Status of Nile Crocodile in north eastern KwaZulu-Natal and conservation management recommendations

Report to the
WATER RESEARCH COMMISSION

by

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EXECUTIVE SUMMARY

BACKGROUND

Establishing and monitoring population trends is essential for implementing informed and timely management decisions and also in the conservation of threatened species. Distribution patterns reflect the interactions of organisms with their environment. Movement patterns and home range is fundamental in understanding the spatial requirements of individuals and is important in generating information for the conservation and management of threatened species. Crocodilians are increasingly being viewed as "sentinel species" because as top predators they are good models for studying environmental threats to their respective ecosystems and the associated food web therein.

Recent Nile Crocodile (*Crocodylus niloticus*) deaths in South Africa have revealed the vulnerability of the species – and the aquatic ecosystems they inhabit – and highlighted the need for urgent study of crocodile populations. As a top predator, crocodiles are a valuable ecosystem component but also a source of management concern due their potential threat to humans. Present threats to the major Nile Crocodile populations in South Africa include pollution, habitat alteration/destruction and poaching. This highlights the importance of identification and protection of other viable and unthreatened Nile crocodile populations which are imperative in the conservation of the species in the country. Investigating reproductive ecology is essential in order to access the population dynamics, particularly of unstudied populations. In addition reproductive output can be a measure of population health. Knowledge of the distribution and abundance of crocodile nests and the threats facing them is essential in calculating recruitment and determining population trends.

RATIONALE

The Nile Crocodiles in KwaZulu-Natal are an important component of the South African population but the effects of the current threats on the separate populations need investigation. The Lake St Lucia estuarine system, Africa's largest and oldest protected estuary, contains the largest Nile Crocodile population in a single waterbody in South Africa. During the first decade of the 21st century, the St Lucia estuarine lake experienced a prolonged drought, streams ceased flowing and in 2006 more than 90% of the total water area evaporated. Ndumo Game Reserve (NGR), in north eastern KwaZulu-Natal bordering Mozambique, has the third largest Nile Crocodile population in South Africa. Impoundments have negative and positive effects on biodiversity. Pongolapoort Dam is one of South Africa's largest man-made water bodies, and is surrounded by several game reserves (state, and/or privately owned and managed). Little is known of the effect of the impoundment of the Phongola river on the Nile Crocodile population numbers and status.

OBJECTIVES AND AIMS

Concurrently we investigated the Nile Crocodile's spatial and reproductive ecology, population status, and health in Lake St Lucia, NGR and Pongolapoort Dam to make management recommendations. The specific aims were to

1. Address the conservation needs of Nile Crocodiles in Zululand, and Southern Mozambique by gathering a suite of ecological, physiological, epidemiological and genetic data. Given recent threats to the species and the global importance of these populations, this research will expand current understanding of crocodilian biology and facilitate long-term Nile Crocodile protection; and
2. Use crocodiles as indicators of ecosystem health.

METHODOLOGY

From 2009-2014 at Lake St Lucia we conducted 10 aerial surveys of Nile Crocodiles. We examined changes in Nile Crocodile population size and changes in the size-class distribution within the population using aerial and ground survey data from 1971-2009 in NGR and in Pongolapoort Dam from 2009-2014. In addition, crocodiles were caught opportunistically for aging, sexing and tagging. We investigated detailed movements and activity for 18 Nile Crocodiles here using GPS-satellite transmitters from 2009-2013 at Lake St Lucia and radio-transmitters at NGR and Pongolapoort Dam. We determined the distribution and abundance of crocodile nests at Lake St Lucia, NGR and Pongolapoort Dam. We also investigated nest predation, hatchling liberation and nest-guarding activities of nesting Nile Crocodile females using remote camera traps mainly at Lake St Lucia. We investigated homing behaviour and specific movements of a Nile Crocodile in Lake St Lucia using a GPS-satellite transmitter by translocating an adult female (2.7 m), with a known home range, ~50 km north (straight line distance) to the False Bay area of Lake St Lucia.

When we captured Nile Crocodiles, morphological measurements were taken. We marked each individual uniquely by scute clipping and fitting of coloured caudal tags. In addition we took urine and blood samples. Analyses of blood, serum and urine from Nile Crocodiles were conducted specifically for crocodile nutritional, environmental contaminant, and epidemiological analyses to construct health/nutrition indexes of wild crocodiles, analyses of bioaccumulation of environmental pollutants

RESULTS AND DISCUSSION

The concurrent research of Nile Crocodiles in Lake St Lucia, NGR and Pongolapoort Dam showed how these differed in their ecology and human pressures so affecting the Nile Crocodiles in different ways and illustrating that "one shoe does not fit all".

Lake St Lucia

From 2009-2013 the majority of Nile Crocodiles at Lake St Lucia were recorded in the Narrows, a ~27 km low salinity channel south of the lake. Above average rainfall at the end of 2010 resulted in the refilling of the lake, and most Nile Crocodiles moved north to the lake. We estimated the sub-adult and adult population at 1005 ± 137 individuals.

The overall activity level of Lake St Lucia Nile Crocodiles was 41.0%, and it differed significantly throughout the day. There was a significant seasonal effect on activity, peaking during autumn (52.0%), while Nile Crocodiles were most inactive in winter (30.5%). Crocodile size and mobility were positively correlated with mean daily movement (1244 m). Adults moved more at night, but sub-adults were significantly more mobile during the day. There was a considerable seasonal variation in mobility, with the longest movements during autumn and the shortest in winter. About 60% of total daily movements were < 1 km per day, but for sub-adults this calculation was 96%.

We recorded complex and varied home range patterns for 14 Nile Crocodiles at Lake St Lucia, resulting from differences in size, sex, reproductive status and habitat. The median home range and core-use area of adults were significantly greater than sub-adults. Three size-related patterns of home range behaviour emerged for adult males; transient, (< 3.0 m TL), topographically confined (3.5-4.0 m TL) and "territorial" (> 4.0 m TL). Adult males revealed an inverse correlation between home range size and crocodile size, while the home range sizes of adult females were generally more homogeneous. All nesting females displayed an explosive increase in mobility and space-use subsequent to the nesting period, and all adults, except one female in the central lake, moved during winter in the drought period to large crocodile congregations south of the lake. Sub-adults occupied significantly smaller home ranges than adults, which were habitat-specific with strict spatial partitioning. They remained in shallow vegetated areas adjacent to deep water, avoiding open deep water altogether.

Nile Crocodile nests at Lake St Lucia have been monitored since 1982, with mean nest abundance = 76.19 ± 6.42, range: 29-141. The macro-level heterogeneity of nesting habitats reflects the spatio-temporal diversity of the Lake St Lucia system, and is possibly unique within a single Nile Crocodile population. Changes in nest abundance and distribution were seemingly related to increased human disturbance and habitat transformation in the northern and southern parts of the lake. Hydrological variability, especially during droughts, combined with the state of the estuary mouth (i.e. open or closed), affected prey abundance/availability contributing to large variation (6.9-56.4%) in nest effort from 1982-2013. All nests were located close to freshwater streams or seepage areas. We confirmed the re-use of the identical nest-site by a female, while other females oviposited in nest-sites occupied by different females during previous years. Despite variable nest effort, the St

Lucia nesting population remains the largest recorded nesting population in South Africa, and least vulnerable to flooding.

The mean home range of Lake St Lucia nesting Nile Crocodile females (0.85 ha) was significantly smaller than non-nesting females (108.41 ha) during the nesting season. Activity levels and mean daily movements on the nest were 8.1 ± 2.5% and 213 ± 64 m, respectively, and increased to 47.9 ± 11.7% and 2176 ± 708 m during the post-nesting period. Overall levels of nest fidelity were 82.8 ± 11.7%, which increased to 87.3 ± 7.8% at night. The highest nest fidelity recorded during incubation was 99.7% over a 96 day period.

We captured 4305 photographs of 19 nest-guarding Nile Crocodile females over four years at Lake St Lucia. Seven nests (36.8%) were raided by the egg predators Water Monitors (*Varanus niloticus*) and Marsh Mongooses (*Atilax paludinosus*), on average 12.1 ± 6.2 days subsequent to trap camera employment. All females settled back on the nest following the first predation event and on average, females returned to their nests three times ± 0.8 between nest raids before finally abandoning the nest. Nest raids continued on average 5.9 ± 1.6 days while on average 18.8 ± 4.0 raids per nest were recorded. Five females were captured by trap cameras liberating hatchlings. During the day females were almost never photographed on the nest, but during the late afternoon or early evening females moved onto the nest and continued to stay there during the night. Females always defended their nests aggressively against non-human intruders.

We found homing behaviour in a translocated adult female Nile Crocodile at Lake St Lucia. Following release, the individual moved a total distance of 178.3 km over 136 days (mean daily movement = 1311 ± 207 m), compared with 60.4 km (mean daily movement = 444 ± 32 m) for the identical time period the previous year. Homing movement was not continuous, but characterised by periods of extensive and directed mobility followed by prolonged periods of inactivity associated with freshwater or low salinity habitats. The translocated crocodile displayed remarkable navigational abilities, even though this required negotiating complex habitat challenges including extensive areas of the lake that were either hypersaline or completely dry, resulting in frequent and extensive overland movements. On 14 Sept. 2012, the individual returned to the same freshwater pool where it was captured 136 days previous. This is the first study to confirm homing behaviour for Nile Crocodiles, and supports growing evidence that crocodilians and other ectothermic taxa possess complex navigational abilities.

Ndumo Game Reserve

We determined the NGR Nile Crocodile population size and changes in the size-class distribution within the population from 1971-2009. The NGR population increased from an absolute abundance of 348 (± 3.4) in the early 1970s to maximum absolute abundance of

992 (± 58.7) in 1994 as a result of a restocking program initiated in the late 1960s and early 1970s. The population structure is currently skewed towards sub-adults and adults, and the current population is in decline. This is a result of low recruitment levels in NGR that is unable to sustain the artificially high population size created by the restocking program. Also contributing to this decline is the poaching of crocodiles, and destruction of suitable and historical nest sites. Sex ratios were skewed towards females in juveniles and sub-adults and towards males in adults, while the overall sex ratio in the population was even. The current NGR Nile Crocodile population is estimated at an absolute abundance of 846 (± 263). We predict that the NGR Nile Crocodile population will continue to decline in the future as part of the natural process, but the decline will be accelerated on account of poaching, uncontrolled harvesting and destruction of nesting habitat. Precision and accuracy of population estimates were affected by water level, season and the use of different observers. Future surveys should occur in austral winter and at low water levels.

The distribution patterns of Nile Crocodiles in NGR, a naturally patchy floodplain environment, were collected using aerial survey data over the last 40 years. Although only 10,000 ha in size, NGR supports one of the largest wild crocodile populations in South Africa, largely because of landscape complementation with neighbouring Mozambique. Distributions within the NGR were influenced by landscape physiognomy and composition as well as connectivity and corridor quality. We conducted 40 diurnal counts at Lake Nyamithi in the NGR between 2009 and 2012 to quantify the effects of environmental conditions on crocodile distribution. Average monthly maximum temperature had an effect on the number of crocodiles in Lake Nyamithi, however environmental variables influenced different size classes of Nile Crocodiles to a varying extent. Anthropogenic disturbances influenced the functionality of the floodplain landscape negatively, with impacts on habitat use and connectivity. It is considered essential that a cross-border conservation program be initiated in order to conserve the current population of Nile Crocodiles in the greater NGR area.

We determined movement patterns of 50 Nile Crocodiles between 202-472 cm total length followed over 18 months in NGR using mark-resight, radio and satellite telemetry. Duration of radio transmitter attachment (131 ± 11.4 days) was significantly and negatively related to total length and reproductive status. Satellite transmitters failed after an average of 15 ± 12.5 days. Home range was calculated for individuals with 10 or more radio locations spanning a period of at least 6 months. There was a significant relationship between home range size and total length with sub-adults (1.5-2.5 m) occupying smaller, more localized home ranges than adults (> 2.5 m). The largest home ranges were for adults (> 2.5 m). Home ranges overlapped extensively suggesting that territoriality, if present, does not result in spatially discrete home ranges of Nile Crocodiles in NGR during the dry season. Larger crocodiles moved further and more frequently than smaller crocodiles. The reserve acts as a winter refuge and spring breeding site for an estimated 846 crocodiles which also inhabit the Rio Maputo during summer months. Nile Crocodile movement out of the reserve and into the Rio Maputo started in November and crocodiles returned to the reserve as water levels in the floodplain recede in May. Movement patterns of Nile Crocodiles show the role that the reserve plays in the conservation of the greater NGR-Rio Maputo Nile Crocodile populations.

We studied the nesting ecology of Nile Crocodiles at NGR from 2009 to 2012. Nesting effort in NGR was comparable to other populations at 18-22%. Historical data suggests that high water levels completely inundate nesting sites within the reserve once every 10 years while predation destroys on average less than 20% of nests annually and can be primarily attributed to the water Monitor Lizard. The number of crocodile nests located in NGR remained similar from 1964-2012 despite their population changes. Stocking programs have increased the number of Nile Crocodiles in the greater Maputo/Phongola rivers floodplain areas but these numbers may not be sustainable as the majority of nests appear to be outside of the reserve in unprotected areas.

