisted with back tracing of animals and contacts. An additional two tissue samples from cattle originating from two different regions (i.e. Chimoio district in Manica Province and Guvuru district in Inhambane Province) in Mozambique were included for comparison purposes. The different animal species sampled as well as their locations are indicated in table 1.

Table 1. Animal species, their origins and numbers of *M. bovis* isolated.

Animal species	Location											
	EC	FS	GP	KZN	LP	MP		NC	NW	WC	MOZ	Grand Total
						KNP	Non-KNP					
Cattle	70	18		30	21		81	7	3	1	2	**232**
Buffalo				32	7	95	34		1			**170**
Baboon				1		3						**4**
Bushbuck							1					**1**
Cheetah					1							**1**
Eland		1										**1**
Hyena							4					**4**
Impala						1	5					**6**
Kudu						3	1					**4**
Leopard						1						**1**
Lion					1	47	8					**56**
Nyala					1							**1**
Porcine	1											**1**
Rhino					1							**1**
Warthog					1	1	5					**7**
Waterbuck							1					**1**
Wildebeest							1					**1**
Grant Total	**71**	**19**	**0**	**63**	**32**	**151**	**141**	**7**	**4**	**1**	**2**	**492**

Keys:

EC, Eastern Cape Province; FS, Free State Province; GP, Gauteng Province, KZN, KwaZulu–Natal Province; LP, Limpopo Province; MP, Mpumalanga Province; NC, Northern Cape Province; NW, North West Province; WC, Western Cape Province; MOZ, Mozambique

Bacterial isolation and *M. bovis* identification

Briefly, tissue samples were processed and decontaminated using 4% sodium hydroxide and 2% hydrochloric acid methods. Bronchial fluids were decontaminated using 4% sodium hydroxide. Samples were inoculated onto Löwensten-Jensen medium supplemented with pyruvate and incubated at 37°C for up to 10 weeks (Alexander et. al. 2002). *M. tuberculosis* complex bacteria were identified by polymerase chain reaction (PCR) using primers that target a sequence encoding the MPB 70 antigen as previously described (Alexander et. al. 2002; Michel et al. 2009). Deletion analysis was performed using primers targeting the RD4 and RD9 regions of difference as previously described for *M. bovis* identification (Warrren et al. 2006).

Template DNA preparation

Genomic DNA extraction from *M. bovis* cells

Genomic DNA from *M. bovis* isolates was extracted as previously described using a PUREGENE DNA extraction kit according to the manufacturer's instructions with minor modifications (Hlokwe et al. 2011).

Mycobacterium bovis lysate preparation

Mycobacterium bovis cells were suspended in 100 µl of sterile distilled water and heated to 95°C for 25 minutes, cooled down briefly and stored at -20°C until required (Hlokwe et al. 2013). Either pure genomic DNA or cell lysate prepared as described above was used for both the PCR-based methods, i.e. spoligotyping and VNTR typing.

Genotyping of *Mycobacterium bovis* isolates

Spoligotyping

Spoligotyping of all isolates was done according to a standardized international method (Kamerbeek et al. 1997), using a commercially available kit (Ocimum Biosolutions, Indianapolis, IN, USA). *M tuberculosis* H37Rv, *M. bovis* BCG and sterile distilled water served as the test controls. The resulting spoligopatterns were compared to those found in the *M. bovis* spoligotype database (www.mbovis.org).

Variable number of tandem repeat (VNTR) typing.

PCR amplifications for VNTR typing were performed using a set of tandem repeat loci recently identified as stable and polymorphic for South African *M. bovis* isolates (i.e. ETR A, B, C, and

E; Qub 11a, b, 18 and 26, MIRU 16, 23 and 26, as well as M. tub 12 and 21 (Hlokwe et al. 2013). The loci were amplified individually as previously described (Le Fleche et al. 2002) and the PCR primer sequences used are outlined in Table 2. The PCR products were separated on a

Table 2. Table 2. Variable number of tandem repeat (VNTR) loci and PCR primer sequences used for the typing of *M. bovis* isolates (Le Fleche et al. 2002).

VNTR locus	VNTR alias	VNTR locus size (bp)	Forward primer (5'-3')	Reverse Primer (5'-3')
2163a	QUB 11a	69	CCCATCCCGCTTAGCACATTCGTA	TTCAGGGGGGATCCGGGA
2163b	QUB 11b	69	CGTAAGGGGGATGCGGGAAATAGG	CGAAGTGAATGGTGGCAT
1982	QUB 18	78	ATCGTCAGCTGCGGAATAGT	AATACCGGGGATATCGGTTC
2461	ETR-B	57	GCGAACACCAGGACAGCATCATG	GGCATGCCGGTGATCGAGTGG
0577	ETR-C	58	GACTTCAATGCGTTGTTGGA	GTCTTGACCTCCACGAGTGC
1955	Mtub 21	57	AGATCCCAGTTGTCGTCGTC	CAACATCGCCTGGTTCTGTA
2996	MIRU 26	51	CCCGCCTTCGAAACGTCGCT	TGGACATAGGCGACCAGGCGAATA
1644	MIRU 16	53	TCGGTGATCGGGTCCAGTCCAAGTA	CCCGTCGTGCAGCCCTGGTAC
3192	ETR-E	53	ACTGATTGGCTTCATACGGCTTTA	GTGCCGACGTGGTCTTGAT
4052	QUB 26	111	AACGCTCAGCTGTCGGAT	GGCCAGGTCCTTCCCGAT
2531	MIRU 23	53	CAGCGAAACGAACTGTGCTATCAC	CGTGTCCGAGCAGAAAAGGGTAT
2165	ETR-A	75	ATTTCGATCGGGATGTTGAT	TCGGTCCCATCACCTTCTTA
1121	Mtub 12	15	CTCCCACACCCAGGACAC	CGGCCTACCCAACATTCC
2347	Mtub 12	57	AACCCATGTCAGCCAGGTTA	ATGATGGCACACCGAAGAAC

