Preliminary investigation into anthropogenic and natural disturbance effects on the Nile crocodile (*Crocodylus niloticus*) in the Mutale River, Limpopo Province

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A Dissertation submitted to the School of Animal, Plant and Environmental Sciences. Faculty of Science, University of the Witwatersrand, in fulfillment of the requirements for the degree of Master of Science

Signed on 30th October, 2014 in Cape Town

Declaration

I declare that this Dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science, at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

____ (Signature of candidate)

30th day of October, 2014

Cape Town

Abstract

My study investigated the significance of spatiotemporal heterogeneity on the Nile crocodile (*Crocodylus niloticus*), a long-lived, apex predator, occupying many African and some South African riverine ecosystems. The scales of study included a long-term investigation of the (indirect) impacts of anthropogenic, landscape scale (100 km^2) disturbances on the population demographics of *C. niloticus*, over 35 years. At the intermediate scale (15 km^2), indirect and direct impacts of flooding and seasonality on the health of the *C. niloticus* population were investigated over a three-year period. This was performed by investigating preferred habitat availability and river quality assessments, including physiochemical variables and rapid bio-assessment measures, which served as the 'smallest' scale (with samples taken every 500 m). All scales were compared with long-term and short-term investigations into crocodile population demographics. Total crocodile population size within the study river increased over time (from 18 in 1981 to 35 in 2013), but the number of adults decreased (from 9 to 3). Human population size increased at a rate of 3300 individuals per year and anthropogenically altered habitat increased over time from 24% total coverage attributable to farmland on the banks of the Mutale River in 1977, to 66% land coverage in 2013. Increases in human-induced habitat alterations also created shifts in preferred crocodilian habitat availability. Investigations into the effects of natural disturbances revealed that physiochemistry was seasonally variable, and changed drastically with changes in climate and runoff. The macroinvertebrate communities in the Mutale River differed in time and space for a multitude of reasons, including climate change and changes in habitat. The results of my study showed that Nile crocodiles were affected by alterations to the environment on multiple scales. The study concludes that the long-term population viability of *C. niloticus* is limited by a combination of these factors.

For my family

“I am the Master of my fate, I am the Captain of my soul”

-William Ernest Henley

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Chapter 1: Introduction

The impact of land-use change and flooding on the persistence of the Nile crocodile (Crocodylus niloticus) in South Africa

Rivers and streams are characterized by spatial and temporal variability in their biological communities, physical characteristics and ecosystem processes (Winemiller et al., 2010). Investigations into the role of temporal variability and spatial heterogeneity on ecosystem processes and biological communities have become common over the last few decades (Benda et al., 2004; Hynes, 1970; Junk et al., 1989; Minshall, 1988; Montgomery, 1999; Thorp & Delong, 1994; Thorp et al., 2006; Vannote et al., 1980; Ward, 1989). Pringle et al. (1988) emphasized the need for researchers to compare environmental conditions and biological communities within and between patches in order to investigate how interactive processes could regulate patterns and dynamics within the stream patch mosaic. The definition of a patch, in this instance, refers to the spatial and temporal scale appropriate for study, depending on the organism under investigation and the question at hand (Pringle et al., 1988).

Patch dynamics is founded on the view that ecosystems are fundamentally heterogeneous, a notion that became an emerging theme described by Palmer and Poff (1997). This theme was that of multi-scale analysis, a concept further developed by Poole (2002), who provided a hierarchical patch dynamics framework for understanding interactions between structure and function in fluvial landscapes. This framework focused on the link between patches within and across scales, occurring as a result of interactions and feedbacks at each scale (Poole, 2002; Winemiller et al., 2010). Rivers are thus multi-faceted amalgamations of habitat types and environmental gradients, typified by considerable spatial complexity and connectivity. Modification of the riverine environment will thus be perpetuated throughout the system at several scales (Allan et al., 1997; Fausch et al., 2002; Schlosser, 1991; Townsend et al., 2003).

Large-scale conversions from pristine to human-dominated landscapes affect ecosystems worldwide. As a result, the quantification of land-use and/ or land cover (further referred to as land-use) has become an invaluable indicator of the condition of ecosystems (Meyer & Turner, 1994). Human interactions at the landscape scale (the largest scale at which rivers are frequently studied) have been shown to impact the persistence and maintenance of the riverine landscape and its associated biota, through alterations to geomorphic processes (Allan, 2004). This frequently results in habitat that is both degraded and has limited heterogeneity. This affects the hydrology of the downstream basin by altering water availability, water quality and the present biota (Costa et al., 2003; Siriwardena et al., 2006) through a multitude of complex pathways (Allan et al., 1997; Strayer et al., 2003; Townsend et al., 2003).

In addition to its direct influence, land-use also interacts with additional anthropogenic drivers, further impacting the health of stream ecosystems. These drivers include the proliferation of invasive species (Scott & Helfman, 2001), building and maintenance of dam walls (Nilsson & Berggren, 2000), and climate change (Meyer et al., 1999). Climate change has been widely recognized as posing a significant threat to these resources (Hartdegen, 2009), especially as several Global Change Models (GCMs) indicate an increased incidence and severity of droughts, floods and other extreme weather events (Conway, 2009). According to Stern (2006), the likelihood of the deleterious impacts of climate change, as well as the cost and difficulty of adaptation, are expected to magnify and hasten, along with the speed of the global climate change.

Flooding induces channel erosion, excess sediment deposition, disturbances of riparian vegetation and associated disturbances of both aquatic and riparian organisms and their habitats (Swanson et al., 1998). These disturbances occur over and above the natural hydrologic variability, which is responsible for the movement and sorting of sediments, which create channel features such as riffles, pools, and islands, through sequences of erosion and deposition. This in turn results in the migration of channels and the maintenance of floodplain connectivity, creating a complex and dynamic interface between land and water (Junk et al., 1989). Allan (2004) graphically presented the possible relationships between stream biological condition and the indirect and direct impacts of anthropogenic influence (Fig. 1).

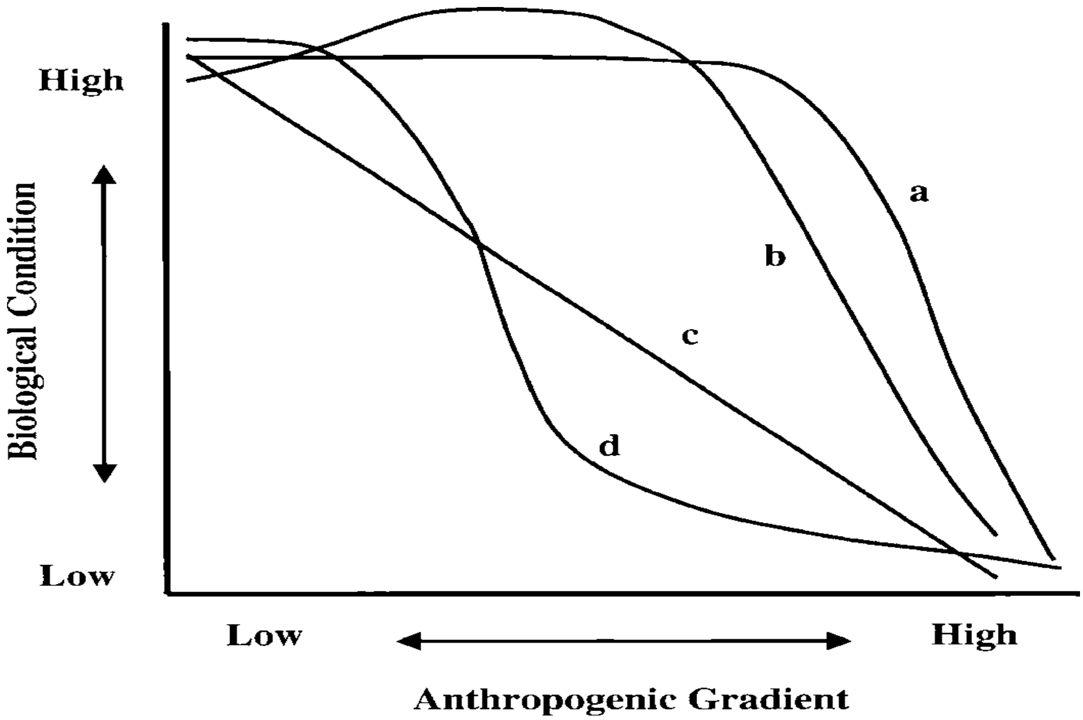

Figure 1: Allan (2004) proposed the above, hypothetical relationship between biological response and anthropogenic gradient. The relationship portrays a series of possible responses of the biological condition of the stream, as measured by a biological index (scaled to a reference, or the highest achievable condition) to a gradient of increasing environmental stress, measured either directly or indirectly (e.g. the state of farmland in the catchment). Proposed responses include (*a*) non-linear response presenting at the high range of the gradient, (*b*) subsidy-stress response, (*c*) linear response, and (*d*) non-linear (threshold) response presenting at the low range of the gradient. Curves are demonstrative of low versus high sensitivity to a stressor (d versus a), as modified from Allan, 2004; Norris & Thoms, 1999; Quinn, 2000.

Biological condition is not only impacted by long-term, large-scale geomorphological impacts, including those depicted in Figure 1, but also through shifts and alterations to intermediate scale factors (Allan et al., 1997; Townsend et al., 2003). An example thereof, is the river channel and individual channel units including riffles or pools (Fausch et al., 2002). These shifts occur due to the movement and sorting of sediments caused in part by natural hydrologic variability (Junk et al., 1989). The alteration of channel features has cascading or far-reaching effects on the local or microhabitat scale. This occurs because habitat quality and complexity greatly affect resident species assemblages (Robinson et al., 2002; Ward, 1998). Therefore, intermediate scale changes are responsible for the creation and maintenance of a complex, ever-changing mosaic of habitat patches for biota at the smaller scale (Allan, 2004; Fausch et al., 2002; Frissell et al., 1986; Montgomery, 1999). In recent years, several studies of spatial and temporal heterogeneity have documented a large variety of interacting factors at the intermediate and smaller scale. These include abiotic factors such as hydrologic disturbance and streambed stability (Bourquin & Death, 2008; Downes et al., 1997; Kilbane & Holomuzki, 2004; Lake, 2000; Lancaster & Belyea, 1997; Matthaei et al., 2000; Riseng et al., 2004; Stevenson, 1997; Suren & Duncan, 1999), microhabitat distributions (Fairchild & Holomuzki, 2002) and habitat connectivity (Bonada et al., 2006), substrate grain size and shape (Holomuzki & Biggs, 2003), channel units (Halwas et al., 2005) and micro-topographic location (Kobayashi & Kagaya, 2004).

The Nile crocodile serves as a valuable indicator species, as the presence of a healthy crocodile population indicates that the ecosystem in question is also healthy (Joubert, 2007; Pooley, 1969). Crocodiles are long-lived (80+ years) and the species has remained morphologically conservative over time. Crocodiles are behaviourally adaptable to changes in their surroundings (Brazaitis & Watanabe, 2011) with an opportunistic feeding strategy, which has allowed for survival of this species over millennia. They are able to travel some distance over land and are thus capable of widespread dispersal, although osmo-regulatory and habitat-related requirements preclude them from dispersing too widely (Hutton, 1989; Leslie & Spotila, 2000). Crocodiles portray biological impacts of freshwater ecosystem processes, at all life-stages, through key aspects of ecology such as food webs, diversity and productivity, as well as freshwater flow (Mazzotti et al., 2009). Life-stages in this context refer to growth stages within the crocodile's life, defined primarily by their habitat necessities. These growth stages include the egg or nesting stage, which requires suitable nesting habitat (Somaweera & Shine, 2013), the hatchling stage, which requires a suitable crèche area and macro-invertebrate diversity and abundance near the nest site (Platt et al., 2002), the juvenile stage, which have generally dispersed from the nursery and require macro-invertebrate and small vertebrate abundance and diversity (Barr, 1997; Tucker et al., 1996), the sub-adult phase, which requires suitable terrestrial and aquatic habitat, especially as territorial behaviour begins to play a role and an abundance of available fish species (Wallace & Leslie, 2008) and the reproductive adult stage, which again requires suitable nesting area, pools for breeding and an availability of larger fish (Games, 1990; Somaweera & Shine, 2013). The responses of crocodiles at each of these life stages are directly related to suitability of environmental conditions and hydrologic change, both of which are directly and indirectly affected by anthropogenic alterations to the environment (Mazzotti et al., 2009). The changes may present as large-scale geomorphological changes to the system or smaller scale macro and microhabitat alterations.

Although the Nile crocodile is able to withstand and adapt to the dynamic ecosystem in which it lives, its survival is becoming increasingly threatened due to human-wildlife conflict. In this instance, human- wildlife conflict refers to both direct, and indirect instances of conflict. Indirect conflict includes competition for resources including terrestrial and aquatic habitat (Combrink et al., 2011) and food sources (Fergusson, 2010). Competition for aquatic habitat is especially prevalent in water-poor countries, as attempts to store and abstract water for agricultural and commercial purposes abounds, leading to the construction of dams and rivers, wetland transformation (Pooley, 1969) and the degradation and pollution of rivers (Blake & Jacobsen, 1992; Ferreira & Pienaar, 2011), as well as uncontrolled water abstraction or release (e.g. nesting site flooding for agricultural use; Jacobsen, 1991). This destruction of natural habitat has affected Nile crocodile populations throughout most of its range (Fergusson, 2010).

Direct conflict between humans and crocodiles typically occurs for several reasons, including retaliation killing for livestock losses or human injury or death (Calverley, 2010; Wallace et al., 2011), as well as deliberate destruction of nesting sites (E.g. Ward, 1985). In Southern Africa, crocodile parts are highly valuable in witchcraft and on the traditional medicine market (Combrink et al., 2011; Ward, 1987). As adults cause the majority of human and livestock injuries and deaths (Aust, 2009; Dunham et al., 2010), reproductively active individuals are the most likely to be targeted, outside of protected areas.

Large-scale and widespread reductions in crocodile populations occurring within protected areas have also increased in frequency in recent years, including population reductions in the three largest crocodile populations in South Africa, namely those within Kruger National Park, St. Lucia and Ndumo Game Reserve (Combrink et al., 2011). This has resulted in the Nile crocodile being recognized as regionally Vulnerable (Branch, 1998).

Due to the hierarchical nature of riverine ecosystems, my study utilized a variety of scale-dependent assessment methods. This was done in an attempt to evaluate the effects of anthropogenic and natural disturbance at multiple scales on a long-lived study species, the Nile crocodile (*Crocodylus niloticus*). The scales examined include large scale (10^3 m), landscape investigations into changes in land-use and human population size along the length of the river. This portion of my study included not only the largest spatial scale, but also the longest time scale. At the intermediate scale (10^1 m), the reach system of individual channel units and the proportion of habitat available to and utilized by crocodiles was investigated. This occurred over a two-year period, and included seasonal assessments of terrestrial and aquatic habitat availability. The smallest scale investigated was that of shifts in the benthic macro-invertebrate community over several seasons and associated measures of river health and biodiversity. These scales were split over two chapters with investigations into land use and anthropogenic alterations to the environment as the first chapter, and the intermediate and smaller scale variables investigated in the second chapter.