Pongolapoort Dam

We investigated the effect of the impoundment of the Phongola river on the Nile Crocodile population numbers and status. Initial surveys from 1981 and 1989 described few crocodiles in the system. Currently Pongolapoort Dam contains a significant Nile Crocodile population that was previously not considered as substantial. A minimum population number of 273 Nile crocodiles was determined for Pongolapoort Dam in 2009-2010 using a combination of large-scale spotlight surveys. A combination of survey methods allowed for a population structure to be identified as having a minimum of 116 (42%) juveniles (< 1.2 m), 75 (27%) sub-adults (1.2-2.5 m), and 82 (30%) adults (> 2.5 m). The high percentage of juveniles suggests a reproductively active population, which is likely to support a viable population into the future. Continued long-term monitoring of the Nile Crocodile population in Pongolapoort Dam is required to determine if the impoundment continues to support a viable population and determine accurate and precise population estimates.

Generally impoundments negatively affect biodiversity and the integrity of the ecosystem. Consequently we investigated the historical and current spatial distribution and use of habitat by Nile Crocodile in Pongolapoort Dam. From the construction of the Pongolapoort impoundment in 1972, water levels fluctuated and the surrounding landscape had been altered. As a result the Nile Crocodiles residing in the area had to adapt to this changing environment. The first general distribution changed after dam wall completion when the dam began to fill. First distributional change was a movement out of the Phongola river gorge section into the newly flooded areas. After the Domoina floods in the 1980s the dam level rose by over 70%, and the crocodiles moved mainly to the current inlet section.

Although dam levels have fluctuated greatly within and between years, crocodiles appear to have adapted successfully here. The majority of the crocodile population is now found concentrated in the inlet section of the Pongolapoort Dam, utilizing the Phongola river in summer months and residing in the inlet section as historical basking sites during the winter months.

We investigated reproduction and nesting of Nile Crocodiles in Pongolapoort Dam, and in particular the effects of the impoundment on these. No previous reproductive effort had been documented prior to this study. Crocodiles congregated at a major basking site where the main tributary entered the dam during August with a 576% increase in numbers. This signalled the commencement of the breeding season. Females with transmitters made short trips upstream during this time. In November, with the first rains, the river rose and the majority of crocodiles moved up the inlet, and females established nests. In 2009 three major nesting areas were identified, two of which were located on the river inlet to the dam. Approximately 30 nesting females were identified during the 2009/2010 nesting season. All nesting areas identified had been used in prior nesting seasons by the presence of old shell fragments. Nests were located on a variety of substrate types, from clay formed through culluvial and fluvial deposits to course river sand. Several of the nests were predated by Water Monitor. Although the number of nesting females was greater than expected, during the study period there was a total recruitment failure of nests along the river due to a flash flood of the Phongola river in January 2010, destroying all nests prior to hatching. As several juvenile crocodiles were found during surveys, this preliminary study suggests that the Pongolapoort Dam Nile crocodile population has a relatively high potential reproductive out-put although their annual successes may vary greatly because of loss of nesting sites as a result of water level fluctuations and predation. It appears that the impoundment has generally had a positive impact on this Nile crocodile population recruitment although suitable nesting sites may become limited.

While KZN Nile Crocodile populations are very different, direct threats to crocodile habitat are similar. Indirect threats are not as well known. Continued monitoring of Nile Crocodile health is recommended. Nutritional, environmental contaminant, and epidemiological analyses are pending and will allow construction of health/nutrition indexes of wild crocodiles

CONCLUSIONS

Our study revealed numerous novel insights into the ecology, behaviour and health of Nile Crocodiles in KwaZulu-Natal, South Africa, and some of the findings may be applicable to other crocodilian taxa. We hope the results will guide the management and conservation of this threatened species and the waterbodies they are associated with. There are concerns about protection of nesting sites, increased anthropogenic disturbance, illegal poaching of crocodiles, and human wildlife conflict.

RECOMMENDATIONS FOR FUTURE RESEARCH

There is an urgent need for ecological, behaviour and health research of Nile Crocodile populations in Kosi Bay, Lake Sibaya and Hluhluwe-iMfolozi Park. Furthermore, the population declines, especially in unfenced populations such as Kosi Bay and Lake Sibaya, are driven by illegal killings for Nile Crocodile body parts, blood and fat. We need to understand the trade in Nile Crocodile products and neighbouring local people's attitude, behaviours and perceptions of Nile Crocodiles, in order to formulate effective conservation programmes for Nile Crocodiles in KwaZulu-Natal. In particular the following recommendations need to be implemented at all study sites for Nile Crocodile conservation:

- Continuation of annual Nile crocodile aerial surveys
- Continuation of annual Nile crocodile nesting surveys
- Limiting anthropogenic disturbance especially destruction of riverine vegetation from unsuitable agricultural activities and the resultant destruction of nesting sites
- Limiting competition for food resources
- Prevention of illegal poaching of live crocodiles
- Reduction of human wildlife conflict
- Reduction in use of led sinkers by fishermen to prevent lead poisoning of crocodiles.

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Fig. i. University of KwaZulu-Natal students involved in Nile Crocodile research (L-R Xander Combrink, Garreth Champion, Peter Calverley, Jon Warner; Mark Summers absent)

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LIST OF ABBREVIATIONS

KZN	KwaZulu-Natal
NGR	Ndumo Game Reserve
EKZNW	Ezemvelo KZN Wildlife

1 INTRODUCTION AND OBJECTIVES

1.1 Why crocodiles?

In the mid-19th Century, Frederick R.N. Findlay, noted that Lake St Lucia "swarmed with crocodiles". Since the onset of colonialism crocodiles were persecuted and eradicated with the sanctioned onslaught continuing until the introduction of the Reptiles Protection Ordinance No. 32 of 1968.

Crocodilians (crocodiles, alligators, caimans, gharials) are top predators as well as charismatic and iconic megafauna within aquatic ecosystems throughout the tropical and subtropical world (Thorbjarnarson 1992, Ross 1998, Combrink 2014). They are implicated in positive effects in their environments as keystone species (Craighead 1968, King 1988, Ross 1998), but as a result of their long life span and high trophic status, are susceptible to exposure and accumulation of environmental contaminants released into their habitats (Rainwater et al. 2007, Guillette and Edwards 2008). Today, crocodilians are increasingly recognised as good indicators in ecosystem monitoring and restoration programmes (Mazzotti and Brandt 1994, Mazzotti et al. 2009, Lane et al. 2013), have significant commercial value for tourism (Ryan and Harvey 2000), the leather industry (MacGregor 2002), and sustainable use conservation programmes (Da Silveira and Thorbjarnarson 1999, Thorbjarnarson 1999, Fukuda et al. 2011), and as a flagship species, have the potential of being a catalyst in wetland conservation programmes (Shirley et al. 2009, Combrink 2014).

However, despite their ecological importance, indiscriminate killing and commercial overexploitation combined with severe habitat loss have resulted in many crocodilian species suffering drastic declines in numbers and reductions in distribution, with several species brought to the brink of extinction (Ross 1998, Combrink 2014). Despite the recovery of numerous species and populations following strict protection (Fukuda et al. 2011), numerous Nile Crocodile (*Crocodylus niloticus*) (Fig. 1.1) populations in South Africa appear to be at risk. Kruger National Park (KNP) and Loskop Dam have experienced large-scale mortalities from broad-scale environmental deterioration leading to contamination (Botha et al. 2011, Ferreira and Pienaar 2011, Lane et al. 2013). Threats to Nile Crocodiles in the Lake St Lucia estuarine system, KwaZulu-Natal province (KZN), are more related to disturbance, habitat transformation, direct killings and hypersaline conditions (Pooley 1973, 1982, Leslie 1997, Combrink et al. 2013). However, the population may not be secure from contaminants due to the increase of human settlements in the catchment combined with agriculture (Fergusson 2010) and potential mining (Combrink 2014).

Knowing the size and structure of a population is typically seen as a prerequisite for effective management of a species (Chabreck 1966; Games et al. 1992; Caughley and Sinclair 2006; Shirley et al. 2012). Changes in such populations should also be monitored in order to achieve successful dynamic management with changes being accounted for by driving factors such as changes in habitat parameters (Primack 2000). Although aerial counts were used to monitor the Nile Crocodile population at Ndumo Game Reserve (NGR) and in the Lake St Lucia estuarine system since the 1960s and 1970s (Pooley 1969, 1974, 1982, Fawcett 1987, Leslie 1997), there is a paucity of information on ecological aspects such as crocodile movements and activity budgets, home range, nesting behaviour and population status, particularly within the context of the recent prolonged drought. The aim of this study was to address these issues and provide management recommendations. This study forms part of a larger bioregional research programme of the Nile Crocodile in Zululand, South Africa, including ecotoxicology and feeding ecology components.

Figure 1.1 Nile Crocodile at Lake St Lucia.

1.2 Status and distribution of the Nile Crocodile in Africa

The Nile Crocodile is considered widely distributed throughout much of Africa, but survey data are non-existent or insufficient for 25 of the 42 countries within its range, particularly in West and Central Africa (Fergusson 2010, Combrink 2014). Recent survey efforts in West (Garba 2008, Shirley et al. 2009) and North Africa (Salem 2010, Shirley et al. 2012) are encouraging and will improved conservation efforts (Combrink 2014).

Despite its extensive biogeography, numerous populations have been depleted during the 1950-1970s (Cott 1961, Gans and Pooley 1976, Pooley 1980) and the species has been extirpated from at least three countries, i.e. Algeria, Comoros and Israel (Leslie 1997, Combrink 2014). Strict protection through national legislation and international trade conventions (CITES) has resulted in the recovery of numerous populations throughout its range (Fergusson 2010). The most recent IUCN Red List assessment was Lower Risk/Least Concern (1996), but the IUCN recognised the need for an update (Combrink 2014).

A metadata analysis of all crocodile surveys conducted in Africa since 1955, concluded that Nile Crocodile populations are declining, despite an increase in the 1990s (Combrink 2014). This trend seemed to be mainly driven by the commercial value of the species. The study included a survey database of Africa which will assist researchers in future survey planning. It also highlighted the importance of knowledge sharing and regional planning of conservation efforts (Laínez 2008, Combrink 2014).

Recently Hekkala et al. (2011) revealed a cryptic evolutionary lineage within the Nile Crocodile based on phylogenetic analysis, and showed that the two Nile Crocodile lineages are distant relatives, but not sister taxa, and proposed that *C. suchus* should be elevated as a distinct species (Combrink 2014). Both lineages apparently occurred historically in the lower Nile River, and in Sudan as recently as the 1920s. The newly discovered evolutionary lineage of African *Crocodylus*, with a predominately western African distribution, seems to be particularly vulnerable to local extinction due to its restricted occurrence, relative rarity and threats such as the bushmeat trade, illegal harvest of skins, and wetland transformation of destruction (Hekkala et al. 2011, Combrink 2014).

1.3 Status and distribution of the Nile crocodile in South Africa

Although South Africa probably never supported Nile Crocodile populations comparable in size with those of equatorial Africa, significant populations formerly existed in rivers of the Limpopo and Mpumalanga Provinces, as well as wetlands, lakes, rivers and estuaries of coastal KwaZulu-Natal as far south as the Dwesa-Cwebe Nature Reserve in the Eastern Cape (Pooley 1976, Loveridge 1980, Blake and Jacobsen 1992, Feely 2010, Combrink

2014). Prehistoric museum specimens of teeth and skulls suggest a further range extension earlier than the 16th century southwest to the area between the Keurbooms and Keiskamma Rivers (Feely 2010). Nile Crocodile have been extirpated from the Eastern Cape since 1903 (Jacobsen 1988), but in 1977 six juveniles from Zululand were reintroduced into the Kobole River of the Dwesa-Cwebe Nature Reserve (Pooley 1980, Jacobsen 1988, Feely 2010, Combrink 2014).

The two largest and possibly secure Nile Crocodile populations remaining in South Africa today are KNP and the Lake St Lucia estuarine system (Combrink 2014). NGR, a very important and large population during the mid-1990s (992 ± 59 individuals) is currently declining, and predictions are the decline will accelerate in future due to illegal killings and destruction of nest-sites (Calverley and Downs 2014b). The Pongolapoort Dam was until recently not considered a substantial population as very low densities were encountered (0.06 crocodiles km^{-1}) during a survey along the Phongola river in the 1980s (Jacobsen 1984). Champion (2011) determined a “conservative estimate” of the dam population at 273 Nile Crocodiles, but the population could be considerably higher (Myburgh, pers. comm., CM Phongolo Nature Reserve). Champion (2011) recorded 30 nests during the 2009/10 nest season and the reproductive frequency of this population might be considerably higher compared with Lake St Lucia and NGR (Calverley and Downs 2014b), highlighting its conservation importance (Combrink 2014).

Numerous smaller and fragmented populations persist in the Zululand region of KZN, e.g. Tembe Elephant Park, waterbodies in iSimangaliso Wetland Park (Kosi Bay, Lake Sibaya, Nsumo Pan, Lake Bhangazi North and South), Enseleni River, Lake Mzingazi, Nyoni River, Hluhluwe-iMfolozi Park, Tugela and Zinkwazi Rivers (Combrink 2014).