2% agarose gels, run at 85 V for at least 3 hours and visualized under 312 nm UV light. A 100 bp or 100 bp ladder PLUS (Thermo Scientific, USA) were included to estimate the sizes of the products. In addition, the DNA fragment sizes were also determined by using Quantity One 1-D analysis software installed in the Gel Doc system (Bio-Rad laboratories, Hercules, CA). These were converted into tandem repeat copy numbers according to Le Fleche and co-workers (Le Fleche et al. 2002) and the resulting VNTR profiles were saved in a spreadsheet.

Determination of the genetic relationships of the *Mycobacterium bovis* isolates

The genetic relationships of the isolates were deduced by the reconstruction of an unweighted pair group mean average (UPGMA) tree, as well as the minimum spinning tree (MST) using the Bionumerics software package version 7.1 (Applied Maths, Belgium).

Statistical analysis

Analysis and comparisons of counts for animal species, provinces, spoligopatterns, VNTR typing profiles and other statistical combinations were done using the Pivot tables (Microsoft Office Professional Plus 2010, Excel version 14.0.6129.5000-Pivot).

Results

Mycobacterial isolation and identification

A total of 492 isolates including 490 originating from 17 different animal species from South Africa (cattle, n=232; pig, n=1; wildlife from KNP, n=151; wildlife from HiP, n=28; wildlife from private game ranches, n=80) and two isolates from cattle from Mozambique were recovered. All isolates were identified as *M. tuberculosis complex* organisms due to the amplification of a 372 bp PCR product from the MPB 70 gene. *M. bovis* was confirmed in all cases by the presence of two specific DNA fragments of 268 bp and 108 bp for RD4 and RD9, respectively.

Spoligotyping

Where more than one animal with an isolate was found in one area, e.g. conservation area or farm, or there was known animal movement and contact between animals, we defined this as an "outbreak" in this report. Analysis of the 490 *M. bovis* isolates from South Africa yielded a total

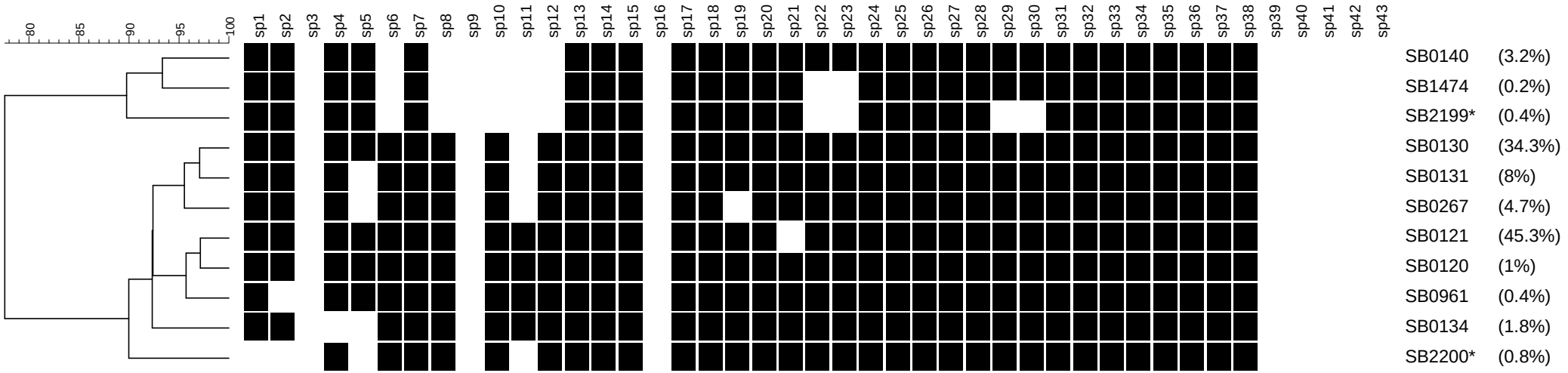

Figure 1. Dendrogram and schematic representation showing relatedness of different spoligotype patterns found among the 490 livestock and wildlife M. bovis isolates from South Africa as well as two isolates from Mozambique analyzed. The newly identified spoligotypes are indicated with the asterisk. SB0961 (Moz) was detected from cattle samples from Mozambique.