My study investigated the impact of large-scale, natural and anthropogenic transformations of river-channel, reach-scale and microhabitat scale effects of flooding within the Mutale River, Limpopo Province, South Africa. I sought to establish whether these multi-scale effects in the system impact the resident population of the Nile crocodile. At present, the majority of crocodile populations in South Africa occur within the boundaries of protected areas (Alexander & Marais, 2007; Calverley, 2010). As the Mutale River's crocodile population is located in an unprotected area, it is important to understand which factors affect their presence in this area. I assessed the impact of land-use change and flooding on the persistence of the Mutale River population of crocodiles outside park boundaries, in this region of South Africa, whilst also considering potential problems with the viability of this population. This thesis is presented with chapters intended to stand alone, excluding the concluding chapter. As a result of this, some repetition within the chapters was unavoidable.

South Africa is recognized as one of the most developed countries on the African continent, and my research is aimed to highlight the important role that South Africa can play in the conservation of the Nile crocodile and freshwater ecosystems in Africa. With legislation such as the National Water Act (36 of 1998) and the National Environmental Management Act (107 of 1998), the regulatory infrastructure is in place. With a deeper understanding of these systems, it is possible to protect crocodiles and freshwater ecosystems in South Africa as a whole, as informed decisions regarding the conservation of this species can be made and implemented using the infrastructure already in place.

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Chapter 2

Changes in land-use, human population and the population of Nile **c**rocodiles (*Crocodylus niloticus*) in the Mutale River

Introduction

Land-use can result in alterations to the riverine landscape at any spatial scale, through direct and indirect effects. Direct influences of human activities on the riverine landscape are reflected by changes in the spatiotemporal distribution of water resources, such as damming (Feng et al., 2011) and extraction of water for the irrigation of farmland. Further direct impacts include the extraction of alluvial material (Rost et al., 2008), and destruction of riparian vegetation (Naiman et al., 2010), both of which have major impacts on the habitat available to terrestrial and aquatic ecosystems (Bawa & Dayanandan, 1997; Ehrlich, 1995; Soulé, 1991). Indirect effects of anthropogenic activity include intensive irrigation and the effects of surface runoff, which can result in the addition of pollutants such as nutrients and pesticides into the system, as well as desertification and salinization of the watershed (Feng et al., 2011). In areas where activities such as mining occur, acidic effluents can leach into the system (Akcil & Koldas, 2006; DWAF, 2001). The effects of water pollutants place enormous strain on aquatic ecosystems (Oberholster et al., 2010; Steyn, 2008; Swanepoel, 1999) as they alter the hydrology, water availability and water quality of downstream riverine habitats (Costa et al., 2003; James et al., 2007; Siriwardena et al., 2006) as well as food web structure and dynamics (Allan, 2004). Alterations to water quality and availability are particularly important when considering the hierarchical nature of riverine systems, as the effects of changes to part of the river will also persist in other reaches of the river.

Because of the direct and indirect effects of landscape-scale changes to the riverine ecosystem, investigations would be particularly illuminating if performed in areas where the changes in human population size and their associated effects are severe. A prime example of this is found in South Africa where, prior to 1994, many people of different cultures were forced into homelands such as Transkei, Bophuthatswana, Venda and Ciskei (the TBVC states; Instigated as the “Bantu Homelands Citizenship Act” No 26 of 1970 which was later repealed in the 1993 “Interim Constitution Act” No 200 of 1993). Rural communities are often poverty-stricken and lack access to potable water supplies, relying mainly on pond, stream, well and river resources for their daily needs (Nevondo & Cloete, 1999). In areas where the surrounding human population directly uses rivers, faecal contamination of the water frequently occurs (Lehloesa & Muyima, 2000; WHO, 1993). Dependence on the river is likely to have resulted in changes in the availability and sustainability of terrestrial and freshwater habitats, especially along small tributaries on which villages depend.

Human reliance on riverine water and drastic increases in human population are likely to have had cascading effects on the riverine ecosystems in former TBVC states. I argue that the effects of the phenomenon, the 'tragedy of the commons' (Feeny et al., 1990), which is frequently portrayed in terrestrial habitats, can also impact the riverine environment. This occurs due to the overuse and consequent depletion of a common resource since it is not owned or controlled by anyone, resulting in drastic shifts and/or declines in biodiversity in terrestrial and aquatic communities. Increases in human population size and associated use of the riverine water are likely to impact riverine health and the availability of terrestrial and aquatic habitats, affecting the flora and fauna which use these habitats. A particularly notable instance of this is the case of the Olifants River, where anthropogenic activities occurring in sections of the river, resulted in major declines in the population of a key species, the Nile crocodile (*Crocodylus niloticus*) (Botha, 2006, 2010a, 2010b; Jacobsen, 1984; Swanepoel, 1999, 2001; Van Vuuren, 2009).

Study species

The Nile crocodile is an apex predator, performing a number of vital functions in aquatic ecosystems (Botha, 2005; Bourquin, 2007). The species helps maintain the structure and function of aquatic ecosystems by way of nutrient recycling, preservation of wet refugia during drought periods and selective predation on fish species (Botha, 2005; Bourquin, 2007; Craighead, 1968; Thorbjarnarson, 1992). Crocodiles are long-lived (80+ years), reaching sexual maturity between 12 and 15 years (Leslie, 1997) at which time they are between 2.62 m and 2.87 m in length for females, and 2.70 m to 2.95 m in males (Kofron, 1990).

Rationale

Freshwater is a limited resource in South Africa and its associated ecosystems are considered highly vulnerable. Of all South African rivers, 82% are considered to be "Threatened", with 44% of these systems considered to be "Critically Endangered" (Driver et al., 2005). These systems are affected by anthropogenic impacts, including the effects of urbanization, industrialization and alterations of the habitat along the length of the river. Growth in demands for water and increases in industrial and agricultural effluents are anticipated for the future (DWAF, 2009). In addition, as the Mutale River flows directly into Makuya Park Nature Reserve, it is important to discover which factors affect the presence of the Nile crocodile in this area, at all spatial scales, in order to assess the population viability of the crocodiles outside the boundary of Makuya Park.

Changes in the Mutale River Nile crocodile population demographics were investigated by comparing data from literature reviews to those collected during field excursions for this study. The first recorded measure of crocodile population size and demographics in this river was made using an aerial survey (Jacobsen, 1984) and successive records include aerial surveys (1988-1989) in Blake and Jacobsen (1992). In 2011, a pilot study (Pearcy, 2011 unpublished) found that a remnant crocodile population still existed in the Mutale River. In this study, I measured the impacts of anthropogenic activity on the health of the river, using the Nile crocodile as an indicator, owing to its susceptibility to pollution (Bourquin, 2007; Thorbjarnarson, 1992) and its longevity. Both these factors help reflect long-term effects on the environment because increases in anthropogenic activity appear to affect the presence of the crocodile throughout its lifespan (Aust, 2009). Each of the life stages of this species involves specific habitat requirements, including the availability of food sources suited to the size of the crocodile (Wallace & Leslie, 2008) and the prevalence of suitable nesting habitat (Somaweera & Shine, 2013). A variety of aquatic and terrestrial habitats should be available for optimal recruitment.

My study focused on the effects of anthropogenic alterations to the land along the macro channel banks of the Mutale River, furthermore, comparisons of patterns in land use change, and human population size were also performed. These changes were then compared and quantified with changes found in crocodile population demographics in the river. These relationships are investigated to broaden our understanding and allow for potential inferences to be made as to indirect anthropogenic effects on crocodile presence at the landscape scale.

Aim

The main aims of my study were to quantify changes in the Nile crocodile population size and demographics since the first aerial survey (Jacobsen, data published 1984). Due to the declines crocodile population sizes in this region (Ashton, 2010; Botha et al., 2011; Calverley, 2011; Combrink, 2004; Ferreira & Pienaar, 2011; Marais & Pooley, 1991; Myburg, 2007; Myburg & Botha, 2009), I anticipate a decrease in the number of crocodiles found in the Mutale River. Further aims of this study were to identify, classify, and quantify changes in land cover patterns along the Mutale River over a 36-year period, by using grid square analysis. Anthropogenically altered landscape is likely to have proliferated throughout this region, as it has globally (Kalnay & Cai, 2003). Another aim of the study is to calculate the rate of change in human population size between 1984 and 2011, along the length of the Mutale River in Limpopo. Human population size is likely to have followed the recent trends for South Africa by exponentially increasing (Cincotta et al., 2000). The final aim of my study is to compare the patterns found in land-use change and human population size, to those of crocodile population size and demographics.

Methods

Study site

The Mutale River is part of the Limpopo catchment in Limpopo, north-eastern South Africa (Fig. 2). The source of the Mutale River is Lake Fundudzi, a site that is sacred to Venda culture. The Mutale River emerges as a spring from below landslide blockage, which created the lake. Lake Fundudzi was reported to hold numerous Nile crocodiles in the past (Davidson, 1995), but occurrence has not been verified recently. The river flows through villages, past agricultural fields and through a 3 km gorge dominated by bedrock rapids. Subsistence farming is currently the primary form of agriculture in the Mutale catchment (DWAF, 2001). Further downstream, Tshikondeni Coal Mine uses tributaries of the river in the mining process and exposure of the pyrite to air and water results in acid leaching into the system (DWAF, 2001). The river then enters Makuya Reserve, where it forms a waterfall. Some distance downstream of this waterfall, the Mutale River joins the Luvuvhu River to flow into the Kruger National Park.

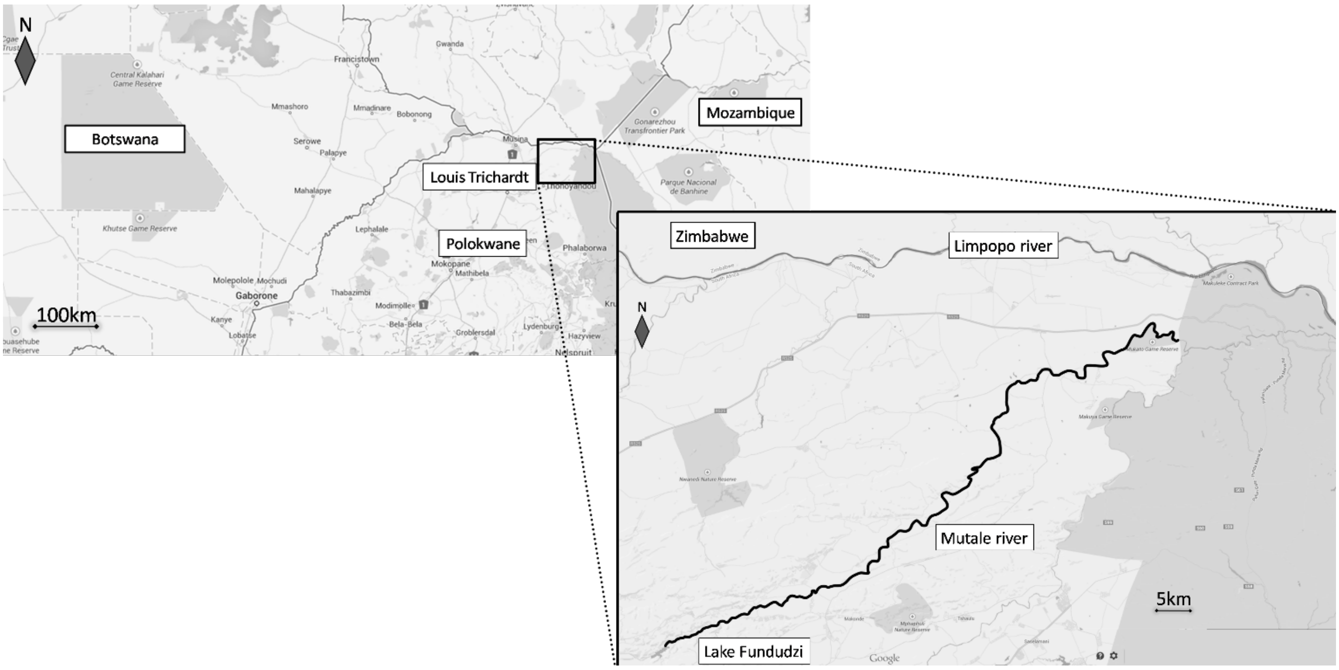

Figure 2: The Mutale River, Limpopo Province, South Africa.

Study design

Crocodile population

Subsequent to the findings of the pilot study (Pearcy, 2011; unpublished), crocodile demographic distribution data were gathered in the course of my study during night- surveys of 23 km of the river between 2011 and 2014. Additionally, 96 km of the Mutale River was also rafted in 2013 and the presence, size and location of additional crocodiles were recorded.

Jacobsen’s 1984 and 1991 aerial surveys (Blake and Jacobson, 1991; Jacobsen, 1984;) were performed in order to estimate numbers and sizes of crocodiles in rivers outside the boundaries of the Kruger National Park. Sizes of crocodiles were placed into the most appropriate categories, according to the following size classes: < 1 m; 1-2 m; 2-3 m; > 3 m. Estimates of the size of the animal in Jacobsen's (1984) study were usually made by comparing the crocodile with surrounding objects such as rocks, trees and shrubs. Estimations of crocodile size may not have been perfectly accurate, but as this was considered a constant factor, it was not pursued in the study (Jacobsen, 1984). A number of animals could not be assessed as they hung in the water or lay partially concealed. These were classified as indeterminate, making up 18% of the total. Survey flights took place in August and September 1979, 1980 (Jacobsen, 1984) and 1991 (Blake & Jacobsen, 1991), when water levels were at their lowest. For both of these surveys, two observers accompanied the pilot, each counting animals seen along one of the banks. The data were recorded on pocket tape recorders, allowing the observers to monitor the river below continuously. Flight speeds varied from 40 to 60 km/h and altitudes of 30 m to 100 m, depending on the terrain and nature of the river course being flown. Flying at a low altitude decreases the area covered while at higher altitudes smaller animals, particularly those partly concealed among rocks or grass, may have been missed (Jacobsen, 1984).

Night surveys for the current study

Crocodile surveys were performed using night survey methods. Since crocodiles are active mostly at night, researchers walked along the river to locate crocodiles, starting 30-45 minutes after sunset. Crocodiles were detected based on their distinctive red-eye shine reflection and length of crocodile was estimated based on surrounding objects (e.g. rocks and reed beds). Where located, evidence of crocodile activity such as -slides and nests were also recorded. These assessments were repeated in January, March and October 2012 and in January and June 2013, and again in April 2014. This was done in order to evaluate the population size and demographics of crocodiles in the Mutale River after the January 2013 floods, as well as the effects of seasonality and potential intermediate and small-scale changes in river health and habitat availability.

Data analysis in the current study

Due to the differences in data collection protocols, my data were organized into two distinct components: 1) A linear regression analysis of the aerial surveys and 23 km night survey section and 2) A linear regression analysis of the aerial surveys and the 2013 full river survey (including both the 23 km stretch, and the river rafting component). The R^2 and p-values for these analyses were then used to assess which survey was more suitable. The population size was quantified as individuals per km (crocodiles/km) to make surveys of different distances comparable. The crocodile population demography was further investigated using a Kruskal-Wallis in order to ascertain whether changes in relative population size were attributable to a single demography. In addition, in instances where the surveys were performed on multiple occasions in one field session, the duplicates were used as a measure of variation.

Measure of body length gives an estimation of life stage, with juveniles measuring approximately one meter or less, sub-adults measuring 1-2 m, and where larger individuals are scored as adults, following the categories specified by Jacobsen (1984), and Blake and Jacobsen (1992). My survey served as a measure of the current demographic distribution of the Nile crocodile throughout the length of the river (2013) and allowed a comparison of population trends over several seasons in the smaller section of the river (2012, 2013 and 2014).

