LION (*Panthera leo*) BOVINE TUBERCULOSIS DISEASE RISK ASSESSMENT

16 – 20 March 2009 Skukuza, South Africa

THE DAVIES FOUNDATION

LION (*Panthera leo*) BOVINE TUBERCULOSIS DISEASE RISK ASSESSMENT

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WORKSHOP REPORT

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South African National Parks
Endangered Wildlife Trust
Conservation Breeding Specialist Group Southern Africa

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The Conservation Breeding Specialist Group (CBSG)
of the IUCN Species Survival Commission

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The CBSG, SSC and IUCN encourage workshops and other fora for the consideration and analysis of issues related to conservation, and believe that reports of these meetings are most useful when broadly disseminated. The opinions and recommendations expressed in this report reflect the issues discussed and ideas expressed by the participants in the Lion Bovine Tuberculosis Disease Risk Assessment Workshop and do not necessarily reflect the opinion or position of the CBSG, SSC, or IUCN.

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31 January 2010

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APNR	Associated Private Nature Reserves
BTB	Bovine Tuberculosis
CDV	Canine Distemper Virus
CFU	Colony forming units
DST	Department of Science and Technology
ELISA	Enzyme-Linked Immunosorbent Assay
EWT	Endangered Wildlife Trust
FIV	Feline Immunodeficiency Virus
KNP	Kruger National Park
KZN	KwaZulu-Natal
NRF	National Research Foundation
SANParks	South African National Parks
TFCA	Transfrontier Conservation Areas

LION (*Panthera leo*)
BOVINE TUBERCULOSIS
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WORKSHOP REPORT

SECTION 1

EXECUTIVE SUMMARY AND CBSG WORKSHOP PROCESS

EXECUTIVE SUMMARY

Changing land-use practices in South Africa and its neighbouring countries have resulted in the loss of habitat for many large carnivores, including African Lion (*Panthera leo*). This restriction in their range, often resulting in lions being confined to relatively small, fenced areas, has resulted in secondary management problems. Isolated populations are more at risk from disease effects due to confinement by fences, and a breakdown in ecosystem function caused by the loss of predators.

Diseases such as Bovine Tuberculosis (BTB), caused by *Mycobacterium bovis*, have become well established in Cape Buffalo (*Syncerus caffer*) and Kudu (*Tragelaphus strepsiceros*) populations in the Kruger National Park (KNP), both being preferred prey species for lion. As BTB is transmitted through direct contact with infected individuals (the most frequent route being droplet inhalation) and both of the aforementioned species are social animals, the potential exists for this disease to spread relatively rapidly. Indeed, it is already considered by some to be an alien disease that has become endemic in the buffalo and kudu populations. The disease can also be transmitted by ingestion of infected organs, which places predators at high risk. An additional route of transmission is percutaneously by scratching and biting and this may facilitate the intraspecific spread of the disease in social species such as lions.

Concern has been raised as to what impact BTB will have on the lion population of the KNP, one of the last strongholds of lion in South Africa, especially in the medium to long-term. Within the scientific and conservation communities of the South African National Parks (SANParks), there is a range of opinions as to the effects of this disease on this population of predators and what action, if any, should be taken to address the issue.

The limited number of diagnostic tools and the absence of a vaccine make it difficult to contain and control BTB within infected free-ranging populations. Veterinary researchers and policy-makers have recognised the need to intensify research and assess the need to develop diagnostic tools and methods for control of this disease, initially targeting buffalo and lion (Michel *et al.* 2006). It was therefore proposed that a specialist workshop be held to identify knowledge gaps and determine impacts of BTB on lions to identify appropriate strategic directions towards addressing the abovementioned issues.

It is essential that a comprehensive understanding of existing and potential disease transmission is developed. The role that other species play as maintenance hosts must be considered and current and future impacts on lions need to be determined. An effective, locally-adapted, management strategy can then be developed and additional research needs can be identified and prioritised. Improved knowledge that will be gained by addressing the knowledge gaps will assist management to determine what intervention action, if any, needs to be taken to mitigate the threat of BTB to the KNP lion population whilst respecting conversation objectives.

The purpose of the workshop was to:

- thoroughly evaluate the current status of lions in the KNP and collate current knowledge of BTB in lions,
- identify knowledge gaps and prioritise the research required to address these gaps,
- review and discuss current research and clinical findings, and
- investigate potential population outcomes through predictive simulation modelling efforts.

THE CBSG DISEASE RISK ASSESSMENT WORKSHOP PROCESS

CBSG has developed tools to model changes in species caused by risk factors such as disease impacts. These disease risk modelling tools are not designed to provide statistically valid, mathematically defensible answers to scientific questions, but rather to better equip the professionals involved in day to day decision making regarding wildlife management. Animal health experts, conservation biologists, regulatory and trade officials, and natural resource agencies are all faced with implementing risk management strategies in the face of relatively little existing information. Risk analysis is a growing field concentrated on accumulating and organising existing information in order to prioritise relative risks to support decision-making in the face of uncertainty.

The workshop was conducted over three and a half days (see Appendix 3 for the workshop programme); and achieved the following initial objectives:

- Identified the major shortcomings in knowledge to predict the potential long-term effects of BTB on the population dynamics of lions at an individual and population level.
- Measured the potential efficacy of mitigation efforts to contain the distribution and limit the rate of spread of the disease while taking existing disease control policies into account.
- Identified whether mitigation is desirable and identify alternative mitigation strategies in the absence of an effective vaccine.
- Initiated the development of a management strategy / policy.
- Assimilated a comprehensive record of the current data available on BTB in South Africa.

In addition there were several objectives initially identified as important but due to time constraints the workshop only dealt with those issues specifically related to lion and did not cover broader issues such as:

- Using disease prevalence data, determine the extent to which BTB may threaten the viability of indigenous, protected and endangered species in ecosystems such as the KNP.
- Assess impacts on wildlife populations and the role of different wildlife species as disease vectors.
- Identify the risk of spill-over infection into the broader Transfrontier Conservation Areas (TFCA) and other species.

Twenty-nine people attended the workshop, representing SANParks (Veterinary Wildlife Services, large mammal population specialists and senior park management), the Department of Agriculture (KNP), various academic institutions, international zoos, conservation organisations and TFCA partners (see Appendix 1 for a list of participants). Several lion ecology specialists and veterinary specialists also attended.

The principle tools used at the workshop included SIMSIMBA (lion biology model; Whitman *et al.* 2004), OUTBREAK (BTB epidemiology model; Pollak *et al.* 2002) and INFECTOR (an OUTBREAK sub-model of lion BTB exposure dynamics; Pollak *et al.* 2009). A disease metamodel was compiled at the workshop, but due to time restrictions, the sensitivity analysis[1] of the model, identifying gaps in the data, and determining potential research management options and priorities were done after the workshop.

[1] A standard sensitivity analyses is done by changing individual variables input values from minimum to maximum to determine changes in the model. Input and output parameter changes are made to find

Based on the modelling requirements the decision was made to address these issues at the workshop by forming the following two working groups:

1. Bovine Tuberculosis Working Group
2. Lion Working Group

The workshop process is comprised of a series of plenary and working group sessions in which working groups complete tasks designed to facilitate free thinking, brainstorming, discussion and debate and, finally, synthesis and consensus building.

WORKING GROUP SUMMARIES

BTB is believed to have entered the buffalo population of KNP in the 1950s from infected domestic cattle on farms bordering the southern boundary of the park. It is now recognised that buffalo are the maintenance host for the disease in the KNP ecosystem. As the primary predator of buffalo in the region, lion experience high levels of exposure to BTB. In addition, their social structure is believed to facilitate transmission of the disease within and between prides.

Although the modelling focused on the KNP area, this project was recognised as a pilot study, with the outcomes possibly being extrapolated to other TFCAs. It is believed that, in time, this disease will spread to the lion populations of Zimbabwe and Mozambique. Workshop participants engaged in lengthy discussions throughout the workshop on the human-wildlife interface. However, while this was not included in the modelling for this workshop, it is important to highlight the fact that the issue is larger and more complicated than just the interaction between lions and buffalos. It was emphasised that attention needs to be paid to the interface between wildlife, livestock and human communities bordering the KNP and other conservation areas.

Additionally, it is important to highlight extensive problem areas for mitigating interface issues. This could allow for policy development and focussing of government resources. More sensitive measures are needed to diagnose infectivity to manage or monitor the disease. The modelling system is vital in understanding and monitoring how this diseases occurs and can be used to develop the most appropriate mechanism for control.

The Bovine Tuberculosis Working Group was tasked with determining parameters for INFECTOR and OUTBREAK (BTB epidemiology models), and the Lion Working Group was tasked with determining the SIMSIMBA (lion biology model) parameters.

1. Bovine Tuberculosis Working Group (pages 17 – 29)

The INFECTOR model is based on the transitioning of the disease from one state to the next. The working group defined the terminology as follows:

- ‘Exposure’ was defined as simple contact only of an individual with the BTB organism.
- ‘Infected’ implies that the organisms will colonise an exposed individual but without any clinical effects or symptoms – these individuals may test positive.
- ‘Diseased’ means the exposed individual becomes infected and displays clinical symptoms of the disease.

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different rates of change on separate variables to assess the sensitivity of the model to those changes (spider plots).

- An ‘Infectious’ state pertains to individuals that are diseased and shedding the organism.

Exposure deals with two transmission routes, buffalo to lion through predation and then lion to lion (in-group versus out-group infection). Prevalence of the disease in buffalos has moved faster than originally thought from the south to the north (i.e. 20 - 25 km per year).

In order to calculate the probability of infection through predation on buffalo, the group worked on the assumption that during a six month period, lions had an 8 – 25 % chance of taking down an infected buffalo in the south (estimated to be a 40 % prevalence zone) and being exposed to the disease. The probability of a lion becoming infected in the south was therefore regarded as 0.8 – 2.5 % in a six month period. There was assumed to be zonal differences in exposure rates with lions, with the north and central districts having a lower probability of becoming infected through predation on infected buffalo. The group therefore modelled a 10-fold reduction in exposure (see INFECTOR parameters on page 18) to the disease of lions in the north. Despite having the highest number of lions, the lions in the central district are considered to have an estimated 50 % reduction in probability of infection through predation on buffalo than those in the south.

The group discussed how the disease is transmitted between lions and agreed that inhalation (pulmonary route) was the primary route of infection. The percutaneous route as a result of biting during fights, such as competing for food or during territorial conflict, was considered secondary. The recurring question was the probability of an uninfected lion belonging to a pride becoming infected and over what time period? The group approximated that, within a 6 month period, lions have a 10 – 30 % chance of BTB infection through “in-group” routes (based on the size of prey taken, the time spent feeding at a carcass, and contact with an infected pride member), and a 10 – 20 % chance through “out-group” routes (contact with a non-pride member). It was recognised that due to the skewed sex ratio in the south of the Park, there is a higher number of interactions between nomadic males and prides. The group agreed that males are compromised when fighting and this increased exposure to BTB through secondary routes of infection, which may have a negative effect on fecundity. Females infected with BTB are less able to look after their young and it was suggested that the modeling team increase post-natal female and cub mortality. Consensus from the group was that, compared to the “in-group” percentage, there is a 10 - 20 fold decrease of infection from “‘out-group” routes of infection.

Lion sex and age was mentioned as influencing BTB epidemiology, but were flagged for later consideration in the model. Another route of infection considered was through milk but there is little evidence to suggest that this is a factor and it was therefore not considered in the model.

Determining the initial frequency of infected animals was difficult to calculate due to a lack of data. Studies show that reactive prevalence in lions using skin tests is 82 % (n=101). This was a random sample of individuals in fair condition in the south of the Park (Keet unpublished data). Once individuals are infected, the rate at which they become diseased and how many infected animals do not get to the diseased state needed to be determined. It was agreed that 20 % remain latent (non-diseased) and of the approximately 80 % of lions that became infected, all became infectious in a five year period.

The OUTBREAK model is based on the premise that once a lion is infected with BTB, it either becomes: 1) latently infected; or 2) develops the disease, becomes clinically affected and dies. The minimum duration of infection is 540 days based on a comparative study (Keet unpublished data 1999 until 2004) and the maximum duration can be a lifetime. The minimum duration of the disease is 14 months based on the observation of the earliest death of a lion in good condition having tested positive. It was cautioned that the maximum duration

of disease is highly variable and it is difficult to determine the window period; however one lion in a study by Keet (unpublished data 1999 until 2004) was infected for 58 months.

2. Lion Working Group (pages 30 – 39)

The SIMSIMBA model required a large number of demographic variables, not all of which were available for the KNP population. Recognising this deficiency, the group supplemented the model with data from the Serengeti population. The latter population is similar to that of the KNP population but does show slight differences in maturation, dispersal and reproduction. Data for age-specific mortality presented the most problems and was probably the most tenuous section of the data. The group assigned quality categories to several data and worked through the parameters to assess whether i) each parameter was relevant to the KNP model and (ii) what levels of each parameter should be used.

FINAL PLENARY SESSION: THE WAY FORWARD

In the original plan, CBSG SA anticipated that a simulation modelling tool to assist in the evaluation of various management options would be completed at the workshop for final write up within two months of the workshop. However, these plans were revised when only the input values for the model were determined for a solid disease metamodel. The modelling team returned to the USA to run the sensitivity analyses on the multiple variables and several models.

LION DISEASE RISK ASSESSMENT MODEL

In the absence of disease, the baseline lion demographic model was constructed in order to produce a population that was neither growing nor declining (growth rate $\lambda = 1.000$). This allowed workshop participants to more easily compare these dynamics to subsequent models that included the impacts of disease. When BTB was added to the baseline model, with best estimates for parameter values that describe the epidemiology of the disease and ecology of the lion population, the population declined at an annual rate of approximately 5%. This rate of decline is considered to be more severe than has recently been observed among the lion population of the KNP, which are seemingly very stable (Ferreira and Funston in press (a)), although localised population declines may have occurred in areas where boreholes have been closed. This prompted workshop participants and model practitioners to question the accuracy of some parameter values in the model.

Sensitivity analysis methods were applied to the baseline disease model to evaluate which disease parameters were most influential in driving lion population dynamics. The analysis indicated that direct disease transmission rate parameters:

- those within territories (prides), here called “in-group” transmission,
- those between territories, here called “out-group” transmission, and
- transmission resulting from predation on infected buffalo

are the most sensitive disease parameters in the model. The model was far less sensitive to the rate of disease transmission from mother to cubs, the initial frequencies of infected and diseased animals, and the duration of time an individual can remain infected or diseased.

A more complex model was developed that included the full complement of lions within the KNP, with 1775 lions distributed among 160 territories. Prevalence of BTB among buffalo was considered to be highest in the south and lowest in the north, thereby promoting higher rates of predation-based transmission of disease among lions in the south. Again, with best

estimates of disease parameters, the models show a significant lion population decline that has not been observed in the recent past within KNP. Additional exploratory models that included lower rates of in-group disease transmission resulted in models showing a robust growth dynamic – in greater accordance with recent field observation of lion populations affected by BTB (Ferreira and Funston in press (a)). This suggests that estimates of disease transmission rate parameters must be studied with great care if they are to be used in predictive models of BTB epidemiology and the impact of the disease on KNP lions.

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WORKSHOP REPORT

SECTION 2

PRESENTATIONS

BACKGROUND INFORMATION ON BTB IN FREE-RANGING AFRICAN WILDLIFE

ROY BENGIS – DEPARTMENT OF AGRICULTURE

In 1990 tuberculosis caused by *Mycobacterium bovis* was first diagnosed in a Cape Buffalo (*Syncerus caffer*) in the Kruger National Park (KNP). This disease, which is not indigenous to Africa's free-ranging mammals, probably originated from infected domestic cattle, and is believed to have entered the KNP from across the southern river boundary in the late 1950's or early 1960's. As an alien multi-host disease in a multi-species system, it poses a potential threat to biodiversity within the Kruger National Park ecosystem as well as the associated transfrontier conservation area (TFCA), and may have the potential to impact on certain species at the population level. The zonal prevalence and spatial distribution of bovine tuberculosis (BTB) in buffalo has progressively increased from south to north in the KNP. The disease in buffalo reached the park's northern boundary in 2006, which is some 350 km from where the disease first entered the park approximately 45 years ago. Subsequently the disease has crossed the Limpopo River and has been detected in buffalo in the Gonarezhou National Park in Zimbabwe in 2009.

Spill over of the disease from buffalo into a total of 12 other species (African Lion (*Panthera leo*), Leopard (*Panthera pardus*), Cheetah (*Acinonyx jubatus*), Spotted Hyaena (*Crocuta crocuta*), Kudu (*Tragelaphus strepsiceros*), Chacma Baboon (*Papio ursinus*), Warthog (*Phacochoerus africanus*), Impala (*Aepyceros melampus*), Honey Badger (*Mellivora capensis*), Bushbuck (*Tragelaphus scriptus*) and Large-spotted Genet (*Genetta tigrina*)) has been documented in the KNP. The disease has also been detected in eland and bush pig on neighbouring private conservation properties.

Buffalo are considered to be the primary maintenance host in the Kruger National Park and kudu and warthog appear to have maintenance host potential. Large predators, especially lions, seem to be highly vulnerable to infection with BTB because they are at the top of the "food chain" and are therefore at a high risk of exposure from infected prey animals or carcasses.

BTB is a declared controlled disease in South Africa and a successful BTB eradication scheme has been implemented for cattle, at great expense, over the past five decades. With the emergence of sylvatic reservoirs of infection, there is an increasing risk of transmission of *Mycobacterium bovis* from infected buffalo to domestic livestock and humans at the park's interface with neighbouring communities.

BOVINE TUBERCULOSIS IN LIONS IN THE KRUGER NATIONAL PARK

DEWALD KEET – CHIEF STATE VETERINARIAN KNP

COMPARATIVE STUDY

A temporal and spatial longitudinal comparative study between a *Mycobacterium bovis* infected and a non-infected lion sub-population in the Kruger National Park (KNP) was undertaken between 1999 and 2004. Longevity, reproduction and recruitment were evaluated using radio-telemetry and direct observations. Thirty-two adult lions from 6 distinct prides were radio-collared while 43 associated pride members were marked. A further 51 peripheral lions were also marked. During the period, necropsies were done on 13 / 32 radio-collared lions. Necropsies done (8 / 8) on southern lions confirmed *M. bovis* infection, while 7 / 8 had advanced tuberculosis in multiple organ systems. No *M. bovis* infection was found in 5 / 5 northern lions. Of the 46 cubs born in the north, 19 (41.3 %) reached one year of age and 9 (19.5 %) lived ≥3 years. Four female cubs were eventually recruited in their natal prides. Of the 30 cubs born in the south, 15 (50 %) reached one year of age and 4 (13.3 %) lived up to 30 months. No lioness was recruited in the south. Two of three southern prides were evicted (male and female components) while all 3 northern prides remained intact. Immigration of unknown lions into the south was recorded. Nine male coalitions were monitored. Pride tenure was longer in the north than in the south. Lion densities were much higher in the south than in the north. This is ascribed to larger prey biomass in the south. Adult sex ratios between the two areas were different. Differences in survival between the two sub-populations were documented.