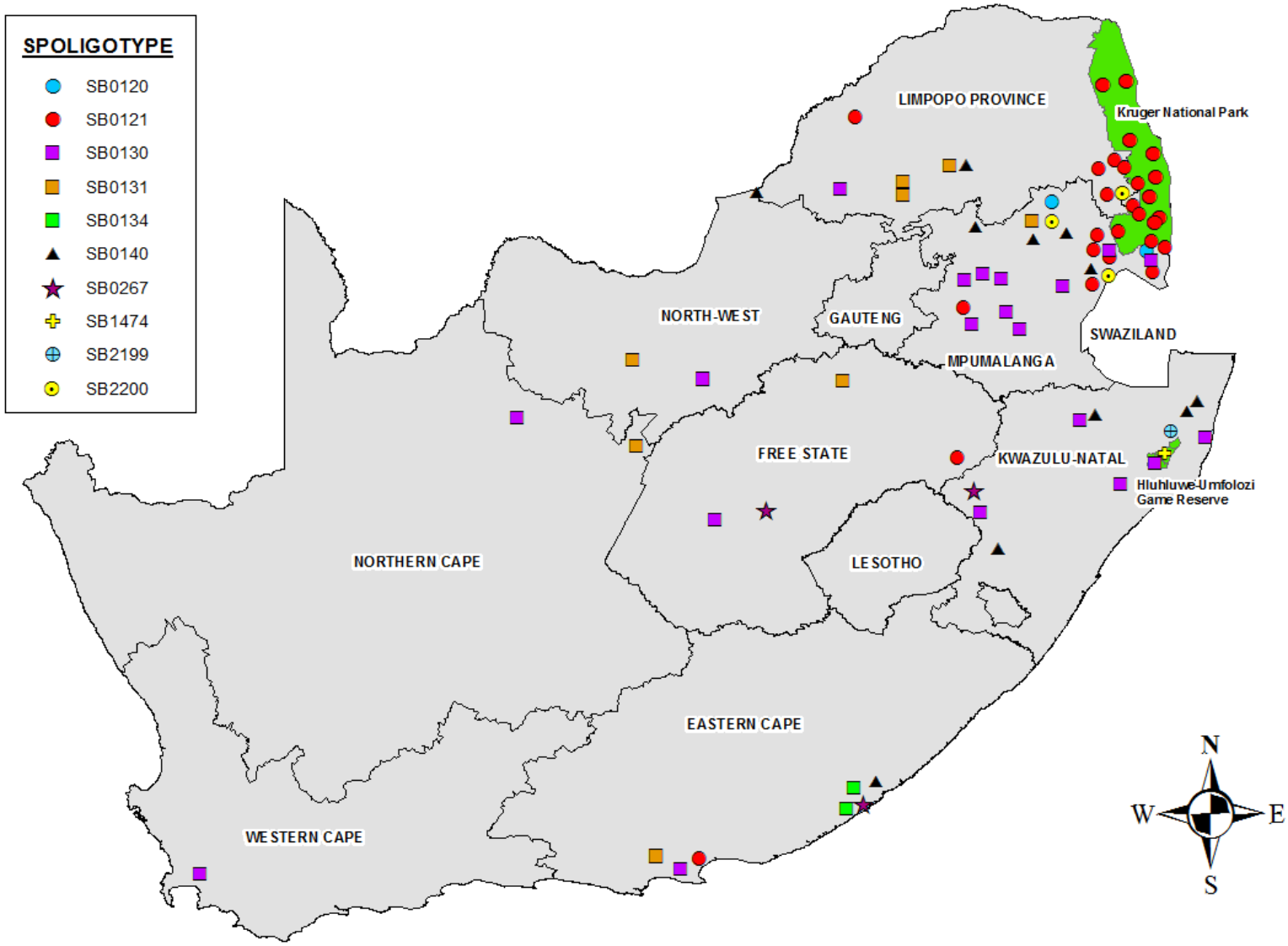

Figure 2. Geographical distribution of spoligotype patterns identified among the 490 M. bovis isolates from South Africa

of 10 different spoligopatterns (Figure 1). Two new patterns were designated the spoligopattern codes SB2199 and SB2200, respectively. Spoligopattern SB2199 had a close genetic relationship with SB1474 and was detected in cattle and a wildebeest. It was characterized by lack of spacers 3, 6, 8-12, 29-30 and 39-43. Spoligopattern SB2200 lacked spacers 1-3, 5, 9, 11, 16 and 39-43 (Figure 1). The geographic distribution of the different spoligotypes as determined in this study is shown in Figure 2. Of the 10 spoligopatterns, five were detected in both livestock and wildlife species (i.e SB0120, SB0121, SB0130, SB0140 and SB2200), four were detected exclusively in livestock (i.e. SB0131, SB0134, SB0267 and SB02199) and a single spoligotype (SB1474) was detected in only one buffalo isolate. In total, nine spoligopatterns were detected in 55 bovine tuberculosis outbreaks in cattle. Spoligopattern SB0130 was found to be geographically most widely distributed and was detected in 34.3 % (168/490) of the total isolates. Spoligotyping results showed that the majority of the epidemiologically related outbreaks (90%) were the result of infection with one *M. bovis* strain. Co-infection (infection with two or more genotypes on a farm or conservation area) was evident on five different cattle farms, (farm 1: SB0134 and SB0267; farm 2: SB0130 and SB0134; farm 3:, SB0120 and SB0131; farm 4: SB0120 and SB0121; farm 5: SB0131 and SB0140) as well as in two private game reserves (reserve 1: SB0121 and SB2200; reserve 2: SB0120, SB0121 and SB0130) and in HiP (SB0130 and SB1474). The latter has been reported before (Hlokwe et al. 2011).