Land-cover

Measures of land-cover were used as a proxy for broad-scale changes in land-use along the length of Mutale River. This was done using an analysis of grid squares from aerial photographs of the river for the years 1977, 1987, 1995, 2004, 2009 and 2013, supplied by the Surveyor-General. These aerial photographs were overlaid and the land-use of the layers compared using Image J (2012), in order to measure and analyze the land-cover changes that occurred within a one km^2 grid square, center over the river. The square was separated into the North and South side of the river macro channel bank, with 500 m^2 polygons of land cover assessed on each side. The separation into North and South side of the river was necessary as the Mutale River serves as a boundary between the Mutale and Thulamela local municipalities (Figure 3).

The primary land-cover categories which were included in the analysis were: Trees (dense, forested cover, >75% of either the North, or the South bank in the grid square covered in trees), bare ground (sparse trees and shrubs, less than 25% tree cover of left or right bank within the grid square), farms (where the land was clearly sectioned off for farming activity and no trees were visible), and villages (where the land was populated by buildings, dams, or other man- made structures, covering >50% of the river bank). These categories were delineated at the beginning of the analysis since they were the most clearly defined land-cover types. Farms and villages were considered as evidence of human disturbance, whereas bare ground and trees were considered natural. In instances where increases in bare ground were likely to have arisen due to over-grazing, this was noted.

Land-cover data were analyzed in Microsoft Excel (2013) using linear regression analysis to calculate the rate of land-use change over time. These results were subsequently separated into human (i.e. the presence of farmland and villages) and primarily natural (i.e. the presence of tree and bare ground) effects. A linear regression was performed comparing both effects to the number of crocodiles found in the Mutale River per kilometer of river travelled. Comparisons per kilometer of river allowed for simultaneous investigations into trends in land-use and the size of the Nile crocodile population.

Human population

Human population census data were obtained from Statistics South Africa, and from the census data available in publications (Lehohla, 2011, 2012). This was done in order to assess the trends in human population size in the municipalities around the Mutale River and compare them with trends in both land-use change along the river and the river's Nile crocodile population. Population census data for municipalities surrounding the Mutale were available for the following years: 1996, 2001 and 2011. The Mutale Local Municipality, and Thulamela Local Municipality were evaluated separately as the Mutale River serves as a boundary between them (Fig. 3). The rate of change was calculated by averaging the slopes of the line of best fit from the linear regressions for the Mutale and Thulamela local municipalities.

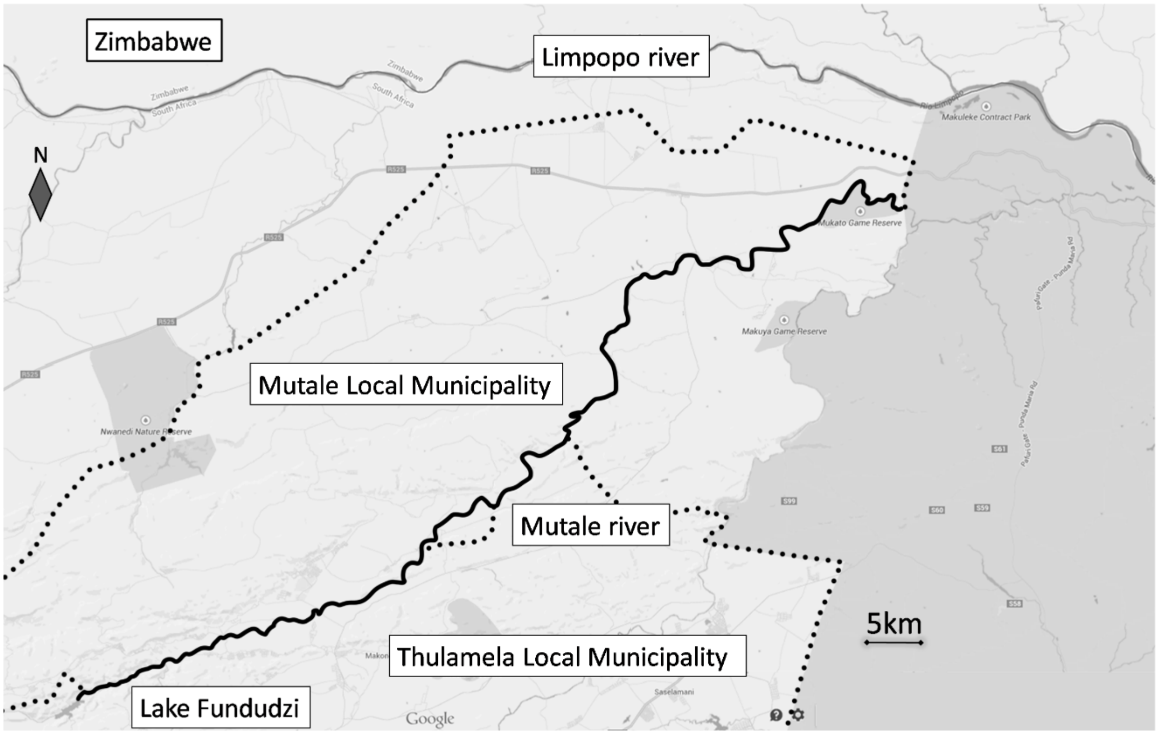

Figure 3: Map showing locality of Mutale and Thulamela Municipality within the district and province.

Results

Crocodile population size

The number of Nile crocodiles per kilometer of the Mutale River has increased significantly over time (Fig. 4; $F_{(1,4)} = 33.89$, $p = 0.01$, $y = 0.04x - 72.69$, $R^2 = 0.92$). This increase occurred when considering the 23 km section of the river (from 0.18 in 1981 aerial surveys, to 0.70 when considering only the 23 km stretch of river covered in the night surveys) and the full river survey, including both rafting and the 23 km night survey (when crocodiles per kilometer was calculated to be 0.34).

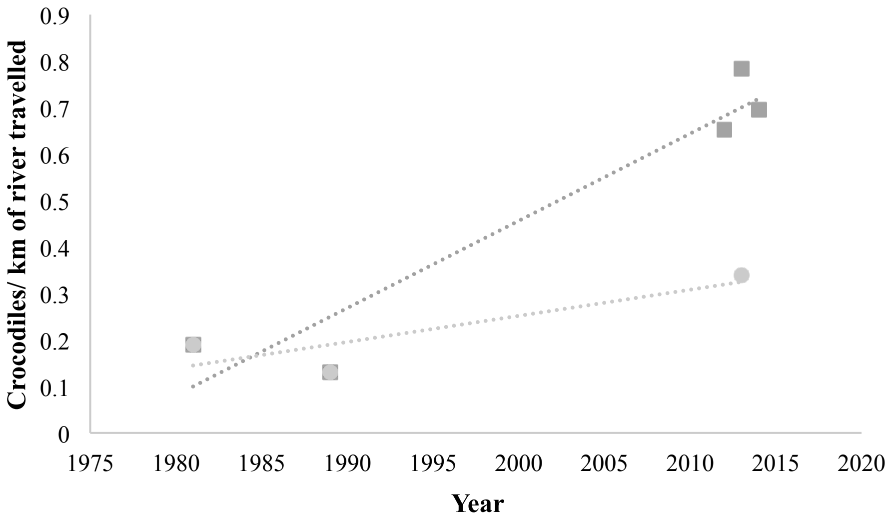

Figure 4: Number of Nile crocodiles per kilometre of Mutale River surveyed over time, including aerial (1981, 1989) and night surveys over the 23 km stretch in 2011, 2012 2013 and 2014 (dark- grey squares) and aerial (1981, 1989) and night surveys (2013) over the length of the river, including aerial (1981, 1989 and rafting + 23 km night survey data) (light-grey circles; $F_{(1,2)} = 3$, $p = 0.33$, $y = 0.01x - 10.99$, $R^2 = 0.75$. Figure includes lines of best fit.

The relative measures of crocodile population size in the Mutale River fluctuated over time (Table 1), with declines in the number of adult crocodiles being particularly notable (from 10 adult individuals, in 1989, to four adult individuals in 2013; $F_{(1,4)} = 29.98$, $p = 0.01$, $R = 0.91$). The population size of the Nile crocodile has increased over time, from 18 to 29 individuals in the space of 32 years (limited to full length river results; Table 1). These increases did not occur in all size classes, with the adult population of individuals greater than 2 m being limited (only 4 individuals recorded). The majority of increases occurred in the juvenile and sub-adult populations, as shown in Table 1. The juvenile cohort was found to fluctuate with different surveys, with peaks in the number of juveniles occurring after flooding seasons (Table 1). The number of sub-adults found during surveys was also found to fluctuate over time, with most peaks occurring during the summer wet seasons. As all sub-adults were sighted multiple times (on different nights surveying the same sections) during every field excursion, this was not considered to be an issue of detectability, but rather due to emigration during high flow periods. Although the results from 2011 and 2012 were not directly comparable to the aerial counts conducted in 1981 and 1989 (as they did not cover the entire length of the river), the 2013 full river survey showed similar, increasing trends to 2011, 2012, 2013 and 2014 crocodile population demographics.

Table 1: Number of Nile crocodiles (n) found in each size class (1 m, juvenile; 1-2 m, sub-adult; and >2 m adult) in the Mutale River, Limpopo Province, over time (Years). Asterisk (*) indicates instances in which the population only includes crocodiles found during night surveys on foot. Letters (a, b, c) indicate multiple surveys, 2013 (a + c) is the total number of crocodiles found in February 2013, including both night surveys (a) and rafting (c).

Year	1 m	1-2 m	>2 m	Unidentified	Total
1981	5	2	9	2	18
1989	0	2	10	0	12
*2011	17	8	3	0	28
*2012 (a)	12	4	3	0	19
*2012 (b)	5	2	1	3	11
*Average	9	3	2	2	15
*2013 (a)	7	9	2	1	19
*2013 (b)	6	9	2	0	17
*Average	7	9	2	1	18
2013 (c)	2	6	2	0	10
2013 (a+c)	9	15	4	1	29
2014	6	7	3	0	16

Crocodile sightings from consecutive nights over the same stretch of river revealed that, of 10 crocodiles which were found in repeats, only one juvenile was not found twice. This leads to an estimation of surveyor accuracy of approximately 90% (Table 2).

Table 2: Number of Nile crocodile re-sightings downstream of Tshulu research camp in the Mutale river, Limpopo Province, over consecutive nights in April 2014

Size class	N (croc) Night 1	N (croc) Night 2
Juvenile	5	4
Sub-adult	3	3
Adult	2	2
Total	10	9

Land cover change

A significant decrease in the number of grid squares classified as having natural vegetation occurred between the years 1977 and 2014 (from 119 of the 137 total grid squares, to 54; Fig. 5, “Trees”; $F_{(1,4)} = 461.83$, $p < 0.05$; $y = -1.73x + 3537.1$; $R^2 = 0.99$ and a coinciding decrease in “Bare ground”; $F_{(1,4)} = 3.67$; $p < 0.05$; $y = -0.1096x + 228.1$; $R^2 = 0.48$), and a simultaneous increase in the prevalence of Farmland, (from 9 grid squares in 1977 to 71 in 2013; $F_{(1,4)} = 431.29$, $p < 0.01$; $y = 1.64x-3234.7$; $R^2 = 0.99$) indicating that much of the natural habitat along the length of the Mutale River has experienced anthropogenic modification and has become more transformed (Fig. 5). This trend also applied to village coverage (from one grid square in 1977 to nine in 2013; $F_{(1,4)} = 20,89$; p <

0.05; y = 0.19x; -391.45; R^2 = 0.84). These changes could be attributed to increases in human population densities.

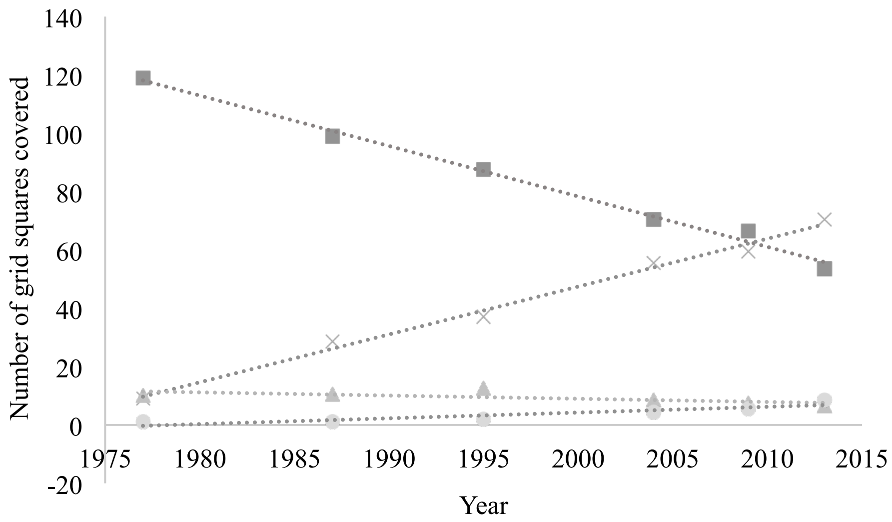

Figure 5: Average land cover change on the macro channel bank of the Mutale River, from the year 1977-2013. Land-cover types include natural habitats such as Bare ground (triangles) and Trees (squares) and altered land cover types include Village (circles) and Farm (cross).

When comparing the number of Nile crocodiles seen per km of river travelled to changes in land-cover, increasing numbers of crocodiles coincided with increases in average proportion of anthropogenically altered landscape cover over time (Fig. 6; $F_{(1,3)} = 4.97$; $p = 0.05$; $R^2 = 0.62$; y = 1.44x + 0.067). In contrast to the overall number of crocodiles per kilometer of river travelled, the number of adult crocodiles was found to decrease, when the proportion of human-induced land cover change (conversion to farmland) increased (Fig. 7; $F_{(1,3)} = 6.51$; $p > 0.05$; $R^2 = 0.68$; y = -0.2364x + 0.11).

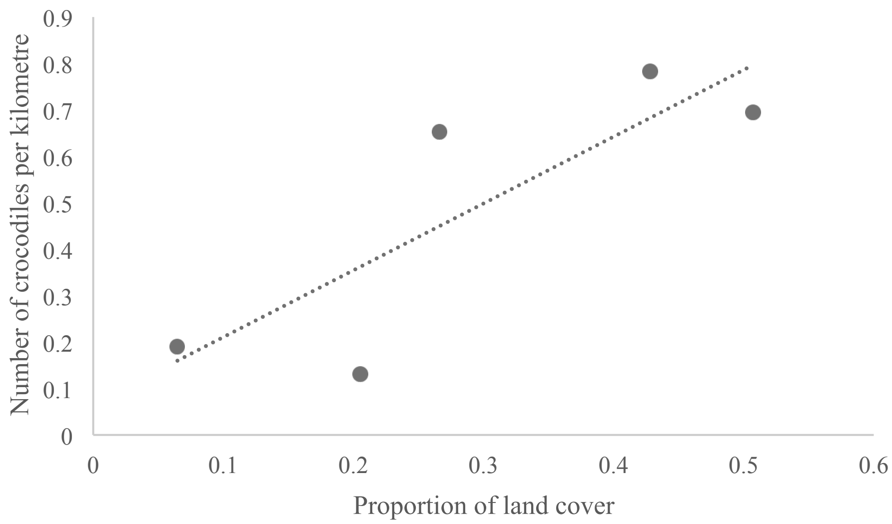

Figure 6: Regression analysis of the proportion of human induced land-cover changes over time, and the total (observed) number of crocodiles found in the Mutale River, per kilometer.