At least two of the six juveniles released in the Dwesa Nature Reserve in the Eastern Cape have survived to adulthood. At least three successful breeding events have been recorded which has resulted in one surviving sub-adult (Combrink et al. 2011, Combrink 2014).

Small and fragmented populations persist in rivers and dams in Limpopo and Mpumalanga provinces outside of KNP, e.g. Flag Boshielo Dam and the Limpopo River. Given current pressures, the continued survival of most of these smaller populations is uncertain (Combrink 2014).

As a result of the depletion of Nile Crocodile populations and escalating threats to the species, their conservation status was classified as Vulnerable in the first South African Red Data Book on Reptiles and Amphibians (McLachlan 1978) and maintained as such in the second revision (Jacobsen 1988) as well as the Atlas and Red List of Reptiles (Marais 2014, Combrink 2014). In order to control trade, Nile Crocodile was listed as a CITES Appendix II species in South Africa under the ranching provision (Resolution Conf. 11.16) in 1994.

Although no recent estimates are available for the total Nile Crocodile populations in South Africa, recent studies suggest that a number of populations are decreasing (Marais and Pooley 1991, Myburgh 2007, Ashton 2010, Botha et al. 2011, Combrink et al. 2011, Ferreira and Pienaar 2011, Woodborne et al. 2012, Calverley 2013, Calverley and Downs 2014b, Combrink 2014).

Twenty years ago, the South African Nile Crocodile population was estimated at 9500 non-hatchlings, based on counts conducted by Jacobsen (1991), Blake and Jacobsen (1992) and Blake (1990)(Combrink 2014). However, comprehensive surveys are required to update the status of Nile Crocodile and to formulate a national conservation strategy for the species, particularly as many of the subpopulations are isolated and all are vulnerable (Combrink 2014).

Nile Crocodile habitat outside of protected areas in southern Africa is becoming increasingly threatened and is in urgent need of protection while populations within protected areas are declining as a result of direct and secondary human activities (Pooley 1969, Combrink 2004, Ferreira and Pienaar 2011; Wallace et al. 2013, Champion 2011, Calverley 2013, Combrink 2014). Public perception of crocodiles in general and their indiscriminate feeding habits on both livestock and humans make colonization of previously occupied areas improbable and the recovery of populations outside of protected areas therefore unlikely; consequently the protection of crocodiles within protected areas is essential.

1.4 Regional threats to Nile Crocodiles

In the past, Nile Crocodile populations in South Africa were reduced as a result of exploitation for their skins, but more recent threats include human competition with their aquatic habitat in a country with relatively low rainfall but large formal and informal agricultural sectors (Jacobsen 1988, Combrink 2014). Other threats include the construction of dams in rivers, wetland transformation, pollution of rivers, degradation of lakes, estuaries and rivers, uncontrolled water abstraction (or release that may flood nest-sites, e.g. downstream of the Pongolapoort Dam) for agricultural and other uses, altered river flow pathways, the release of pesticides or herbicides in waterbodies, the killing of crocodiles by farmers in rivers or dams, on or adjacent to their property (Pooley 1969, Jacobsen 1991, Blake and Jacobsen 1992, Calverley 2013, Combrink 2014).

Direct conflict between humans, their livestock and Nile Crocodiles invariably leads to sanctioned or illegal killing of crocodiles (Ward 1985, Calverley 2013, Calverley and Downs 2014b, Combrink 2014), as well as the deliberate destruction of nest-sites (Bruton 1979, Ward 1985, Ward 1986, Calverley and Downs 2014b, Combrink 2014). Exotic invasive vegetation (e.g. Triffid Weed, *Chromolaena odorata*), especially when forming dense stands at nest-sites reduces crocodile nesting and the shading effect might alter sex ratios of hatchlings (Leslie and Spotila 2001). Crocodile eggs, blood, fat, brains and other organs have high value in the traditional medicine market (Ward 1985, 1987) and this demand has led to their decline in some areas. Other causes of mortalities include fishtraps (Kyle 2008), wire snares (Calverley and Downs 2014a,b, Combrink and Warner, pers. obs.), baited hooks (Combrink, pers. obs.), gillnetting (Ward 1985, Kyle 1999, 2008, Calverley and Downs 2014a), and the bioaccumulation of toxins following the release of uncontrolled pollution from factories, mines and unprocessed sewerage in rivers and dams (Myburgh 2008, Botha et al. 2011). Such escalating environmental problems are related to the outbreaks of pansteatitis and subsequent crocodile deaths in Loskop Dam and the Olifants, Letaba and Sabie Rivers in KNP (Myburgh 2008, Myburgh and Botha 2009, Ashton 2010, Botha et al. 2011, Ferreira and Pienaar 2011, Woodborne et al. 2012, Lane et al. 2013). Habitat destruction, development and disturbance along rivers and other natural corridors (e.g. floodplains) has led to increased fragmentation between sub-populations (Calverley and Downs 2014a) and potential loss of genetic diversity of Nile Crocodiles (Champion 2011, Calverley 2013, Combrink 2014).

1.5 Lake St Lucia

The Nile Crocodile has a broad distribution in Africa and Madagascar, but populations have been depleted throughout much of its former range, including local extinctions in three countries (Fergusson 2010, Combrink 2014). Formerly widespread throughout the waterbodies of eastern South Africa, viable Nile Crocodile populations are now restricted to three disjunct protected areas in Limpopo, Mpumalanga and KwaZulu-Natal. Growing evidence suggests that even protected populations are declining (Ashton 2010, Botha et al. 2011, Combrink et al. 2011, Ferreira and Pienaar 2011). As a result of depleted populations and escalating threats, the conservation status of the Nile Crocodile in South Africa is listed as Vulnerable (McLachlan 1978, Jacobsen 1988, Marais 2014, Combrink 2014).

Lake St Lucia estuarine system, Africa’s largest estuary (Begg 1978) and first estuary in the world declared a protected area (Perissinotto et al. 2013), was listed a Ramsar Wetland of International Importance in 1986 and included in the iSimangaliso Wetland Park World Heritage Site in 1999 (Porter 2013, Combrink 2014). Lake St Lucia contains the largest Nile Crocodile population in a single waterbody in South Africa, hosts one of only a few remaining viable breeding populations in the country and might be the largest Nile Crocodile estuarine population (Combrink et al. 2013). Consequently, its population status is of heightened conservation interest, especially due to a recent prolonged drought (Combrink 2014).

1.6 Ndumo Game Reserve

NGR in northeast KwaZulu-Natal, South Africa, is one of the oldest game reserves in South Africa (Calverley 2013). Established in 1924 as a sanctuary for Hippopotami (*Hippopotamus amphibius*), the reserve coincidentally protects habitat equally suitable for Nile Crocodiles. This unintentional protection did not extend as far as the animal itself and Nile Crocodiles were viewed as vermin and actively persecuted both inside and outside of game reserves in South Africa until 1969 (Leslie 1997, Wallace et al. 2011). In an effort to restock game reserves in KwaZulu-Natal with Nile Crocodiles, a breeding centre was established in NGR in the 1960s and over 1200 yearling crocodiles were released into the reserve from the late 1960s to the early 1970s (Pooley 1982). A monitoring program was initiated in 1971 by Pooley and conducted sporadically thereafter as successive counts showed a gradual population increase. The NGR Nile Crocodile population was thought to be at an acceptable level to implement a harvesting program as early as the 1990s (W.S. Mathews pers. comm., Calverley 2014).

1.7 Pongolapoort Dam

South Africa is a semi-arid, water poor country, with freshwater being a very limited and highly sought after resource (Steyn 2008, Champion 2011). The flow rates of Southern Africa's river systems are sporadic as a result of the semi-arid climate of the region (Jacobsen and Kleynhans 1993). Furthermore, river systems in South Africa have been and continue to be drastically degraded (Kingsford et al. 2011, Ferreira and Pienaar 2011). This is a result of impoundment, inter-basin transfers, catchment degradation, water abstraction, pollution and introduced species (O'Keefe et al. 1989). As a result of this and the increasing pressure for water resources, the impoundment of rivers in South Africa is often unavoidable in order to create permanent water supplies for anthropogenic use (Jacobsen and Kleynhans 1993). River impoundment by dams has great effect on downstream waterways, disrupting hydrological processes, effecting water quality, geomorphology, ecology and ecosystem services (Heath and Plater 2010). The degradation of South Africa's river systems and the associated riverine habitat has threatened many biota, which are dependent on these habitats (Roux et al. 2008). The designing of protected areas to conserve freshwater biodiversity has been seldom considered (Nel et al. 2009). The negative effects of such impoundments, lowering river ecological integrity, are undeniable (Zhai et al. 2010). However, despite this loss of riverine habitat, there is now a need to correctly manage the existing impoundments to conserve the freshwater species now threatened as a result of habitat degradation (Champion 2011).

An example of the potential negative and positive effects of an impoundment on a riverine system in terms of conservation is Pongolapoort Dam, KwaZulu-Natal, South Africa (Champion 2011). The formation of this dam has disturbed the natural functioning of the lower Phongola river flood plain, threatening a number of aquatic species found there (Mwaka et al. 2003). It has however also created a new stable fresh water habitat and sanctuary for a number of species. Such species include common hippopotamus, Nile Crocodile and tiger fish *Hydrocynus vittatus* all of which are listed on the IUCN red list of threatened species (Combrink et al. 2011). Although these species occur downstream of the dam, those populations are currently at great risk as a result of over exploitation, poaching and habitat destruction (Calverley and Downs 2014a,b).

Pongolapoort Dam is one of South Africa's largest man-made water bodies, and is surrounded by several game reserves (state, and/or privately owned and managed) (Champion 2011). Pongolapoort Dam was completed in 1972, however only first filled significantly in 1984 (13 to 86%), as a result of large-scale floods during Cyclone Domoina (Rossouw 1985; van Vuuren 2009a). The exact number of crocodile contained in the Dam after construction is unknown as is the number of crocodiles that may have emigrated down from the upper Phongola river. Jacobsen (1991), however, did survey the upper Phongola river and the northern sections of the Pongolapoort Dam during 1981 and 1989, recording 11 and 16 crocodiles respectively. The Dam has, in recent years, been labelled a "white elephant" due to its relatively low economic use and has been steeped in controversy, as a result of its politically driven construction under the previous government of South Africa (van Vuuren 2009a). Despite this, from a conservation point of view, it may now however have great purpose, potentially having one of the few unthreatened and viable Nile crocodile populations in South Africa. In order to fulfil this conservation potential, it is imperative that knowledge on this crocodile population in terms of numbers and demography be obtained (Da Silveira et al. 1997).

The Pongolapoort Dam is South Africa's third largest dam by volume, with a holding capacity of 2 500 million m^3 of water (van Vuuren 2009b). Although large, about 45% of the dam perimeter has little suitable habitat for Nile crocodiles (Champion 2011). The dam is relatively new, completed in 1972 but only first filled significantly in 1984, as a result of large-scale floods during Cyclone Domoina (Mkwaka et al. 2003). The Pongolapoort Dam was completed on the Phongola river and this section of river supported a relatively low, however unquantified, number of Nile crocodiles prior to dam completion (Jacobsen 1991). In addition the majority of the crocodiles occurred in the gorge section prior to impoundment (K. Landman pers. comm.; Champion 2011).

1.8 Aims and objectives

Crocodilians are increasingly being viewed as "sentinel species" because as top predators they are good models for studying environmental threats to their respective ecosystems and the associated food web therein. Recent Nile Crocodile deaths in South Africa have revealed the vulnerability of the species – and the aquatic ecosystems they inhabit – and highlighted the need for urgent study of crocodile populations. As a top predator, crocodiles are a valuable ecosystem component but also a source of management concern due their potential threat to humans. Our research included the following components: spatial ecology and habitat use; diet, foraging ecology and nutrition; reproduction and nesting; population ecology; external threats to crocodiles (e.g. poaching, environmental contaminants); and conservation management strategies to contribute to the protection and understanding of Nile Crocodiles in north eastern KwaZulu-Natal (Zululand), and Southern Mozambique.

In South Africa, three of the 15 sites inscribed on the list of Wetlands of International Importance are located within the iSimangaliso Wetland Park (formerly the Greater St. Lucia Wetland Park), a UNESCO World Heritage Site. The Lake St Lucia system (155,000 ha), Lake Sibaya (7,750 ha) and the Kosi Bay system (8,000 ha) are critical wetland areas both from a local socioeconomic perspective and a global biodiversity viewpoint (Bate et al. 2011). A keystone species is the Nile Crocodile, a Threatened species in South Africa and flagship species for the iSimangaliso Wetland Park (Meffe and Carroll 1997; Branch 1998; Taylor et al. 2007). The Nile Crocodile is the top aquatic predator within these iSimangaliso water bodies. Two other populations in the nearby Pongolapoort (Jozini) Dam and NGR are also of importance as part of the Zululand metapopulation. This north eastern KwaZulu-Natal Nile Crocodile population (>1000 individuals) is of global importance, as comparable subtropical populations of the species do not exist. However, despite the environmental importance of crocodiles, little is known regarding the ecology, life history, and population dynamics of Nile Crocodiles in South Africa. Less well understood is the impact and degree of specific anthropogenic and environmental threats to the species; threats that have far reaching ramifications for aquatic ecosystems and food webs. Given confirmed and suspected recent die-offs of Crocodilian populations, both within and outside of South Africa, Nile Crocodiles merit serious scientific study if the species and its wetland habitats are to be adequately protected and managed.