Variable number of tandem repeat (VNTR) typing analysis

Analysis of typing results from 490 South African isolates was based on 13 VNTR loci and yielded a total of 97 VNTR profiles (Figures 3 and supplementary information 1). In this study we defined a cluster as a group of *M. bovis* genotypes which were ≥70% similar according to the dendrogram in the Supplementary information. The threshold used is unique to this study, and is

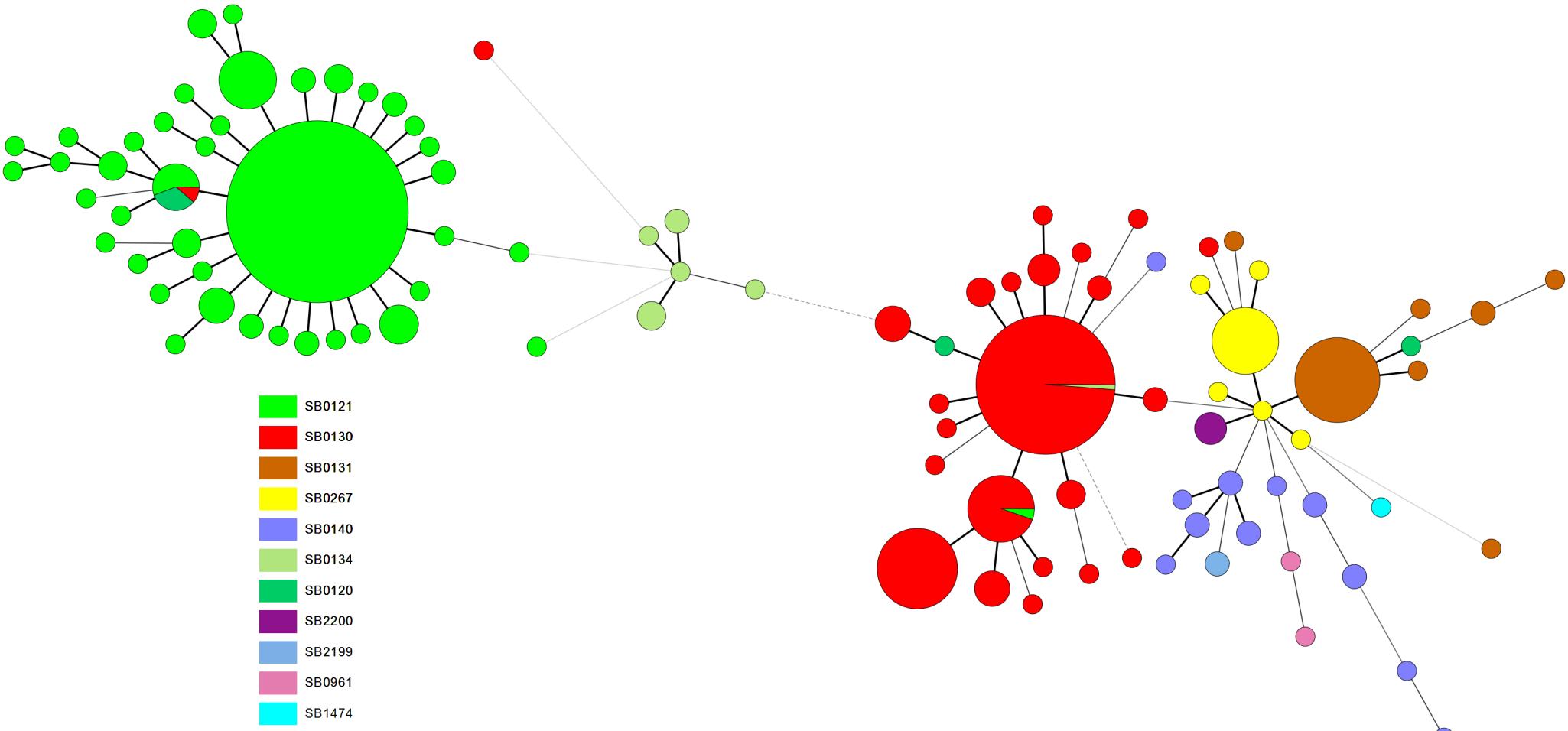

Figure 3. Minimum spanning tree (MST) for the phylogenetic relationship of the 490 M. bovis isolates analyzed based on the VNTR profiles in relation to spoligotypes obtained.

based on empirical data derived from isolates from the Greater Kruger National Park Complex (GKNPC) where the epidemic can be traced back to one unique *M. bovis* strain. Of main interest was the KNP cluster consisting of approximately 40% of the total profiles corresponding to SB0121 (Figures 3 and supplementary information 1). Within this cluster, VNTR-1 was the KNP's dominant genotype. The genotypes of the KNP cluster were found in eight known infected wildlife species within the KNP as well as in private game reserves which form part of the Greater Kruger National Park complex (GKNPC). Overall, a total of nine VNTR profiles were shared among cattle and different wildlife species, whilst 46 and 42 VNTR types were found in cattle or wildlife species only, respectively. Some VNTR genotypes (e.g. genotypes corresponding to SB0130) were widely distributed.