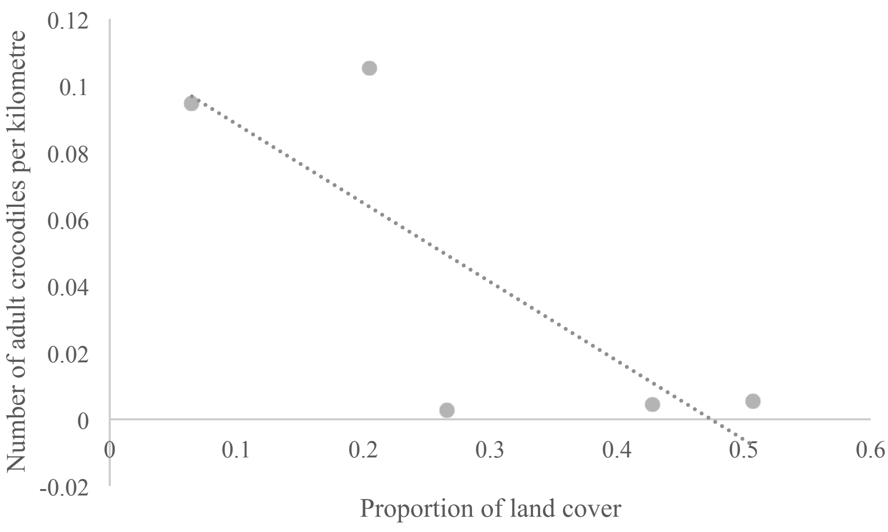

Figure 7: Regression analysis of the proportion of human induced land-cover change over time, and the number of (observed) adult Nile crocodiles found in the Mutale River, per kilometer.

Human population size

The rate of change in the human population in the Mutale and Thulamela Local municipalities was 1200 people per year and 5400 people per year, respectively (Fig. 8; Mutale; $F_{(1,1)} = 13.76$; $p > 0.05$; $y = 9278.5x + 45578$; $R^2 = 0.99$; Thulamela; $F_{(1,1)} = 13.76$; $p > 0.05$; $42353x + 408492$; $R^2 = 0.99$). This equated to an average rate of increase of 3 300 people per year for these municipalities. The increase in human population along the banks of the Mutale River correlated with decreases in the total adult population of Nile crocodiles (Data not shown; $F_{(1,3)} = 6.51$; $p > 0.05$; $R^2 = 0.68$; $y = -0.2364x + 0.11$). The number of adult crocodiles more than halved over time, from 9 and 10 adults in 1981, to only 4 adults in 2013. Once again, human impact was found to correlate with decreases in the number of adult crocodiles. The increase in the human population in the Mutale and Thulamela municipalities were found to correlate with decreases in the adult crocodile population (Data not shown), though these results were not significant ($F_{(1,1)} = 1.14$; $p > 0.05$, $F_{(1,1)} = 1.42$; $p < 0.05$), respectively.

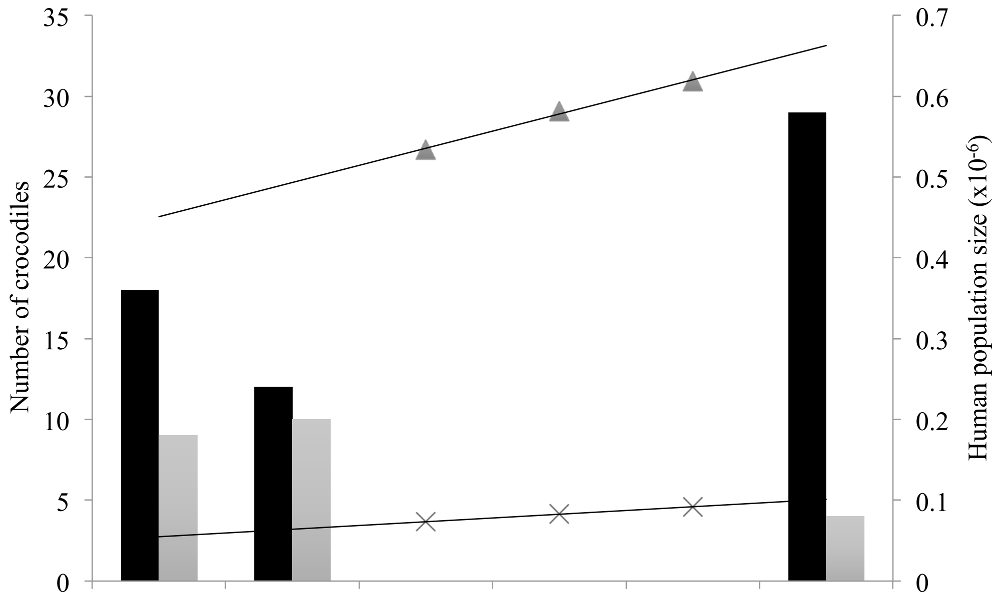

Figure 8: Human population size (1996-2011) in Thulamela (Grey triangles) and Mutale (Grey crosses) local municipalities over time, compared with the total number (black bars) and the number of adult (grey bars) *C. niloticus* individuals.

Linear regression analysis of the increase in farmland, compared with the human population size indicated that farmland increased, with a corresponding increase in human population size (Fig. 9; $F_{(1,6)} = 9.22$; $p < 0.05$; $y = 502.08x - 130.48$; $R^2 = 0.61$).

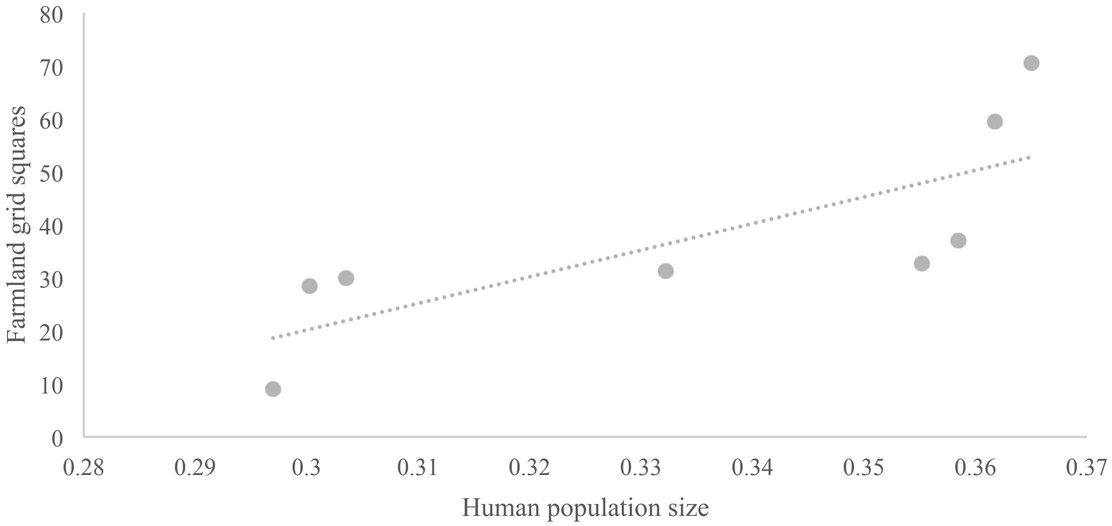

Figure 9: Regression analysis, combined human population size of Mutale and Thulamela Local Munivipalities on the North and South bank of the Mutale River vs farmland grid squares along the length of the river .

The percentage of land-cover type increased more rapidly between pre- and post-flood (1999-2004; 2009-2013) than changes occurring during periods that did not experience flooding (2004-2009) (Fig. 10). The increase in anthropogenic activity is also highlighted, revealing an almost 40% change in farmland cover over a 14-year period, with most change occurring after flooding. During all flooding, there was an increase in the intensity of anthropogenic alteration to the environment. Typically, there was twice as much change in time periods characterized by floods.

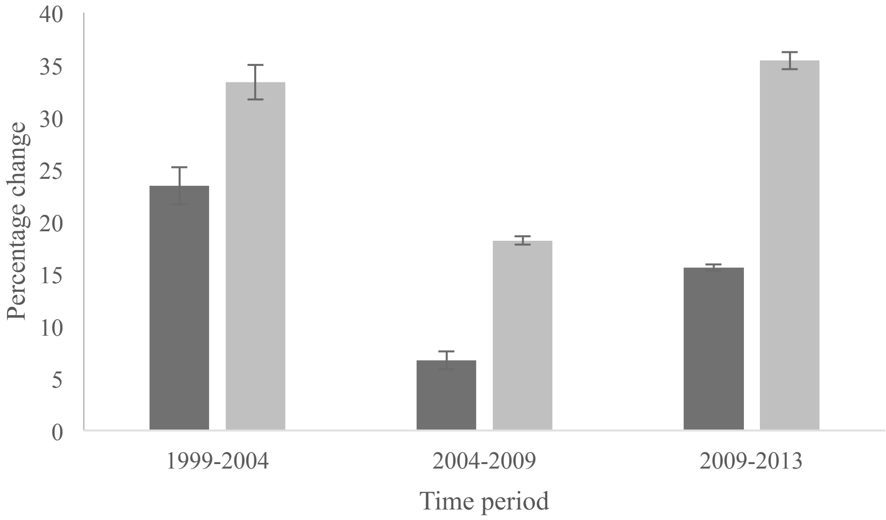

Figure 10: Change (%) in anthropogenically altered land-cover type along the banks of Mutale River. Including flooding (1999-2004; 2009 - 2013) and non- flooding (2004-2009) periods.

Discussion

The increase in the number of Nile crocodiles per km of river surveyed over time was found to contradict expectations when considering the recent history of declining trends crocodile population sizes in South Africa (e.g. Ashton, 2010; Branch, 1998). In contrast to total population size, however, the number of large, reproductively active individuals decreased over time (from 9 individuals > 2.5 m in 1984, to 4 individuals > 2.5 m, in 2013; Table 1). This difference between the overall population sizes, may have been overestimated, as aerial surveys are more likely to miss juvenile crocodiles as they are more likely to be found in densely vegetated areas with plenty of covering. As it was not possible to perform ground-truthing in order to estimate the probability of sightings during aerial survey and compare these directly with night surveys, no measures of relative detectability can be made. The data from the night surveys, however, account for much of the most recent data, and crocodile sightings from consecutive nights over the matching stretch of river, lead to an approximation of assessor accuracy of 90% (Table 2).

The decrease in the number of adult Nile crocodiles in the Mutale River gives rise to concern as to the viability and sustainability of the remaining population, as declines in the effective population size can negatively impact future population viability (Bishop et al., 2009). Several instances of decreases in adult crocodiles have been recorded in the recent past, and it is difficult to attribute their demise to a single factor. The data in my study strongly suggest that changes in land-use affect the adult crocodile population in the Mutale River region. My study also suggests that the Mutale River remains valuable habitat for the Nile crocodile, outside of the boundary of protected areas, as recruitment is still possible.

At the landscape scale, anthropogenic alterations to land-cover frequently result in the degradation and increased homogeneity of land-cover and habitat (Costa et al., 2003; Siriwardena et al., 2006). After a flood, the riverine floodplains may be especially vulnerable to increases in anthropogenic activity, as the flattening of trees and destruction of sections of the riparian zone can result in increases in land available for farming. A steady increase in anthropogenic activity surrounding the Mutale River over the past 30 years is apparent. Increases in the acreage of farmland resulted in an average of 71 km of land within 500 m of the banks of the Mutale River being covered (Fig. 5). This increase is substantial (44% of total land use conversion), especially since the Mutale River is only 139 km in length. It may be partly due to it being more cost-effective to plant crops close to the river, reducing the cost of transporting water for irrigation. This increase in farmland reduces the quality of the habitat, exhibited as declines in riverine habitat indices and greater bank instability (Richards et al. 1996; Roth et al., 1996; Wang et al., 1997), with demonstrable increases in the deposition of sediment within the streambed. In studies by the Department of Water and Forestry (as part of the River Health Project initiative), sediment deposition and channel erosion were recorded as negatively impacting the biota living in the Mutale River (DWAF, 2001). Sediments in runoff from farmland and livestock trampling (Quinn, 2000; Strand & Merritt, 1999) are regarded as being particularly influential in the impairment of stream ecosystem process and function (Waters, 1995). Livestock trampling occurs along several sections of the Mutale River (DWAF, 2001), which corresponded to observations in the field.

In addition to the large-scale alterations to the river through direct land-cover change on the river banks, pollutants may become a problem in the future. Examples of the effluents which could already be present in the system include the excretory products of livestock utilizing the river directly (DWAF, 2001; Leopold, 1968), road runoff (there is a road adjacent to a large section of the Mutale River) and the percolation of sewerage into the groundwater especially with the universal use of long-drop toilets in this part of Venda (Wheater & Evans, 2009). Further effluents could include those from poorly-regulated industrial facilities (such as the Tshikondeni coal mine). Even in the absence of direct impacts, a long-term legacy of soil and groundwater pollution from agricultural and industrial effluents is often experienced (Wheater & Evans, 2009). These pollutants are thus likely to affect the river at multiple scales both spatially and temporally.

In contrast to farmland, many of the increases in village/otherwise occupied areas were found to fill grid squares previously occupied by bare ground (70%), as opposed to trees or farms (30%). These changes were possibly a result of increased human settlement in certain areas, during the classification of the TBVC states. In Venda, areas were communally owned and frequently over-used for many years, especially prior to the abolishment of apartheid in 1994. As over-grazing by cattle and goats frequently result in areas becoming barren, the phenomenon known as the “tragedy of the commons” (Feeny et al., 1990), is likely to play a role in this system. The impacts of the tragedy of the commons, such as desertification of the land surrounding the rivers, can result in further degradation of the surrounding habitat. This will likely affect the riverine biota at multiple scales, especially in species that rely on terrestrial and freshwater components of the landscape, such as the Nile crocodile.

As mentioned above, declining trends in the adult Nile crocodile population size and increases in land-use and human population were found to occur simultaneously in my study. The average rate of change in human populations surrounding the Mutale River is 3 300 people per year, which is especially important when one considers that these increases occur within a small area (9721 km^2 in total; 0.34 humans per kilometer increase per year). These changes may be limited at present, but with future increases in human population size further declines in the viability of the crocodile population are probable. The implementation of conservation measures would be instrumental in preventing further declines of the crocodile population in the Mutale River.

My study revealed that anthropogenically-driven land-use and occupancy correlated with decreases of adult crocodile numbers. These changes could be attributed to several causes, including changes in river quality, habitat availability, and the presence of pollutants in the water (indirect effects). However, the changes could also be contributed to a an increasing trend noted in many parts of South Africa, where large crocodiles are often targeted in retaliation killings for the loss of livestock and/or injury of humans (Calverley, 2010; Wallace et al., 2011). Larger crocodiles are also easier to track, especially in the dry season, when they are restricted to the few deep pools remaining in the river. This impact poses an important threat to the persistence of the population. Without immigrant adults to augment the population, and with smaller individuals being more vulnerable to predation, drowning in high water levels and pollutants, it seems likely that this crocodile population will not survive without additional management.