The recent die-off of crocodiles in the Kruger National Park and at Loskop Dam have revealed the vulnerability of the species and highlighted the need for urgent study of Nile Crocodile populations in southern Africa. The KZN population is second in size only to the Kruger population, and the governing conservation organization, EKZNW, has the obligation to conserve this important population effectively (Taylor et al. 2007). As a top predator the

Nile Crocodile is a valuable ecosystem component but also a source of management concern, as individuals can cause problems when they leave protected areas (Taylor et al. 2007).

If crocodile populations are sick or in decline, it is a serious reflection on the health of their associated water bodies and other organisms in the food web. Mitigation of threats to crocodiles is important for protection of aquatic habitats at an ecosystem level and has a positive “trickle down” effect on sympatric aquatic species. Lake St Lucia and environs represents one of only three major breeding areas for the Nile Crocodile in South Africa (Branch 1988). Crocodiles require large areas of undisturbed wetland (e.g., Lake St Lucia) to maintain large, stable populations (Botha 2005). As water levels fluctuate, movements of crocodiles within and out of particular areas become ecologically important to individuals and populations (Swanepoel 1999). Environmental fluctuations are suspected to affect the demographic stability of crocodile populations because of their direct and indirect influences on recruitment, mortality and food availability (Cott and Pooley 1972; Pooley 1982; Leslie 1997).

New breakthroughs in Crocodilian research have showed links between environmental contaminants and gene expression (Cramp 2008), decreased reproduction and development (Kohno et al. 2008) and trace element concentrations in individuals (Almli et al. 2004). Stable isotope ratios of carbon and nitrogen can be used to trace food pathways in crocodiles and determine the working of trophic networks (Kelly 2000). Zululand, Southern Limpopo, Eastern Mpumalanga and Southern Mozambique Nile Crocodiles (hereafter referred to as the study area) need to be studied within these frameworks, as their aquatic habitats are subjected to a variety of environmental contaminants (e.g., the suspected botulism outbreak at the St. Lucia sewage works, pesticide runoff from sugarcane farms, eutrophication, mercury ingestion from fish, etc.). Because crocodiles are top predators in St Lucia, establishing health indices for individuals will yield direct information about overall ecosystem health. Biochemistry and physiological research on crocodiles in the study area combined with the proposed ecological research will significantly update the knowledge of Nile Crocodiles and allow hidden threats to the species to be identified and moderated. The Crocodile Centre in St. Lucia is an asset to crocodile research in the greater iSimangaliso area, as it allows for comparative ecophysiological studies with captive “baseline” crocodiles of various age classes and species.

The conservation and management of Nile Crocodiles requires working understanding of their ecology from scientific study so that long-term population viability can be facilitated and risks to humans can be mitigated. The proposed crocodile research is also in response to research needs identified in the crocodile management strategy (Taylor et al.

2007). It is hoped that this focus which is directed at management needs identified in this strategy will provide input and direction for management.

This project aims to address the aforementioned conservation needs of Nile Crocodiles in the study area by gathering sound data on a suite of ecological, physiological, epidemiological and genetic components for the species. Additionally, it aims to analyze the specific threats to crocodiles (human-, environmental- and disease-related) while simultaneously generating novel solutions of risk reduction for both sides of the crocodile-human interface. Information from field and lab studies will be used to produce predictive models of population viability and change that are needed to support proper long-term management of Nile Crocodile populations in the study area.

The study is a programme that included researchers of diverse scientific backgrounds and fields of expertise from various institutions. Such a collaborative programme is needed to analyze and understand the complexity of the Zululand and Southern Mozambique Nile Crocodile populations and all the biological and social aspects that pertain to them. Given recent novel threats to the species and the global importance of the these populations, this research has the potential to significantly expand current understanding of Crocodilian biology and provide information that will facilitate pragmatic, long-term Nile Crocodile protection as well as the water systems they inhabit. As a programme it is divided into several interlinked components: Spatial Ecology and Habitat Use; Diet, Foraging Ecology and Nutrition; Reproduction and Nesting; Population Ecology; External Threats (including Condition and Health); Repatriation; and Conservation Management. These will contribute to understanding the importance of Nile Crocodiles to water health, and aquatic ecosystems in the greater study area.

The specific aims were to

1. Address the conservation needs of Nile Crocodiles in Zululand, and Southern Mozambique by gathering a suite of ecological, physiological, epidemiological and genetic data. Given recent threats to the species and the global importance of these populations, this research will expand current understanding of crocodilian biology and facilitate long-term Nile Crocodile protection; and
2. To use crocodiles as indicators of ecosystem health.

2 METHODS

2.1 Study sites

2.1.1 Lake St Lucia estuarine system

The Lake St Lucia estuarine system, the oldest protected estuary in the world (Whitfield et al. 2006) is situated in north-eastern South Africa in the province of KZN (Fig. 2.1, Combrink 2014, Combrink et al. in prep. a,b). At ~67 km in length, which includes the ~27 km long Narrows channel that connects the lake to the ocean, and an average of 6 km in width when filled to capacity, it is the largest estuarine system in Africa (Cowan 1997), but nonetheless very shallow with a mean depth of 0.98 m. Daily mean water temperature measured in the Narrows and Charters Creek during the four year study period (2009 to 2012) was 23.7°C ± 0.1 S.E., range 13.6-30.29°C, but water temperatures vary across the lake, particularly with changing depth. Daily mean air temperature measured at St Lucia village was 21.5°C ± 3.4 SD, range 12.15-29.14°C. The minimum and maximum water and air temperatures recorded during the study were 10.6°C and 40.6°C and 6.6°C and 44.2°C, respectively (Combrink 2014).

The Lake St Lucia system is dynamic and driven by varying environmental and ecological processes, each occurring at differing spatial and temporal scales (Taylor 2006, Combrink et al. in prep. a,b). A tidal channel (~27 km long, 100-200 m wide) known as the Narrows, connects the main St Lucia estuarine lake body to the Indian Ocean. At mean water level, Lake St Lucia is ~35 000 ha with a shoreline of ~400 km (Taylor et al. 2006). The key hydrological and geomorphological features are freshwater inputs from groundwater seepage and five small streams (Mkhuze, Mzinene, Hluhluwe, Nyalazi and Mphathe), salinity levels from seawater input at the estuary mouth, water loss and gain in the large shallow lake basin from evaporation and rainfall, and the role of the Mfolozi River and its state of connectivity to the system (Taylor 2006). The complex interactions of these features have a profound impact on the reproduction, growth, distribution and survival of the crocodile population through food availability – mammals, birds, reptiles, fish, amphibians and macro invertebrates (Mazzotti et al. 2009), and habitat features such as nesting and winter basking sites (Combrink 2014, Combrink et al. in prep. a,b).

Unlike fish and other true aquatic animals, Nile Crocodiles respond behaviourally to extreme conditions such as hypersalinity, droughts and depressed estuarine functioning by moving from the lake to more favourable microhabitats such as freshwater shoreline refugia, swamp forests and burrows (Pooley 1982b, Combrink et al. 2013, Combrink 2014, Combrink et al. in prep. a,b). Nonetheless, the lake experienced unprecedented fluctuations in water level and salinity in the period 2002 to 2011 and there was a need to assess the extent that the prolonged closure of the estuary mouth might have had on the crocodile population (Combrink et al. in prep. a,b).

Freshwater is lost by outflow through the estuary mouth (when open), but the main lake basin of the estuary is not affected by tides (Combrink 2014, Combrink et al. in prep. a,b). Average annual rainfall is 911 mm (Taylor and Fox, Ezemvelo unpublished data) with a distinct dry/wet cycle of about 10 years (Tyson and Preston-Whyte 2000). Large salinity fluctuations may occur when the mouth is open (Blaber 1980, Pitman 1980), and seawater circulating within the estuarine system results in a geographical salinity gradient ranging from seawater at the mouth to fresh water at the stream input localities. When stream flow into the estuarine system subsides during droughts, salt is concentrated by evaporation, leading to hypersaline conditions in the northern reaches of the lake furthest from the mouth. Historically, the Mfolozi River and St Lucia estuary shared a common mouth, but accelerated sediment accumulation (primarily from the Mfolozi) promulgated a decision to manually separate the mouth of the Mfolozi in 1952. In 1956, a separate mouth was opened for the St Lucia estuary (Taylor 2011, Combrink 2014, Combrink et al. in prep. a,b).

In July 2002 the estuary mouth closed, with the exception of seven months in 2007, resulting in a constant salt load but dynamic salinity levels dependent on water volume (Taylor 2006, Combrink 2014, Combrink et al. in prep. a,b). In 2003 as a result of below average rainfall and little input from the five streams, the lake divided in a number of compartments with varying salinities, increasing towards the north, and by June 2006 approximately 90% of the lake surface was exposed and dry (Whitfield and Taylor 2009). During this time most Nile Crocodiles were either concentrated in the south of the system in the Narrows, or they utilised freshwater seeps adjacent to swamp forests, often with associated burrows (Combrink 2014). The removal of 5000 ha of exotic plantations on the Eastern Shores contributed to the rehabilitation of groundwater discharge and subsequent shoreline seepage creating favourable habitats (refugia). Vrdoljak and Hart (2007) suggested that such seepage during periods of low lake levels appears to provide a stable freshwater habitat for freshwater fishes providing a persistent supply of fresh water, even during times of extreme droughts. Good rainfall in Dec. 2010, Jan., July and Nov. 2011 as well as Cyclone Irina passing ~125 km offshore in March 2012 resulted in a restoration of water coverage throughout the lake system (Combrink et al. in prep. a,b). During March 2012 a beach spillway was established between the Mfolozi River and St Lucia estuary using a tracked excavator and on 6 July 2012 the Mfolozi River were re-linked with the St Lucia estuary after 60 years (Combrink 2014).

The Lake St Lucia estuarine system is situated in the north-eastern corner of KZN (Fig. 2.1, Combrink 2014, Combrink et al. in prep. a,b). It consists of a ~35,000 ha main lake basin, 6 km wide when filled to capacity, and a shoreline length of ~400 km (Taylor et al.

2006). The system is ~67 km in length including the Narrows, a ~27 km, 100-200 m wide tidal channel connecting the lake to the Indian Ocean. Five seasonal streams (Mkhuze, Mzinene, Nyalazi, Hluhluwe and Mphathe) flow into the lake system (Stretch and Maro 2013) and two perennial streams (Nkazana and Tewati) drain groundwater to the lake shoreline (Taylor et al. 2006). The Mfolozi River, just south of the estuary, carries more water than all other rivers entering St Lucia combined (Taylor 2011). However, development in the Mfolozi catchment, sugar cane farming and canalisation/drainage of the Mfolozi Swamp has greatly increased the sediment load reaching the estuary (Van Niekerk and Huizinga 2011). In 1952, a new mouth was dredged for the Mfolozi River, and in 1956 a separate mouth was mechanically opened for the St Lucia estuary (Taylor 2011, Combrink et al. in prep. a,b).

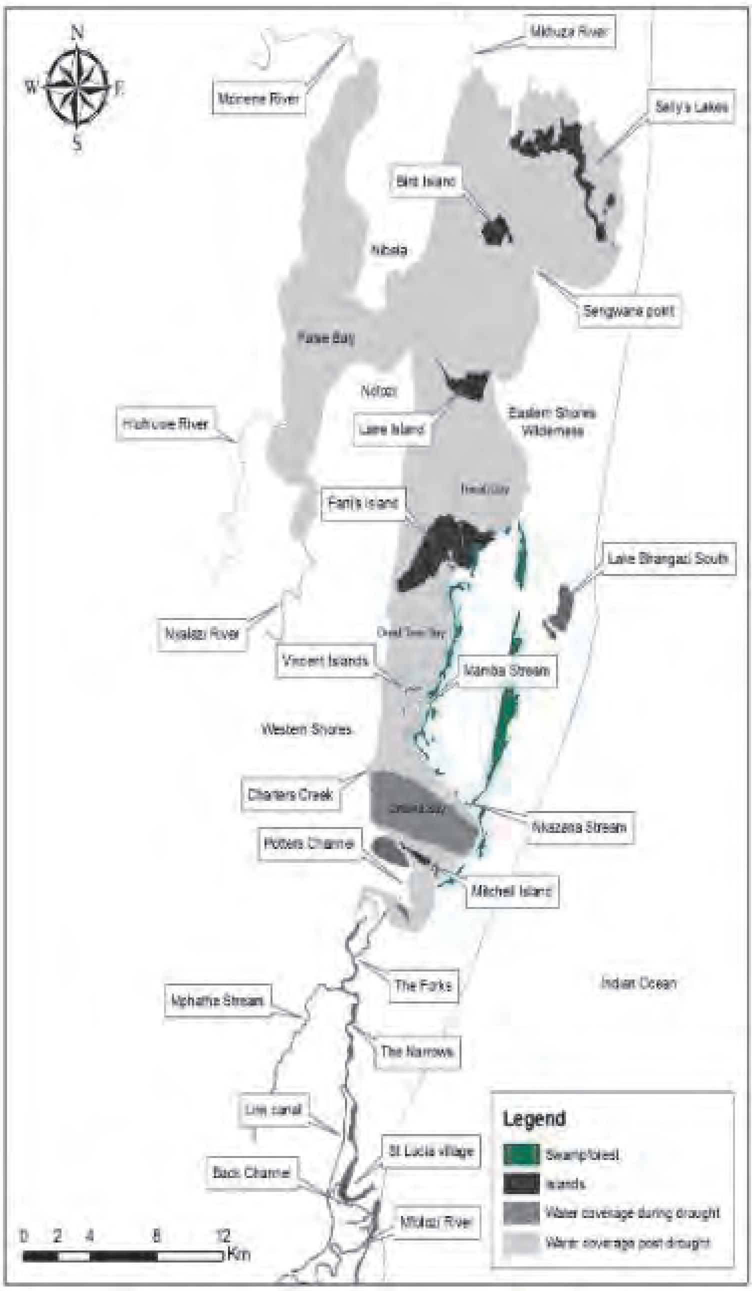


Figure 2.1 The Lake St Lucia estuarine system (from Combrink 2014).