Discussion

Initial studies conducted in South Africa targeted specific ecosystems or species to determine the genetic diversity of *M. bovis* (Michel et al. 2008; Michel et al. 2009). The current study aimed to establish a database of *M. bovis* genotypes which allows the determination of genetic relationships between outbreaks not only among the 490 isolates characterized to date, but they can serve as reference for future isolates. The study aimed at further evaluation of the 13 VNTR loci panel across a variety of outbreaks in epidemiologically related and unrelated events. Information based on spoligopatterns is known to contain sufficient phylogenetic signals to construct recent events with some level of confidence (Smith et al. 2003). In addition, strains bearing the same spoligotype pattern are assumed to be a set of individuals derived relatively recently by clonal replication from a single ancestral cell. The VNTR typing tool applied here had the ability to recognize such clonal variants, allowing the genetic diversity of South African *M. bovis* strains to be studied at country level.

In this study, a total of ten spoligotype strains were detected, of which nine were detected in cattle isolates in 55 bovine tuberculosis outbreaks in different regions of the country. Most outbreaks (n=25) occurred in Mpumalanga Province (Figure 2). The widespread distribution of some of the spoligotype strains (i.e. SB0130 and SB0131) could have started during the historical importation of cattle into South Africa from other countries in previous centuries. On the contrary, SB0120 and SB0134 appear to be geographically localized in Mpumalanga and Eastern Cape Provinces, respectively. It is of concern that outbreaks described in this study most likely resulted from the persistence of seven *M. bovis* strains (about 70% of the *M. bovis* spoligotypes) previously detected in the country between 1993-2003 (Michel et al. 2008), suggesting that very few or none of the strains were effectively removed by control measures during these years. Movements of infected animals, possibly unknowingly, from one region to another seem to be the most likely route of transmission of the strains. Further noteworthy is the isolation of new strains, namely SB2199 and SB2200. SB2199 was detected in cattle originating from a research station in the Hluhluwe region, located approximately 80 km from HiP. SB2199 is genetically closely related to SB1474 which was detected for the first time in buffaloes from HiP. Both SB2199 and SB1474 seem to have evolved from SB0140 as their common ancestor (Figure 1). The research station exclusively farms and breeds Nguni cattle. Cattle from this research station were initially sourced from iShowe and Kokstad regions (both in KwaZulu-Natal Province) in the 1980's. However, this particular animal from which SB2199 was detected, was born and bred in the station. In Mpumalanga Province, we detected spoligotype SB2200 from cattle on two epidemiologically unrelated farms, which may suggest that this novel strain could be more widespread than currently detected, as it was also detected in a blue wildebeest within the GKNPC. All infected cattle and the blue wildebeest also shared the same VNTR profiles.

The persistence of the ‘old’strains and the detection of new emerging strains is an indication of active, ongoing BTB transmission, increasing the risk of spill over to wildlife species in currently uninfected game farms and parks.

Mycobacterium bovis was also detected in tissues from a pig. This is only the second time in the past decade that *M. bovis* has been isolated from pigs in South Africa, reason being that pigs and cattle are rarely kept together commercially in S.A. In contrast, *M. tuberculosis* is more frequently isolated from pigs, reflecting the high human tuberculosis incidence (Michel, unpublished data). On the other hand there is a complete lack of information regarding the occurrence of *M. bovis* in free-ranging pigs in communal farming areas as these animals are not marketed through abattoirs.

The majority of wildlife derived *M. bovis* isolates in this study were from the KNP (58%), confirming the ongoing transmission of *M. bovis* between and within species in the park. The VNTR profiles detected, which all corresponded to spoligopattern SB0121, formed what we described as the KNP cluster. Genotype VNTR-1 dominated within this KNP cluster (Hlokwe et al. 2013). Spoligotype SB0121 clonal complex had originally descended from SB0120 through the loss of spacer 21. It is tempting to speculate that the success of SB0121 is at least partially caused by a higher transmissibility compared to its ancestor SB0120. This could, on the other hand, however, be severely flawed by the fact that SB0120 occurred only in farming areas where BTB control measures were applied. Hence there was a possibility of containment or even active elimination of SB0120 through test and slaughter, while SB0121 occurred within the GKNPC which is a free-ranging ecosystem with a high rate of intra-and interspecies contacts in the absence of any BTB control measures. We did not find any evidence suggesting an active spread of SB0121 clonal variants in other regions of the country except in private game reserves of the

Greater Kruger National Park Complex. The possibility of direct spread of the disease from wildlife species in the GKNPC to cattle and other wildlife species in neighboring areas remains a risk to neighboring communities.