In conclusion, contrary to expectations, increases in anthropogenic activity and human population size were found to positively correlate with an increase in the Nile crocodile population. However, the decrease in the number of reproductively-active individuals, linked to increases in anthropogenic activity, are likely to compromise population viability of Nile crocodiles in the Mutale River in the future, especially as these are the individuals most likely to be targeted by humans. Although this does raise concern, the increase in smaller size classes, indicates that reproduction is nevertheless still occurring. As a result, I argue that the crocodile population in the Mutale River could be afforded at least some level of protection. If this is possible in Mutale River, it would not only benefit the crocodile population occurring here, but would supplement the meta-population of Nile crocodiles occurring in north-eastern South Africa, which is the southern range limit of the species.

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Chapter 3

The effects of natural disturbances on the Nile crocodile (*Crocodylus niloticus*) in the Mutale River, Limpopo Province

Introduction

Natural disturbances such as flooding, result in a cascade of physical processes such as erosion, sediment deposition and associated changes of both aquatic and riparian organisms in their habitats (Swanson et al., 1998). Species-specific traits and substrate characteristics including heterogeneity and stability, dictate biotic responses to patch disturbance in a stream (Holomuzki & Biggs, 2000, 2003; Olsen et al., 2007; Townsend et al., 1997). Though regional populations of fauna adapt to the local prevailing climate through physiological and behavioral responses (McMichael et al., 2006), extreme events often stress populations beyond these limits. A variety of aquatic species are thought to be at risk as their ability to adapt through natural selection is limited and because anthropogenic alterations to the environment reduce the dispersal and migration potential of organisms, limiting their ability to find suitable habitat (Angeler, 2007). Moreover, synchronization between life-cycle events and seasonal changes in habitats may be disrupted (Harper & Peckarsky, 2006; Winder & Schindler, 2004), limiting the ability of organisms to reproduce and persist in the face of climate change.

Freshwater ecosystems are vulnerable to climate change (Alvarez-Cobelas et al., 2005; Carpenter et al., 1992; Firth & Fisher, 1992; Kundzewicz et al., 2008; Lake et al., 2000; Lodge, 2001; Magnuson et al., 1997; McCarthy et al., 2001; Poff et al., 2002; Schindler, 2001; Woodward et al., 2010). Global Change Models (GCMs) indicate an anticipated increase in the frequency and severity in extreme weather events such as droughts and flooding (Collier et al., 2008; McMichael et al., 2006). In 2003, the Department of Agriculture indicated that South African rivers are already frequently affected by erratic and unpredictable climatic extremes such as drought and flooding (M' Marete, 2003) and increases in these events would result in heightened flood risk. In the context of my dissertation, flood risk is defined as the combination of the probability of a flood event and its negative consequences. The latter is a function of flood intensity, exposure and vulnerability of the system to flooding (Angeler, 2007). Worst-case scenarios of climate change depict increased extinction rates and loss of biodiversity resulting from physiological stress, interactions with invading species, habitat conversion and habitat loss (Hughes, 2000; Root et al., 2003; Thomas et al., 2004; Vitousek, 1994). Increases in flooding and associated changes in the riverine habitat could result in the reduction or degradation of suitable terrestrial and aquatic habitat being available to Nile crocodiles (*Crocodylus niloticus*). Flooding has been shown to result in direct mortality of crocodile eggs (Magnusson, 1982) and the resultant rise in nest failure, if compounded by decreases in habitat availability, would increase the vulnerability of crocodiles to the effects of climate change.

Excessive alteration of the Mutale catchment occurred in 2000 when high rainfall in Mozambique and the north- eastern region of South Africa resulted in flooding of large areas in Limpopo Province (Christie & Halon, 2001). The Mutale River, was altered from a narrow, deep river associated with a gorge and a riparian area, to a flat, shallow river with a multitude of small pools and limited riparian forest growth (pers comm. Bunn, 2012; pers comm. Allan, 2012; Pearcy, *unpublished*). Despite the low likelihood of such an event occurring on multiple occasions in a short time-span, flooding in January 2013 further flattened the Mutale River and altered the river channel while shifting large amounts of sediment downstream (pers. obs.). These changes in channel morphology, and the possibility of increased frequency of floods of this magnitude is likely to result in the degradation of habitat available to Nile crocodiles and may also have cascading effects on water quality.

Rationale

The floods of 2000 and 2013 in the Mutale River resulted in shifts in the locations of optimal crocodile nesting habitat availability and sheltered pools and runs suitable for crèches available to the Nile crocodile (Pearcy*, unpublished*). By investigating the extent and the subsequent effects of flooding, I sought to supplement current knowledge on flooding effects on river quality, including crocodile abundance and distribution outside of a protected area. The emerging patterns can then be used by future studies to model the impacts of flooding on small riverine systems. In addition, the regular collection of river quality data and crocodile population demographics can serve as a useful tool in monitoring river health in this region.

Aims

The aims of my study were fourfold: 1) to investigate changes in river quality, including physiochemical variables such as pH, water temperature and turbidity, as well water quality measured by the South African Scoring System (SASS5) rapid Bioassessment method (Dickens and Graham, 2010), 2) to examine pre- and post-flood changes in the riverine landscape, including rapid habit assessments of available habitat to the Nile crocodile and the potential (indirect) effects of land-use change, 3) to assess the abundance of crocodiles and their nests in subsections of the Mutale River and 4) to compare these results to changes in the crocodile population to better understand the overall impact of natural disturbances on the riverine environment. River quality variables were anticipated to fluctuate between seasons, due to changes in insolation and the associate effects of shifts in temperature and water availability (Palmer and Poff, 1997). Land use change effects were hypothesized to increase sandbank presence due to sediment deposition, though these effects could have been curtailed due to seasonal shifts in deposition (Allan, 2004). As the population of crocodiles in the Mutale river occurs outside a protected area, decreases in the population size were anticipated (Combrink et al., 2011).

Methods

Study site

The primary study site for the intermediate and small-scale data collection was located in Hamakuya, a cluster of 19 villages in the rural Thulamela Local Municipality of the Vhembe District in Limpopo Province. Sample collections took place from Lamvi, a 7 km section upstream of a 3 km, inaccessible gorge. Collections continued 8 km below the gorge, upstream of the research base (Tshulu, Fig. 11), and 8 km below the gorge, downstream of the base (Fig. 11). Sampling was limited to this area, which is accessible on foot. The gorge itself is not frequently utilized by villagers from the surrounding areas as there is little or no grazing available for livestock and the banks of the river are not suitable for farming. Fishnets observed in the lower stretches of the gorge indicate that it is at least partly utilized and as one moves away from the gorge, both further up and down-stream, there are a progressive increase in the exposure to direct anthropogenic alterations of the environment.

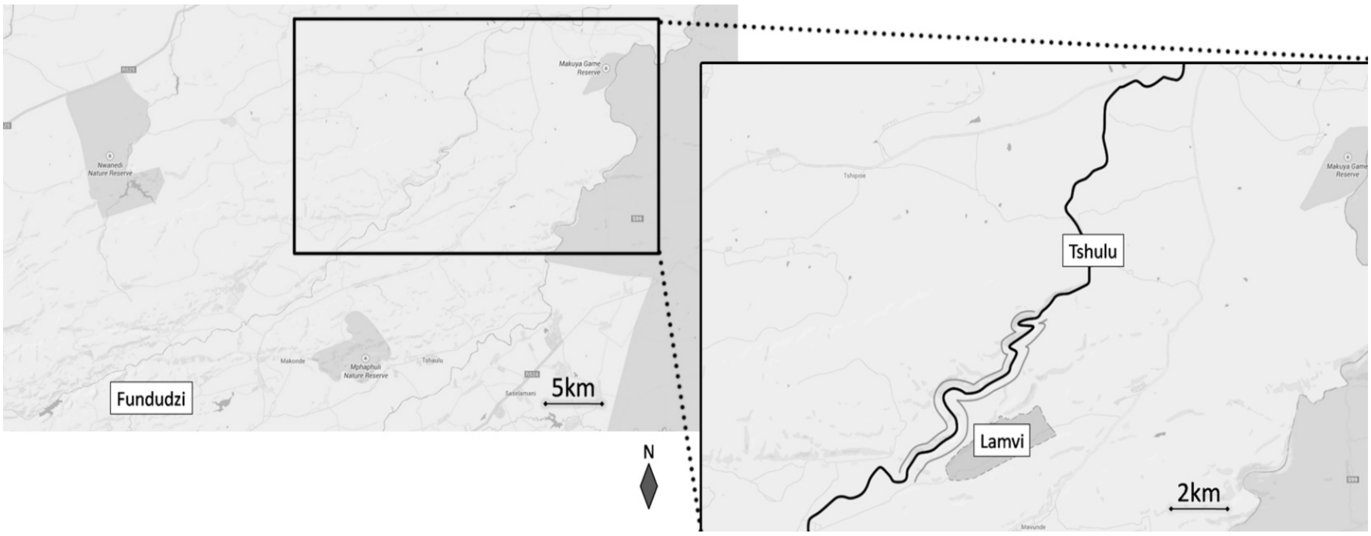

Figure 11: Sections of the Mutale River, Limpopo, covered in seasonal surveys and pre- and post-flood, intermediate and small scale surveys. Surveys and samples were performed along the portrayed section of the river (indicated in black), excluding the three kilometre gorge (indicated in grey).

Study Design

The methods described below are the same as those used in studies conducted in December 2011, March 2012, October 2012, December 2012 (pre-flood) and March 2013, June 2013, October 2013 and April 2014 (post-flood), in a 23 km subsection of the river. Data were available for a two and a half year period, for the winter and summer seasons. These data were used to compare river quality by indicating 1) crocodile presence, 2) The river quality, assessed using SASS 5 Rapid Bioassessment Method (Dickens & Graham, 2010), 3) changes in the riverine habitat (using rapid habitat assessments) with particular attention to crocodile nesting and potential crèche habitat, and 4) the combined effects of water quality, habitat availability and changes in land-use on the Nile crocodile.

Crocodile surveys

Night surveys of crocodiles were conducted as described in Chapter 2. These were performed each night on the return journeys from sample collections (described below), or separately on the nights succeeding days where sampling did not occur.

Habitat Assessment

Habitat assessments were processed over a time-period of three days. Each morning, researchers walked upstream or downstream along the river, (as specified earlier and represented in Fig. 9; black line, excluding grey gorge areas). As they progressed along the bank of the river, the presence, position and length of predetermined habitat types (terrestrial and aquatic) were recorded for the north and south banks, and within the river channel. GPS co-ordinates for each change in habitat were recorded. The habitat types were categorized during the first data collection period (in 2011) and correlated with habitats that could be considered as valuable to crocodiles (such as sandy banks; found to be the primary nesting site for the Nile crocodile; Leslie & Spotila, 2001). Terrestrial habitat types included sand (with more than 70% coverage of sand), rocks (boulders and basking areas were included in this) and unusable areas (including gorge walls, cliff walls and any other areas that would otherwise be inaccessible to crocodiles). Overlap of habitat types was rare, but those that were observed were recorded; e.g. sand banks interspersed with rock. Terrestrial habitat types recorded along the north and south banks were limited to a distance of 7 m away from the river. A 7 m zone is the accepted distance from the river edge that crocodiles will lay eggs (Mabuwaya Foundation, 1993) and is the distance away from the water's edge that nests were located along the river. The presence of any exposed sand, rocks and reeds in the river was also included in habitat descriptions.

The distribution of Nile crocodiles of different life-stages is likely influenced by the size of pools and the rate of flow along the length of this river, as these factors impact the spatial distribution of prey items in the river (Palmer & Poff, 1997). Juveniles are likely to remain close to sections with relatively deep, slow moving water as these are ideal fish nurseries (Mosepele et al., 2009) and crocodiles of all sizes tend to actively avoid rapids

(Hutton, 1989). As such, riverscaping data included the presence of rapids (white water), runs or pools.

Garmin BaseCamp (2012) was used to measure the lengths of the different habitat areas of the river by calculating the distances between the co-ordinates of the beginning and end point for each specific habitat type (both terrestrial and aquatic). These data were entered in Microsoft Excel (2013) and the proportion of each habitat type was calculated using the total length of distance travelled, compared with the actual distance for each habitat subsection, including overlaps of each individual habitat type.

Water quality

Physiochemical variables including measurements of water temperature, pH, velocity, turbidity, elevation, and depth were recorded every 500 m along the river, for January 2012, March 2012, October 2012, March 2013, June 2013 and April 2014. Water temperature was measured with a thermocouple thermometer and elevation with a Garmin GPS System (GPSmap 60CSx). Turbidity was assessed by counting the number of consecutively smaller dots (five) that could be seen through a clear plastic bottle filled with sample water. Velocity was measured by recording the time taken for a meter-long string attached to a water-soaked apple to fully extend. Using a tape measure to find depth, three randomly selected points were measured as close to the middle of the river as possible. In some instances, it was not possible to wade out to the middle, due to the presence of crocodiles or the depth of the water. This sometimes precluded us from doing totally random measures. Three macro-invertebrate community samples were collected every kilometer within each survey section of river, in March 2012, October 2012, March 2013, June 2013 and April 2014. For safety, these samples were collected in rapids since Nile crocodiles tend to avoid fast flowing water, but were otherwise collected according to SASS5 guidelines (Dickens & Graham, 2010). The collected taxa were identified using an invertebrate identification guide (Gerber & Gabriel, 2002).

The river quality data were assessed using SASS5 Average Score Per Taxon (ASPT). This score was calculated for the samples of macro-invertebrates found in each site. ASPT was used, instead of SASS scores, as a conservative estimate of river quality (Dickens & Graham, 2010), especially since data from previous years were collected during times of varying flow. This allowed for comparison of data across the years with previously collected samples.

Data analysis

Night surveys of Nile crocodiles were analyzed using two-sample T-tests in order to determine whether upstream and downstream populations were significantly different, as upstream areas were less frequently utilized by humans, due to the presence of the gorge and less arable farmland, as mentioned before. An Analysis of Variance (ANOVA) was used to test whether the number of crocodiles in each size class was significantly different between months (seasonal observations). In addition, the proportion of total crocodiles found in each habitat type was compared. Findings were assessed by calculating the relative importance of each habitat type, by dividing the relative abundance of crocodiles in each habitat type with the relative abundance of the habitat type, as per the calculation:

$$\frac{Pcroc}{Phab}$$

Where $Pcroc$ refers to the proportion of crocodiles found in the habitat and $Phab$ refers to the proportion of the available habitat type. This calculation was performed for terrestrial and aquatic habitat types.

Habitat availability was assessed by calculating the proportion made up by each habitat type. I tested for differences between years using a single-factor ANOVA, with the year as the independent variable, and the habitat type as the dependent variable. In addition, the proportion of terrestrial habitat availability calculated for 2013 was compared with land-use data for 2013.

Land-use data were collected in the same manner as presented in Chapter 2 (within the 500 m polygons), but limited to the section of the river traversed in this study (Fig. 9) and to a single survey (March 2013). Data were compared using GPS location to determine where each habitat type was situated along the banks of the river, within the 7 m polygon directly adjacent to it, and what land-cover type was present within the 500 m polygon on the same bank. Each 500 m polygon for the year 2013 was investigated in this way, as this was the most recent aerial survey data available for this region. Within the 500 m polygon, the proportion of each habitat type along the banks of the river was calculated. This measure was repeated along the length of the surveyed section of the river, resulting in 23 comparisons (as each 500 m polygon and corresponding habitat type data was considered a single data entry). This was analyzed using a single factor ANOVA, with Land Cover type as the independent variable, and Habitat availability as the dependent variable. As this information was investigated as proportions, all data were first Arcsine transformed to normalize the variables.