2.1.2 Ndumo Game Reserve

NGR is a relatively small (10,000 ha, Fig. 2.2) reserve in northeast KZN, situated in the Mozambique Coastal Plain (26°52'01.1"S 32°15'01.2"E; datum = WGS84). The reserve has an elongated trapezoid shape with the longitudinal east-west axis (Calverley, 2013). The Usuthu River forms the northern boundary of the reserve and the southern boundary of Mozambique, while the Phongola river and its associated floodplain run along the eastern boundary of the reserve. The confluence of these two major river systems in the north east corner of the reserve and the flat nature of the Mozambique Coastal Plain combine to inundate over 40% of the NGR during times of high rainfall (Pooley, 1982). The Usuthu River forms the northern boundary of the reserve and the southern boundary of Mozambique while the Phongola river and floodplain run along the eastern boundary of the reserve. The confluence of these two river systems in the northeast corner of the reserve, and the flat nature of the Mozambique Plain, result in large tracts of the reserve becoming inundated with flood waters during times of high rainfall (Pooley, 1982) or water releases from Pongolapoort/Jozini Dam (Heath and Plater, 2010).

The Usuthu River feeds two pans; Banzi and Shokwe (Fig. 2.2, Calverley 2013, Calverley and Downs 2014a,b, 2015a,b); Banzi Pan is the largest pan in the NGR at 270 ha. Upon entering the reserve, the main course of the Phongola river bifurcates forming an old and a new course. The old course meanders through the western periphery of the floodplain following a contour at the base of Ndumo Hill while the new course carves its way through the eastern periphery of the floodplain. The old and the new courses are linked through a bifurcation of the old course in the region of Lake Nyamithi as well as by numerous feeder channels and Hippopotamus pathways which traverse the floodplain linking all of these courses with one another as well as with 10 permanent and ephemeral pans (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b).

The largest permanent pan in the Phongola floodplain is Lake Nyamithi (157 ha; Fig. 2.2), which also has the highest density of Nile Crocodiles in the NGR (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b) and served as our focal point of study. Lake Nyamithi is irregularly ovular in shape with the 4.2 km longitudinal axis running east to west and a maximum width of 700 m. During summer, high water levels the pan may reach depths of 5 m while the average depth during winter is less than 1 m (Pooley, 1982; T. Forbes and N. Demetriades, personal communication). The large surface area combined with the relatively shallow nature of the pan results in warmer water temperatures in Lake Nyamithi than in the deeper and shaded channels of the Phongolo River, particularly during the winter months (Pooley, 1969). The northern shore is characterized by a fringe forest of Fever Trees (*Acacia xanthophloea*) with gently sloping lawns of Couch Grass (*Cynodon* *dactylon*). The southern shore is somewhat more rocky and steeper in slope. Lake Nyamithi is fed by the seasonal Balamhlanga Stream from the west that creates a narrow channel which cuts through the shallower mud flats and *Cynodon* lawns that define this part of the pan. However, although at a slightly higher elevation than the floodplain Lake Nyamithi receives water primarily through back-filling from floodwaters of the Phongola or Usuthu Rivers via the outlet in the eastern periphery of the pan. Here a channel is maintained by Hippopotami and serves as a water course considerably deeper than the surrounding mudflats (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b).

The confluence of the Usuthu and Phongola rivers in the north eastern corner of the NGR marks the start of the Rio Maputo and its associated floodplain (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). The river channel is characterized by a low gradient, so much so that tidal fluctuations in water level are noticeable 70 km upstream from the mouth (Kramer, 2003). The Rio Maputo floodplain has been drained in the past for agricultural purposes and the only major water bodies that remain are Lake Pandejene and Machana pan, both of which are 10 km downstream of the NGR (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b).

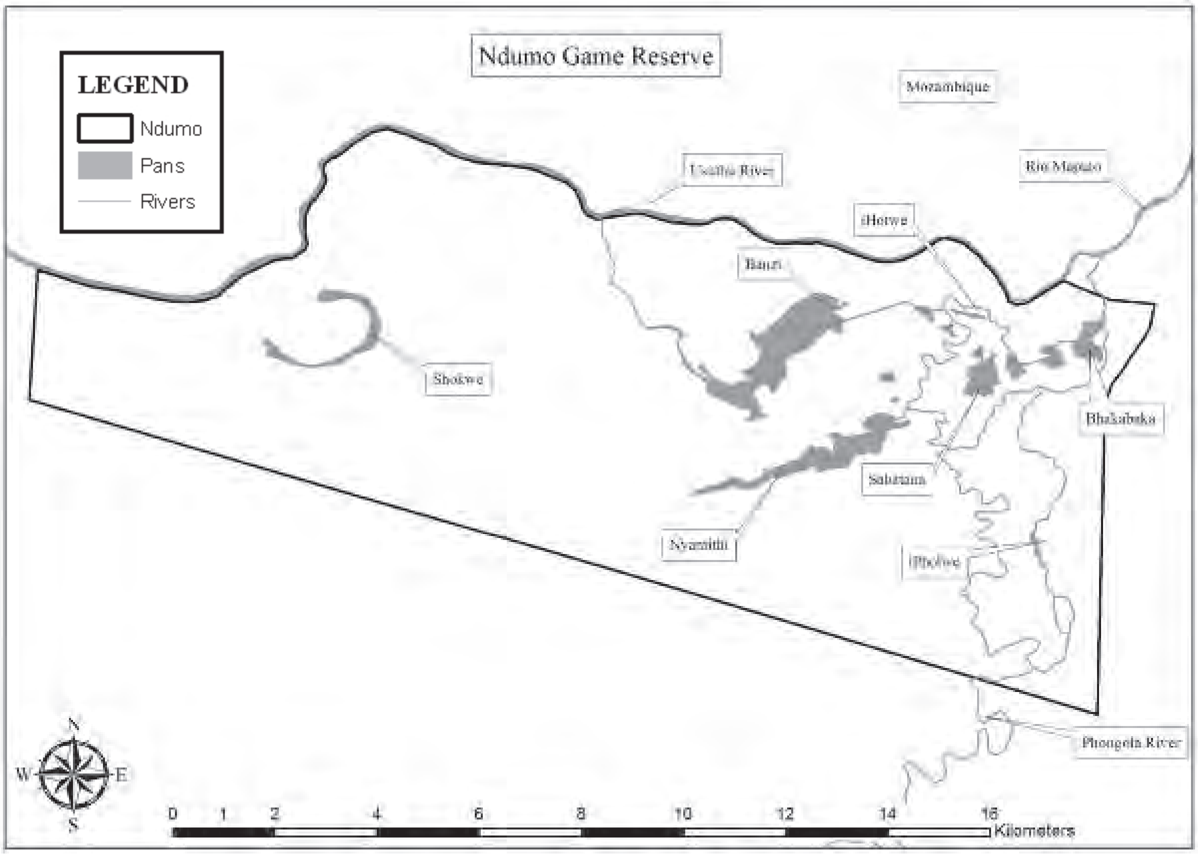


Figure 2.2 The Ndumo Game Reserve, KwaZulu-Natal, South Africa, showing the major pans and rivers that make up the hydrology of the reserve (from Calverley 2013).

2.1.3 Pongolapoort Dam

Pongolapoort Dam is located on the east flowing Phongola river, in northern KZN (27°22’10.81” S; 31°51’22.49” E to 27°31’23.74” S; 31°59’48.84” E, Champion 2011, Champion and Downs in prep. a,b,c). The dam is located between the towns of Golela, Jozini and Mkuzi, running along the western side of the Lebombo Mountains (Fig. 2.3). The area has a sub-tropical climate, with summer months hot (24.5°C average) and wet, whilst the winters months are mild (15.8°C average) and dry, giving the area its sub-tropical climate (Heard and Whitley 2009), with most of the 600 mm mean annual rainfall falling between the months of November and March (Rutherford *et al*. 2006). The study on Nile crocodile in Pongolapoort Dam began in April 2009 and continued to the end of June 2010. The total study area included the entire Pongolapoort Dam and a short section of the Phongola river inlet to the dam, up to the N2 highway bridge (Champion 2011, Champion and Downs in prep. a,b,c).

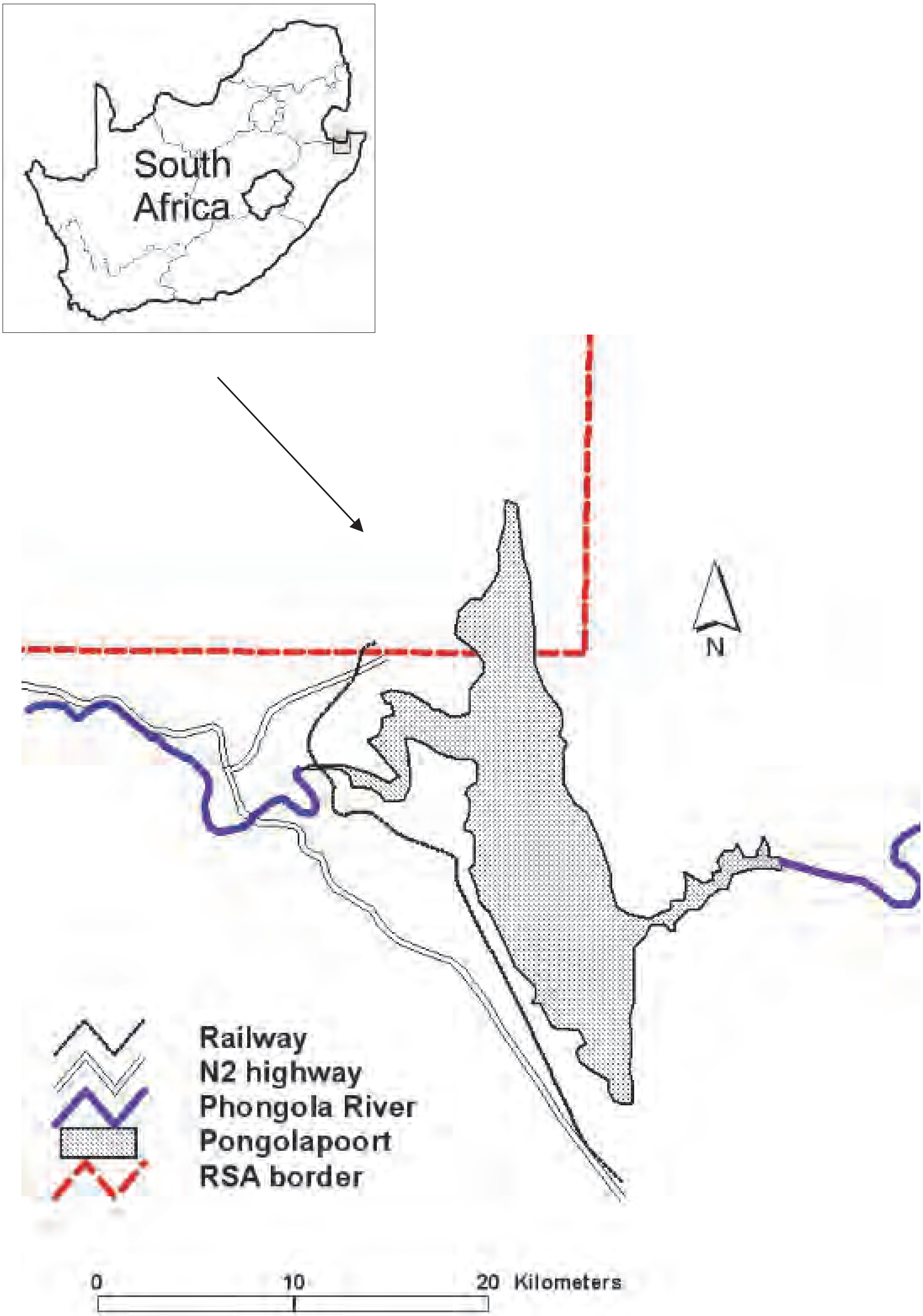
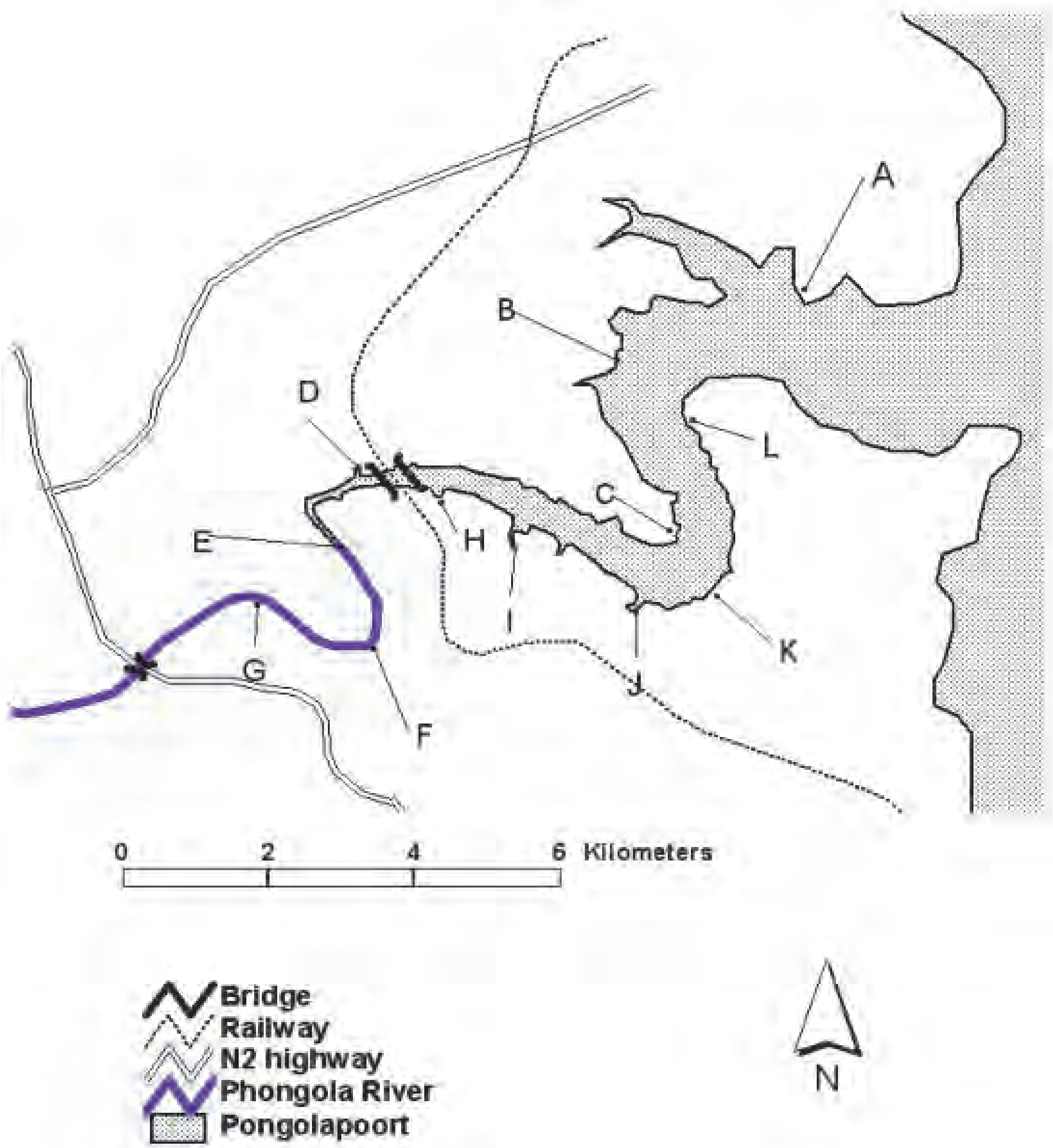