Our results showed that bovine tuberculosis had spread to previously uninfected (or unknown status) game farms and reserves in Mpumalanga, Limpopo, KwaZulu-Natal, Free State and North West Provinces. In addition, this study reports for the first time, *M. bovis* infection of a blue wildebeest in South Africa. The wildebeest was on a private game reserve in the GKNPC and carried the novel *M. bovis* strain SB2200, indicating the introduction of a new *M. bovis* genotype in the GKNPC ecosystem, most probably effected by the repeated translocation of blue wildebeest into the reserve (Reininghaus, personal communication) Infection with *M. bovis* was first reported in two wildebeests in the Serengeti ecosystem in Tanzania (Cleaveland et al. 2005). Consistent with the previous report, the wildebeest in the current study did not present with any visible lesions during post mortem examination, but *M. bovis* was isolated from lung tissue. The animal was culled because it escaped from the reserve. In South Africa, movement control of any buffalo is instituted in order to prevent spread of BTB out of infected conservation areas (www.daff.gov.za/publications). The spread of bovine tuberculosis in this country may also be facilitated by infected buffaloes escaping from the game parks/reserves due to compromised fences after floods etc. Infected but undiagnosed wildlife species (as in the case of the wildebeest and other cases) can potentially play a role in the spread of the disease since their movement is not controlled. Over 50% of the isolates in this study were from wildlife species, of which 65.6% (170/259) were from buffaloes, emphasizing their role as carrier status and their role in the epidemiology of the disease in the country.

Genotyping methods applied in this study were useful in determining the possible sources of infection or true origins of buffaloes on a game farm located south of the KNP co-infected with 3 different strains of *M. bovis* (SB0120; SB0121 and SB0130). Our results confirmed that buffaloes had been initially sourced from HiP, based on the isolation of strains endemic in the latter conservation area. The resident SB0121 strain recovered from buffaloes and warthogs on the farm was likely to originate from the KNP. The source of infection could, however, not be established for one buffalo harboring SB0120 strain type and could either stem from a persisting infection in the immediate neighborhood or the strain could have been introduced during movement of game onto the farm.

We have analyzed two isolates from different regions in Mozambique, which borders South Africa in the east. Spoligopattern SB0961 was detected in both the cattle isolates and not recovered from any of the South African isolates. The absence of SB0961 in South Africa may indicate that the *M. bovis* populations in the two countries are largely unrelated based on historical livestock trading partners, a hypothesis which remains to be further investigated. The Greater Limpopo Transfrontier Park links South Africa and Mozambique through the partial removal of park fences which has resulted in unrestricted movements of wildlife. In South Africa, only BTB test negative buffaloes can be moved between properties, while other wildlife species and cattle outside the foot and mouth disease control zone can be moved freely. Monitoring of BTB in wildlife and livestock populations including genetic characterization of *M. bovis* recovered from these populations in the transfrontier park is therefore of high importance for animal and human health at this wildlife/livestock/human interface.

Conclusion

We have analyzed a larger *M. bovis* sample size and it is suggested that both typing tools can be applied in future molecular epidemiological investigations of *M. bovis* infection in order to have a better knowledge of their genetic diversity and distribution in the country. Our findings showed that besides cattle, at least 16 different animal species in S.A contracted the infection, and highlight a strong evidence of inter- species transmission of *M. bovis*. Although bovine tuberculosis is a controlled disease in South Africa in terms of animal health legislation, eradication of the disease in the near future is elusive. Despite the fact that national control of BTB is applied in commercial cattle, there is a high diversity of *M. bovis* persisting in the country, highlighting the importance and need for intensified diagnostic testing and consideration of alternative control measures such as vaccination. In the light of these most recent findings, screening of the BTB status of wildlife species before translocation is urgently recommended as prevention of the disease introduction remains the most effective control approach.

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Conflict of interest

The authors declare no conflict of interest.

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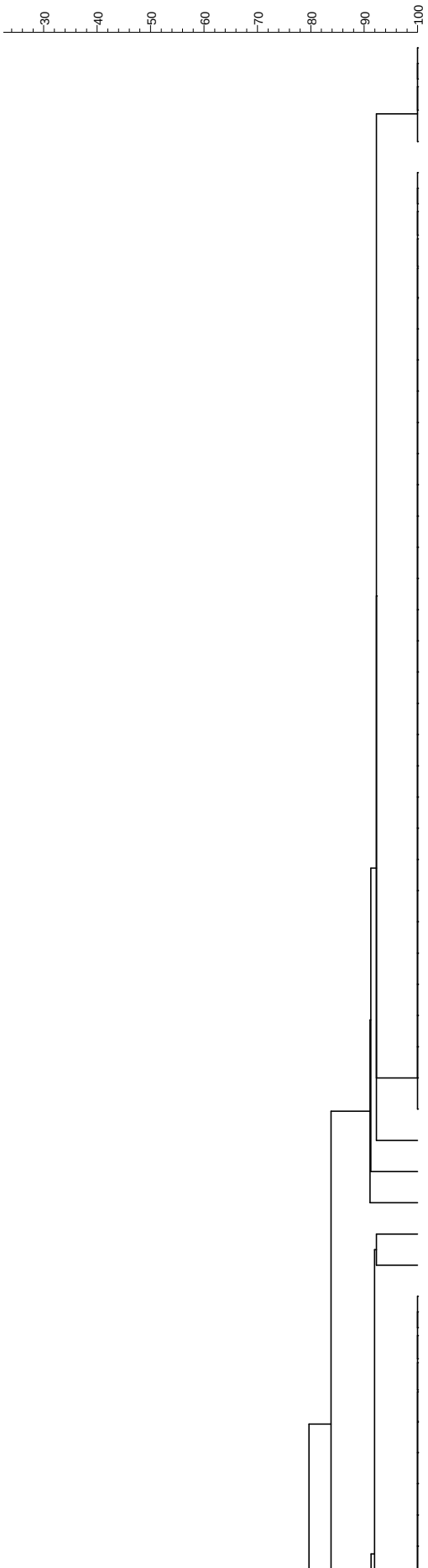
Supplementary information 1. Dendrogram and schematic representation demonstrating the genetic relatedness of the 97 VNTR profiles obtained from the 490 M. bovis isolates from South Africa as well as VNTR profiles obtained from isolates from Mozambique based on a 13 loci VNTR panel.