During three separate intensive surveys during the study period 174 different lions arrived at all night calling stations with bait provided. Seventy six (76) were identified in the north and 98 in the south. Adult sex ratios vary significantly between the north (1 male:1.75 females) and south (1:1.06). This was found to be statistically significant $p < 0.00$ (T Test). When considering all ages, the sex ratio in the north was still skewed towards females while it remained 1:1 in the south. This may imply that male survival in the north is not high or that sub adult males do not lodge in natal territories due to low prey biomass availability.

ANTE-MORTAL DIAGNOSTIC TECHNIQUE

Historically, reliable detection of mycobacteriosis in lions was limited to necropsy and microbiological analysis of lesion material collected from emaciated and ailing or repeat-offender lions. A method of cervical intradermal tuberculin testing of lions and its interpretation was capable of identifying natural exposure to *M. bovis*. Infected lions (n = 52 / 95) were identified by detailed necropsy and mycobacterial culture. A large proportion of these confirmed infected lions (45 / 52) showed distinct responses to bovine tuberculin Purified Protein Derivative (PPD) while responses to avian tuberculin PPD were variable and smaller. Confirmed uninfected lions from non-infected areas (n = 11) responded variably to avian tuberculin PPD only. Various non-tuberculous mycobacteria (NTM) were cultured from 45 / 95 lions examined, of which 21 / 45 were co-infected with *M. bovis*. Co-infection with *M. bovis* and NTM did not influence skin reactions to bovine tuberculin PPD. Avian tuberculin PPD skin reactions were larger in *M. bovis*-infected lions compared to uninfected ones. Since NTM co-infections are likely to influence the outcome of skin testing, stricter test

interpretation criteria were applied. When test data of bovine tuberculin PPD tests were considered on their own, as for a single skin test, sensitivity increased (80.8 % to 86.5 %) but false positive rates for true negatives (18.75 %) remained unchanged. Finally, the adapted skin test procedure was shown not to be impeded by persistent Feline Immunodeficiency $Virus_{Ple}$ co-infection.

CLINICAL SIGNS AND PATHOLOGY

Clinical signs are typically non-specific and consist of varying degrees of emaciation with deterioration of skin quality. Focal areas of partial alopecia of varying size are seen in most cases. Visible, palpable and marked enlargement of superficial lymph nodes as seen in various other species does not occur. Hygromas of the elbow are found to be a reliable indicator of *M. bovis* infection. They are more frequently seen in females than in males. Undetermined or non-specific lameness due to swollen, inflexible stifle and hock joints associated with muscular atrophy of affected appendices occur in older lions. Dermal wounding with an apparent inability to heal is seen in a number of cases. Older males often develop large swellings above or below the hip joint. Large ulcers subsequently develop on the surface of these swellings. This is often bilateral but varying in size. Varying degrees of mane loss and deterioration are seen in most males necropsied. Testis atrophy is consistently present in these cases. None of 86 females were pregnant at the time of necropsy. Tachypnoea and dyspnoea was seen in cases with advanced pulmonary lesions. Ocular lesions are seen in a small number of cases and central nervous system impairment in only one. Hair covering the ventral aspects of the neck, thorax and abdomen appears to be longer and white in inactive females.

Gross lesions in the carcass of a lion are not typically caseous-necrotic. They are rather fibrous and proliferative and seldom associated with abscess formation. The sarcomatous appearance of mycobacterial lesions in domestic cats frequently leads to misdiagnosis in cats and lesions in lions have a similar sarcomatous appearance. Lymph nodes are only slightly enlarged but mostly rather severely atrophied. These lymph nodes reveal sinus ectasia associated with cortical and paracortical lymphoid hyperplasia. Pulmonary lesions are the only category identifiable with a certain degree of accuracy. However, they also appear distinctly different from lung lesions seen in ruminant, primate, rodent, swine and lagomorph species.

Microscopic lesion patterns observed in various organs were of a granulomatous nature consisting of macrophages, epithelioid cells, lymphoplasma cells and numerous neutrophils, suggestive of mycobacterial infection. Severe generalized lymphoid atrophy was sometimes seen in association with granulomatous lesions. Pulmonary lesions comprised of granulomatous interstitial pneumonitis or granulomatous bronchopneumonia often associated with bronchiectasis. Intestinal lesions showed mononuclear macrophage predominance suggestive of mycobacterial mural enteritis. Granulomatous osteitis, periosteitis and osteosis were found in most of the well-developed cases frequently associated with myositis.

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MODELLING PREDATOR-PREDATOR POPULATION DYNAMICS IN THE CONTEXT OF BTB

PAUL VAN HELDEN AND PIETER UYS– DST / NRF CENTRE OF EXCELLENCE FOR BIOMEDICAL TUBERCULOSIS RESEARCH

Researchers know that the African Lion (*Panthera leo*) in the Kruger National Park (KNP) has been diagnosed with Bovine Tuberculosis (BTB) and may therefore hypothesize that there may be a change in the lion population. Since lions are the apex predator, the hypothesis is that there may be expected changes in the dynamics of other predators, based on interactions between these species.

From available literature, certain information regarding birth and mortality rates and interactions between predators can be obtained. Using this data, and assuming an additional mortality rate for lions, the Department of Science and Technology (DST) / National Research Foundation (NRF), Centre of Excellence for Biomedical Tuberculosis Research has developed a model to predict what may happen to populations of other predator species. Any mortality rate can be used in the model. Using a 5% additional mortality rate as an example, over a period of 10 - 20 years, the model predicts that lions will decline in number (by definition), whilst Cheetah (*Acinonyx jubatus*) and Spotted Hyaena (*Crocuta crocuta*) numbers will rise marginally. Leopards (*Panthera pardus*) and African Wild Dogs (*Lycaon pictus*) are expected to increase fairly substantially, whilst jackals (*Canis* spp.) are expected to decline in numbers drastically.

A survey amongst rangers and staff, who have been in KNP for many years, reveals that jackal numbers have indeed declined dramatically, whilst leopards are abundant. While simplistic, this model has some value and observations suggest some accuracy for it.

LION POPULATION DYNAMICS

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Researchers generally use direct observations, sample surveys, or indices to assess some of the population features of carnivores. When determining lion population numbers, repeated estimates for the same area may allow calculation of population growth rates. Variance in population estimates results in uncertainty of growth rate usually overcome by long time series. Such detailed data sets only exist for the Serengeti Plains and, to a lesser extent, for a few other populations. In addition, sex- and age structures, as well as birth and death rates are demanding to estimate. Few lion populations thus have reliable estimates of population size, trends in these, or demographic assessments.

The research team calibrated call-up stations to develop a statistically robust way to estimate population sizes and age structures. The calibration found that lions within a 4.3±0.9 km (mean ± SE) radius from a sampling location responded to call-ups. Of those within an effective sampling area, 73.4±7.6 % and 28.6±7.9 % of groups without and with cubs responded respectively. Within responding groups, 95.7 % and 90.7 % of individuals in groups without and with cubs responded respectively. Correcting for these response probabilities, it was estimated that 1684 (95 % CI: 1617 - 1751) lions lived in the Kruger National Park (KNP) in 2005 and 2006. These estimates together with those extracted from previous studies suggest that lion numbers did not change in the KNP for some time. However, power to detect a trend was low. These results suggest that even a statistically robust approach to estimate lion population features may have limited application in the absence of other demographic measures.

Given that lion populations experience a range of ecological and human influences that affect their demography, the statistically robust approach was used to evaluate the perceived threat of bovine tuberculosis (BTB) in landscapes of varying prey biomass in the KNP to lion populations. Density and survival rates were associated with prey biomass - density and survival being higher at high biomass. However, some of the variation in survival was associated with the prevalence of BTB in lion prey - density was lower, but survival higher in areas that had high prevalence of BTB compared to areas with low BTB prevalence after the effect of prey biomass was accounted for. Male survival was lower than that of females disregarding the effects of prey biomass or BTB prevalence. Body condition of lions was high with scores lower at low to medium prey density. In addition, survival declined with lion density once the effect of prey biomass was accounted for. The results suggest that prey biomass and intra-specific competition in areas of the KNP where lions live in high densities may mask the effect of an exotic disease, if present, on lion population dynamics. However, drought could disrupt the hierarchical influences of prey biomass, intra-specific interactions, and BTB prevalence on lion densities and survival. Hence, to evaluate the effect of an exotic disease on lion demography, future surveys should include age- and sex-structure assessments complemented by focal studies of fecundity and survival.

LION (*Panthera leo*) BOVINE TUBERCULOSIS DISEASE RISK ASSESSMENT

16 - 20 March 2009

Skukuza, South Africa

WORKSHOP REPORT

SECTION 3

WORKING GROUP REPORTS

Bovine Tuberculosis Working Group

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INTRODUCTION

The working group debated a multi-host disease model and considered the role other species play as maintenance hosts for bovine tuberculosis (BTB) (e.g. Kudu (*Tragelaphus strepsiceros*) and Warthog (*Phacochoerus africanus*)). However, the group ultimately focused on the dynamics of exposure to disease resulting from predation on buffalos and from lion-to-lion contact. The human-livestock interface was also discussed and the group agreed to concentrate on lions but recognised that future assessments would have to consider other species.

MAJOR QUESTIONS IDENTIFIED BY THE GROUP:

Questions that can be explored through models:

- How does BTB prevalence change in lions as it changes in buffalos? What is the impact or threat?
- What is the impact of varying buffalo densities on disease prevalence in KNP on lions?
- Does BTB disease affect the spatial use of the landscape among lions?
- Does exposure equate to infection in the model?

Questions that have a broader significance and require additional field data:

- Are lions serving as maintenance hosts or spill-over hosts?
- What are the consequences for wildlife and livestock at the interface?
- What is the importance of BTB as a driver in an ecological system?
- What is the public health issue potential(s) in South Africa?
- What does the role of concomitant diseases play in susceptibility to disease from parasites, or other infections such as Feline Immunodeficiency Virus (FIV)?

- How is infection with BTB confirmed in infected and diseased animals: culture, necropsy? Difficulty in diagnostics exists and there is a need for improvement. *M. bovis* data prevalence in lion and buffalo is currently determined using culture methods.
- What is the contribution of lions to spill-over to other species, including infected prey carcasses, e.g. scavengers feeding on lion kills?
- What is the infective dose, and is it dose-dependent?
- As this is a multi-host disease, sustaining infection within the system, what other species can be affected?
- How strong a driver is rainfall in affecting infection rates in lions?
- What are the regulatory and political ramifications of sustained BTB infections in wildlife at national and international levels?
- Does BTB cause declines in other species, e.g. there may be important effects on jackals.
- What are the actual pathological effects of BTB in lions?

GENERAL MODEL INPUT VALUES FOR INFECTOR AND OUTBREAK:

The group defined and used the following terminology in the model:

- 'Exposure' was defined as simple contact of an individual with the BTB organism.
- 'Infected' implies that the organisms will colonise an exposed individual but without any clinical effects or symptoms – these individuals may test positive.
- 'Diseased' means the exposed individual becomes infected and displays clinical symptoms of the disease.
- An 'Infectious' state pertains to individuals that are diseased and shedding the organism.

INFECTOR PARAMETERS

The INFECTOR is a sub-model that controls exposure of lions to BTB, with reference to individual status within the population. The parameters were provided to the group by the modelling team and the values associated with the inputs were discussed and agreed upon by the group. Recognising that data of variable quality and different sources would be necessary to fully populate the model, the group assigned data to several different quality categories as follows:

1. Serengeti - known parameters obtained during field studies in the Serengeti.
2. Kruger - known parameters obtained during field studies in KNP.
3. Informed opinion - best guess of experts.
4. Derived - obtained from other studies

Three sources of infection were identified: i) intrinsic sources which include infected "in-group" or members of the same pride; ii) extrinsic sources which include infected lions from outside the pride, i.e. "out-group" individuals, including nomadic animals and members of other prides and iii) predation on infected prey species.

The group also questioned the development of lion tolerance or resistance to BTB and agreed that there does not appear to be any selection for any genetic type. In buffalos, adults in high prevalence herds may have some genetic component, but further study is required and it was suggested that this may be a new population (different strain of *M. bovis*). As the pathogen is slow in developing and the infection

is chronic the group questioned if there are any predators known to show resistance to BTB.
Note that all probabilities within INFECTOR are expressed in terms of a six-month time-step, in line with the default time-step used in SIMSIMBA.

Probability of infection per lion through predation on buffalo: *0.025*

Two decades of information are available on buffalo and currently the average regional prevalence of infected individuals is 40 % in the south and only 4 % in the north of KNP. The spread of BTB has been 20 - 25 km per year, and the disease took 16 years to move from south to north, with the disease first detected in 1990 in the south of KNP and finally recorded at the northern Limpopo boundary in 2006. Lions kill every 4 – 5 days and may eat small infected nodes, resulting in up to 50 exposures per year. The variety of prey in the south of the KNP is more diverse than the north and buffalo are a lower prey choice for lions in the south (Mills and Shenk 1992, Funston *et al*. 1998). However, in the north, buffalo are more abundant and thus a more common prey source.

The probability of infection per lion was estimated, where a lion in the south has contact with an infected buffalo once every 6 months on average. The assumption is that in a 6 month period, 12 of these buffalo will be BTB positive. The model assumes that one out of three buffalo are infected and there is an 8 – 25 % probability of taking down an infected individual in a 40 % prevalence zone. In southern KNP, 73 % of the kills made by non-territorial lions, 36 % of the kills made by territorial males and 18 % of the kills made by females were buffalo (Funston *et al.* 1998) suggesting that particularly young male lions face a relatively higher risk of infection.

The zonal differences in KNP were determined as follows. The probability of a lion becoming infected is between 0.008 to 0.025 per buffalo predated in a six month period in the south. There is a 10-fold reduction in the probability of becoming infected in the north, as compared to the south. The central district has the highest number of lions and probably a 2-fold reduction in the probability of becoming infected as compared to the south. The probabilities of a lion becoming infected with BTB due to predation of buffalo in a six month period were: south (0.025), central (0.0125) and north (0.0025).

[Data category: 3, informed opinion]

Note: A formula is available to determine the annual risk of infection based on age; however the formula was developed in humans and so applicability to lions may not be accurate (Van Helden pers. comm.)

Probability per lion of "in-group" infection:..... *0.10*

The probabilities of "in-group" or "out-group" exposure rates are important, as exposure to the disease does not immediately mean infection in the model and the model does not account for dose-dependence.

It has been determined that *M. bovis* is resistant to stresses immediately after becoming airborne, 94 % surviving the first 10 minutes after aerosolisation. Once airborne, the organism is robust, its viability decreasing with a half-life of approximately 1.5 hours (Gannon *et al.* 2007). Feeding on infected carcasses is

therefore probably the most common method of transmission. Lions have their heads close together in the prey's body cavity, often growling and breathing heavily while feeding, which are ideal conditions for transmission. It was noted that territorial pride females kill small prey every 2 days and larger prey every 4 - 5 days, generally spending longer time on the larger carcasses, thus increasing their chance of aerosol transmission.

It has always been assumed that infection in lions was due to eating infected prey (particularly of organs); however it has been shown that intrinsic infections within prides (within territories) through factors such as aerosol transmission, inhalation, and wounds do occur. Aerosol transmission can also take place during social interactions and roaring in close contact.

It is also important to look at the location of the lesions and distribution of the bacteria in lions – pathogenesis is very different because there are major subdivisions of infection. A high percentage of infected lions have pulmonary lesions, which are the most consistent lesions seen.

[Data category: 3, based on informed opinion (from data on humans), took conservative decision]

Probability per lion of "out-group" infection: *0.005*

This parameter defines the probability of a lion being exposed to BTB from an extrinsic source, i.e. a source outside its pride which would include prey that are consumed, or contact with infected lions from other prides. The probability of transmission from an out-group (extrinsic) source in a 6 month period was assumed to be 10 – 20 times lower than the probability of infection from an "in-group" (intrinsic) source.

There was some debate within the group, due to a lack of quantitative data, as to the probability of an uninfected animal becoming infected by a member of another pride or nomadic male. Based on "in-group" transmission rates being 10 – 30 %, some working group members suggested that the "out-group" rate should be lower and a figure of 10 – 20 % was agreed on. It was recognised that the ratio of male to female lions is skewed towards males (R. Bengis pers. comm.). This phenomenon has been reported previously in several ecosystems including KNP. It is important for the model to distinguish whether adult sex ratios vary among regions of the KNP. A greater skew towards males in the southern region indicates the presence of a higher proportion of nomadic males compared to the northern areas of KNP. This represents an increased risk of infection in southern prides from contact with "out-group" individuals. It has been noted that southern lions have more peripheral lesions from fighting than other lions in KNP and more peripheral lymph nodes cultured positive for *M. bovis* than from other regions.

It was proposed that FIV infection as well as sex differentiation (i.e. males have a potentially higher risk of becoming infected by BTB than females) be incorporated into the model. Lions with co-infection have far more severe BTB lesions and more organ systems are infected with BTB. Sex differentiation is important because of the social effects of males becoming infected earlier than females and males exposed more frequently than females to oral infection (D. Keet pers. comm.). While this is important and possible to incorporate into the model, it would need to be done at a later point when the time and resources become available. Additionally, separate infection areas for FIV and BTB can be included; however the model will need to be modified substantially.

[Data category: 3, based on informed opinion]

Probability per cub of infection through nursing cubs: *0.0*

Cubs suckle for up to nine months but will start to take solids at six weeks (R. Bengis pers. comm.). Lactational transmission was discussed and it was noted that, very few females (ten out of 37 positive lionesses) had mammary lymph node lesions (Keet unpublished data) and therefore this variable was set at 0. However, it was cautioned against drawing conclusions on lactational transmission because there is transmission of the BTB organism via milk in cattle (A. Michel pers. comm.).

[Data category: 2, based on low transmission in livestock (Michel)]

Initial frequency of infected animals: *0.5*

The initial frequency of infected animals is defined as the proportion of animals in the population that have been exposed and are infected with the pathogen. The zonal prevalence of infection with BTB in buffalo in the southern KNP is 40 %, while 80 % of lions test positive on the intradermal skin test for the disease (Keet in press). The working group questioned why the infection rate was so high. It was noted that of the animals necropsied in 2000 – 2004 by Keet, 71 % (41/58) cultured positive (Keet unpublished data). It was pointed out that these samples comprised animals that were obviously sick, problem animals, and those with zero prognosis so the necropsies probably represented a biased sample. Keet's necropsies from all the lions captured were taken and cultured following a standard method (sampling lesions and nodes), and at least five sets of samples were taken from each individual. During the early phase of the disease, lesions are small and may be missed even in infected nodes (N. Kriek pers. comm.). Indeed, the earlier the case, the more difficult it is to get positive test results, unless a comprehensive necropsy and culture is done. Macroscopically only lung lesions and some bone lesions can be identified as being tuberculous. Lesions in lions need to be confirmed to be of a granulomatous nature through histology and ultimately cultured to confirm the presence of *M. bovis*. The majority of lions in bad condition had at least 3 organ systems affected. The group estimated the initial frequency of infected animals as there were no available data. It was however recommended that a sensitivity[2] analysis be done.