River quality (physiochemistry and SASS data) pre- and post-disturbance was also compared in order to assess the effects of flooding on these variables. Physiochemistry was analyzed using a Principle Component Analysis (PCA), performed in Primer (Clarke, 2006), with pH, velocity, water temperature and average depth as inputs. The PCA is considered to be an unbiased method, revealing associations or variations in chemical and physical constituents, which could be indicative of seasonal influences on the physiochemical data. Physiochemical variables were compared using Kruskal Wallis analysis of variance, in STATISTICA (StatSoft, 2007) to test for seasonal differences. Macro-invertebrate data were analyzed using STATISTICA (StatSoft, 2007), and were subjected to an ANOVA of the ASPT scores when categorized by month, and subsequently using a post-hoc Tukey test in order to determine the difference.

ASPT scores were compared with the habitat availability using the average ASPT scores per habitat type and per location in order to establish whether the surrounding habitat type, seasons or flooding effects, significantly influenced ASPT changes. All data were discussed in relation to the Nile crocodile.

Results

Crocodile surveys

The average number of Nile crocodiles found in the 23 km stretch of Mutale river was 20.63 p.a. (±2.70). This equates to one crocodile per 1.03 km of river. Crocodiles were seen more frequently during the wet season than in the dry season, but there was no significant difference between years for any size class ($F_{(2,6)} = 3.13$; $p > 0.05$; Wilks = 0.01) or total numbers between seasons ($F_{(1,4)} = 3.03$; $p > 0.05$; Wilks = 0.08). Furthermore, no significant differences were found between the population sizes downstream and upstream of Tshulu Camp ($F_{(4,1)} = 3.02$; Wilks = 0.08; $p > 0.05$), (Fig. 12). The number of crocodiles did not fluctuate significantly from year to year ($F_{(2,6)} = 1.37$; $p > 0.05$; Fig. 12). Observations of juvenile crocodiles were highest in 2011 (17 Juveniles; Figure 12), though no significant difference was found between years ($F_{(3,2)} = 1.93$, $p > 0.05$). Adult crocodile population size remained similar between years ($F_{(3,2)}= 0.27$; $p > 0.05$).

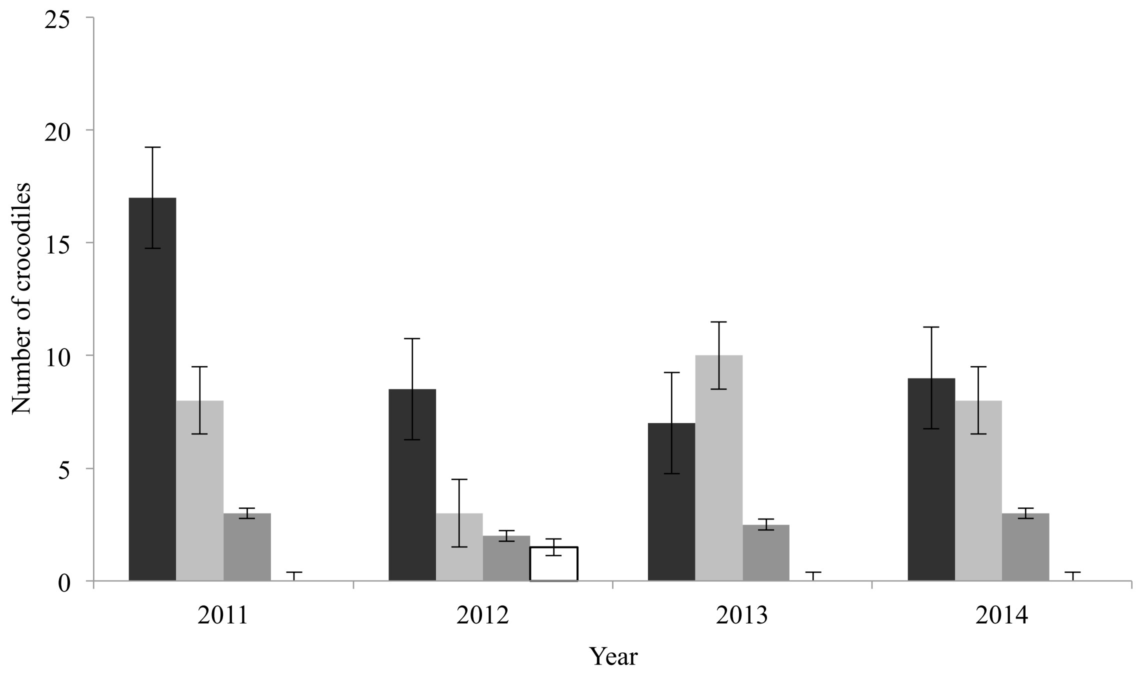

Figure 12: Number of Nile crocodiles sighted in Mutale River, Limpopo Province, during night surveys according to size class (Juvenile, black; Sub-adult, light grey; Adult, dark grey; Unidentified, white.)

The Nile crocodile in the Mutale River did not equally favor all terrestrial habitat types. The majority of crocodiles (72%) were found in sandy areas (Table 3). During the night surveys, crocodiles were also frequently found in rocky areas (20%), and seldom in areas where habitat was considered unusable (8%). The relative habitat importance of sand, was found to be >1, indicating that crocodile distribution in this habitat was not completely random. The proportion of crocodiles found in unusable habitat, and the relative importance of the habitat (<1; Table 3), indicates that crocodiles actively avoided habitats, which were considered unusable.

Table 3: Proportion of Nile crocodiles found in each terrestrial habitat type. The proportion of habitat types available and the probability of finding crocodiles in each habitat type in the walked section of the river, in March 2013.

	Proportion of crocodiles	Proportion of habitat available	Relative importance of habitat
Rock	0.20	0.24	0.83
Sand	0.72	0.53	1.36
Unusable	0.08	0.21	0.35

In addition to favoring certain terrestrial habitat types, the Nile crocodile was also found to favor specific aquatic habitat types over others. The majority of crocodiles (72%) were associated with slow-flowing and quite deep runs (Table 4). Only 17% of the crocodiles were found in deep pools, though this is probably a function of pool availability and detectability of crocodiles throughout the river, especially when one considers the relative importance of this habitat (3.4; Table 4). Crocodiles were found to actively avoid rapids (<1; Table 3). They were somewhat evenly distributed in Runs; the most common habitat type (48%).

Table 4: Proportion of Nile crocodiles found in each aquatic habitat type, the proportion of habitat types available and the probability of finding crocodiles in each habitat type in the walked sections of the river in March 2013.

	Proportion of crocodiles	Proportion of habitat available	Relative importance of habitat
Rapid	0.11	0.47	0.23
Run	0.72	0.48	1.5
Pool	0.17	0.05	3.4

Habitat assessment

When comparing land-cover type and the associated percentage of habitat cover, it was found that the proportion of habitat cover for each land-use type was significantly different ($F_{(9, 209.45)} = 4.99$; $p < 0.05$; Fig. 13). Tukey post-hoc comparisons revealed that bare ground and farm encompassed significantly different habitat distributions to areas covered by trees. This is visually represented in Figure 13, in which land-use polygons specified as trees have even distribution of sand, rock and unusable areas.

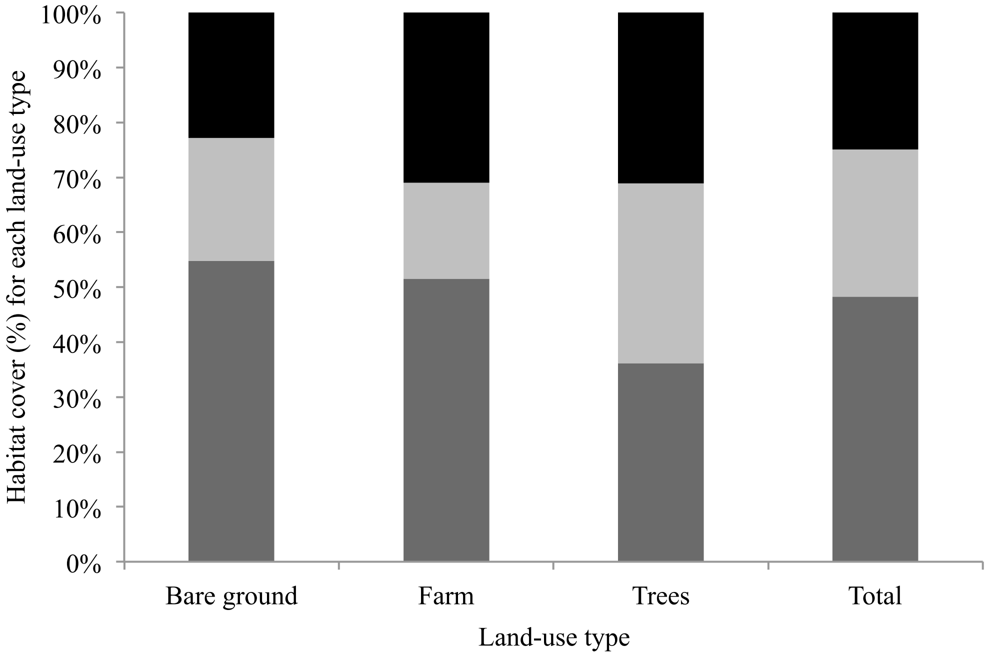

Figure 13: Percentage habitat (%) found under each land-use type on the banks of the Mutale River. Total indicates the average percentage of the river that was covered by the habitat types (Sand, dark grey; Rock, black; Unusable, light grey).

The proportion of terrestrial habitat availability was found to fluctuate over time (Figure 14; Wilks lambda = 0.01; $F_{(12, 8.23)} = 3.08$; $p = 0.06$). Increases in sand coincided with seasonal changes (e.g. October 2012), but a general decrease in sand occurred over time. Rock and unusable habitat showed opposing trends after October 2012, with higher proportions of rock coinciding with lower proportions of unusable territory.

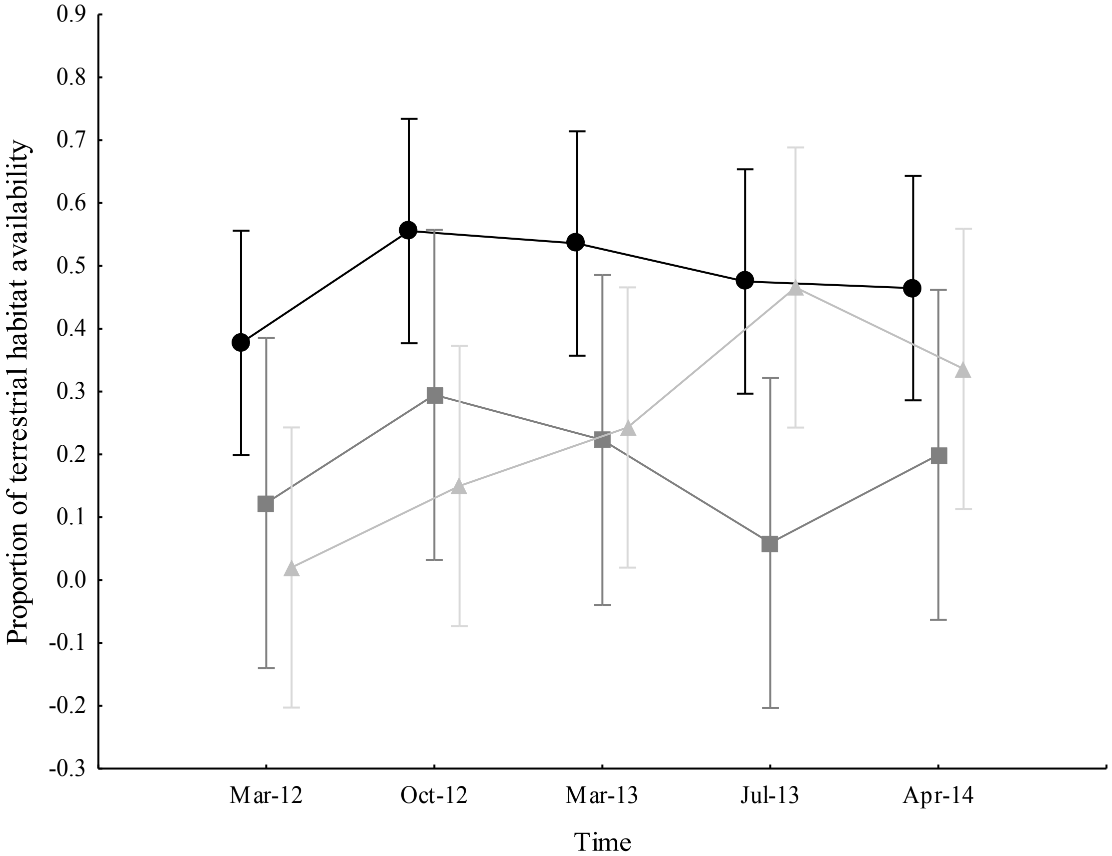

Figure 14: Proportion of terrestrial habitat availability (Sand, black with circles; Unusable, dark grey with squares; Rock, light grey with triangles), over several seasons (March 2012, October 2012, March 2013, July 2013, April 2014), in the Mutale River .Vertical bars denote 95% confidence intervals.

The proportion of aquatic habitat availability along the banks of the Mutale River, was also found to fluctuate over time (Wilks lambda = 0.00, $F_{(12, 8.23)} = 21.93$; $p < 0.05$, Fig. 15). July 2013 showed a marked decrease in rapids; directly after the dry season. Runs fluctuate seasonally as well. A decrease in pools was found after the 2013 flood.