Qub 11a	Qub 11b	Qub 18	Qub 26	MIRU 16	MIRU 23	MIRU 26	Mtub 12	Mtub 21	ETR-A	ETR-B	ETR-C	ETR-E	VNTR-type	Key	Animal species	Location	Spoligotype	Year
11	4	3	4	2	4	6	4	3	6	4	5	3	11434246436453	TB 8008G	Cattle	MP	SB2200	2011
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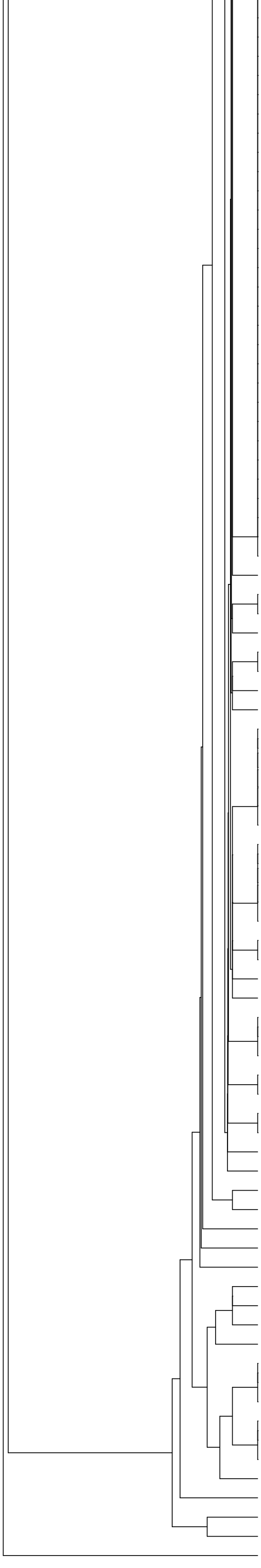