[Data category: 3, based on opinion for purposes of sensitivity testing]

Initial frequency of diseased animals: *0.08*

The initial frequency of diseased animals is defined as the proportion of animals in the population that contract the disease (with or without clinical symptoms) and are infected with the pathogen. Once individuals are infected it is important to determine the rate at which they become diseased and how many of the infected individuals never get to the diseased state. It was agreed that 20 % remain latent (non-diseased). Of the 16 positive animals tested and monitored for 5 years by Keet (unpublished data 1999 - 2004), 7 / 10 converted from infected to diseased and one lioness that was fatally injured when her pride was taken over did not have extensive lesions but was considered infectious. Therefore, 80 % of the lions that became infected, all became infectious in a five year period, and it was initially calculated that roughly 8 % of lions became infected in a six month period.

[Data category: 2, based on fact that animals in the south test 80 % positive (Keet in press)]

[2] Standard sensitivity analyses change individual variables input values from minimum to maximum to determine their effects in the model. Input and output parameter changes are made to find different rates of change on separate variables to assess the sensitivity of the model to those changes.

The parameters determined above are shown in Figure 1.

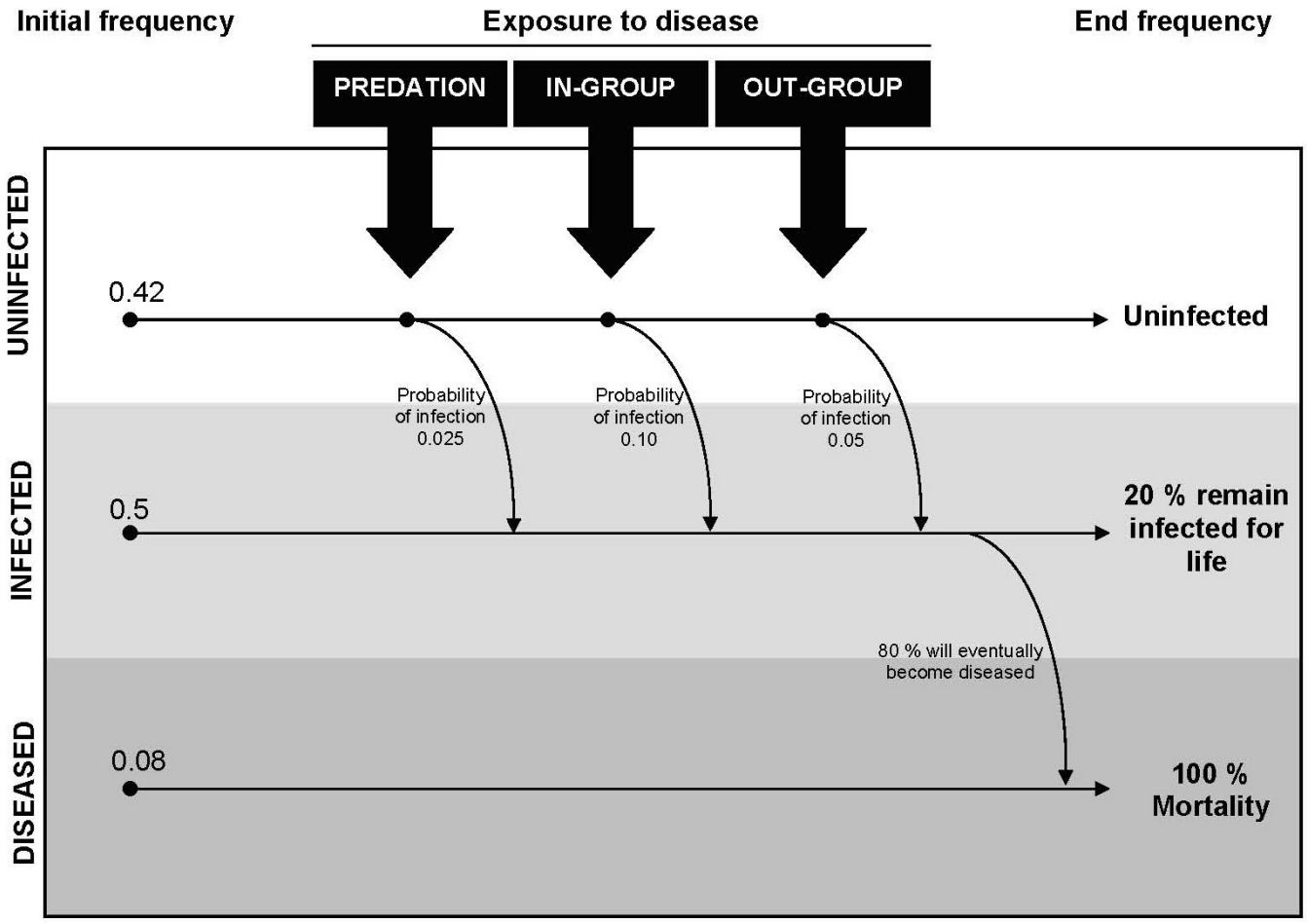

Figure 1: Flow chart depicting the conversion stages from exposure to the diseased stage.

OUTBREAK PARAMETERS

The OUTBREAK model is an individual-based stochastic simulation of wildlife disease epidemiology and controls progression of BTB exposure to clinical infection. It was determined that once a lion has become infected, disease progression can follow one of two routes: i) shows no clinical symptoms of the disease provided no other immunosuppressant complications occur (reactivation has never been demonstrated in animals but could occur, although rare in humans); or ii) it develops the disease, sheds the organism and dies.

Although all the probabilities within SIMSIMBA and INFECTOR are expressed in terms of a six-month time-step, OUTBREAK remains a daily time-step model.

Minimum duration of infection: ..... 540 days (18 months)

This parameter is defined as the minimum amount of time an individual will remain infected, before becoming capable of transitioning into the active diseased state. The earliest that cubs feed on an infected carcass was estimated to be four months, based on feeding studies conducted by Keet (unpublished data 1999 - 2004) on 16 lions. In this same study by Keet, two of the 16 lion showing skin-reactions did not develop generalised BTB disease and each lived to 12 and 13 years of age. Expert judgement within the working group led to the conclusion that a minimum of six months would pass between the time an individual become infected and when that individual could be capable of transmitting BTB to other lions (i.e. diseased).

In clinical trials in which buffalo were injected with the BTB organism into the left tonsil, the animals showed signs of primary exposure and infection within six weeks (De Klerk *et al.* 2006). The trials included injecting the buffalo with varying doses of BTB; low doses were calculated at 300 colony forming units (cfu's) (n=11) versus 3000 cfu's (n=11); 5 animals were used as a control and monitored over 4.5 months. Results suggest that higher doses of BTB may shorten the time to shedding while with low doses, the individual may not become diseased at all.

A comparative study conducted by Keet (unpublished data 1999 - 2004) on 16 BTB positive lions in good condition (4 - 8 years of age) showed that those testing positive died within five years, with mortalities (BTB related) occurring within 14, 19, 23, 25, 26, 28, 41 and 58 months. Within five years (60 months), the majority of infected animals became diseased / potentially infectious and began shedding. Some (7) lions did not test positive for FIV initially, but later tested positive for FIV and then lost condition rapidly and died of advanced BTB. Although FIV infection is believed to be a very important factor, it has not been included at this stage for model simplicity.

Of the infected lions not showing clinical signs of the disease, 52 (54.8 %) out of a sample of 95 lions cultured positive (D. Keet pers. comm.), 84 of which originated from the central and south regions. Fifty one of these animals cultured positive and 45 were positive on skin tests. These were all mostly emaciated animals and some problem animals that were permitted to be captured for the study (Keet in press). Eleven uninfected animals in the north were included to act as negative controls to validate the test.

[Data category: 2, based on a comparative study by Keet]

Maximum duration of infection: .....*4815 days*

This parameter is defined as the maximum amount of time an individual will remain infected, before becoming capable of transitioning into the active diseased state. Given the estimate of the earliest age of infection being four months and the minimum length of time of remaining infected as 540 days (18 months), lions will begin transitioning from infected to disease at approximately 660 days (22 months) of age at the earliest. For this analysis, it was assumed that the generalised maximum lifespan for KNP lions, combining data for both males and females, is about 5475 days (15 years). The maximum length of time a lion will remain infected is (5475 – 660) = 4815 days. However, *OUTBREAK* does not have an explicit parameter that describes the proportion of individuals that never transition out of the infected state. To account for this, an "effective" maximum duration is captured that exceeds the lifespan of the lions so on average, 20 % of infected individuals do not make the transition to diseased. This effective duration, $D^*_{Max,}$ is calculated by setting up the equality

$$[(100\% - 20\%) / 4815d] = [100\% / D^*_{Max}]$$

which gives D^*_{Max} = 6019 days. These calculations are shown graphically in Figure 2.

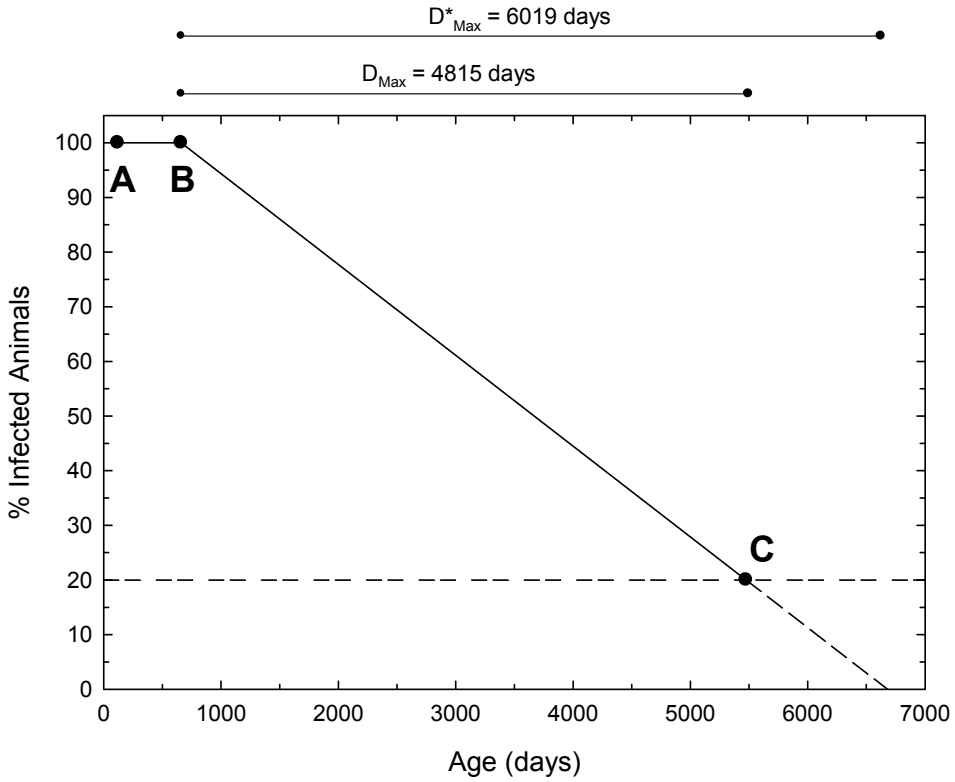

Figure 2: Graphical depiction of the timeline of [Infected – Diseased] transition among lions infected with BTB. Lions can first become infected at four months of age through feeding (Point A). Following infection, individuals can begin transitioning into the Diseased state after a period of about 18 months (total age is then 660 days: Point B). This transition occurs at a constant rate among Infected lions throughout their lifespan. This assumes the average lifespan across males and females to be 15 years (5475 days, Point C), with 20% of Infected lions never transitioning to the Diseased state before reaching their maximum age. Given this observation, and for the purposes of model construction, an "effective" maximum infection duration, D*Max, is calculated

by extrapolating the transition curve to the point where all Infected lions would have transitioned to the Diseased state (% Infected = 0.0).

[Note: Models described in this report were constructed with D*Max = 6205 days, obtained through a mathematical error. While this error may affect absolute numerical results, albeit slightly, the relative robust nature of the results will be unaffected. Subsequent extensions of the modelling exercise will be undertaken with the revised parameter values described above].

[Data category: 2, based on Keet's data that lions tested positive and still alive after 5 years]

Proportion of individuals that remain permanently infected: .....*20 %*

20 % of the individuals that become infected will remain infected throughout their lifetimes. Keet's data showed that of 10 animals two survived (20 %). It should be noted that of the original infected group of 16 lions, Keet lost track of 6 during the 5 year period.

[Data category: 2, based Keet's data: 2 out of 10 survived 5 years without developing disease]

Minimum duration of disease: ..... *14 months*

The parameter is defined as the minimum length of time between an animal becoming diseased and its death from the pathogen. The working group decided to use 14 months as minimum duration of disease based on the study by Keet (unpublished data) where 16 lions in optimum condition tested positive for BTB and the first recorded deaths occurred 14 months later.

[Data category: 2, Keet's data: based on observation of earliest death from animals in good condition testing positive]

Maximum duration of disease: ..... *58 months*

The parameter is defined as the maximum length of time between an animal becoming diseased and its death from the pathogen. The group made an educated guess on the length of the diseased stage. It was cautioned that the maximum duration of disease is so highly variable that it is difficult to determine a window of time (D. Keet pers. comm.). One lion in Keet's study was infected for 58 months before dying. Based on the death of all except two of Keet's 16 animals that were monitored, it can be assumed that once diseased, most animals die within 14 – 58 months.

Due to a lack of data a discussion followed about Keet's study. The main concern lay with categorising shedders from non-shedders of the organism, as it is not clear whether lions that appeared thin should be considered shedders. However, eight out of 20 lions that tested pulmonary positive based on cultured samples had a body condition of 4 / 5 (these are lions in good condition). Keet confirmed that up to 40 % could be infectious and shedding the organism.

Of all the animals that progressed from infected to diseased, 80 % died and 20 % were still infected but probably died of natural causes. Infected animals are defined as non-shedding as far as the model is concerned. The model assumes that 20 % of infected animals do not shed and do not die from BTB. It was cautioned that some

lions may be intermittently shedding and it was questioned how long this phase might be. It could last a few days or months, but for the purpose of this model the group assumed that they will not shed.

[Data categories: 2, Keet's data based on observation of latest death from animals in good condition testing positive. Shorten time by 3 months since animals separate from the pride]

Note: Craig Packer stated that a maximum of 6 months can be taken off the 14 months estimated as the minimum duration of disease and 58 months from the maximum duration of disease as a sick animal does not associate with the pride in the last 6 months (sensitivity measure is needed). This has not been added to current models but can be incorporated in later versions of the analyses.

Mortality from disease at end of infectious period: ..... *100 %*

This is defined as the probability of dying from BTB during the period of time that an animal is in the diseased state. Based on the calculated rate at which lions progress from the infected to diseased state, the modelling team questioned the age of the youngest lion getting infected.

An individual lion could die as soon as 14 months after infection and all young lions seen losing condition died within 6 months – the maximum period before death once showing clinical signs (D. Keet pers. comm.). Keet's study shows that 20 % of those that become infected did not die; however it was highlighted that only those lions that appeared emaciated or were problem animals were captured. Of the 14 radio-collared emaciated lions that were followed to see if they recovered, all died within a period of 6 months.

A number of emaciated lions associated with the prides were also monitored; however they died shortly after they were ultimately captured and fitted with radio-collars. Due to the limitations in capturing and doing necropsies on healthy looking animals, it is difficult to determine the length of time from exposure to infectious / diseased status. Not all lions had pulmonary lesions, so were probably not necessarily infectious even though they had the disease (D. Keet pers. comm.).

[Data category: 2, Keet's data based on all study animals died that showed clinical signs]

The parameters determined above are shown in Figure 3.

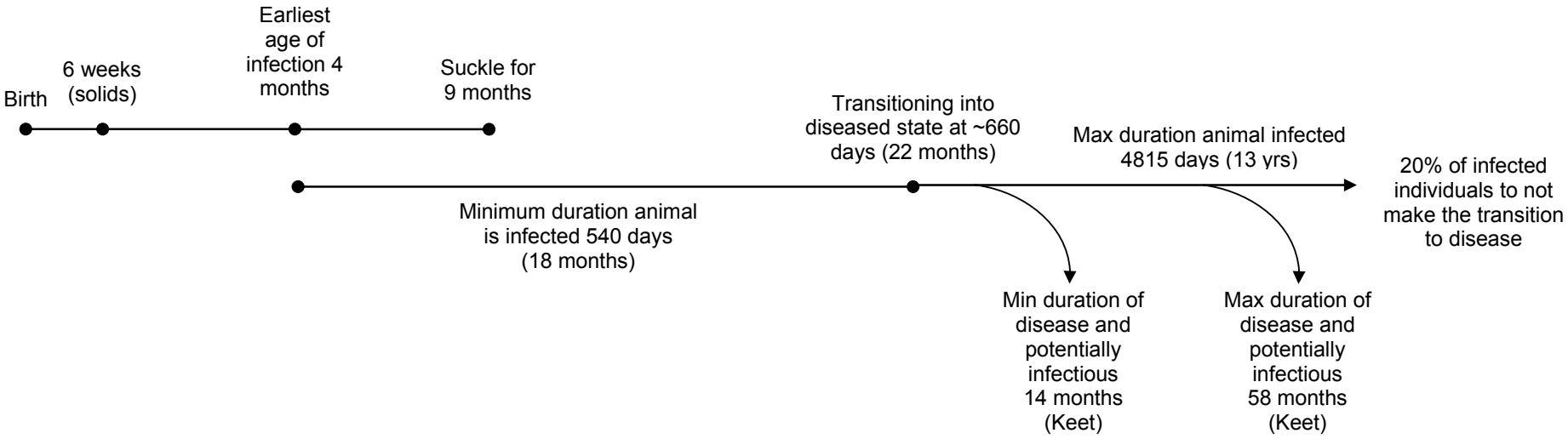

Figure 3: Graphical depiction of the OUTBREAK parameters.

Research gaps identified by the group participants:

- Need to compare the rates of exposure in buffalo within the southern, mid and northern zones. Using data at hand, predict the spread of disease in KNP in the future.
- Need to investigate the likelihood of a lion becoming infected when feeding on an infected buffalo.
- Determine the tenure of a male lion coalition, for example, 2 - 5 years in the different zones. This varies from 13 to 63 months in the south, tenure in the north was longer and less variable, but this needs more study to actually quantify (D. Keet pers. comm.). This should provide more accurate data on the probability per lion of "out-group" infection.

Suggested criteria for modelling

Participants suggested the following additional criteria for modelling during their discussions:

- Determine how other species will be affected by the loss of lions?
- Sex-based and age differences can affect transmission loads and in some cases these were found to be statistically significant and should therefore be considered in the final model, and particularly for sensitivity analyses. Age-specific distinction of individuals is also needed in the model as prevalence increases with age and there is a delay before reaching the maximum (80 %) prevalence as shown in the original data model (D. Keet pers. comm.).
- Differentiating between FIV infected individuals due to social interactions (e.g. males become infective earlier than females and males more frequently exposed than females to oral infection). The modelling team suggested that separate infection areas for FIV and BTB are included, once the model has been modified.
- Drought should be incorporated into the model as it has been described as an influencing factor on the demise of lions in the KNP. A 10-fold increase in exposure probability can be found during drought periods with good records being kept on rainfall in KNP (M. Miller pers. comm.).
- Produce plausible scenarios and identify critical areas that are driving the population so as to determine essential research areas. The modelling team suggested that the sensitivity analysis would help identify which parameters need to be considered to obtain the information needed for the model.