Figure 2.3 Pongolapoort Dam, KwaZulu-Natal, South Africa (from Champion 2011).



A	KZN Wildlife Camp Site	G	Causeway Bend
B	Houseboat Jetty	H	Hissing Bay
C	KZN Point	I	Croc Bay
D	Mvubu Jetty	J	Mpalane Jetty
E	Buffalo Bend	K	Inkwazi Lodge
F	Cliff Ledges	L	Cliffs End

Figure 2.4 North Western section of Pongolapoort Dam and inlet section (from Champion 2011).

2.2 Population estimate and spatial use

2.2.1 Lake St Lucia

The total survey distance for crocodiles in Lake St Lucia is ~600 km, which include the shoreline length of the Narrows, streams, rivers, channels, Lake Bhangazi and all islands (Combrink 2014, Combrink et al in prep. a,b). The majority of the lake's shoreline is exposed with little vegetation, facilitating good observation of crocodiles from an airplane. However, streams and rivers flowing into the main lake are all heavily vegetated, making it difficult to count crocodiles from the air. Freshwater intrusions and seepage and their affiliated aquatic macrophytes (reeds and sedges such as *Phragmites australis* and *Juncus kraussii*) also obscure visibility. Additionally, the estuary mouth closed in 2002, and since 2004 salinities in the Narrows channel have decreased due to freshwater intrusion from the nearby Mfolozi River through the Backchannels and Link canal, leading to a sharp increase in shoreline vegetation and submerged macrophytes (e.g. *Stuckenia pectinata*), increasing visibility bias. Lake St Lucia is a longitudinal, shallow waterbody with a mean depth of 0.98 m (Hutchison 1974), and features high turbidity due to wind effect and wave action (Taylor 2006). This impedes observing crocodiles in the water, and submerged crocodiles will be missed altogether. Variations in catchment rainfall patterns, often between consecutive years, can have a considerable effect on lake levels and salinity, influencing the distribution and visibility of crocodiles and the accuracy of censusing. Historically, crocodiles were distributed from the Mkhuze River in the north, along the eastern shoreline and western shoreline south of Hell's Gate, Mphathe Stream and Narrows to the Mfolozi and Msunduzi Rivers in the south (Fig. 2.1) (Combrink 2014, Combrink et al in prep. a,b). During the last twenty years, human disturbance (e.g. increased settlements, small scale farming, water extraction and illegal gillnetting) especially in the northwest and southwest, led to a contraction of crocodiles away from the north and south. Therefore, connectivity with other Nile Crocodile populations in the region (e.g. Hluhluwe-iMfolozi and uMkhuze Game Reserves) is unlikely given increasing and extensive human disturbance and development along the feeding rivers (Combrink 2014, Combrink et al in prep. a,b).

2.2.1.1 Aerial surveys

Aerial surveys are the most effective method to census crocodile populations over extensive or remote areas where rough terrain and subject behaviour make other forms of survey unfeasible. To improve accuracy, these surveys typically occur during winter months when Nile Crocodiles are aggregated around permanent water sources and spend more time basking out of the water, and are therefore easier to count (Champion 2011, Calverley 2013, Combrink 2014).

We conducted ten aerial surveys between 19 June 2009 and 13 June 2013 to record the distribution, relative abundance and seasonal movement pattern of Nile Crocodiles in Lake St Lucia (Combrink 2014, Combrink et al in prep. a,b).. Fixed-wing Cessna 182 (four-seater), a Bushbaby (two-seater) aircraft, and a Microlight Trike were used. The primary observer (Combrink) was present during all surveys and additional observers all had previous experience in crocodile aerial surveys. For the June (= winter) surveys, weather conditions were regarded as acceptable if wind speed was < 20 km/hour and cloud cover < 25%. Aircraft departure always occurred after 10:00 in order to maximise the number of basking (= visible) crocodiles in the survey area (Downs et al. 2008). The position of each crocodile or group of crocodiles was marked with a GPS, and number of individuals recorded. Crocodile localities and the survey track were mapped in ArcView 9.3 (ESRI, Redlands, USA) (Combrink 2014, Combrink et al in prep. a,b). In order to interpret historical Nile Crocodile distribution and movements in relation to the recent drought period, we obtained spatial and abundance records from journals, theses, published survey reports and maps from the former Natal Parks Board (now Ezemvelo KZN Wildlife (EKZNW)), the Ezemvelo St Lucia research office and Ezemvelo St Lucia Crocodile Centre (Combrink 2014, Combrink et al in prep. a,b).

2.2.1.2 Spotlight surveys

We conducted 10 spotlight Nile Crocodile boat surveys in the Narrows, Lake St Lucia from 19 June 2009 to 21 June 2012 with aim to record their density and seasonal movement patterns (Combrink 2014, Combrink et al in prep. a,b). The Narrows channel was the only component of the study area deep enough for boat access. We used two 100 Watt spotlights (Lightforce 240, Australia), each connected to a 12V battery. Crocodiles observed were counted and their sizes estimated. Crocodiles that were too far away, or dived before a size estimate was possible, were recorded as “eyes only”. The position of each Nile Crocodile along the survey transect was recorded with a GPS and then plotted on orthophotographs along with the survey track (Combrink 2014, Combrink et al in prep. a,b).

2.2.1.3 Determining biases for aerial and spotlight surveys

In Lake St Lucia we quantified diving bias of Nile Crocodiles by calculating the ratio of submerged (underwater) individuals to emerged individuals for 17 crocodiles fitted with GPS-satellite transmitters (Combrink 2014, Combrink et al in prep. a,b). This gave us the proportional time a given crocodile was above the water surface and therefore able to record a GPS-position. Conversely, a submerged transmitter was unable to record a GPS-position at the pre-set scheduled time (i.e. 1-4 h intervals). Hourly water temperature data were collected over three years using iButton DSL 1922 Thermochron temperature data loggers (Maxim Integrated, San Jose, USA) in Catalina Bay and the Narrows, as these sites were the only areas in the entire lake and estuarine system sufficiently deep (i.e. > ~75 cm) throughout the study period. Data loggers were secured to a pole in the water 30 cm from the bottom and the data were stored on the thermochron monitors until uploaded in MS Excel for analysis. Temperature was accurate to ± 0.5°C (http://www.maximintegrated.com) (Combrink 2014, Combrink et al in prep. a,b).

We compared successful GPS-observations with unrecorded/unsuccessful, but scheduled "missed-observations" for the periods 10:00-14:00 ("day"), 19:00-01:00 ("night") and between months (Combrink 2014, Combrink et al in prep. a,b). These time periods are representative of the hours aerial and spotlight surveys were conducted, respectively. We summed the successful observations and missed-observations for day and night periods separately to obtain mean total and monthly emergence ratios. Factorial ANOVA was used to test for significant differences between months and time periods. Finally, we used the emergence ratios to estimate correction factors for diving bias during aerial and spotlight surveys (Combrink 2014, Combrink et al in prep. a,b). Observer bias (the proportion of visible crocodiles in the observers field of view missed during a survey) was quantified through a double-counting technique (Magnusson et al. 1978, Hutton and Woolhouse 1989, Williams et al. 2002). Derived correction factors were used to estimate observer bias during past surveys and can be applied to future surveys using a single airplane, which is standard procedure for St Lucia Nile Crocodile surveys (Combrink 2014, Combrink et al in prep. a,b).

2.2.1.4 Population estimate

We estimated the 2013 Lake St Lucia Nile Crocodile population (N) using a simultaneous double count technique, see (Eltringham 1972, Magnusson et al. 1978, Combrink 2014, Combrink et al in prep. a,b). We used two independent groups of observers, one in a Cessna 182 airplane and a second in a Bushbaby airplane, flying simultaneously but in opposite directions around the lake and feeder streams. Both airplanes counted and recorded geographical positions of crocodiles according to the aforementioned aerial survey procedure. The model we used is equivalent to the Lincoln-Petersen closed population mark-recapture estimate (Magnusson et al. 1978, Williams et al. 2002), with data allocated into one of three categories: crocodiles seen and mapped by both airplanes (B), crocodiles counted exclusively from the Bushbaby (S_1), and the number of crocodiles counted exclusively by the Cessna (S_2):

(1) $$N = \left(\frac{(S_1 + B + 1)(S_2 + B + 1)}{(B + 1)} \right) - 1$$

(2) $$Var\left(\hat{N} \right) = \frac{(S_1)(S_2)(S_1 + B + 1)(S_2 + B + 1)}{(B + 1)^2 (B + 2)}$$

(3) $$\text{Standard error} = \sqrt{Var(N)}$$

(4) $$\text{Coefficient of Variation } (CV) = \left(\frac{\sqrt{V}}{N} \right) \times 100$$

The assumptions of this approach were that sightings by both groups of observers were independent, detection probabilities were homogeneous, individual or group positions can be identified (GPS) in order to establish which individuals were “marked and recaptured” or “marked but not recaptured,” and that the population was closed between the two surveys (Williams et al. 2002, Combrink 2014, Combrink et al in prep. a,b).

2.2.2 Ndumo Game Reserve

Our efforts to capture Nile Crocodile in the NGR took place in Lake Nyamithi. The shallow nature of the lake and high density of crocodiles favoured noosing as a capture technique (Calverley 2013, Calverley and Downs 2014a,b). Nile Crocodiles were caught using this technique between March 2009 and June 2010. Crocodiles were taken ashore for morphometric measurements, sexing, unique scute notching and colour tagging before being released (Calverley, 2013). Historical records of Nile Crocodile surveys were obtained from the EKZNW and from Pooley (1982) (Calverley 2013, Calverley and Downs 2014a,b).