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8	2	4	4	3	4	5	4	2	6	4	3	4	8244345426434	TB 8158	Lion	MP	SB0121	2012
8	2	4	4	3	4	5	4	2	6	4	3	4	8244345426434	TB 8179A	Hyena	MP	SB0121	2013
8	2	4	4	3	4	5	4	2	6	4	3	4	8244345426434	TB 8179B	Hyena	MP	SB0121	2013
8	2	4	4	3	4	5	4	2	6	4	3	4	8244345426434	TB 8179C	Hyena	MP	SB0121	2013
8	2	4	4	3	4	5	4	2	6	4	3	4	8244345426434	TB6884A	Buffalo	KNP	SB0121	2008
8	2	4	4	3	4	5	4	2	6	4	3	4	8244345426434	TB7761E	Impala	MP	SB0121	2010
8	2	4	4	3	4	5	4	2	6	4	3	4	8244345426434	TB7762C	Warthog	MP	SB0121	2010
8	2	4	4	4	4	5	4	2	6	4	3	4	8244445426434	TB 7027B	Buffalo	KNP	SB0121	2008
8	2	4	4	3	4	5	4	2	4	4	3	4	8244345424434	TB 4175E	Lion	KNP	SB0121	2004
8	2	4	4	3	4	5	4	2	4	4	3	4	8244345424434	TB 4184B	Lion	KNP	SB0121	2004
8	2	4	4	3	4	5	4	2	5	4	3	4	8244345425434	TB 6974C	Lion	MP	SB0121	2008
6	2	4	4	3	4	5	4	2	6	4	3	4	6244345426434	TB 4649A	Buffalo	KNP	SB0121	2004
6	2	4	4	3	4	5	4	2	6	4	3	4	6244345426434	TB 5057D	Buffalo	KNP	SB0121	2005
7	2	4	4	3	4	5	4	2	6	4	3	4	7244345426434	TB 7818B	Buffalo	KNP	SB0121	2010
10	2	4	4	3	4	5	4	2	6	4	3	4	10244345426434	TB 5167A	Buffalo	KNP	SB0121	2005
8	2	4	4	3	4	6	4	2	6	4	3	4	8244346426434	TB 5530A	Buffalo	LP	SB0121	2006
8	2	4	4	3	4	6	4	2	6	4	3	4	8244346426434	TB 5530B	Buffalo	LP	SB0121	2006
8	2	4	4	3	4	6	4	2	6	4	3	4	8244346426434	TB 5547	Buffalo	LP	SB0121	2006
8	2	4	4	3	4	6	4	2	6	4	3	4	8244346426434	TB 7170A	Lion	KNP	SB0121	2009
8	2	4	4	3	4	6	4	2	6	4	3	4	8244346426434	TB 7913A	Buffalo	MP	SB0121	2011
8	2	4	4	3	4	6	4	2	6	4	3	4	8244346426434	TB 7913B	Buffalo	MP	SB0121	2011
8	2	4	4	3	4	4	4	2	6	4	3	4	8244344426434	TB 4850D	Buffalo	KNP	SB0121	2005
8	2	4	4	3	4	4	4	2	6	4	3	4	8244344426434	TB 5147B	Buffalo	KNP	SB0121	2005
8	2	4	4	3	4	4	4	2	6	4	3	4	8244344426434	TB 5151A	Buffalo	KNP	SB0121	2005
8	2	4	4	3	4	4	4	2	6	4	3	4	8244344426434	TB 7778E	Hyena	MP	SB0121	2010
8	2	4	4	3	4	4	4	2	6	4	3	4	8244344426434	TB 7830F	Lion	KNP	SB0121	2010
8	2	4	4	3	4	3	4	2	6	4	3	4	8244343426434	TB 3898E	Buffalo	KNP	SB0121	2003
8	2	4	4	3	4	3	4	2	6	4	3	4	8244343426434	TB 3898F	Buffalo	KNP	SB0121	2003
8	2	4	4	3	4	1	4	2	6	4	3	4	8244341426434	TB 4844A	Cattle	MP	SB0121	2005
8	2	4	4	3	4	2	4	2	6	4	3	4	8244342426434	TB 5002B	Buffalo	KNP	SB0121	2005
8	2	4	4	3	4	5	4	2	6	4	3	3	8244345426433	TB 4984B	Buffalo	KNP	SB0121	2005
8	2	4	4	3	4	5	4	2	6	4	3	3	8244345426433	TB 6707B	Lion	KNP	SB0121	2008
8	2	4	4	3	4	5	4	2	6	4	3	3	8244345426433	TB 6922B	Buffalo	KNP	SB0121	2008
8	2	4	4	3	4	5	2	2	6	4	3	4	8244345226434	TB 4695	Buffalo	MP	SB0121	2005
8	2	4	4	3	4	5	2	2	6	4	3	4	8244345226434	TB 8002C	Lion	MP	SB0121	2011
8	2	4	4	3	4	5	4	2	6	4	2	4	8244345426424	TB 3603	Warthog	KNP	SB0121	2002
8	2	4	4	3	4	5	4	2	6	4	2	4	8244345426424	TB 8145	Buffalo	MP	SB0121	2012
8	2	4	4	3	4	5	4	3	6	4	3	4	8244345436434	TB 3423A	Buffalo	KNP	SB0121	2002
8	2	2	4	3	4	5	4	2	6	4	3	4	8224345426434	TB 7895G	Kudu	MP	SB0121	2011
8	2	4	4	3	4	5	4	2	3	3	3	4	8244345423334	TB 4581F	Buffalo	KNP	SB0121	2004
8	2	4	4	3	4	5	4	2	6	3	3	4	8244345426334	TB 5234	Lion	LP	SB0121	2006
8	4	4	1	3	4	5	4	2	6	4	3	4	8441345426434	TB 7485	Cattle	LP	SB0121	2009
8	2	4	4	3	2	4	4	2	6	4	3	4	8244324426434	TB7277	Cattle	MP	SB0121	2009
7	2	4	4	3	4	5	4	2	5	4	3	4	7244345425434	TB 7818B2	Buffalo	MP	SB0121	2010
8	2	4	5	2	2	5	4	2	6	4	3	4	8245225426434	TB3417	Warthog	MP	SB0121	2002
8	2	4	4	2	2	5	4	2	6	4	3	4	8244225426434	TB4841	Cattle	MP	SB0121	2005
8	2	4	3	2	2	5	4	2	6	4	3	4	8243225426434	TB5656	Impala	MP	SB0121	2006
8	2	4	5	2	2	5	4	3	6	4	3	4	8245225436434	TB7823C	Lion	MP	SB0121	2011
8	2	4	5	3	2	5	4	2	6	4	3	4	8245325426434	TB6442	Cattle	MP	SB0121	2007
8	2	4	5	3	2	5	4	2	6	4	3	4	8245325426434	TB7002B	Lion	MP	SB0121	2008
8	2	4	5	3	2	5	4	2	6	4	3	4	8245325426434	TB7464	Waterbuck	MP	SB0121	2009
8	2	4	3	3	2	5	4	2	6	4	3	4	8243325426434	TB5697D	Cattle	MP	SB0121	2007
8	2	4	3	3	2	5	4	2	6	4	3	4	8243325426434	TB6312	Bushbuck	MP	SB0121	2007
8	2	4	3	3	2	5	4	2	6	4	3	4	8243325426434	TB6313	Impala	MP	SB0121	2007
8	2	4	5	3	2	5	4	2	5	4	3	4	8245325425434	TB6974J	Lion	MP	SB0121	2008
8	2	4	5	4	4	3	4	2	6	4	3	4	8245443426434	TB 7087	Buffalo	MP	SB0121	2009
8	2	2	4	2	4	5	4	2	6	4	5	4	8224245426454	TB 4567	Cattle	EC	SB0121	2004
8	2	2	4	3	4	5	4	2	6	4	5	3	8224345426453	TB 5437	Cattle	EC	SB0121	2006
6	3	5	1	1	5	5	4	2	2	3	4	3	6351155422343	TB 3477B	Buffalo	KZN	SB0130	2002