Plenary session - notes and discussions following a report back from the BTB Working Group:

Presentation by Dr Peter Buss - below are the questions raised by the workshop participants:

Q: Concern was raised as to whether sampling methods have missed some infected herds because of clustering effects of herds in the different zones.

Infected herds were definitely missed as not all herds were sampled and there is great individual movement between herds. After the most recent sampling in KNP, it is safe to assume that all herds south of the watershed between Mopani and Shingwedzi Rest Camps are infected to a lesser or greater degree (D. Keet pers. comm.). There is a risk that the current data are disjointed rather than providing actual movement since some herds of buffalo are known to move from 60 to over 100 km. This means that testing for infection should be set up in more locations.

Q: Assuming that 20 % of the lions remain latent and re-infection is an issue, lions are repeatedly exposed – is there a dose dependency?

Studies show that animals in general need a large dose of the organism to become infected. This can drastically affect the outcome of the model as it is difficult to quantify the extent of repeated exposures. Dose and frequency of exposure data are needed but the model currently is unable to accommodate these types of data. The model assumes a six-monthly exposure period through predation. The dose during feeding on a kill is probably lower than inhalation. A high rate of exposure, especially repeated exposures, would probably lead to a higher probability of infection and is relevant for lions preying on buffalo. There are definitely zonal differences in KNP with northern and far northern lions being exposed less often to BTB because there are far fewer buffalo with extensive lesions.

Lion Working Group

WORKING GROUP PARTICIPANTS

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2.	Davies-Mostert, Harriet:	The EWTs Carnivore Conservation Group
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INTRODUCTION

The Lion Working Group was tasked with determining the SIMSIMBA (lion biology model) parameters.

MAJOR QUESTIONS IDENTIFIED BY THE GROUP:

- Is additional mortality from BTB on top of background rates of natural mortality enough to push the population down?
- What level of mortality would BTB have to inflict in order to decrease the population?
- Does infection with BTB affect fecundity in any way? For example, by altering interbirth intervals, litter size and cub mortality.
- Do infected and uninfected animals display differences in age-specific survival patterns?

GENERAL MODEL INPUT VALUES:

The SIMSIMBA model is an individual-based stochastic simulation of socially-structured lion population dynamics. This model is parameterised by a large number of demographic variables, some of which have been well studied in some lion populations, but others for which data are scant or non-existent. Recognising that data of variable quality and from different sources would be necessary to fully populate the model, the group therefore assigned data to several different quality categories as follows:

1. Serengeti - known parameters obtained during field studies in the Serengeti.
2. Kruger - known parameters obtained during field studies in KNP.
3. Informed opinion - best guess of experts.
4. Derived - obtained from other studies.

The group worked through the parameters in the model to assess whether (i) each parameter was relevant to the Kruger model and (ii) what levels of each parameter should be used.

SIMSIMBA PARAMETERS

Note that SIMSIMBA incorporates density dependence through its specification of territory numbers, size and lion composition.

Maximum female age:..... 16 years
Maximum male age:..... 13 years

Parameters regarding maximum ages of females and males

- The model kills all lions at above the maximum age.
- It is important to have two parameters: (i) age at last reproduction, and (ii) maximum age, as old animals might be infectious and therefore influence disease transmission.
- The group decided to use the average maximum years (informed opinion): 16 for females, 13 for males (Smuts *et al.* 1978a, 1980, Ferreira and Funston in press (b)).

[Data category: 2, based on Funston's data]

Average maximum females per pride: 5

This parameter is defined as the average maximum number of females per pride (Figure 4).

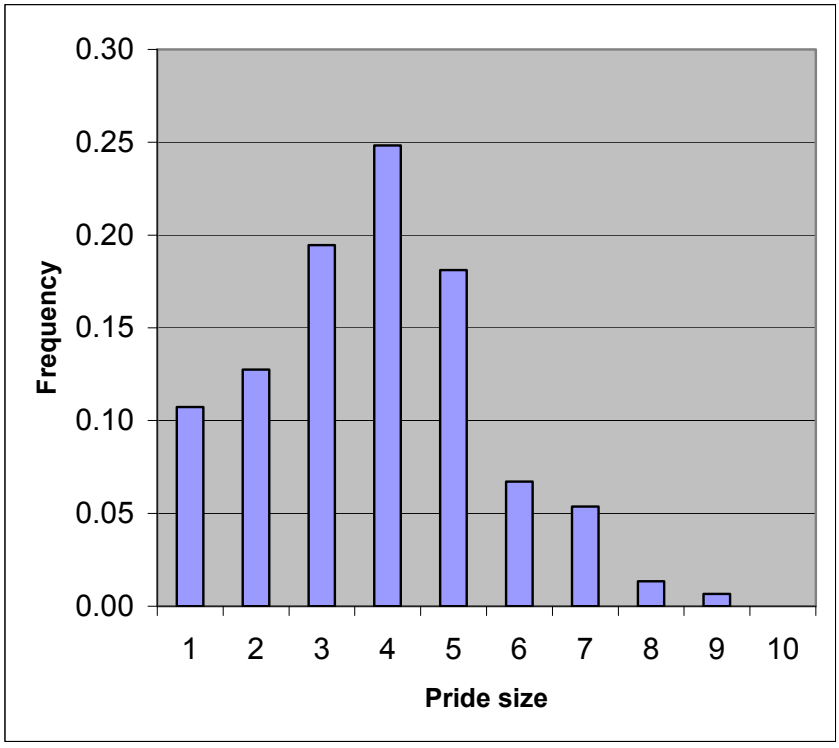

Figure 4: The frequency distribution of pride sizes (number of adult females)

Maximum sizes for prides (females):

- This parameter is important as is regulates the recruitment of females into their natal prides and governs whether they disperse or not.

- The biggest prides on record in terms of number of adult females are between 13 and 15 females, and these groups can become very large if males and cubs are added.
- The group decided that the average maximum would be used and this was set at between 5 and 9 lionesses. This includes all females older than 3 years (Smuts 1976, Smuts *et al.* 1978b, Funston *et al.* 2003).

[Data category: 1, 2, based on Funston's data]

Average maximum males per coalition: *10*

- This governs the size which male coalitions can reach.
- This number is not important to the model, because in practice it is rarely, if ever, obtained (Smuts 1976, Smuts *et al.* 1978b, Funston *et al.* 2003).

[Data category: 2, based on Funston's data]

Male reproductive age:..... *3.5*
Female reproductive age: *3.5*

Reproductive age for males and females (age at first reproduction).

- Lion social reproduction: females 3 years, males 3 years (Smuts *et al.* 1978b)
- A discussion ensued about whether this should be the physiological or social age at first reproduction. It was agreed that males would only be likely to breed at 6 years and females at 4, but this would be controlled in the model by the fighting matrix. The chosen model parameters were lower than the values in the population, because other components of the SIMSIMBA model contribute to these processes and therefore breeding at such an early age would be unlikely.

[Data category: 2, based on data from Smuts]

Maximum male reproductive age:..... *12*
Maximum female reproductive age:..... *13*

Age at last reproduction

- Females breed throughout their adult lives. Females last reproduce at 13 years.
- It is suspected that males will not breed much beyond their 9th or 10th year but occasionally older males will breed. Males: 12 years.

[Data category: 2, Smuts *et al.* 1978a, 1980, Ferreira and Funston in press (a)]

Male adult age:..... 5
Female adult age: 5

This parameter was discussed below.

Survivorship per 6 months (0 months to 6 months): *0.707*
Survivorship per 6 months (6 months to 12 months): *0.775*
Survivorship per 6 months (12 months to 24 months): *0.906*
Survivorship per 6 months (males 2 - 5 years): *0.877*
Survivorship per 6 months (females 2 - 5 years): *0.964*
Survivorship per 6 months (males 6+ years): *0.949*
Survivorship per 6 months (females 6 - 13 years): *0.929*

Survivorship per 6 months (females 14+ years): *0.548*

These are age-specific background mortality rates which exclude death from additional causes (disease, fighting or infanticide):

- In SIMSIMBA age classes in the model are: juveniles (0 – 6 months, 7 – 12 months), sub adults (1 - 2 years, 2 – 4 years) and adults (+4 years, etc.)
- It was suggested that juvenile age classes are not that important for disease transmission, and that adult age classes might be more important as these classes are likely to have more impact on disease transmission. Suggestions included 2 year age classes for adults (5 - 6, 7 - 8, 9 - 10, etc.).
- It is important to have an age class that encompasses the age at which males become territorial and are establishing themselves as at this age the mortality schedule might be different.
- The group discussed the effects of prey biomass on lion survival and mortality and agreed that this should be made spatially explicit to incorporate the patterns likely to be observed in KNP.
- In Serengeti age-specific mortality typically follows a J-curve. But there are also periods when the population just declines, and at these times the survival curve is a flat line. Approximately ¼ of cub mortality is due to infanticide and about ⅓ is due to poor nutrition. The rest is possibly due to disease (parvovirus, etc.) (Packer *et al*. 1988).

The population structure is currently:

- 48 % of females are adults (4+ years)
- 23 % males are adults (5+ years)
- Adult sex ratio is 2.2 females per male as determined in 2005 / 2006 which included over 500 lions (Ferreira and Funston in press (a)).

The method used to estimate survival rate:

In addition to the above, the working group made use of a Leslie matrix (Caswell 2000) to estimate survival rates. For this the group defined a fecundity schedule assuming that lions have an age at first birth of four years and the last litter of cubs at 13 years of age. The average litter size was set at 3.2 cubs with an interbirth interval of three years and the group assumed an equal offspring sex ratio at birth.

For input into the Leslie Matrix Model, the group defined:

$$Fx = \frac{\text{Litter size x Sex ratio}}{\text{Birth interval}}$$

Age at first birth ≤ χ ≤ Age of last birth having zero fecundity. This defines age χ, however χ has to be equal or larger than the age of first birth and equal or smaller than age at last birth. Any age χ outside that range will have no fecundity.

The working group then used the age structures smoothed from the survey data in KNP and estimated survival rate. This allows for only a common survival rate across all ages. For females these varied from 0.71 to 0.85 across six different zones of prey biomass and BTB prevalence in prey (Ferreira and Funston in press (a)). Funston noted survival in KNP during 1 - 2 years of age as 0.82 (Funston *et al.* 2003).

To overcome this challenge, the group used a maximum likelihood approach to estimate the survival rate of females (Ferreira and van Aarde 2008) 0 - 6 and 7 - 12

months old assuming that the female age distribution recorded in 2005 / 2006 (Ferreira and Funston in press (b)) is stable. The working group used reproductive variables noted in 1976 (Smuts *et al*. 1978a) and the age distribution data extracted from (Ferreira and Funston in press (b)) and adopted a population growth of lambda (λ) = 1 from (Ferreira and Funston in press (a)). For females older than three years the group used age-specific survival rates from the Serengeti (Table 1) as input into the Leslie Matrix Models. This provided a survival rate estimate of 0.65 for both age classes of 0 - 6 months and 7 - 12 months.

The working group then assumed that males and females may have similar survival to the age of 2 years. Making use of observed adult sex ratios of females (4 years - 16 years): Males (5 years – 12 years) of 2.2 (Smuts *et al.* 1978b, Funston *et al.* 2003), as well as observed male age distribution where 23.3% of males are older than 5 years, survival rates of males 3 - 5 years and >5 years were estimated.

The above approaches made key assumptions as follows:

1. Reproductive data did not change over time.
2. Survival of females is similar in KNP and Serengeti.
3. Fecundity and survival schedules are stable which leads to a stable age distribution.
4. Population is not changing.

Table 1: Survivorship data from the Serengeti

Age	Survival
3 yrs	0.89
4 yrs	0.95
5 yrs	0.95
6 yrs	0.92
7 yrs	0.93
8 yrs	0.89
9 yrs	0.91
10 yrs	0.83
11 yrs	0.80
12 yrs	0.70
13 yrs	0.68
14 yrs	0.60
15 yrs	0.20
16 yrs	0.10
17 yrs	0.00

[Data category: 2 and 4, Funston *et al.* 2003, Ferreira and Funston in press (a), Ferreira and van Aarde 2008, Smuts *et al.* 1978b]

Survivorship per 6 months (orphaned cubs): *0.5*
Survivorship per 6 months (females without territory): *0*

Survivorship per takeover (cubs 0 mo. to 6 mo.): *0.01*
Survivorship per takeover (cubs 6 mo. to 12 mo.): *0.25*
Survivorship per takeover (cubs 12 mo. to 24 mo.): *0.65*

- This includes infanticide as a result of pride takeovers. Paul Funston never recorded infanticide in his study area and records from other reserves also

suggest that the rates of infanticide are low. Infanticide seems to be much more prevalent in East Africa. However, Dewald Keet recorded cubs being killed by incoming males in two of the three southern prides that were studied (Keet unpublished data).

[Data category: 1]

Survivorship per defending mother per takeover: *0.09*

- Fighting female mortality which arises when females are defending their cubs during take-overs.

[Data category: 1]

Survivorship per male per takeover (defending, winning): *0.97*
Survivorship per male per takeover (defending, losing): *0.40*
Survivorship per male per takeover (attacking, losing): *0.50*
Survivorship per male per takeover (attacking, winning): *0.97*

- Fighting-related male mortality is the biggest cause of mortality for males in the Serengeti.
- Defined as separate mortality rates for whether they are attacking or defending and whether they live or die.
- Keet has found far more intra-specific aggression when sex ratios are male-biased and when prey biomass is high (Keet unpublished data). Reduced periods of tenure might also lead to the possibility of consequent infanticide.
- The fighting outcome needs to be adjusted for BTB status as males who are weakened by BTB are less likely to win fights.
- In the Serengeti, this additional mortality accounts for a large proportion of overall mortality.
- It is always the ousted males that challenge the resident males, and there is an associated probability of there being a fight and the outcome depends on the relative size and age of the coalition. It is very difficult to determine these rates as it is not easy to observe where males go.
- It was agreed to use Serengeti data (due to no specific data being available from KNP) for these rates of additional mortality as there is no reason to suspect that they should be significantly different, although the BTB interaction could have an effect.

[Data category: 1]

Litter Size is 1 Probability: *0.05*
Litter Size is 2 Probability: *0.05*
Litter Size is 3 Probability: *0.75*
Litter Size is 4 Probability: *0.15*

- Litter size was set at 3.2 – average (Smuts *et al.* 1978b)
- A probability is set for each of 4 litter sizes (1, 2, 3 and 4) with 3 being the most likely.
- Females will not have cubs while they have dependent cubs.
- The probability of pregnancy is set at 100 % but this can be changed (i.e. a female with no cubs and with males in her territory will become pregnant 100 % of the time).

[Data category: 2, Funston, Smuts]

Probability newborn is male: *0.50*

Litter sex ratio at birth:

- Taken to be 50:50 on average as this has been found in a number of lion populations.
- In some areas there are deviations from the 1:1 sex ratio but in general it averages out to 1:1.
- The sex ratio in the south of KNP is very male-biased. It would be interesting to understand why there is such an over-representation of young adult males. Paul Funston suggested that there may be areas that are attractive to young males.
- Could capture this in the "habitat heterogeneity" parameter of the model.

Dependency on the pride:

- Offspring usually stay dependent until 36 months for both sexes.
- Inter-birth interval is not a parameter specified in the model but is controlled through the parameter describing dependency of offspring.
- It appears that reproduction is slower in the KNP than in the Serengeti and this is possibly due to the deceased availability of food resources. Alternative reasons for the slower reproduction is birth intervals increase, females give birth for the first time later, females stop giving birth earlier, or litter sizes decrease.

[Data category: 2, Funston, Smuts]

Number of territories nomadic males move in 6 months: *3*

The parameter is defined as the number of territories that can be traversed by non-resident males in a 6-month period. Movement parameters need to be able to incorporate habitat / zone heterogeneity for the various variables. The territories might be dimensionless in terms of the probability of in-group interactions.

- Funston has data from Lower Sabie and this value is set at 3 (Funston *et al.* 2003).

[Data category: 2, Funston]

Distance in territories sub-adult males can go from home territory in 6 months: *1*

The number of territories that sub adult male coalitions can be exposed to for *ad hoc* unions with females (per 6-month period)

- This was set at 1.

[Data category: 2, Funston *et al.* 2003]

Table 2 describes the number and position of territories across the park, shown graphically in Figure 8. This figure is a virtual landscape map based on the six zones which are based on BTB prevalence and prey biomass. The group discussed whether to include the Limpopo National Park, Mozambique, as this might be an important destination for dispersers; however the group decided to exclude it from this analysis as there were not enough data available to realistically model its inclusion.

Table 2: KNP sections, with the number of pride territories and density (Ferreira and Funston in press (a)).

Section	Estimated number of prides (territories)	Estimated density (lions / 100 km^2)
North West block	29	5.0
North East	24	8.3
Central West	16	7.3
Central East	45	17.4
South West	25	8.1
South East	5	11.2
APNR (incl. Sabi Sands)	16	7.3
Total	160	

Chance coalition of 2 males takes a second territory in given 6 months: 0.0001
Chance coalition of 3 males takes a second territory in given 6 months: 0.33
Chance coalition of 3 or more males takes a third territory in a given 6 months:... 0.01

The number of prides that a coalition can be resident in (monopolise). This parameter is described by a probability of how many prides that coalitions of different sizes can cover. The parameter was set at the same levels as for the Serengeti model (Whitman *et al.* 2004).

i. Coalition of 1: up to 1 prides
ii. Coalition of 2: up to 2 prides
iii. Coalition of 3: up to 3 prides

[Data category 1: Funston]

Plenary session - notes and discussions on the baseline data

Presentation by Dr Phil Miller - below are the questions raised by the workshop participants:

Q: Would a purely demographic model work in modelling the effects of BTB on lions?

The group want to explore the details of interactions and therefore it is important to set up a model that incorporates sex- and age-specific details. It is possible to work backwards to obtain age-specific mortality rates from the stable aged distribution as long as the fecundity is known.

BTB-related mortality:

- A very small number of older animals have been confirmed to have BTB. Frailty displayed by old animals may be a combination of physiological senility and the long-term accumulation of the effects of disease.
- Dewald Keet managed to do necropsies on 8 of the 16 BTB positive animals. 2 / 10 (6 unaccounted for) females were still alive at the end of the study. (Keet unpublished data).
- These mortality data will be very useful to add to the disease components of the metamodel (OUTBREAK and INFECTOR). BTB-related mortality will be modelled in the other models.

BTB might disrupt (through increased mortality and social instability) and subsequently affect the number of dispersal groups that are moving through the area. This might have consequences for conflict on park boundaries.