2.2.2.1 Aerial surveys

Aerial surveys at NGR carried out in 2009 give distribution patterns for the dry season only. In 2009, a helicopter was available for Nile Crocodile counts only in the wet season (Calverley 2013, Calverley and Downs 2014a,b). Following historical methods employed in all the surveys at NGR, the helicopter (AS350 Ecureuil helicopter; Eurocopter) was used with four observers including the pilot. Flight speed (75 km/h) and altitude (25 m above ground level) were relatively low, and weather conditions were favourable. Crocodiles observed within each region of the NGR were recorded and totals indicated on a map (scale =

1:50,000). Counting areas were divided amongst observers, with observers on the left of the helicopter searching only the left and those on the right searching only the right. The survey lasted 1 h, and water levels in the NGR were high on account of heavy rainfall in the Usuthu catchment area (Calverley 2013, Calverley and Downs 2014a,b).

Figure 2.5 Aerial survey conducted at NGR by Paul Dutton and Peter Calverley (Calverley unpublished data).

A Piper Supercub aircraft with two observers seated longitudinally was used during the dry season in an effort to achieve a count comparable to previous surveys (Fig. 2.5, Calverley 2013, Calverley and Downs 2014a,b). This also allowed for the investigation of seasonal changes in abundance as surveys were carried out in 2009 during high, medium and low water levels in austral summer and winter. The right window was opened to facilitate counting and the aircraft flown that all counting was done on this side. On larger water bodies, where both banks could not be observed from the right hand window, transects were flown to cover both shorelines. A Vista® Cx Global Positioning System (Garmin, Kansas, USA) was synchronised with a dictaphone (Hewlett-Packard PDA, California, USA) so that commentary of the flight and GPS data were recorded simultaneously at waypoints of 50 m intervals (Calverley, 2013). An EOS 400D digital camera (Canon, Tokyo, Japan) was used to record areas of high crocodile density when counting from the aircraft proved inaccurate. The number of crocodiles in photographs were counted after the survey and added to the total amount counted during the survey (Calverley, 2013). Initial weather conditions were favourable, but winds became gusty towards mid-morning. Temperature ranged between 18-20°C. The survey occurred from 08:42-10:22, including take-off and landing from Tembe

National Elephant Park (within 32 km), with an average flying speed of 139 km/h at an average altitude of 173 m (Calverley 2013, Calverley and Downs 2014a,b).

2.2.2.2 Correction factors

Aerial surveys give an indication of the relative abundance of crocodiles and correction factors that negate sources of bias should be calculated to obtain an indication of the absolute abundance of a population (Combrink 2004, Calverley 2013, Calverley and Downs 2014a,b). Generally, where different aircraft types are used for surveys (helicopter and airplane) survey yields are not comparable. This raises some questions as to the comparability of results obtained via fixed wing aerial surveys in 2009 versus the historical data obtained using helicopters (1971-1994). Correction factors for aerial surveys are normally calculated by conducting follow up spotlight surveys (Bayliss et al., 1986). In areas such as the Phongola and Usuthu floodplains, however, accurate spot light surveys were not possible due to the shallow, sinuous, heavily vegetated waterways interspersed with marshes, swamps, pans, impenetrable vegetation and the danger of Hippopotami (Leslie, 1997; Combrink, 2004). For example, a fixed wing survey yielded 21% more crocodiles at Lake Nyamithi (part of the Phongola river basin) than a diurnal survey conducted one hour later, and 34% more than a spotlight survey conducted the previous night (Calverley, 2013). Therefore, reliable correction factors for aerial surveys could not be calculated, and relevant literature was consulted in order to identify a suitable correction factor (Calverley 2013, Calverley and Downs 2014a,b).

Correction factors for surveys of Nile Crocodiles using fixed or rotary wing aircraft in a variety of suitable habitats in the region range from 1.28 to 2.0 (Combrink 2004, Botha 2005, 2010, Bourquin 2008, Fergusson 2010, Ferreira and Pienaar 2011, Calverley 2013, Calverley and Downs 2014a,b). We applied the most conservative of these multipliers (1.28; reported by Bourquin (2008) and Ferreira and Pienaar (2011) to all historical survey data that were collected using a helicopter in order to better estimate the absolute abundance of the NGR population. For the fixed wing surveys, we calculated a minimum and maximum absolute population estimate and used the mean of these two values to estimate absolute abundance. All estimates and an indication of their precision are reported as means ± 1 SE (Calverley 2013, Calverley and Downs 2014a,b).

2.2.2.3 Stratification

The NGR was divided into the same strata as earlier surveys (Calverley 2013, Calverley and Downs 2014a,b). All surveys from 1971-2010 separated the study site into two major regions each with numerous sub-regions: Region 1. The Phongola river system consisting of the following sub-regions: Nyamithi Pan, main course Phongola river and floodplain east, Phongola old course and floodplain west, and Bakabaka/Shabatana. Region 2. The Usuthu River system consisting of the following sub-regions: Shokwe, Banzi/Diphini, and Usuthu River. During aerial counts, the numbers of crocodiles were recorded for each sub-region. Our analyses examined relationships between and within regions and sub-regions to improve precision. Consecutive counts conducted by the same observer were viewed as separate strata to improve accuracy and precision.

2.2.2.4 Spatial use

We conducted our study from March 2009 to November 2012 at two spatial and temporal scales in NGR (Calverley 2013, Calverley and Downs 2014a,b). At the microscale, population fluctuations were observed at Lake Nyamithi on a monthly basis and related to environmental and social factors over the 3.5-year period. At the mesoscale, annual distribution patterns were observed for the entire reserve and the Rio Maputo floodplain by making use of aerial survey data initiated in 1971 through to 2012 (Calverley 2013, Calverley and Downs 2014a,b).

Between March 2009 and November 2012 a total of 40 diurnal counts were conducted at Lake Nyamithi (Calverley 2013, Calverley and Downs 2014a,b). A vehicle was driven around the 9.5-km periphery of the lake with an average search time of 3 h 14 min. Location and size of individual crocodiles (observed using binoculars) was recorded as were the date, time, duration of each survey, and weather conditions. Minimum and maximum temperature (°C), humidity (%) and rainfall data (mm) were collected at the NGR Head Office, 5 km southeast of Lake Nyamithi. Water levels for Lake Nyamithi were obtained from the Department of Water Affairs website (http://www.dwa.gov.za/hydrology/HyDataSets.aspx?Station=W4R004) (Calverley 2013, Calverley and Downs 2014a,b).

Data obtained from 13 Ezemvelo KZN Wildlife Nile Crocodile aerial counts in NGR from 1971-2009 were used to examine the spatial distribution of abundance of Nile Crocodiles in the NGR (Calverley 2013, Calverley and Downs 2014a,b). The Bateleurs (non-profit organization who provide pilots and aircraft for conservation projects) assisted with an additional aerial survey in 2010. A private pilot and aircraft was hired for a survey of the Rio Maputo in 2012. In total, data from 15 aerial surveys conducted from 1971 to 2012 were examined. We also included data from an aerial survey of the Rio Maputo conducted in 2010 by the Mozambique Provincial Directorate of Environmental Affairs. The methods employed in the 1971-1994 surveys as well as the 2009-2012 survey are presented elsewhere

(Calverley, 2013; Calverley and Downs, 2014). We report size classes of crocodiles in total lengths: <150 cm, 150-250 cm, 250-350 cm, 350-450 cm, and >450 cm (Calverley 2013, Calverley and Downs 2014a,b).

In order to analyze any differences in the proportion of crocodiles found in each river system in NGR over the last 40 years, as well as the sub-regions within each system, we used an arcsine square root transformation on our data (Calverley 2013, Calverley and Downs 2014a,b). We then used one-way ANOVA to detect any differences in the proportions of Nile Crocodiles counted in the Phongola and Usuthu regions, as well as for the respective sub-regions within these systems from 1971-2009. To minimize the effects of autocorrelation between some of the environmental variables, we used regression analyses to assess the importance of continuous environmental variables (e.g., water level, temperature, rainfall) on the density of Nile Crocodiles in Lake Nyamithi (based on estimates of relative abundance). When reported, means of raw data are presented ± 1 SE (Calverley 2013, Calverley and Downs 2014a,b).

2.2.3 Pongolapoort Dam

A minimum population number approach was used rather than a population estimate or density estimate as this was a baseline study where the dynamics, particularly presence and abundance of Nile crocodiles in Pongolapoort Dam, and the effects of water levels and season on these had not been previously documented (Champion 2011, Champion and Downs in prep.a,b). Precision and accuracy of determining reliable population estimates requires prolonged monitoring, and correction for the particular survey biases of the system as has been shown in other studies (Ferreira and Pienaar 2011). Furthermore, in the current study it was found that the comparability of surveys was affected by variation in conditions between surveys. Consequently each survey was treated as a separate count rather than a replication and a minimum total determined (Champion 2011, Champion and Downs in prep.a,b).

The Pongolapoort Dam system was perceived as a “closed system” (Champion 2011, Champion and Downs in prep. a,b,c). Any movements by Nile crocodiles out of the dam, up the Phongola river past the N2 highway bridge were presumed to be short-term movements during the rainy season, with crocodiles returning in the dry season when the river became unfavourable habitat (Jacobsen 1991). In order to establish a minimum population number and structure of Nile crocodile in Pongolapoort Dam, a combination of survey methods was used. In each method crocodiles were counted and recorded with an associated location and size classes. Size classes were categorised as juveniles (< 1.2 m), sub-adults (1.2-2.5 m), adults (> 2.5 m) and “eyes only” (unknown size class). In all surveys each crocodile sighted was recorded with an associated total length (TL) estimate and its location using a hand held Global Positioning System (Garmin, eTrex, Kansas, USA) (Champion 2011, Champion and Downs in prep. a,b,c).

2.2.3.1 Aerial surveys

We conducted an aerial count of the entire Pongolapoort Dam including the inlets was on 22 August 2009 using a fixed-wing Cessna 210 aeroplane (Champion 2011, Champion and Downs in prep. a,b). The aim of the survey was to obtain baseline data of minimum number and for future estimates of total abundance of adult crocodiles (> 2.5 m), not including juveniles due to their associated visibility bias (Games 1994, Ferreira and Pienaar 2011). Timing of the aerial survey in winter and after 10h00 increased the likelihood of crocodile sightings as they generally bask then (Downs et al. 2008). The survey crew consisted of four people, two observers, a pilot and a scribe. The survey began at 10h00 at the southernmost point of the dam. Weather during this survey was favourable, with little wind, clear skies and good visibility. The plane was flown at approximately 100 m above the ground and travelled at an average speed of 120 km h^{-1}. At this speed and height, observers found the ability to sight crocodiles acceptable. The survey continued northwards up the western shore of the main dam body (Pongola Game Reserve, Fig. 2.3), towards the inlet section. The entire shore line of the dam (Fig. 2.3) was followed in this clockwise direction. The survey included the entire shore line of the main dam, including the section into Swaziland. The narrower dam section in the north west, up to the railway bridge, was also included in the clockwise circumnavigation (Fig. 2.3). Each crocodile seen was noted together with its estimated size category and location (recorded on an aerial photograph of the dam for later transfer to an electronic map). Areas with high densities of crocodiles were on occasions circled in order to obtain a secondary, more conclusive count. A section of Dam not included in this survey was the gorge section leading to the dam wall (Fig. 2.3). This has high cliffs and little shoreline terrain, and it was decided that the area was both too dangerous to navigate at a height that observations would still be possible and there was unlikely to be any significant number of crocodiles in the gorge (Champion pers. obs. 2009). The aerial survey was concluded at 11h00, once the eastern shore line of the main dam body had been flown and the original starting position reached (Champion 2011, Champion and Downs in prep. a,b).

A second aerial survey of the north western section of Pongolapoort Dam (Fig. 2.3) took place during favourable weather conditions, on 23 November 2010, using an AS350 Ecureuil Helicopter (Champion 2011, Champion and Downs in prep. a,b). As this survey technique is costly, the entire dam could not be included. Instead the inlet and river section was surveyed, where the majority of crocodiles were expected to occur (G. Champion pers obs. 2009, Champion 2011). The survey began at 09h00 and finished at 10h00, following a predetermined route. The survey crew consisted of 4 observers, including a pilot and a scribe. The survey route followed the Phongola river, starting from the N2 bridge going downstream towards the railway bridge. During this section (7 km) of the survey both sides of the river were surveyed simultaneously as the river was narrow and observers had a clear view of both banks. After reaching the railway bridge, denoting the beginning of the dam, the survey continued along the shoreline in an anti-clock wise direction, keeping the shore line on the left-hand side of the helicopter, including the exploration of bays (Fig. 2.3). During the survey, 7 km of the river, 11 km of western shoreline and 7 km on the opposite, eastern bank on return to the railway bridge were surveyed. Again during the survey, any crocodiles seen were recorded along with their size class and location (Champion 2011, Champion and Downs in prep. a,b).