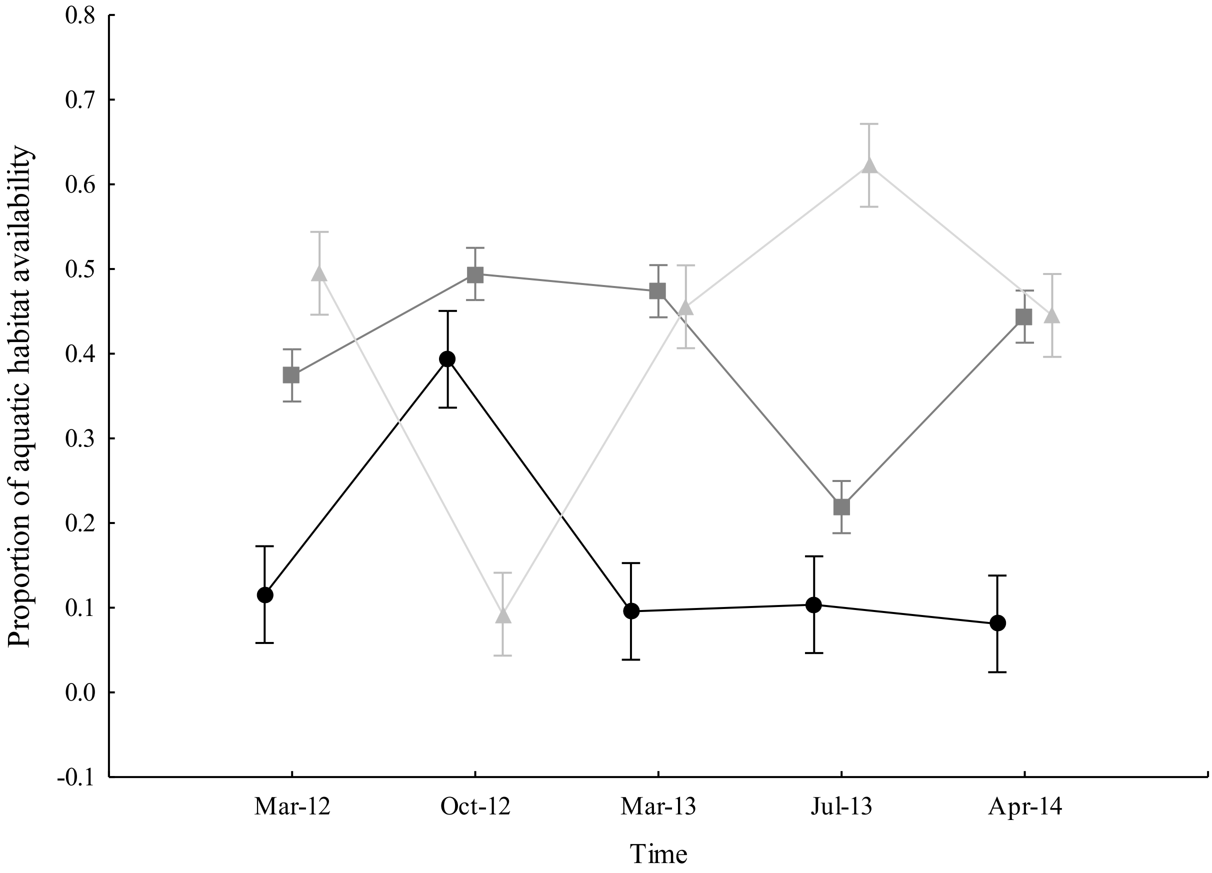

Figure 15: Proportion of aquatic habitat availability (Pool, black circles; Rapid, dark grey squares; Run, light grey triangles) over several seasons in the Mutale River. Vertical bars denote 95% confidence intervals.

River quality

Physiochemical variables

The physiochemical variables investigated in this study (Water temperature, pH, velocity and depth) clustered according to the seasons in which they were recorded (Fig. 16), with significant differences between seasons for each of the variables (Depth: $F_{(5,91)} = 29.76$; $p < 0.001$; pH: $F_{(5,91)} = 20.31$; $p < 0.001$; Velocity: $F_{(5,91)} = 20.31$: $p < 0.001$; water temperature: $F_{(5,91)} = 94.73$; $p < 0.001$) when analyzed using ANOVA. March 2013 data (post-flood) were overlapped with October 2012 data (pre-flood, end of dry season) in the PCA. Post 2013 flood data separated completely from the rest of the data. A potential flood signal was represented in the shift from the riverine physiochemistry in October 2012 to October 2013, as these would be expected to look similar had the river returned to a natural fluctuation.

April 2014 data overlapped once more with March 2013 data. PC1 was driven primarily by water temperature (Eigenvector = -0.66), followed by velocity (Eigenvector = -0.58) and pH (Eigenvector = -0.45), thus accumulating a total of 45.1% variation represented by PC1. A further 25.9% of variation was represented by PC2, and was driven primarily by depth (Eigenvector = 0.89).

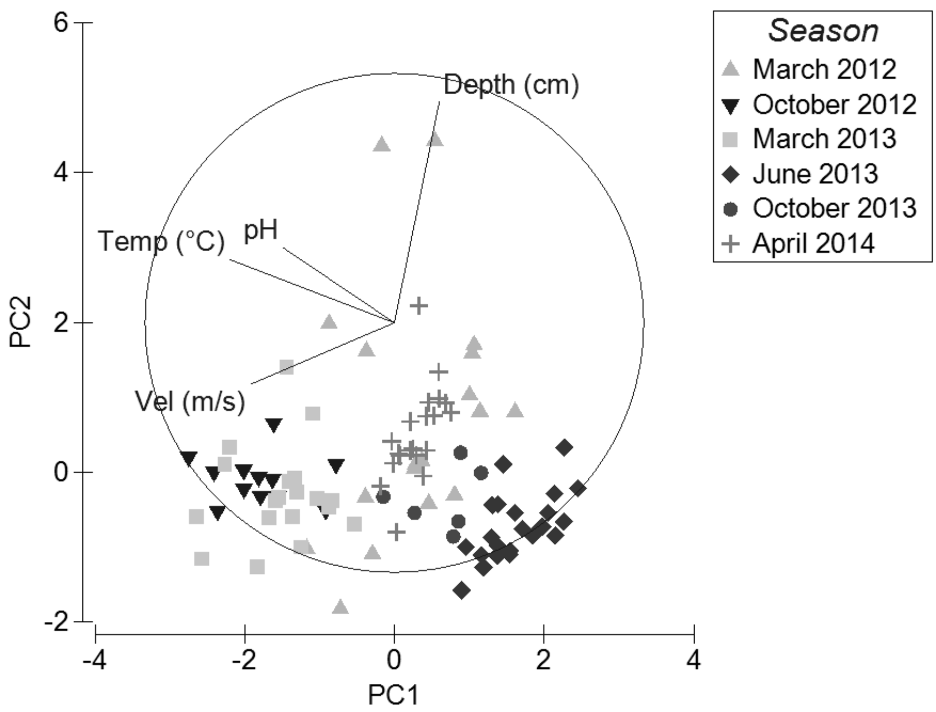

Figure 16: Principle components analysis of physiochemical variables including water temperature (°C), pH, velocity (m/s) and depth (cm) in the Mutale River, Limpopo Province.

Macroinvertebrate assessments

The SASS5 scores revealed that the ASPT along the surveyed sections of the Mutale river differed significantly, in several instances ($F_{(6,19)} = 10.291$, $p = 0.00$) from one another (Fig. 17). The ASPT was found to be higher soon after the flood in March 2013 than in any other month (Tukey post- hoc; MS = 1.81, df = 59). January 2012 saw significantly lower ASPT scores than other months.

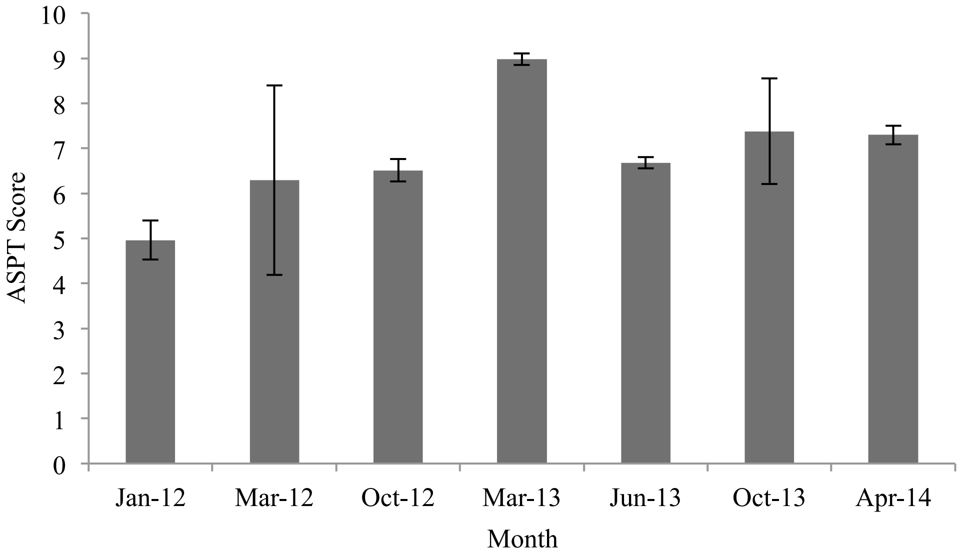

Figure 17: Histogram of the average ASPT scores of the Mutale River, over time (Months, January 2012-April 2014).

At the intermediate scale, despite the absence of common trends, individual changes in terrestrial habitat availability were noteworthy (Fig. 18a). After the January 2013 flood, a 62% increase in the proportion of rocky habitat accompanied a 24% decrease in the sandy habitat availability (October 2012-March 2013). Between March 2013 and July 2013, an increase in rocky habitat coincided with a further decrease in sandy habitat and greater exposure of the rock-bed, which was noticeable after the floods had receded.

Alterations in the aquatic habitat were also notable (Fig. 18b). Between March 2012 and October 2012, decrease in river flow after the dry period resulted in an overall increase in slow-flowing pools. Following the October 2012 dry period, the 2013 floods and wet period resulted in a major increase in the presence of 'runs' (medium to fast flowing water, excluding white rapids). The Mutale River had so much more water flowing through it at this point that in many deep areas previously classified as pools, the increased velocity altered this classification. Increases in fast flowing water and rapids between October 2012 and April 2014 were likely to result in decreases in the availability of suitable/valuable Nile crocodile habitat. As the proportion of rapids increased by 102% (twice as many rapids between July 2013 and April 2014), there was in the past year an increase in habitat that was actively avoided.

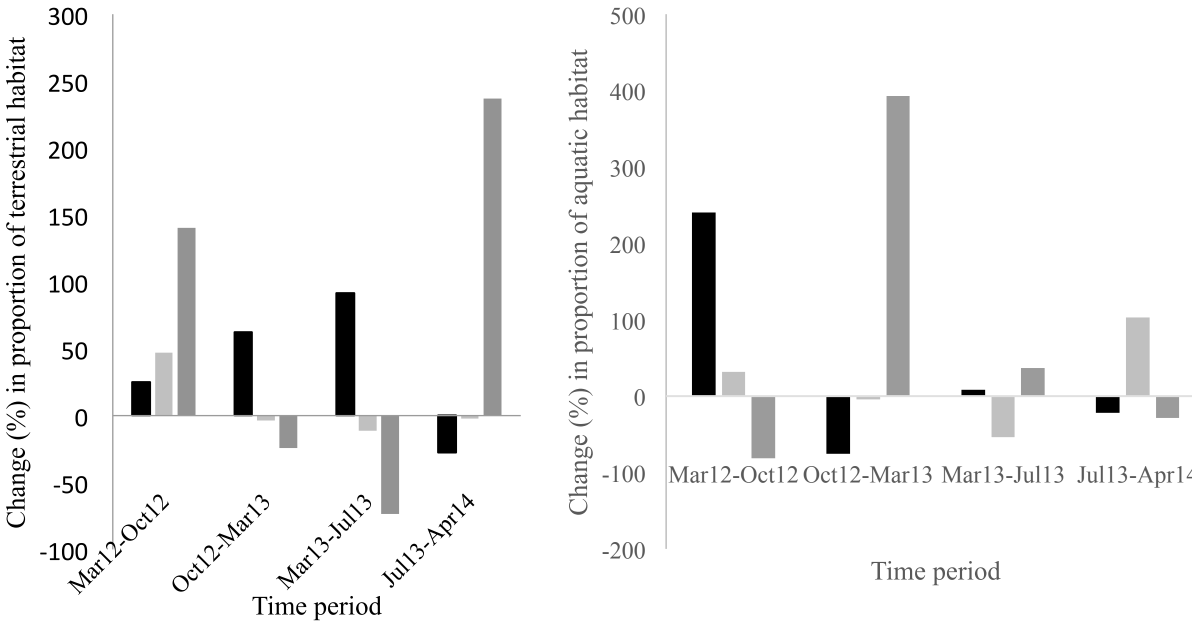

Figure 18: Change (%) in a) terrestrial (rock-black; sand- light grey; unusable- dark grey) and b) aquatic habitat (pool- black; rapid- light grey; run-dark grey) along the surveyed section of Mutale River, including flooding (October 2012-March 2013) and non- flooding (March 2012-October 2012; March 2013-July 2013; July 2013-April 2014) periods.

At the small scale, ASPT scores increased by 37.3% after the January 2013 floods; this increase is likely to have occurred as a result of the initial scouring effect of the flood (Fig. 19). The fluctuating SASS scores indicate that the percentage change is greater in periods of lower flow than during flooding. This could occur because of a shift in biota associated with seasonality (Wolda, 1988).

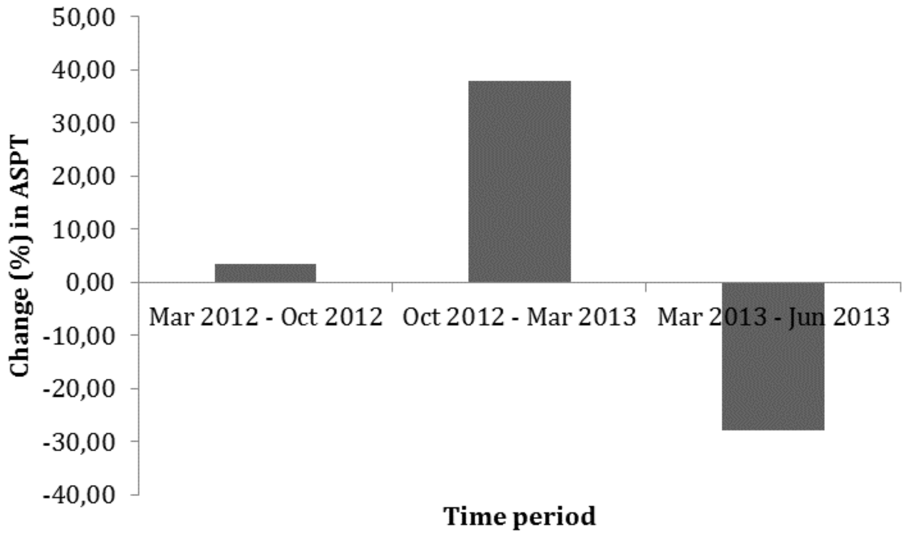

Figure 19: Change (%) ASPT scores along the surveyed section of Mutale River, between flooding (October 2012-March 2013) and non-flooding (March 2012-October 2012; March 2013-June 2013).

Discussion

The density of Nile crocodiles in the Mutale River was one individual per 1.03 km of river traversed. This density is relatively low when compared with populations of crocodiles found elsewhere in South Africa (e.g. the Olifants River; Ashton, 2010). As this population occurs outside a protected area, lower numbers in the population sample were anticipated (Combrink et al., 2011). The results also indicate that the Mutale River population of reproductively active crocodiles has been relatively similar over a short period of time (2011-2014). The adult population did not change during this time period, and the presence of adult individuals in the same areas in every survey, lead to the assumption that the same individuals were found each season. This indicates that the adult crocodile population in this section of the river remained stable, despite the flooding event in 2013. The high levels of variability in the number of hatchlings found per year was probably due to predation on hatchlings during their most vulnerable life stage (Hutton, 1987). The number of adults remained constant throughout the year as these were resident and less prone to predation. The stability of this crocodile population along the Mutale river was likely also linked to the prevalence of preferred habitat within these areas.

The Nile crocodile has a preference for sandy habitats, with the majority of crocodiles being found in these areas (Table 3; >70%). Crocodiles were found to have a particular preference for sandy terrestrial habitats, as there was a greater proportion of crocodile present than could reasonably be expected from a random distribution. Sand has frequently been recognized as a valuable habitat for nesting and basking (Hutton, 1989; Kofron, 1989). In contrast, few crocodiles were found in areas classified by the observers as 'unusable', indicating active avoidance of these areas, as presence was found to be lower than expected by chance alone. Crocodiles also favored specific aquatic habitat types. A majority of individuals were associated with runs, however, crocodiles were found to have a greater preference for pools. The absence of any crocodiles in rapids suggests the active avoidance of this habitat type. With increasing flooding anticipated in the future, flooding is likely to induce a higher prevalence of rapid habitat in the river. As rapids are actively avoided, this would be detrimental to the crocodile population.