Q: Is this model (and the associated disease models) really going to get to the issues where SANParks might be able to intervene in terms of improving population persistence and reduction of human-lion interaction?

It is important to capture the key persistence parameters relating to survival and dispersal. For example, if there are major changes in lion behavioural ecology due to BTB interactions does this affect buffalo / cattle interactions? Is there any reason to think that BTB might change lion spatial use and what would be the consequences for the spatial use of buffalo, and the knock-on effects on livestock at the park's periphery?

It is important to note data reliability when building the model as this will help us to determine whether data for especially sensitive parameters need further investigation.

Plenary session - notes and discussions following a report back from the Lion Working Group:

Presentation by Dr Paul Funston - below are the questions raised by the workshop participants:

Q: Was female recruitment included in the model?

The modelling team confirm that female recruitment had been included in the survivorship parameters.

Q: Can one distinguish between territorial and non-territorial coalitions of males, as this could be important for mortality rates?

This is captured through the fight matrix as larger coalitions are likely to become territorial.

Q: Can one link available prey biomass to each of the 7 regions? There is a distinctly different available prey biomass and this may affect the lions, for example by altering lion / buffalo encounter rates?

Available prey biomass is captured through the input map which determines the size of territories (i.e. the number of territories) in each of the zones. Territory size serves as a proxy for available prey biomass

The group discussed whether there should be different datasets for each zone. However, the method used to derive background mortality rates mean that all types of mortality are actually captured in these rates (including BTB and management). This reflects the total mortality and not the true background mortality. It was necessary to assume that population size is static and that there is a stable age distribution. It is essential when modelling forward to remember that background BTB-related mortality has already been included. However, since we want to examine the effects of BTB in future models, we need to ensure that the background rates we have calculated do not include BTB mortality. Keet's data suggests increased mortality due to BTB. However these samples were drawn from the 4 % of

KNP that is covered by roads that are visible to tourists and so might not be representative of the population at large. Of the 16 lions sampled in the south, the fates of 10 were known: 2 were still alive and 7 / 8 had advanced BTB. In the north, 3 necropsies were conducted. A difference in survival was also significant between the combination of males and females from the north and south. When only females were considered differences only approached significance. 150 necropsies have been conducted (emaciated and repeat offender animals) south of the Olifants river (D. Keet pers. comm.). Sixty seven came from a high prevalence zone south of the Sabie River, the remainder (n=83) from the central district. Of the samples from the high prevalence zone, 26 animals were negative and 41 positive. It was suggested that the data from Dewald Keet's two studies be combined (the disease survey and the comparative study) as this might be the best way to incorporate existing information in to the models (Table 3).

Table 3: Data from Keet's combined disease survey and comparative study in the different prevalence zones

	Positive	Negative	Total
High Prevalence Zone	41 (61 %)	26	67
Medium Prevalence Zone	32 (38.6 %)	51	83
Low Prevalence Zone	5 (35.7 %)	9	14
Zero Prevalence Zone	1 (6 %)	15	16
Total	**79**	**101**	**180**

Of the 180 cases examined most (150) were taken south of the Olifants river. Most were generalised BTB cases (i.e. the cause of death was likely to be BTB). The way that these animals were sampled (i.e. from tourist, staff reports) is likely to lead to a bias in the data.

Roy Bengis reported that his department receives approximately 2 lions for necropsy each month. These largely come from the 4 % of the park that is covered by tourist roads and there may be many more lions that are being missed. Most of the animals are adults (6+ years). It was noted that the 4 % penetration rate is an average for all the tourist roads throughout the park, and as the density of tourist roads is much higher in the south, the area of exposure to tourists probably covers an area larger than 4 %.

During Paul Funston's call-up survey in 2005, less than 5 % of the 850 lions seen were in poor condition. However, it is possible that there is a differential response to calling stations between emaciated lions and healthy lions. It was suggested that the call-up data be compared to opportunistic sightings (n=450 all of which were seen within 100 metres of the roads), as this will give a less biased estimate of the proportion of sickly animals.

In the first survey there were 260 stations - the second had a few less. Another factor leading to a bias in opportunistic lion "sightability" is that all the waterholes in KNP have a road leading to them, and this is often where lions spend their time.

The female mortality data in the model is equivalent to background mortality but the male mortalities include the effects of BTB. The observed population decline over the past 10 - 20 years has also been partly attributed to the closure of water holes throughout KNP and this should be flagged. However as the KNP population has only been censused once ever, SANParks has no idea whether the lion population is actually declining. The best available information suggests that the population has not actually undergone any major changes.

Baseline Model Dynamics

All of the models discussed below are based on estimates of lion population dynamics and BTB disease epidemiology and ecology that are as realistic as practicable given the data at hand. The initial models focused on a hypothetical population of lions inhabiting KNP which is much smaller in size than the true population. An assumed initial population size of 213 lions distributed across 19 territories was used with a simple geometry of territory location on the generic landscape (Figure 5). This abstraction allowed for immediate model results to be obtained and simplified the process of sensitivity analysis as discussed in more detail below.

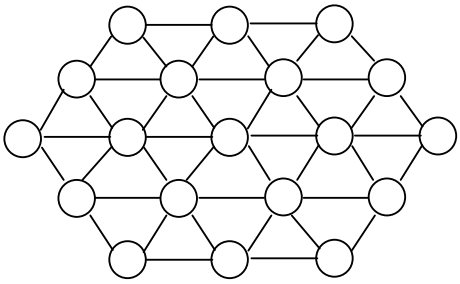

Figure 5: Spatial arrangement of the 19 territories used in the basic sensitivity analysis scenarios.

As intended through the parameterisation of the underlying lion demographic model, the simulated baseline lion population demonstrates stable census size throughout the simulation when disease is absent from the model (Figure 6, solid line). This model, with a population growth rate $\lambda = 1.000$, provides a baseline to compare the results of other models where BTB is included.

The baseline disease model, which includes best initial estimates of BTB epidemiology and ecology, resulted in a simulated population growth rate that is considerably lower than the disease-free lion model (Figure 6, dashed line). The 5 % annual rate of decline in this population leads to a final population size of 18 lions after 50 years, showing a 91.5 % decrease in lions over this period. The absolute number of lions in the baseline analysis is considerably less than the true number of lions thought to inhabit KNP; it is therefore more instructive to evaluate the model output in terms of the rate of population decline. Using this comparative metric, the predicted 5 % rate of lion population decline in the presence of BTB is greater than what has recently been observed on the KNP landscape. Assuming a reasonable understanding of recent lion population trends in KNP, it is likely that this discrepancy results from unrealistic assignment of values to one or more parameters[3] in the disease model. In order to make more realistic predictions of future demographic trends in the true population of lions within KNP, more accurate values for BTB epidemiology and / or ecology are needed in the models.

[3] This refers to any of the INFECTOR / OUTBREAK parameters or perhaps more narrowly, those to which the metamodel is most sensitive (Table 4).

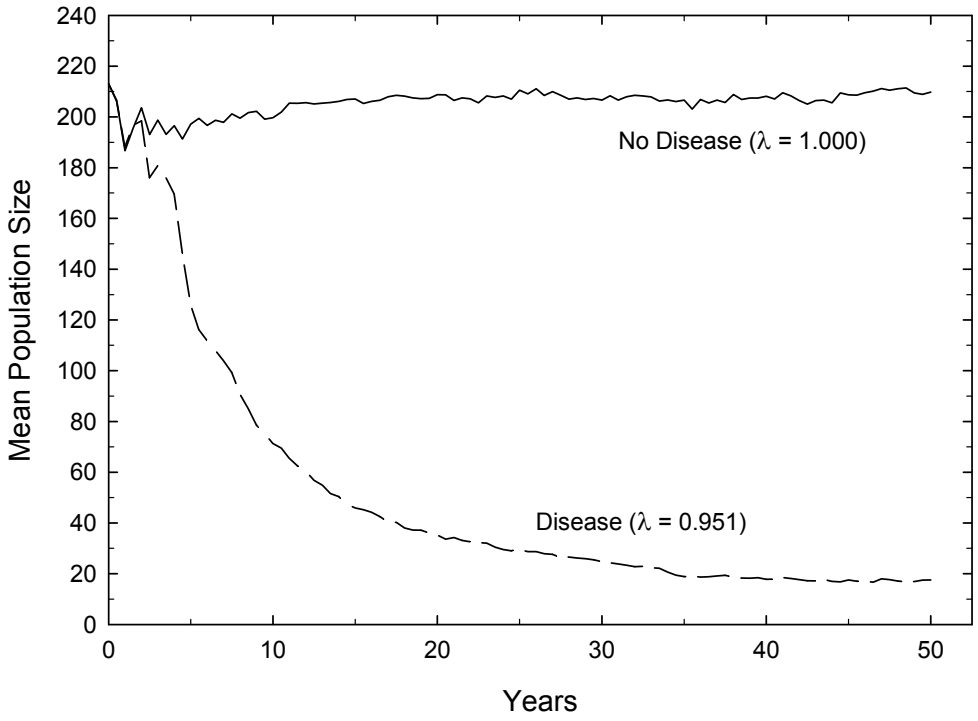

Figure 6: Size trajectories for simulated KNP lion populations in the absence (solid line) and presence (dashed line) of BTB, using demographic and epidemiological parameter estimates developed by workshop participants. Mean annual population growth rate for the alternative models indicated by λ.

SENSITIVITY ANALYSIS

During the development of the baseline input datasets, it became apparent that a number of characteristics of BTB epidemiology and ecology were being estimated with varying (and often high) levels of uncertainty. This type of measurement of uncertainty, which is distinctly different from the annual variability in demographic rates due to extrinsic environmental stochasticity and other factors, impairs the ability of the model to generate predictions of population dynamics with any degree of confidence or precision. An analysis of the sensitivity of the models to this measurement of uncertainty could be an invaluable aid in identifying priorities for detailed research and / or management projects targeting specific elements of the species' population biology and ecology.

As it was beyond the scope of the workshop, sensitivity analyses on the basic demographic parameters that define the lion population of KNP were not conducted. In the limited time available, it was decided to focus instead on the epidemiological dynamics of BTB in lions due to a lack of data compared to the extensive literature available on lion demographics.

A set of disease parameters with uncertain estimates were identified to conduct the sensitivity analysis. A range of values were developed for these parameters (see Table 4). A set of simulations were constructed for each parameter, with a given parameter set at its prescribed value, with all other parameters remaining at their baseline value. With eight parameters identified in the analysis, and recognising that

the aggregate set of baseline values constitute a single baseline model, Table 4 allowed for the construction of a total of 30 alternative models whose performance (defined here in terms of average population growth rate) can be compared to that of the starting baseline model. All sensitivity models used the simplified lion population with 100 iterations per scenario.

The results of the sensitivity analysis are shown in Table 4 (rightmost column) and graphically in Figure 7. Those lines with the steepest slope – namely, predation exposure rate, out-group transmission rate, and in-group transmission rate, show the greatest degree of response in terms of population growth rate to changes in those parameters and, hence, the greatest sensitivity.

Based on this analysis, it can be concluded that those parameters with the greatest sensitivity can be targeted in subsequent field activities for more detailed research and / or active management, where appropriate. However, it is important to remember that sensitivity parameters, such as those identified here, may not always be the subject of demographic impairment through local human activity. Thoughtful analysis of the mechanisms responsible for such impairment should accompany the development of effective population management strategies.

Table 4: Uncertain input parameters and ranges for use in disease sensitivity analysis for lions of KNP. Highlighted rows indicate those disease parameters that show the highest sensitivity as identified graphically in Figure 7

		Estimate	
Model Parameter	Minimum	Baseline	Maximum
Maternal transmission rate	0.0	0.0	0.1
In-group transmission rate	0.0	0.1	0.1
Out-group transmission rate	0.005	0.005	0.1
Predation transmission rate	0.0	0.025	0.1
Initial frequency infected	0.125	0.5	0.5
Initial frequency diseased	0.02	0.08	0.08
Residence time as infected (days)	6205	6205	8212
Residence time as diseased (days)	1740	1740	2300

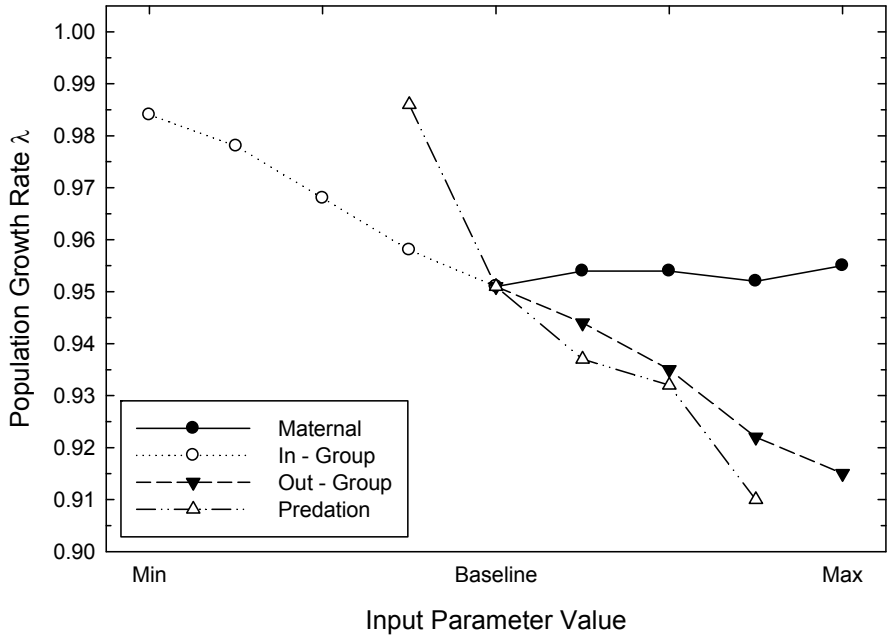

Figure 7: Sensitivity analysis of a generalised population of lions inhabiting KNP. Curves with the steepest slope indicate the model parameters with the greatest overall sensitivity. (Results for infected and diseased state initial frequency and residence time models not displayed here but are shown in Figure 6).

FULL KNP POPULATION ANALYSIS

The baseline lion demographic, movement, and disease parameter values were used to evaluate model results when applied to the full KNP landscape. A virtual landscape map was constructed of KNP based on estimates of lion density and pride size for each region of the park (Northeast, Northwest, Central East, Central West, Southeast, and Southwest). The landscape consists of a total of 160 territories distributed throughout the six regions, with an initial population size of 1775 lions distributed on the landscape. Dispersal rates were specified for sets of territories within and between regions in order to create a realistic set of movement patterns across the landscape. The spatial arrangement of territories on this virtual landscape is shown in Figure 8.

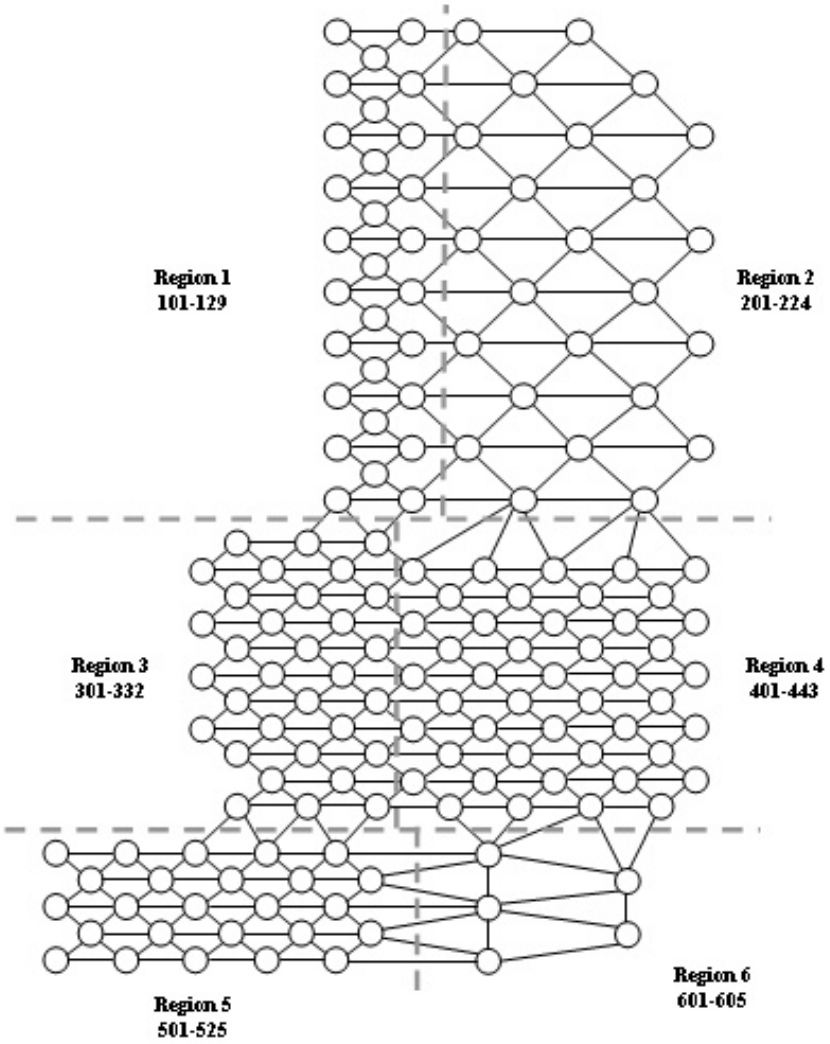

Figure 8: Virtual landscape map of the 160 territories comprising the lion population in KNP. Numerical designations across the six regions of the landscape correspond to territory ID numbers used as model input.

The maternal, in-group and out-group disease transmission parameters were kept constant (baseline value), as were the residence time of individuals in both infected and diseased states (see Table 5 for these values). The predation transmission rate and the initial proportion of infected and diseased lions vary by park region, with the highest values in the south and the lowest values in the north. This regional specificity is intended to simulate the higher prevalence of BTB among buffalo in the southern and central regions of the park.

Table 5: The region-specific parameter values.

Region	Predation trans. rate	Initial freq. Infected	Initial freq. Diseased
South	0.0250	0.50	0.080
Central	0.0125	0.25	0.040
North	0.0025	0.05	0.008

As with the sensitivity analysis scenarios discussed above, all full KNP models were run with 100 replicates.

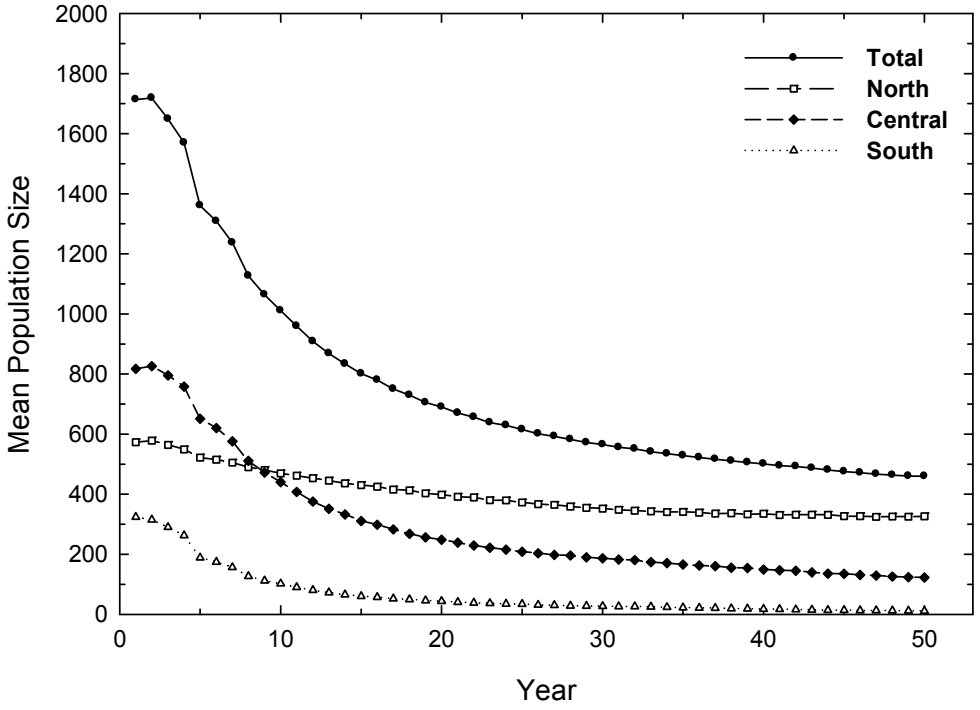

Figure 9: Mean trajectory of a simulated KNP lion population in the presence of BTB. Values for predation-based disease transmission rates and initial disease prevalence are region-specific, with the highest rates in the south. All other disease parameters are at their baseline values.

Figure 9 shows the results of an initial full KNP lion population model. The figure shows a steady rate of decline in the overall population, with growth rate = 0.973. The population in the southern region shows the most rapid rate of decline (λ = 0.934), while the northern population displays the highest degree of relative stability (λ = 0.989) and, after 50 years, appears close to reaching demographic equilibrium at approximately 325 individuals. The population in the central region loses over 75 % of its lions and is still declining after 50 years (λ = 0.962). Overall, the full KNP population appears likely to stabilise at approximately 25 % of its initial population with the majority of animals in the north. This can be explained most easily by the fact that the initial frequency of BTB in the lion population is lowest in the northern region of the park, and the rate of predation-based transmission of the disease is also the lowest due to the low prevalence of tuberculosis in the buffalo population. This long-term projection of lion population dynamics assumes that the prevalence of BTB in the KNP buffalo population will not change over time, which may be unrealistic.

Disease prevalence for this scenario varies by region (Figure 10). After initial fluctuations, the percent of infected and diseased individuals approaches equilibrium. In the northern regions, 6 – 7 % of lions are infected, while 3 % are diseased. In the central regions, 10 – 12 % are infected and about 5% are diseased. In the southern region, 13 – 16 % are infected and 6 – 8 % are diseased.

This scenario assumes the prevalence of disease among KNP buffalo does not change over time. Consequently, the population in the northern region escapes most of the effects of BTB. Meanwhile, the parameters for disease in the south are so harsh that lions cannot survive; in fact, the continued survival of small numbers of lions in the south is likely due to immigration from the central region.

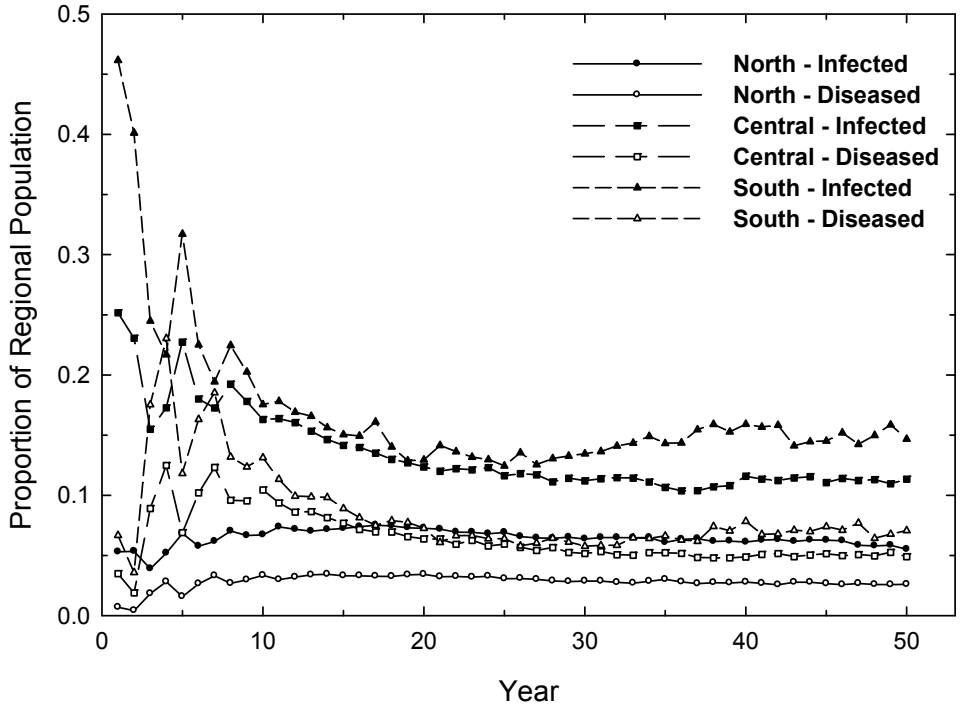

Figure 10: Prevalence of BTB in a fully simulated population of lions in KNP. Values on the Y-axis give the proportion of lions in either Infected or Disease states over the course of the 50-year simulation.

As the model output for this scenario suggests that large-scale lion mortality within KNP should have occurred (particularly in the southern portions of the park) it is likely that the disease parameters are unrealistically severe. Recall from the sensitivity analysis that predation-based transmission, as well as lion-to-lion transmission rates, both within and among groups, were the primary drivers of disease-mediated lion population dynamics. To investigate the effect of a change in one of these parameters on the model output using the full KNP landscape map, a second model scenario was developed. In this new scenario, the same parameter values are used as in the first scenario with the exception of a change to the in-group transmission rate from 0.1 to 0.025.

The results for this scenario (Figure 11) show an early drop in population size across all regions, then a much more rapid and pronounced approach to equilibrium. The overall population stabilises at about two-thirds of its initial size, as compared to 25 % in the initial scenario. Populations in the north, central, and southern regions all appear stable at about 85 %, 65 %, and 35 % of their initial populations.

Unsurprisingly, disease prevalence in this scenario is also lower than the initial full population scenario (Figure 11). In the northern regions 2 % of lions are infected and 1% are diseased; in the central regions 6 % are infected and 2 – 3 % are diseased; and in the south 8 – 9 % are infected and 4 % are diseased.

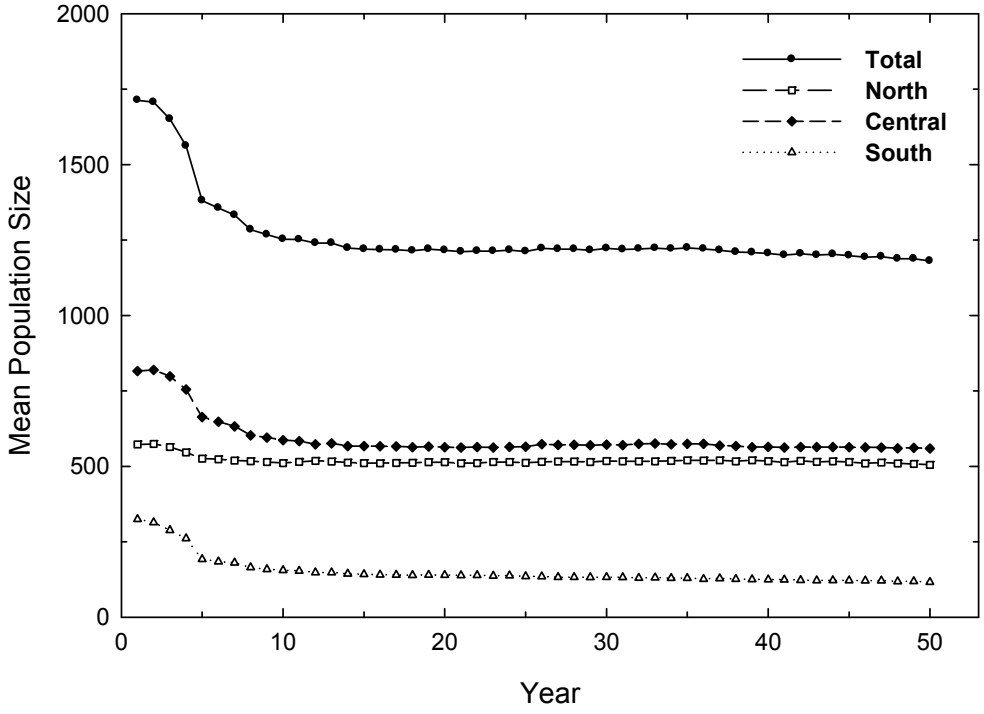

Figure 11: Mean trajectory of a simulated KNP lion population in the presence of BTB. All parameter values are as described for the initial full KNP lion model (Figure 9 and Figure 10), with the exception of a decrease in the in-group transmission rate to 0.025.

The results of this second scenario do not necessarily indicate that the parameter value being used for in-group disease transmission is wrong, rather that it *may* be too high and / or the buffalo-to-lion transmission rate *may* be too high. Careful attention must be paid to the value chosen for the three most sensitive disease transmission parameters in these scenarios. Furthermore, the assumptions being made when determining these values need to be carefully considered.

In addition, both scenarios show a marked drop-off in population before stabilising. This is likely due to the initial proportion of lions that are infected and diseased. These initial conditions can be reduced to reflect the eventual equilibrium prevalence levels and thereby removing the initial drop-off. The actual prevalence levels expected in the lion population given the expected mortality rates of lions that contract BTB need to be carefully considered.

Figure 12 shows prevalence of BTB in a fully simulated population of lions in KNP.

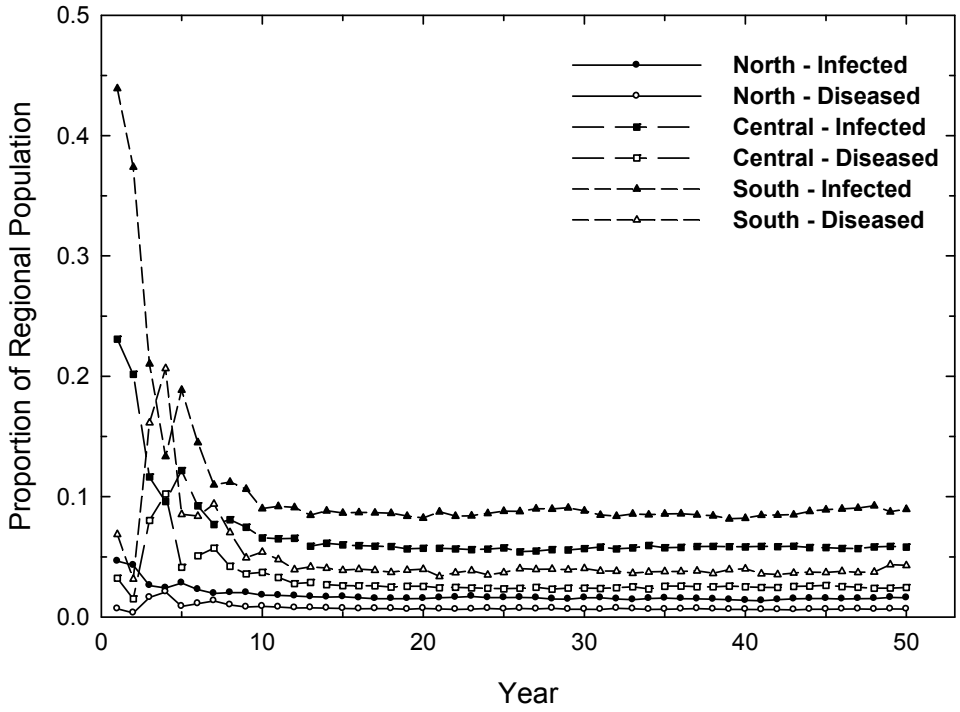

Figure 12: Prevalence of BTB in a fully simulated population of lions in KNP, with reduced in-group disease transmission rate as described in Figure 10. Values on the Y-axis give the proportion of lions in either Infected or Diseased states over the course of the 50-year simulation.

Joint Group Discussions

PREY EXPOSURE

Given the input values for SIMSIMBA, OUTBREAK and INFECTOR outlined in section 3 (Working Group Reports) of this report, a joint group discussion was held to identify additional significant exposure sources of prey for lions.

Buffalo are considered the primary source of prey for lions, followed by kudu and warthog in KNP. In the Serengeti, warthog are an important prey source for lions and since warthogs are burrow dwellers, it may be easier for them to transmit infection to other individuals as they are more clustered than other prey species (R. Bengis pers. comm.). The number of diseased kudu found in KNP is low (estimated 2 - 3 found per year) as they tend to be more isolated, dwelling in smaller groups. They can however be important transmitters when infectious (shedding). Lesions in the draining head lymph nodes, intestinal tract and kidneys were described in a kudu bull (Keet 2001). This means that there are broader spectrum infection modes in kudu with advanced disease.

There does not appear to be any difference in BTB prevalence among buffalo between the eastern and western parts of the KNP; however buffalo are the only prey species that has been studied (L. de Klerk-Lorist pers. comm.). In the south of KNP, the BTB prevalence in buffalo is 40 %, the prevalence in kudu is unknown and the BTB prevalence in warthog on farms south of the KNP is 37 % (Mpumalanga Directorate of Veterinary Services – Annual Reports). Prevalence in warthog is probably lower in the KNP as the population densities of warthog are not as high. Impala (*Aepyceros melampus*), the most common ruminant in the KNP, have not been found to have BTB, and only one case has been recorded in Bushbuck (*Tragelaphus scriptus*). BTB has not been found in Chacma Baboons (*Papio ursinus*) following a previous localised outbreak, and only one case has been reported in a Large-spotted Genet (*Genetta tigrina*) and another in one Honey Badger (*Mellivora capensis*). In central KNP, buffalo prevalence is 20 % and in the north it is 4 %. It is difficult to get proper coverage from the central region for other prey species such as kudu, because there have been so few reports which may indicate lower prevalence, but also could be a result of observation bias due to fewer tourists and lower road density.

Prevalence of BTB in buffalo calves is generally low. A survey of prevalence in calves younger than two years showed 25 % prevalence in the south, 10 % in the central area and 2.5 % in the north (L. van Schalkwyk pers. comm.). Of the prey taken by lions over a normal or above average rainfall year in the south, 27 were calves, 17 were subadults and adults were rarely recorded (P. Funston pers. comm.). Prey frequency was considerably different in the north and central zones. Data are available from Owen-Smith and Mills (2008) on mortalities reported by rangers at KNP for anthrax surveillance and it was suggested that these data are used to investigate what prey species are selected for by lions in the different zones, particularly in the north.

There is a 0.025 probability of infection from carcasses in the south where the prevalence of BTB in buffalo is 40 %. It was agreed to use a range of 25 – 40 % prevalence in the south, 10 – 20 % in the central region and 1 – 4 % in the north. This was used in the initial model. Contrary to the north-south gradient, de Klerk-

Lorist's work shows no difference in the east-west gradient. It was noted that these regions have different soil types, iron content, and different rainfall patterns, all of which should affect BTB prevalence (R. Bengis pers. comm.).

GENERAL CONCERNS DISCUSSED BY THE GROUP

In addition to prevalence, the following issues were also discussed by the group:

- **Testing of animals to investigate BTB prevalence in a natural system**. To determine if the organism is spreading, some countries now test animals at the top of the food chain (predators) rather than prey species, especially when the prevalence is low. The rationale behind this is that it is easier to test a smaller number of lions than to take samples from buffalos who live in herds numbering up to the hundreds. However, this will only indicate that the disease is already present (N. Kriek pers. comm.). Both buffalo and lion were tested in the KNP and the results showed that the proportion of lions that tested positive was double the proportion of buffalo testing positive (Figure 13). It was cautioned that the first lion to test positive in KNP only did so about four years after the first buffalo, prevalence in buffalo at the time was approximately 15 % (Keet *et al.* 1996).

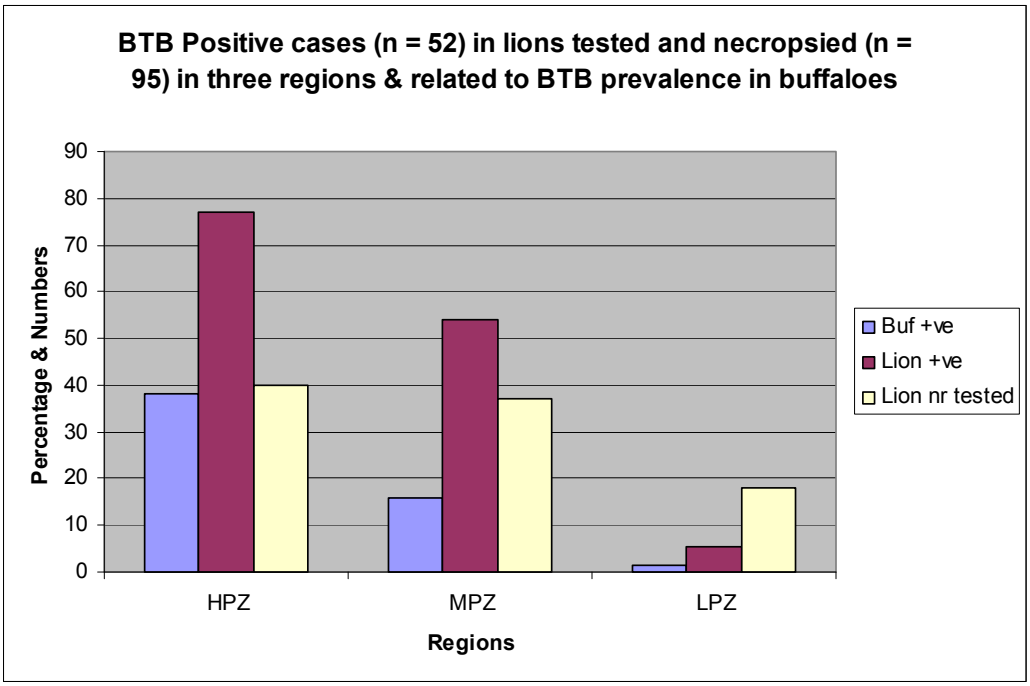

Figure 13: Zonal BTB test results in lion and buffalo according to Keet (unpublished data), High Prevalence Zone (HPZ), Medium Prevalence Zone (MPZ) and Low Prevalence Zone (LPZ).