The prevalence of sand along the Mutale river was found to decrease over time, between March 2012 and April 2014 (Fig. 14). In contrast, the proportion of rock was found to increase (despite seasonal fluctuations) over time (Fig. 14). At the intermediate scale we therefore see the drastic effect of flooding, owing to the shifting of sediment to areas further downstream after high rainfall seasons (March 2013, April 2014). Shifts in sediment and exposure of rock of this magnitude are likely to have a detrimental effect on the Nile crocodile habitat in the Mutale, as rocky areas do not constitute preferred conditions, and more exposure would result in degradation of suitable habitat for the reptiles. Between July 2013 and April 2014, an increase in the proportion of unusable terrestrial habitat was observed to occur as a result of bank erosion (pers. obs.). Increases in unusable habitat affect the crocodiles as they tend to avoid these areas (Table 2).

These results indicate a decline in preferred Nile crocodile habitat availability post-flood. Although the actively avoided, 'unusable' habitat was found to fluctuate with season (primarily due to the exposure/submergence of rock beds, depending on the season), with no particular increasing or decreasing trend. Rocky habitat, however, is not a particularly favorable habitat, and was found to increase substantially between March 2012 and April 2014, from approximately 12% habitat coverage, to 30% habitat coverage, for the respective years. As mentioned above, Further increases of unusable terrestrial area and rapids in aquatic habitat are likely to impact on crocodiles in the river, due to the unfavorablity of these habitat types.

Riverine systems exhibit seasonal variability in factors such as biotope availability (Armitage et al., 1995; Pardo & Armitage, 1997): hydrology (McElravy et al., 1989), and physiochemical variability such as water temperature (Hawkins et al., 1997). This was reflected in my study as physiochemical variables investigated were found to group together according to seasons (Fig. 16). The overlap in data from pre- and post-flood indicates that flooding resulted in a disturbance in the otherwise natural variation between seasons. Shifts in the physiochemistry directly after the 2013 floods were found to be returning to pre-flood conditions over time. This indicates that the river was returning to a pre-disturbance state. The time taken between the shift in conditions, and the return (approximately 1 year), indicates that this system is sensitive to flooding. Subsequent floods may result in longer restoration periods. This would negatively affect the Nile crocodile because shifts in physiochemistry for extended periods could be detrimental over time. Alterations in land-use on the adjacent riverbanks are likely to further alter the physiochemistry of the Mutale River. Effluents in the river should also be monitored, as these are likely to affect the physiochemical variables already mentioned.

Seasonal variations in the physiochemistry of the river also influence the variation in the distribution and abundance of benthic macro-invertebrates (Dallas, 2004). This is due to presence of specific habitat requirements, which may only be met in certain seasons. In addition, the seasonal patterns of occurrence and abundance of invertebrates depend on their life history and behavioral characteristics (Beche et al., 2006; Wolda, 1988) and fluctuations in flow structure (particularly flooding and drying) in stream communities (Beche et al., 2006). This was portrayed in the fluctuating ASPT scores of the Mutale river, as there were differences between macro-invertebrate communities from different seasons, despite the similarity in the habitat type (all data were collected in rapids). A potential reason for this, is that samples were taken only three months after flooding occurred, allowing sufficient time to re-establish the environment to a more pristine, pre- flood state. Subsequent to this, it is likely that ASPT scores decreased due to excess algal growth in sections of the river that had previously produced some of the higher ASPT values (pers. obs.), with only low scoring species persisting in this state. Many of the species contributing to differences between seasons were highly tolerant of pollution (with a low average score per taxon) and physical disturbances. Due to the fact that the dissimilarity was a feature of these highly tolerant species, the results indicate that tolerance is a determining factor in community composition in different seasons. The water quality of the Mutale River was shown to fluctuate over time, and the overall health of this river was found to be somewhat low. The presence of more tolerant species may indicate an increase in pollution within this river. Shifts in community composition and in water quality over time are bound to also affect the Nile crocodile population, as previous studies have shown that increasing pollution has been linked with die-offs in the past (Botha, 2005).

In this study, as in previous studies, it was found that the flooding and seasonal movement of water across the landscape not only influences the biodiversity within the river, but also impacts the ecology of the river across a broad range of spatial and temporal scales (Junk et al., 1989; Poff et al., 1997; Poff & Ward, 1990; Sparks, 1995; Vannote et al., 1980). The shape and size of river channels, the distribution of rapid and pool habitats, and the stability of the substrate are all largely determined by the interaction between the flow regime and local geology and landform (Cobb et al., 1992; Frissel et al., 1986; Newbury & Gaboury, 1993).

In summary, it was evident at all scales within my study that, excluding the ASPT scores, that there were more changes in the Mutale river during a flooding period, than would normally be the case. At the landscape scale, change increased by as much as four fold compared with inter-flood periods. It is evident that the immediate effects of flooding were often greater than at a longer scale (e.g. the dramatic shifts in aquatic habitat availability that occurred as a result of the increases in river flow). At the smallest scale, the immediate effects of flooding on ASPT (October 2012-March 2013) were greater than during normal, seasonal fluctuations (March 2012-October 2012). As a long-lived animal, the Nile crocodile is likely to experience both large-scale, long-term changes to the riverine environment, as well as short-term, intermediate and small-scale changes. The crocodile is highly adaptable, but clearly prefers certain types of habitat to others. Overall, results showed that seasonality, intermediate and small-scale flooding will impact the freshwater community. With increases in the occurrence of flooding anticipated with climate change, these shifts in the community may become greater and eventually cause cascading effects across space and time.

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Chapter 4: Conclusion

Natural and anthropogenic disturbance effects at multiple scales, and their impact on *Crocodylus niloticus* population demographics in a South African river

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Lotic communities are strongly influenced by alterations to the surrounding environment at multiple scales (Allan et al., 1997; Fausch et al., 2002; Naiman et al., 1987; Schlosser, 1991; Townsend et al., 2003; Vannote et al., 1980; Ward & Stanford, 1983). In chapter 2, I investigated the significance and the prevalence of large-scale, anthropogenic impacts, including changes in land use and trends in human population size, as compared with the Nile crocodile populaton in the Mutale river. Chapter 3 focused on reach-scale changes, such as shifts in aquatics and terrestrial habitat availablity serving as the intermediate scale, and smaller scale fluctuations in water quality and physiochemistry. This chapter serves as a discussion of these findings in order to create a coherent, detailed picture required for effective and relevant management decisions.

In my study, the combined impacts of anthropogenic (Chapter 2) and natural (Chapter 3) disturbances on the Nile crocodile (*Crocodylus niloticus*) population in the Mutale River were investigated through comparisons of the state of the river, pre- and post-flooding. In this context, 'state' referred to 1) the change in anthropogenic land cover on the banks of the river (within a 500 m radius) as a proxy for long-term, large-scale change, 2) the terrestrial and aquatic (preferred) habitat availability, a short-term, intermediate-scale change and 3) the rapid biodiversity assessment value, short-term, small-scale changes in the benthic macro-invertebrate community composition.

This study was done with the aim of informing management decisions and instilling the importance of future projections for the Nile crocodile population in Mutale River, the Limpopo region, and southern Africa as a whole. This is of particular importance when considering the 'Vulnerable' status of the crocodile within South Africa, and the decrease of the primary populations of crocodiles within the boundaries of nature reserves (Ashton, 2010).

The investigations in this study, were performed at multiple scales, in order to depict the short-term, small-scale effects of flooding, and contrast them with the larger, long-term effects of flooding and anthropogenic alterations to the environment. The data revealed that Mutale River is undergoing major changes, which resound across space and time. The trends of land-use clearly showed flooding effects, as anthropogenic land-cover consistently increased after flooding events (Figure 10, Chapter 3). This is likely to have occurred as a result of the destruction of riparian vegetation that frequently occurs during periods of flooding (Swanson et al., 1998). Areas that were previously inaccessible were exposed and farming has encroached. In addition, major shifts in sediment deposition resulted in the widening and flattening of the river, making the areas more accessible to villagers from surrounding areas. These shifts in land-use are likely to exacerbate the effects of future floods, as increases in urban areas and farmland are known to result in increases in water runoff over time (Niehoff et al., 2002). The cumulative effect described above is likely to be further exacerbated by increases in the frequency and intensity of future flooding events (IPCC, 2001).

Anthropogenic effects have resulted in an amplification of the instantaneous flooding effects occurring in Mutale River. All of these effects will magnify with increases in land-use change, not only because of the indirect effects of farming and sedimentation or the direct effects of mining point source pollution, but also because there is already a steady increase in the human population in municipalities on either side of the river (Thulamela and Mutale; Fig. 8). Climate change predictions, in addition, indicate an increase in the frequency and intensity of flooding events in southern Africa (Bubeck et al., 2011). The shifts in land-use, degradation in habitat availability and the increased likelihood of frequent, intense flooding in future years, creates a troubled scenario for the future of Nile crocodile presence in the Mutale River. Increasing land-use and increased human presence coincide with decreases in the adult population of Nile crocodiles. These changes may also be related to an increase in retaliation killings of crocodiles in the area, especially the largest individuals (pers. obs.). In addition, Figure 19 shows that during flooding periods the creation of farmland increased greatly directly after the events, especially farmland within 500 m of the riverbank, resulting in limited restoration of the riparian vegetation on the banks of the Mutale (data not shown).

The shifts in habitat abundance on the banks directly adjacent to the river and the increase in unusable terrain, in the most recent data (April 2014) resulted in an increase in unfavourable territory (Table 3, Chapter 3; Fig. 13, Chapter 3). These shifts are likely to be compounded with an increasing frequency in flooding events, as flooding frequently results in channel erosion (Tang et al., 2005). These shifts in the habitat may eventually result in areas which become increasingly homogenous, especially as there were clear increases in the rocky habitat between March 2012 and July 2013 (Fig. 18). Declines in habitat heterogeneity are often associated with decreases in riverine species diversity (Allan, 2004), which is likely to put pressure on the Nile crocodile population, as a lower abundance and diversity of both their own required habitat and food could result in declines in recruitment and the survival of hatchlings.

As mentioned before, Nile crocodiles are keystone species in aqautic ecosystems (Thorbjarnarson, 1992). As such, they impact ecosytem processes (Bourquin, 2007) and the loss of any species of crocodilian would represent a significant loss of biodiversity and economic potential (Ross, 1998). Throughout their life span, crocodiles play a key role in maintaining the structure and function of aquatic ecosystem processes (Bourquin, 2007). This occurs by way of nutrient cycling, and selective predation on fish species (Thorbjarnarson, 1992; Botha, 2005; Bourquin, 2007). Due to the value of this species, it is in our interests to conserve and maintain the few populations we have left. This is particularly important, as crocodilian persistence is related to the suitability and prevalence of favourable environmental conditions, which are directly and indirectly affected by anthropogenic alterations to the environment (Mazzotti et al., 2009).

Although *C. niloticus* is able to adapt to the dynamic ecosystem in which it lives, its survival is becoming increasingly threatened through the destruction of its natural habitat, water extraction, water pollution (Ferreira & Pienaar, 2011) and increasing instances of human-crocodile conflict (Thorbjarnarson, 1992; Fergusson, 2010). In the advent of Climate change, these effects are likely to be exacerbated, as further competition for limited resources (such as habitat availability and water; Combrink et al., 2011) and greater pollutant loads in rivers due to higher runoff and precipitation (Kundzewicz et al., 2008) is likely to bring about more cases of direct and indirect human- wildlife conflict (as described in Chapter 1) and also may increase the probability of further pansteatitis outbreaks in the future (such as those in the Kruger National Park (Lane & Huchzermeyer, 2013). Limited numbers of fecund individuals may also decrease genetic variability resulting in lower viability of crocodile populations, both inside and outside of nature reserves (Bishop et al., 2009). This would likely be particularly noticeable outside of reserves, as populations of Nile crocodiles are few and far between.

Management options

In the case of the Nile crocodile in the Mutale river, there are two major management questions to consider. Firstly, would management of the catchment and related water and land usage be enough to preserve the Nile crocodile in this area, and secondly, is that enough? When considering catchment relate management options, dams and other forms of water management should be carefully considered before implementation, especially as there have been discussions of building a dam within the Mutale River (DWAF, 2012). The first management option would be to restrict the usage of the banks and floodplains of the Mutale River for farming. I would also suggest that the extraction and utilization of water from the river should be limited by instigating better irrigation practices (such as a drip irrigation method).

The changes in macro-invertebrate community structure and changes in the physiochemical variables in the Mutale River are likely to increase dramatically with increased flooding, and this may result in gradual decline in water quality. This can be mitigated if there is no additional point source pollution of the system. Pollution not only decreases water quality (Tang et al., 2005), it is also likely to magnify the effect of flooding. The above management decisions revolve around the exclusion of anthropogenic change to the riverine environment, which is not a viable option. But if there is sufficient incentive to generate active community involvement in maintaining the river, it could help to slow the process of degradation, thereby creating a sustainable environment in which the Nile crocodile could thrive.

An alternative management option, on a larger scale, is that of crocodile farming and/or sustainable harvesting. Although wildlife farming is a contentious measure of conservation (Nogueira & Nogueria-Filho, 2011), in instances where the 'wild' population have been depleted to a point close to non-viablity, it could be a valuable method of preserving or maintaining a species. This, however, is dependent on market- related supply and demand, as legalized farming of the Nile crocodile could result in increases in poaching of the crocodile due to competitive marketing (Moyle, 2013). As such, crocodile farming could have one of three outcomes; that flooding the market will depress prices and limit poaching, that farming crocodiles could encourage wild harvesting and that this increase in wild-harvesting could compete against farming (Moyle, 2013). As mentioned before, limited Nile crocodile populations occur outside of park boundaries in South Africa (Combrink et al., 2011), meaning that wild harvesting becomes more difficult, though also more threatening to dwindling population sizes. As South Africa has limited fresh water resources, and due to anticipated increases in the frequency and intensity of drought in this region, limitations to Nile crocodile habitat will become inevitable. As such, I suggest that the farming of Nile crocodiles could become a valuable conservation measure in South Africa, especially in light of climate change.

Increases in the human population and anthropogenic change do not necessarily indicate doom for what remains of Mutale Nile crocodile population. With a greater number of people, a larger municipal drive toward education is possible. With more people and projects such as the River Health Project helping to collect valuable data, increased awareness of present and future benefits could lead to more environmentally friendly thinking. These principles, combined with legislation such as the National Water Act (Act 36 of 1998) and the National Environmental Management Act (Act 107 of 1998), create a framework that could contribute to a manageable and sustainable future.

South Africa has an advanced economy that actively promotes eco- tourism, such as visits to the nearby Kruger National Park. As the southern range limit for the Nile crocodile, this country has regulatory infrastructure in place for the conservation of crocodiles outside the boundaries of nature reserves. The situation can be utilized to the advantage of the local and wider communities. Using the available infrastructure, the amplified effects of flooding can be mitigated through development regimes. These regimes could embrace more sustainable farming practices, helping to decrease erosion and sedimentation along the river, which is a valuable regional resource. The instigation of certain sections of the river as fishing reserves could help to bolster seasonal fish and crocodile populations. In addition, optimizing water re-use programmes could help to limit pollution entering the system. Along with sustainable use of Mutale River, these management options would benefit the Nile crocodile, the flora and fauna living within South Africa, and society as a whole.

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