- **Implications for stakeholders outside the park and the zoonotic potential**. The most likely way lions affect BTB transmission outside KNP will be to chase buffalo through the KNP fences onto neighbouring properties. Recent BTB surveys in cattle in Mpumalanga Province, west and south of KNP showed that there is currently very little BTB circulating in these herds. During 2008 and 2009, a total of 27,850 cattle were tested for BTB in the Nkomazi, Nelspruit, Bushbuckridge and Orpen State Vet Areas, and all but one isolated herd in southern Nkomazi tested negative for BTB (Mpumalanga Directorate of

Veterinary Services – Annual Reports). Communal herds around KNP are thought to show low prevalence. Further discussion followed on the interface between wildlife and livestock and the concern regarding zoonotic transmission. Environmental factors can cause the organism to mutate, increasing the possibility of transmission to humans. Managing people and cattle may be easier than managing buffalo provided the necessary resources are available. However, countries such as Canada, New Zealand, the UK and the USA, have tried to eradicate BTB in humans and livestock but have not been able to deal with a persistent source in wildlife (Bengis, 1999).

- **Lowering of BTB prevalence in buffalo herds in KwaZulu-Natal (KZN)**. Since 1999, KZN has captured large numbers of buffalo, euthanasing BTB positive buffalo and releasing negative animals. A spill-over effect has been observed in the predator population which has immunocompromised lions that were severely affected by BTB when it was at a peak. This was a result of underlying factors such as immunosuppression due to inbreeding. Control or eradication of BTB may be achievable in a small ecosystem. The scale of the KZN area is 1 / 20th the size of KNP so such an operative would be impractical in KNP. The cost of such a programme was discussed as well as the stress factor on the animals. The full consequences of the programme are not yet known e.g. the spill-over of BTB to other species such as rhinoceros species (D. Cooper pers. comm.). Initially KZN had a prevalence of 40 %, but more recently it has been reduced to 10 %. While the spill-over consideration is important, its effect on other animals is unknown. BTB transmission between rhinoceros in captivity (zoos) and other species has been recorded but it is unclear which way the transmission occurred, i.e. rhinos to other species or vice versa (M. Miller pers. comm.). Rhinoceroses are perissodactylids, and in general, the disease is reported to be extremely rare in those species (R. Bengis pers. comm.). However, tapirs speices are quite susceptible (M. Miller pers. comm.).

VACCINES AND DIAGNOSTIC TESTS

Two tools that are essential to understanding and managing BTB are: 1) better diagnostic tests with single immobilisations for the species of concern; and 2) the development of effective species-specific vaccines. Of the two, the diagnostic test is the most critical, due to identification of infected / diseased animals being paramount in applying the vaccination (ideally only uninfected animals should be vaccinated), understanding the disease dynamics and for allowing safe translocation of lions (R. Bengis pers. comm.). Vaccinating animals will not, however, cure them if already infected. In humans, the notion of vaccination has not met with approval as people have been vaccinated since 1921. The lack of success can be attributed to the fact that Tuberculosis is an intracellular parasite and gives a cellular immune response (i.e. involves sensitised lympho / reticular cells). This immune response is less efficient than the humoral (blood fluid response), which results in antibodies (protective proteins) being formed and is the basis of most of the excellent vaccines currently available (e.g. polio, measles, distemper, rinderpest, etc). Therefore, developing a vaccine is difficult and if there is going to be a breakthrough it will be in humans where the majority of resources are invested. Work is being done on post-infection vaccines (immunotherapy), but progress has been slow.

In humans, the diagnostic tests are not ideal because the organism is found in so many different organs and it is difficult to obtain the appropriate sample for testing (P. van Helden pers. comm.). A further major problem with the current diagnostic method

is the 72 hours incubation period to examine skin test results (C. Foggin pers. comm.). A new diagnostic method (Stat-Pac from Chem-Bio Diagnostics) has been tested and this appears to have a high specificity and sensitivity to detect BTB in fresh samples (only 40 cultured and necropsy samples have been tested to date), but the test was not as effective if the samples were frozen and thawed (M. Miller pers. comm.). The test results can be obtained within 15 minutes. Although the results are preliminary, the positives appear to be accurate, but there is still some question as to whether false negatives could result from early infections, especially if the samples have been frozen for some time. Before considering the current enzyme-linked immunosorbent assay (ELISA) test, it should be kept in mind that the sensitivity is far less than 60 % and, although specificity is better, it will not provide a confident indication of prevalence.

SUGGESTED RESOURCE ALLOCATIONS

1. In humans and wildlife there is completely inadequate longitudinal data and follow-up from the same cohort, leading to the need for educated guesses to be made regarding the data needed to populate the model (P. van Helden pers. comm.). More longitudinal research needs to be done before designing effective research and management of BTB.

2. There is a strong subjective impression that the southern KNP may be losing lions at an escalating rate and are being replaced by lions from central KNP. In order to accurately determine what is happening, the movement of nomadic lions on a longitudinal basis and a longevity study on radio-collard animals to test the source-sink hypothesis should be conducted (R. Bengis pers. comm.). Keet suggested that monitoring a small group of lions with poor reproductive success and poor recruitment would be a more objective method to determine the ultimate consequences.

3. DNA microsatellite analyses and mitochondrial DNA samples of lions in the KNP should be performed (D. Keet pers. comm.). Lions in the south are becoming less related due to the increased mortality and influx from neighbouring areas and because individuals start to associate to form new prides (Figure 14 and Figure 15). DNA analysis will give more information on dispersal of different ages to understand subpopulation movements throughout the KNP. Data collected from very old genetic samples will need to be compared with new genetic samples, from animals in different regions of the park.

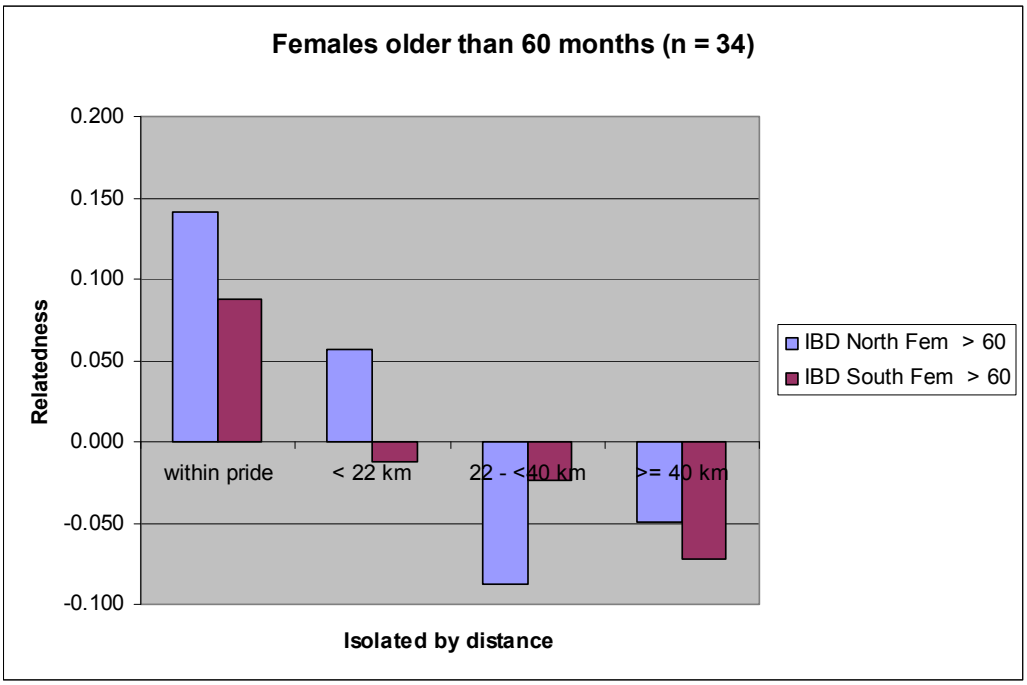

Figure 14: Results from DNA microsatelites analysis on female lions older than 60 months conducted by Dr. Pim van Hooft on unpublished data provided by Keet.

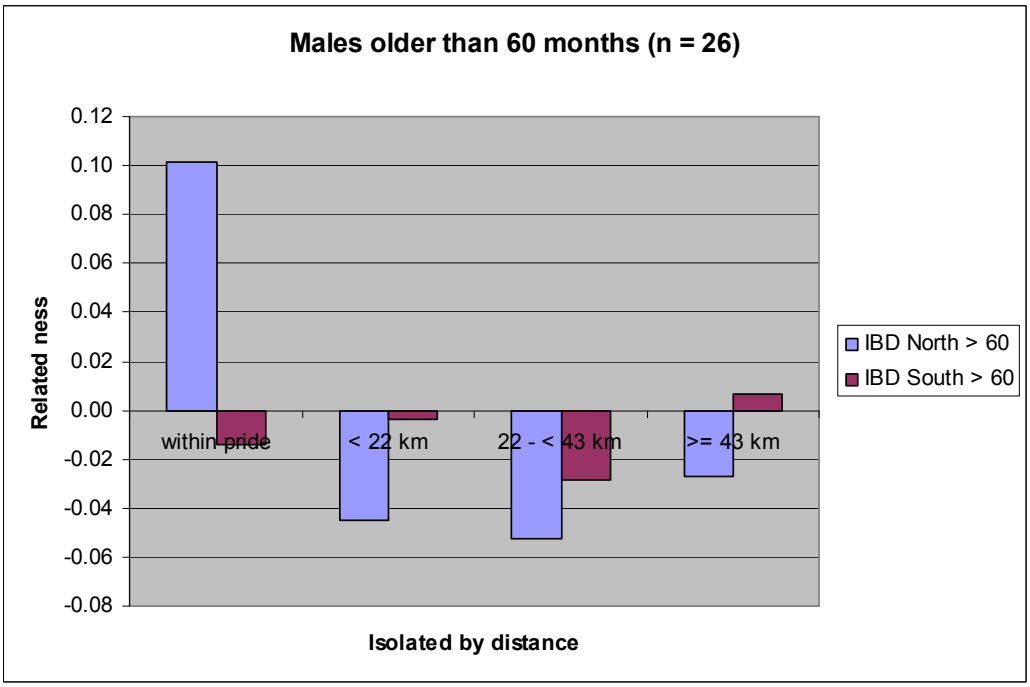

Figure 15: Results from DNA microsatelites analysis on male lions older than 60 months conducted by Dr. Pim van Hooft on unpublished data provided by Keet.

4. It was suggested that random sampling of animals in optimal condition be done (lethal examinations with full necropsies and the full battery of testing) from randomly selected prides. Such studies would provide calculations of a more realistic picture of pathology in very early cases than what has previously been accomplished in more advanced cases. This would also resolve the issue of whether or not respiratory transmission or predation of infected buffalo was the main culprit for infection. However, to accomplish this, the euthanasia of healthy animals would be necessary, a factor which is not acceptable to the current management (SANParks), media, general public and some workshop participants. It is possible to detect lung lesions in advanced cases by x-ray without euthanasia, but that is non-specific and difficult to diagnose (D. Keet pers. comm.). It was suggested that a STAT-PAK test (Greenwald *et al*. 2009) be used on healthy animals, which may provide a better idea of how the infections are initiated as assumptions are still being made on pulmonary versus other routes of infection. This is potentially problematic for lions but the use of domestic cats as a substitute was suggested. Domestic cats have been used as models for certain studies but were in general a very difficult model to work with (M. Miller pers. comm.). An alternative strategy is to capture apparently healthy animals, test them and euthanize those that test positive. A limitation is that newly infected animals may test negative.

5. Studying inter-birth intervals in lions and other changes may give some indication of what is going on with the population over time and should be considered.

6. Reference was made to an age-structured demographic matrix model (Van Vuuren *et al.* 2005) to determine the long-term viability of a lion population that is subjected to persecution. Sensitivity analyses indicated that adult female survival ability alone is the most important component of the model. This raised the question as to whether the loss of one adult female in a pride would cause the pride numbers to gradually decline. Would losing one to two lionesses to BTB per year affect the pride population long-term? In some circumstances, the population may respond by producing more female cubs (P. Funston pers. comm.); however others believed that recruitment would replace those individuals (C. Packer pers. comm.). The duration of tenure of a coalition of lions was discussed but available data has not yet been adequately analysed. Indications also show that the duration may be longer in the north (D. Keet pers. comm.). Participants at the workshop stressed the importance of determining pride composition and sample size for project design to account for inherent variability in pride composition. Populations in the Serengeti can survive in equilibrium for up to 20 years, with good recruitment of cubs, but much is dependent on environmental factors such as rainfall (C. Packer pers. comm.).

7. A longitudinal study on age-specific mortality requires research on 30 prides (10 in south, central and north) over 5 years. Each pride is revisited on a daily or weekly basis and measures of BTB status are done every 6 months to a year, so as to build a non-lethal data set. A spatial component between prides in different zones can be incorporated so as to determine the prevalence of the disease and interaction with prey.

8. A proposal was made to conduct vaccine trials in which BTB negative lions would be fed with BTB infected buffalo. This was suggested 13 years ago and rejected. It was also suggested that captive lions be exposed to BTB in a confined environment to determine rates of horizontal transmission. More data have since been obtained so this suggestion could be revisited. Some participants felt that even if this was allowed, the costs involved with keeping and feeding these lions

would be prohibitive. Others raised concern about the welfare issues with such a project.

9. A more advanced necropsy protocol with a scoring system for lesions is needed in order to understand the progression of the disease. It was suggested that a necropsy protocol is developed as per Dewald Keet's study (Crawshaw *et al*. 2008).

10. Areas outside the KNP in the transfrontier parks are important regards the movement of the disease across borders and a policy should be developed.

RESEARCH VERSUS MANAGEMENT PRIORITIES

Workshop participants fleshed out the parameters that needed changing in the model and listed research versus management priorities.

Questions raised during this session:

1. What happens when the prevalence of infected buffalo (currently at 40 % in the south) is uniform throughout the KNP, with no more lions to disperse?
2. What would the effect be if a programme similar to that of KZN was applied in KNP (reducing the number of infected buffalo)? It was noted that lion birth and cub survival rates were different prior to the outbreak of BTB infection in buffalo.
3. What needs to be done to reduce the prevalence of BTB in KNP and what is an acceptable level?
4. What are the effects of extreme climatic fluctuations (droughts)? Need to consider the decline in buffalos and the increase in infections in lions. At present the model sees it as a cyclic event, but this needs to be changed in the model.
5. What is the duration of disease from when lions become infectious until they die? Model time of infection until death, infect at 2 years or up to 9 years (now believe that diseased animals will die within 5 years).
6. What would the effect be with the introduction of catastrophic events when approximately 35 % lions die? Other diseases that can exacerbate BTB infections by immunosuppression.
7. What are the effect(s) of co-infection with FIV? Need to determine what the impact, survival and extended probability is on the survival and the prevalence of BTB. In addition, the potential immunosuppressive effect of the Canine Distemper Virus (CDV) was also queried. In eastern Africa, CDV is acute in lions for no more than three months however BTB was not prevalent (C. Packer pers. comm.).
8. How do changes to background mortality rates affect the model?
9. What happens when BTB prevalence in buffalo is greater than 40 %?

Research projects for setting management priorities:

1. The lion source-sink hypothesis due to the escalating loss of lion in the south.
2. Improved diagnostic tests for lions and other species.
3. Repeat longitudinal monitoring of lions in the north compared to the south. (It was noted that this may be expensive, long-term and difficult).
4. Ongoing surveillance of buffalo and lions.
5. Study relative transmission of prey-to-lion versus lion-to-prey (pathogenesis studies).
6. Predator cascade: predator relationship studies.
7. Development of effective vaccine options.

The group agreed that all items listed above should be considered high priority and some are already ongoing. The group further agreed to the suggestion of taking the data collected to-date and validating the information to determine if the estimates placed in the model were correct. Once these data were validated this was considered an ideal stage to run additional scenarios by looking at other variables and determining gaps before starting new projects.

The modelling team was tasked with providing details of critical parameters and identifying areas for more research so as to validate the estimated values used in the model.

SUMMARY CONCLUSIONS

The workshop aimed to determine the impacts of BTB on the lion population of the KNP and determine the appropriate strategic directions to address the knowledge gaps. The workshop report clearly shows that many of the parameter input values still need ground-truthing and therefore the focus must be to address critical knowledge gaps.

The INFECTOR model determined the transitioning of disease from one state to the next: in this case, transitioning of hosts from exposed to infected to diseased (infectious) states. Parameters were determined for the three sources of infection (exposure groups): i) within-group (intrinsic); ii) between-group (extrinsic) and iii) predation on infected prey, as well as for initial frequencies of both infected and diseased animals. These parameters were then used to model the transition of the disease within each exposure group. Insufficient data from the study population required the use of data from other studies as well as (in most instances), informed opinion, which may introduce variability. Focus for further studies include disease transmission rates (within-group, between-group and transmission from predation).

OUTBREAK is a BTB epidemiology model used to determine minimum and maximum durations of both infection and the diseased state, as well as the proportion of permanently infected individuals and mortalities. Shortcomings are possible data bias, as studies were limited to one single population in feeding studies conducted by Keet (unpublished data 1999 – 2004).

Additional research needs were highlight during the process:

- Zonal analysis comparing rates of exposure in buffalo is required to predict the future spread of the disease.
- The likelihood of infection from predation needs to be investigated.
- Further study is required on male lion coalition tenures to provide more accurate data for “out-group” infection.
- Sex and age data should be included in the model.
- The effect of FIV should be included in the model.
- The effect of drought and the closing of waterholes need to be incorporated.
- The effect of a reduced lion population on other species.
- To examine the effects of BTB in future models, morality rates calculated should not include BTB.

The SIMSIMBA lion biology model provided the parameters for a number of demographic variables for the KNP lion population.

Focus for future research includes:

- Key persistence parameters related to survival and dispersal.

- Spatially explicit data for prey biomass on lion survival and mortality

The baseline disease model using a hypothetical lion population predicted a more drastic decline in the lion population than has been observed. This was most likely due to unrealistic values being assigned to one or more of the parameters, and suggested that more accurate data for BTB disease epidemiology and ecology are required to reduce levels of uncertainty. In addition, demographic sensitivity analysis was conducted using the disease parameters with uncertain estimates. The model showed the greatest sensitivity to predation exposure rate, between-group transmission rate and within-group transmission rate and this should guide priority-settings for future research and / or management activities. A full KNP population analysis was conducted using lion demographic, movement and disease parameters. The initial baseline model data suggested that large-scale lion mortality should already have occurred, which is not supported by field data, suggesting that the disease parameters were unrealistically severe. A second model with a reduced value for within-group transmission produced a more realistic model. This highlights the importance of assumptions made when assigning values to parameters, particularly those shown to be most sensitive. The process of populating the models with data brought to light that there are large baseline knowledge gaps. Subsequent research studies could inform and validate input values before the model is reassessed.

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LION (Panthera leo)
BOVINE TUBERCULOSIS
DISEASE RISK ASSESSMENT

16 - 20 March 2009

Skukuza, South Africa

WORKSHOP REPORT

SECTION 4

FINAL PLENARY: WAY FORWARD

The Way Forward

A plenary discussion was held on finalising the workshop report and determining the way forward. Phil Miller stated that a fairly solid disease metamodel had been compiled during the workshop, however this needed to be tested further and the modelling team would run the sensitivity analyses on the multiple variables and several models back in the USA. The modelling group would complete this section in a few months and preliminary results would be sent to the workshop participants for comment. Modelling results would be discussed with workshop participants by remote means and various management recommendations made. During this time a full report on the proceedings of the workshop would be compiled and distributed.

Douglas Armstrong suggested that the workshop report present an action plan supported by the actual model results. At this point Markus Hofmeyr reiterated the importance and need for examining research gaps, due to the limited available resources. An understanding of the population dynamics was essential and suggestions are needed on how to expand on the current studies on diseased lions.

Sam Ferreira cautioned the group about making management recommendations that might not align with SANParks policies, but welcomed the identification of research gaps. He also cautioned around the intellectual property rights of the data collated for the workshop and strongly recommended that the outcome of this workshop not be published. Yolan Friedmann explained that CBSG only provides a workshop report without drawing conclusions or prematurely providing recommendations. All participants would be requested to review and correct the report before it is finalised. Yolan Friedmann welcomed input from participants on how to improve on the workshop model and process given that it is the first time that this type of disease risk workshop had been held. The workshop provided a valuable learning experience for the CBSG in terms of the additional time and effort needed to ultimately develop a useful and workable model beyond the limitations of the workshop.

Roy Bengis urged all participants to continue with regular buffalo monitoring in different sectors of the park. Markus Hofmeyr highlighted the need for some kind of management end point recommendation to justify the costs and resources to continue these studies.

Dave Cooper was urged to continue updating the KNP veterinary staff as to the progress of BTB-related programmes in KZN. Sam Ferreira asked whether the removal of diseased lions for study, would affect the population dynamics. Dewald Keet stated that diseased lions should be removed to remove infectiousness in the group; however this was risky as it does influence the social structure of the pride. Craig Packer said that this depends greatly on the understanding of the probability of horizontal transmission.

Nick Kriek questioned the risk of a new outbreak, if a diseased lion was placed in a clean environment. Keet stated that there was certainly a risk of inter-specific aggression and the infection of buffalo at an unsuccessful hunt; however he stated that this would be very difficult to quantify. Roy Bengis cautioned around how members of the public were sensitive to the presence of clinically diseased animals and there would potentially be bad press if sick animals were not removed. Markus Hofmeyr said that it is important to realise that there are quite a number of such occurrences in other species in KNP and public pressure should not prevent SANParks from developing appropriate management methods to reduce the chance of disease transmission.

LION (*Panthera leo*)
BOVINE TUBERCULOSIS
DISEASE RISK ASSESSMENT

16 - 20 March 2009

Skukuza, South Africa

WORKSHOP REPORT

SECTION 5

APPENDICES

Appendix 1: Lion Workshop Participants List

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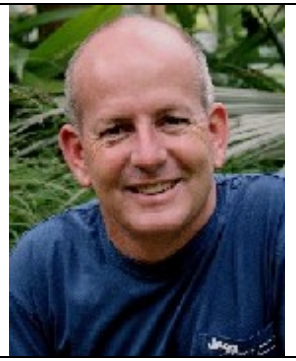
Burroughs, Richard University of Pretoria P.O. Box 254, Derkepark, Pretoria, 0035, South Africa +27 12 529 8508 +27 12 529 8315 +27 82 568 5896 richard.burroughs@up.ac.za		Buss, Peter SANParks P.O. Box 86, Skukuza, 1350, South Africa +27 13 735 4149 +27 13 735 4057 +27 82 905 4665 peterb@sanparks.org	
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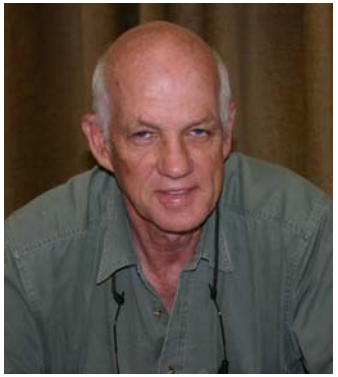
Ferreira, Sam SANParks P.O. Box 202, Skukuza, 1350, South Africa +27 13 735 4189 +27 76 600 4152 samf@sanparks.org		Foggin, Chris Wildlife Veterinary Unit, Department of Veterinary Services Private Bag BW 6238, Borrowdale, Harare, Zimbabwe +263 4 253185 / 6 / 7 +263 4 253188 +263 912 524089 +263 11 631588 chris@kigelia.net or cfoggin@zol.co.zw	
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LIST OF INVITEES UNABLE TO ATTEND THE DISEASE RISK ASSESSMENT WORKSHOP

Invitee	Institution
Albert Machaba	SANParks
Cathy Greaver	SANParks
Craig Tambling	University of Pretoria (Mammal Research Institute)
Danie Pienaar	Scientific Services, SANParks
David Zimmerman	SANParks
Dawn Zimmerman	Memphis Zoo
Don English	SANParks
Elissa Cameron	University of Pretoria (Mammal Research Institute)
Freek Venter	Conservation Services, SANParks
Gus Mills	Kgalagadi Cheetah Project (SANParks)
JP Pollak	Outbreak Software developer / troubleshooter
Julie Napier	Omaha's Henry Doorly Zoo
Lombard Shirindza	SANParks
Louis Olivier	SANParks
Luke Hunter	Wildlife Conservation Society International
Mark Stetter	Disney's Animal Kingdom
Michelle Larsen	Albert Einstein College of Medicine
Miriam Maas	University of Minnesota
Nick Kapustin	Jacksonville Zoo and Garden
Nick Zambatis	Conservation Services, SANParks
Norah Fletchall	John Ball Zoo Society
Peter Novellie	SANParks
Ray Waters	National Animal Disease Center, Agricultural Research Service, US Department of Agriculture
Sarah Cleaveland	Centre for Tropical Veterinary Medicine, University of Edinburgh
Stefanie Freitag	SANParks
Steve Osofsky	Wildlife Conservation Society (AHEAD)

Appendix 2: Participants Goals and Hopes

Workshop participants were asked to write down the answers to the following three questions:

1. What do you hope will be accomplished during this workshop?
2. What do you hope to contribute to this workshop?
3. What, in your view, is the primary challenge for successful management of bovine tuberculosis in the KNP lions over the next 25 years?

I wish to accomplish	I wish to contribute	Primary challenge
Identify whether tuberculosis is a problem for the predator using a clearly defined scientific plan and then determine if management is required Personal goal – application of new techniques for monitoring and detection of infection in lion populations.	Logistical / financial resources are limited. Application of scientific techniques to field collection of data in a systematic manner.	Immunological background / immunodiagnoctics knowledge from other species.
Learn from the experts. Defining what needs to be done and determine an action plan.		Lack of data: Need to fill information gaps to be able to propose effective management tools if needed.
Using a combination of content and process tools to help experts at the workshop make more informed management decisions.	Risk assessment methodologies and group discussion facilitation tools.	
To explore implications of BTB in lions in Kruger based on the current understanding of lion populations and BTB.	Quantitative and modelling skills.	Lack of Data
To learn more about the issue of wildlife and BTB in Kruger; explore possible contributions and collaborations; identify what actions if any needs to be taken relative to the core issue.	Facilitation.	Sufficient data to identify appropriate management actions.
Make a contribution regarding research and the way forward. Increased networking with the possibility for the future research grant applications.	Knowledge in BTB over nearly 20 years. Ideas for research, areas for research. Increase my personal networking with knowledgeable people.	I do not think we can “manage” it in 25 years. We need more information before intervention. Need research tools and methods developed.

I wish to accomplish	I wish to contribute	Primary challenge
Contextualising the importance of BTB as a long-term population driver on lion population persistence. Indentify gaps in trying to answer this question.	Four years of working on BTB prevalence study in buffalo with vet clinical experience.	Suitable diagnostic test. Suitable control measure Addressing public perception that seeing thin lions means collapse of the population.
Personal goal: understanding the dynamics of bovine BTB in lions in a complex multi-host system (BTB susceptible and infected species).	Background experience and guard against basing logic on false assumptions (face up to reality).	If they are a maintenance host, how to deal with the matter should there be a significant negative effect on lions.
Learn more about population / distribution / ecological effects of disease in a / many spp. Get to a realistic point of agreement of the factors driving BTB, which should lead to some useful outcomes on its impact.	Probably not too much. Limited knowledge on the epidemic in buffalo from active surveillance.	1st understand disease dynamics in the system before touching management!
Understanding of existing information. Definition of research needs.	Ecological thinking to bridge the application of productionists paradigms to ecosystem based conservation management.	Ensure the understanding that disease evolution will not lead to local extinction. Ensure the understanding that disease and emergent diseases are desirable for maintenance of ecological integrity. Ensure that the wildlife-livestock interface does not impose on ecological outcomes!
Understanding the BTB dynamics and effect on population dynamics within lion populations and prides. Form a comparison between Hluhluwe-Imfolozi Park (BTB buffalo control) and KNP (no BTB control). Answer: will uncontrolled BTB infection lead to local extinction of lion in KNP?	Practical knowledge and experience from Hluhluwe-Imfolozi Park with BTB control in buffalo and observed effects on Hluhluwe-Imfolozi Park lions.	Sensitive / specific and practical diagnostics is key! Identify key issues and areas of research are needed to decide whether management (active) is required (policy).
Identify solutions that will avoid the spread and transmission of disease from lions to another animal in the Great Limpopo Transfrontier Park.	With some experience as field veterinarian sharing knowledge that will contribute to the controlling of a spreading disease.	Develop a vaccine for wildlife species. Develop an effective diagnostic test.

I wish to accomplish	I wish to contribute	Primary challenge
BTB just confirmed in buffalo in Gonarezhou National Park (Great Limpopo Transfrontier Park). Home to take back some ideas on surveillance and control of BTB for Zimbabwe. Hope to see integrated plan and making relevant contacts. Nota bene: Great zoonotic potential of BTB in Gonarezhou.	Probably not much. Do not have any entrenched ideas on BTB in wildlife and may have unencumbered perspective.	To have Vets and Ecologists agree on what BTB is doing to lion populations. Accurate monitoring of effects of BTB in lions. A decision on if any intervention is necessary / feasible.
Understand disease dynamics better within the greater ecosystem (Transfrontier Conservation Area) with a more holistic approach to dealing with BTB - broadly speaking.	Broad based overview of health issues across the Great Limpopo Transfrontier Conservation Area landscape and concerns and consequences for the Republic of South Africa's neighbours.	Determining the impact of this disease (long-term) not only with lion but within the ecosystem has a whole and the potential public health threat within the Great Limpopo Transfrontier Conservation Area. The unknown, the linkages.
To become more familiar with the problem of BTB in Kruger and the tools that may be used to address it. Clear identification of gaps in our knowledge with recommendations of how to fill these.	To participate in discussions and try to keep the issues within the broader context of carnivore conservation in the region.	Collecting and understanding the right quantities of the right type of data.
Adequate risk evaluation and assessment that can lead to formulation of a policy to manage BTB in lions.	Essentially networking within the workshop to help facilitate this goal.	Small sample size / information, limited by temporal spread of data. Ecological approach.
Learn from others Collaborate with others Quality document Better collaboration with more research fund possibilities.	Experience in vaccine trials (difficulty). Experience in wildlife pathology (disease).	Lions are maintenance hosts. No cure. No vaccine.
Identify areas for future research of BTB in lions to improve knowledge to be applied in realistic modelling of future trends.	Experience in lion BTB.	The current inability to manage the situation now. Increase and distribution will make future management impossible because of the lack in prevention. Increased spread.
Knowledge sharing, working together and assessment (however tenuous) on the risks lions face from BTB and a clearer vision on how to move forward.	Knowledge Energy	Confronting perceptions with good science i.e. using science to inform adaptive management.

I wish to accomplish	I wish to contribute	Primary challenge
To understand more about the dynamics and diagnosis of BTB in lions. To catalogue the data required to formulate relevant responses.	An understanding of the relationships between 'parasite" / pathogen and host versus disease / lesions and biological costs.	Stakeholder education / communication. Relevant data.
Learn about non-veterinary, broader aspects of the effects of BTB on the lion and prey populations to be taken into consideration in the future management of BTB in KNP.	Aspects of BTB diagnosis and molecular epidemiological studies	No diagnostic tests are available to easy and accurately identify infected / diseased lions. No effective vaccine is available to control BTB in buffalo and lions.
Identify major parameters to be studied e.g. latency, impacts in mortality, fecundity). Develop work plan for measuring these parameters.	How to develop a model, how to measure parameters and how to design long-term study.	Decide whether or not to intervene.
Development of possible scenarios through modelling which look at the long-term effects of BTB on the KNP lion population to facilitate the identification of research focuses areas.	Knowledge of disease in KNP. Some understanding of logistical issues regarding working with BTB in the KNP (Great Limpopo Transfrontier Park) system.	Development of diagnostics for the disease. Managing the disease if required to maintain biodiversity in KNP.
Understand the knowledge gaps currently related to the impact / consequence of BTB in lions in KNP. Set direction on future research projects related to lion population dynamics and disease risk.	Our building and facilities. Our knowledge related to work already done. Enacting and facilitating future research in lions and BTB (related to persistence, understanding disease dynamics and risk to lion populations. Influence management policy related to improved knowledge of BTB in the lion population and the overall intervention required or not required.	Develop better diagnostics related to BTB in lions and other species. Test vaccine efficiency to reduce disease of BTB in lions. Ensure that we evaluate carefully all risks and consequences of any management action linked to BTB in lions and other species.
Development of improved methods for monitoring lion population dynamics. Development of animal side tests for BTB status.	Ideas Experience Debate	Monitoring and detecting population effects of BTB. Improved BTB diagnostics. Development of effective and safe vaccine.
Contribute to a successful workshop process.	Produce a quality workshop report to be used by others.	Working together to make the right decisions on a way forward.

Appendix 3: Workshop Programme

LION BOVINE TUBERCULOSIS WORKSHOP

16 - 20 March 2009

Kruger National Park Veterinary Wildlife Services, Skukuza, South Africa

MONDAY 16TH	**MARCH 2009**
14h00 –	Delegates arrive and register at the Kruger National Park Veterinary Wildlife Services Building.
16:30 – 19:00	"5 minutes" Water Hole (Icebreaker)
TUESDAY 17TH	**MARCH 2009 - DAY 1**
07:00 – 08:00	**BREAKFAST**
08:30 – 09:00	Welcome - Hector Magome (SANParks)
09:00 – 10:30	Presentations (20 minutes) ▪ Background information on BTB in free-ranging African wildlife (Roy Bengis, Department of Agriculture) ▪ Bovine Tuberculosis in lions in the Kruger National Park (Dewald Keet, Director of Veterinary Services) ▪ Modelling predator-predator population dynamics in the context of BTB (Paul van Helden, DST / NRF Centre of Excellence for Biomedical Tuberculosis Research) ▪ Lion Population Dynamics (Sam Ferreira, SANParks)
10:30 – 10:45	**TEA BREAK**
10:45 – 11:30	Participant Introductions
11:30 – 12:00	Introduction to the CBSG, CBSG SA and the workshop process (Yolan Friedmann)
12:00 – 13:00	Introduction to OUTBREAK and SIMSIMBA (Phil Miller)
13:00 – 14:00	**LUNCH BREAK**
14:00 – 15:00	Plenary Session: Identify key issues
15:00 – 15:20	Formation of Working Groups and overview of task one
15:20 – 15:50	**TEA BREAK (future breaks self-regulated)**
15:50 – 17:30	Working groups convene and begin on first task
19:00 – 20:00	**DINNER**
WEDNESDAY 18TH	**MARCH 2009 - DAY 2**
07:30 – 08:30	**BREAKFAST**
08:30 – 10:00	Plenary – Working Group reports on first task
10:00 – 10:30	Working groups convene to make changes to first reports

10:30 – 11:00	**TEA BREAK and group photos taken**
11:00 – 11:15	Introduction to goals / solutions and filters
11:15 – 13:00	Working groups convene and begin second task
13:00 – 14: 00	**LUNCH BREAK**
14:00 – 15:00	Working groups convene and complete second task
15:00 – 15:30	**TEA BREAK**
15:30 – 17:00	Plenary session to present and discuss goals / solutions
17:30 – 18:00	**DINNER**
18:00 – 23:00	Lion Darting
THURSDAY 19TH	**MARCH 2009 - DAY 3**
07:30 – 08:30	**BREAKFAST**
08:30 – 09:30	Plenary session to complete task two
09:30 – 10:30	Discussion of third task: Strategies and Action plans
10:30 – 11:00	**TEA BREAK**
11:00 – 13:00	Working Groups reconvene to carry on with task three
13:00 – 14:00	**LUNCH BREAK**
14:00 – 15:00	Working Groups reconvene to carry on with task three
15:00 – 15:30	**TEA BREAK**
15:30 – 17:30	Plenary Session to report back on and finalise task three
19:00 – 20:00	**DINNER**
FRIDAY 20TH	**MARCH 2009 - DAY 4**
07:00 – 08:00	**BREAKFAST**
08:00 – 10:30	Working Groups reconvene to finalise reports Group integration: Prioritise all solutions
10:30 – 11:00	**TEA BREAK**
11:00 – 12:30	Plenary session to present working group reports, discuss management recommendations and report completion
	Workshop closure
13:00 – 14:00	**LUNCH BREAK**
	Departure by delegates

Appendix 4: The Endangered Wildlife Trust and CBSG Southern Africa

The Endangered Wildlife Trust (EWT) is one of the largest non-governmental conservation organisations in southern Africa and was established in 1973. Widely recognised by its prominent red cheetah spoor logo, the EWT conserves biodiversity through the hands-on conservation of threatened species and their habitats, in a sustainable and responsible manner. Coordinating more than 100 field-based conservation projects and with 18 specialist Working Groups operating throughout southern Africa, Endangered Wildlife Trust programmes cover a wide variety of species and eco-systems and play a pivotal role in conserving southern African biodiversity and natural resources.

The Endangered Wildlife Trust with its access to a rich and diverse range of conservation expertise established CBSG Southern Africa in partnership with the CBSG, SSC / IUCN in 2000. Nine CBSG regional networks exist worldwide, including CBSG Indonesia, India, Japan, Mesoamerica, Mexico, Sri Lanka, Europe and South Asia. Regional CBSG networks are developed in regions requiring intensive conservation action and each network operates in a manner best suited to the region and local species. CBSG tools are adapted according to the needs and requirements of regional stakeholders and species and local expertise is utilised to best effect.

CBSG Southern Africa's mission is: *To catalyse conservation action in southern Africa by assisting in the development of integrated and scientifically sound conservation programmes for species and ecosystems, building capacity in the regional conservation community and incorporating practical and globally endorsed tools and processes into current and future conservation programmes*.

CBSG Southern Africa, operating under the banner of the Endangered Wildlife Trust is a non-profit, non-governmental organisation, serving the needs of the *in-situ* and *ex-situ* conservation community in southern Africa through the provision of capacity building courses, species and organisational Action Planning, Population and Habitat Viability Assessment (PHVA) and Conservation Assessment and Management Planning (CAMP) workshops, communication networks, species assessments and a host of other CBSG processes for species and ecosystem conservation. CBSG Southern Africa works with all stakeholders in the pursuit of effective biodiversity conservation throughout southern Africa.

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