2.2.3.2 Day and Night boat surveys

The whole dam could not be included in boat surveys due to logistical constraints and associated costs. However, based on the aerial survey and other feedback, the section of dam where the majority of the crocodiles resided was surveyed (G. Champion pers. obs. 2009, Champion 2011, Champion and Downs in prep. a,b). Consequently we used regular boat surveys to determine the minimum number of Nile Crocodiles in the northern section of the Pongolapoort Dam. This area was estimated to contain approximately 80% of the crocodile population in the dam (G. Champion pers obs. 2009, Champion 2011). In addition, the ratio of juvenile, sub-adult and adult crocodiles in the survey area was determined. Locations of observed crocodiles were also recorded for general crocodile distribution and habitat use for the various size classes (see Champion 2011). The northern section of Pongolapoort Dam was divided into five transects of approximately 15 km long. Areas not covered in the north, included the Swaziland section (restricted) and the upper river inlet section depending on water levels (Champion 2011, Champion and Downs in prep. a,b).

We used a 4.5 m aluminium boat, powered by a 30 hp outboard Yamaha engine (Hamamatsu, Japan). A total of 80 h of boat surveys were done between May 2009 and July 2010 (Champion 2011, Champion and Downs in prep. a,b). We conducted surveys along shoreline routes both at night and during the day each month. With night-spotlight counts being identified as most accurate method for determining numbers of crocodiles and day counts were best used for determining ratios of size classes (Combrink 2004). On some occasions areas with known high densities of crocodiles were not reachable by boat due to water depth or presence of aquatic weed (*Hydrilla verticillata*) and therefore these clusters could not be included directly in boat surveys (Champion 2011, Champion and Downs in prep. a,b).

During daylight surveys, the number of observers present varied from one to three (Champion 2011, Champion and Downs in prep. a,b). The shoreline was followed closely, travelling approximately 50 m from the shoreline, where conditions allowed. Once a crocodile was spotted the boat was stopped. The locality and size class of the crocodile was recorded, as well as the distance to nearest neighbouring crocodile and any other observational information was recorded (including presence of identification tags, Champion 2011). These surveys usually lasted between 2-3 h covering a number of transects on a particular day (Champion 2011, Champion and Downs in prep. a,b).

Large-scale night-spotlight counts of the northern section of Pongolapoort Dam were done twice during the study period, on the 31 October 2009 and 12 June 2010 (Champion 2011, Champion and Downs in prep. a,b). The surveys consisted of a number of survey teams sampling transect sections simultaneously using various motorised boats. Each survey team surveyed a predetermined route, with the combination of survey routes covering the entire northern half of the dam, except for few areas inaccessible by boat such as the upper river section or restricted Swaziland section (Fig. 2.3). Each survey team had a minimum of three crew members, a skipper, a spotlight operator and a scribe. Survey teams were briefed prior to survey in order to standardise survey methods'. The entire survey took approximately 3 h with all teams starting simultaneously at a predetermined time and ending with in 20 min of one another. Crocodiles were identified by eye-shine. Each crocodile seen was recorded along with its location and estimated size class when possible. In cases where the crocodile became submerged prior to an accurate size estimate being made, the crocodile would be recorded as “eyes only” (E.O). Such recordings would aid in number estimates but would not be included in size class structure calculations. Location was mapped on a collection of detailed aerial photos of the dam shoreline. At the start and end of the survey environmental conditions were noted (Champion 2011, Champion and Downs in prep. a,b).

Figure 2.6 Capture of a Nile Crocodile at Lake St Lucia (Unpublished data Combrink and Warner).

2.3 Capture methods, transmitters and movement

We used a combination of Nile Crocodile capture techniques to maximise success under diverse habitat conditions (Figs 2.6, 2.7, Champion 2011, Calverley 2013, Combrink 2014). The preferred capture technique was noosing, i.e. securing a self-locking cable around the crocodile's head, but detachable harpoons, treble hooks and traps were also used (Champion 2011, Calverley 2013, Combrink 2014).

At Lake St Lucia we used GPS-satellite transmitters (African Wildlife Tracking) in combination with a GSM download system, while one GPS-satellite transmitter transmitted data via the Iridium system Combrink 2014, Combrink et al. in prep. c,d,e). Units were attached to crocodiles subcutaneously with orthopaedic stainless steel wire. Capture methods, transmitters and transmitter attachment are described in Combrink 2014, Combrink et al. in prep. c,d,e.

Figure 2.7 Nile crocodile a. capture at Lake St Lucia and b. crocodile fitted with a transmitter

2.3.1 Lake St Lucia

2.3.1.1 Partitioning of seasons

The Nile Crocodile is an aquatic ectotherm and ambient temperature plays a crucial role in thermoregulatory behaviour (Cott 1961, Combrink 2014, Combrink et al. in prep. c,d,e). Temperature gradients in water are often sharp with deep water providing a refuge from high temperatures while shallow surface water are used for heat gains (Smith 1979). Past aerial surveys at Lake St Lucia indicated considerable seasonal variation in basking behaviour, peaking in winter while during summer most crocodiles bask very little (Pooley 1982a, Leslie

1997). In order to analyse movement and activity, we used water temperature to partition a calendar year into four unequal length seasons. This allowed for comparisons with other crocodilian studies, as most authors referred to seasons in their discussion (Joanen and McNease 1970, Joanen and McNease 1972, Taylor et al. 1976, Goodwin and Marion 1979, Taylor 1984, Kushlan and Mazzotti 1989, Hocutt et al. 1992, Rootes and Chabreck 1993, Botha 2005, Bourquin 2007, Calverley 2010, Champion 2011, Calverley 2013, Combrink 2014, Combrink et al. in prep. c,d,e).

Hourly water temperature data were collected in Catalina Bay (Charters Creek Ezemvelo management jetty) and the Narrows (St Lucia Wilds jetty) as these sites were the only areas in the entire lake and estuarine system sufficiently deep (i.e. > ~75 cm) throughout the study period (Combrink 2014, Combrink et al. in prep. c,d,e). We calculated mean water temperature per week, over three years using iButton DSL 1922 Thermochron temperature data loggers (Maxim Integrated, San Jose, USA). Thermochron monitors record time and temperature, and the data were stored on the device until uploaded in MS Excel for analysis. Temperature was accurate to ± 0.5°C (http://www.maximintegrated.com). Water temperatures were recorded every 30 minutes at recording stations in the southern Narrows (St Lucia Wilds jetty, St Lucia town) and Charters Creek (close to Ezemvelo jetty). Data loggers from three other recording stations (Hell's Gate, Dead Tree Bay and northern Narrows) were removed. Data loggers were secured to a pole in the water 30 cm from the bottom. The coldest mean weekly temperature was 16.8°C, and the warmest 28.7°C, range = 11.9°C. We divided the range into three equivalent thermal bands of 4.0°C respectively, i.e. a warmer "summer" thermal band (> 24.7°C) corresponding with the following dates: 8 Nov. to 7 April (151 days), a cool "winter" thermal band (< 20.8°C) from 22 May to 30 August (102 days) and a transitional thermal band (20.8°C to 24.8°C) "autumn" and "spring", from 8 April to 21 May (44 days) and 1 Sept. to 7 Nov. (68 days) respectively. Activity and movement analysis were reported in daily values, to allow for comparisons between unequal length seasons (Combrink 2014, Combrink et al. in prep. c,d,e)

2.3.1.2 Movement analysis

Prior to analysis, Greenwich Mean Time (GMT) data obtained for transmitter Nile Crocodiles in Lake St Lucia were converted to South African local time, GMT + 2 h (Combrink 2014, Combrink et al. in prep. c,d,e). Despite some seasonal variation in daylight, for the purpose of the analysis we defined the period 06:00 to 18:00 as "day" and 18:00 to 06:00 as "night". The displacement between two successive GPS points x_1y_1 and x_2y_2 was calculated using the following equation: 1000 x (6371.1 x ((2 x asin (sqrt ((sin((radians(y_1) –radians(y_2))/2)^2) + cos (radians (y_1)) x cos (radians(y_2)) x (sin((radians(x_1) –radians (x_2))/2)^2)))))).

Displacements between GPS point locations were considered an interval along the shortest path connecting them. Therefore, displacements should be considered a minimum, as the actual distance would not have been a direct line (Combrink 2014, Combrink et al. in prep. c,d,e)

Nile Crocodiles spend a proportion of their time underwater and Hutton and Woolhouse (1989) have shown through a mark-recapture programme, that up to 37% of undisturbed crocodiles may be submerged at any given time (Combrink 2014, Combrink et al. in prep. c,d,e). When a transmitter-fitted crocodile was submerged, the unit was unable to record a scheduled GPS position and the unrecorded displacement value (between the two GPS points) would remain unknown. Furthermore, if the crocodile remained submerged, all successive (scheduled) GPS positions were unrecorded until the crocodile re-surfaced, enabling the unit once again to record a GPS position. Displacements could only be calculated between successfully recorded points. Therefore, a particular displacement value may have included a number of scheduled, but unrecorded GPS points. Furthermore, if the transmitter failed to record a GPS position, for instance, at the end of the day (i.e. 0:00), the next successfully recorded point could have include a certain proportion from the previous day, resulting in erroneous movement values for both days. If not accounted for, these factors will influence the analysis over 24 h, months and seasons. In order to partition displacements into set hourly temporal periods, we calculated the mean value for the unknown displacements, based on the first successfully recorded displacement value, divided by the number of missing schedules (Combrink 2014, Combrink et al. in prep. c,d,e).

Probability-Probability (P-P) plots were used to determine if the theoretical normal distribution fitted the observed data (Combrink 2014, Combrink et al. in prep. c,d,e). Non-normal datasets were logarithmic transformed. Kolmogorov-Smirnov and Shapiro-Wilk normality tests were used to determine if the transformed data were appropriate for parametric tests. Alternatively, appropriate non-parametric tests were used (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.3 Activity levels

We determined activity levels for Nile Crocodiles in Lake St Lucia through investigating displacements between GPS fixes. We defined displacements < 20 m as zero movement and displacements > 20 m as a movement event, irrespective of the length of the movement (Combrink 2014, Combrink et al. in prep. c,d,e). The distance of 20 m was used to account for accuracy limitations of the GPS transmitter. As explained earlier, a submerged transmitter was unable to record a GPS point and if this was not accounted for, scheduled but unrecorded GPS duty cycles would spatially inflate the value of the first successfully recorded displacement. Therefore, if one or more consecutive scheduled GPS recordings were unsuccessful (i.e. submerged transmitter), we calculated the mean value for the unrecorded schedules, and if these were less than 20 m were considered to represent zero movement. However, if the unrecorded displacement value(s) were > 100 m, it was considered a movement event, irrespective of the number of consecutively missed GPS schedules. We determined the proportion of times a crocodile moved, or did not move, per time period (02:00-06:00; 06:00-10:00; 10:00-14:00; 14:00-18:00; 18:00-22:00 and 22:00-02:00), per 24 hours, calendar month and season. Significance levels were determined using Pearson Chi-square in Statistica 7.1 (Tulsa, Ok, USA) with activity level expressed as a percentage (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.4 Mean daily movement (MDM)

We used the subtotal function in Microsoft Excel to calculate total movements of Lake St Lucia Nile Crocodiles per day (Combrink 2014, Combrink et al. in prep. c,d,e). If transmitter longevity extended over seasons, we grouped total movements per day by season and calculated the mean daily movement (MDM). We fitted the data to P-P plots in order to check for normality, and non-normal distributions were logarithmic transformed. Kolmogorov-Smirnov and Shapiro-Wilk normality tests were used determine if the transformed data was appropriate for parametric tests. Normally distributed datasets were analysed using One-way and Factorial ANOVA (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.5 Diel movement patterns

We determined diel and seasonal activity patterns for Lake St Lucia Nile Crocodiles (Combrink 2014, Combrink et al. in prep. c,d,e). Six temporal periods (i.e. 02:00-06:00; 06:00-10:00; 10:00-14:00; 14:00-18:00; 18:00-22:00 and 22:00-02:00) of four h were selected, corresponding with the lowest GPS duty-cycle of four hours per 24 h, allowing comparisons between individual crocodiles on dissimilar duty cycles (i.e. 24, 12 or six fixes per 24 h period). We accounted for scheduled, but unrecorded GPS duty cycles, see "Movement analysis" section under "Methods". We fitted the data to P-P plots in order to check for normality, and non-normal distributions were logarithmic transformed. Kolmogorov-Smirnov and Shapiro-Wilk normality tests were used determine if the transformed data were appropriate for parametric tests. Normally distributed datasets were analysed using One-way and Factorial ANOVA (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.6 Nocturnal and diurnal movements

Nocturnal and diurnal movements of Nile Crocodiles were determined at St Lucia (Combrink 2014, Combrink et al. in prep. c,d,e). Despite some seasonal variation in daylight, for the purpose of the analysis we defined the period from 06:00 to 18:00 as “day” and from 18:00 to 06:00 as “night”. We accounted for scheduled, but unrecorded GPS duty cycles. We fitted the data to P-P plots in order to check for normality, and non-normal distributions were logarithmic transformed. Kolmogorov-Smirnov and Shapiro-Wilk normality tests were used determine if the transformed data was appropriate for parametric tests. Normally distributed datasets were analysed in using One-way and Factorial ANOVA (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.7 Total daily movements

We investigated total daily movements as an additional indicator of Lake St Lucia Nile Crocodile activity (Combrink 2014, Combrink et al. in prep. c,d,e). We calculated total daily movements as the sum of successfully recorded displacements and mean values for unrecorded scheduled displacements, over a 24 h period. Total daily movements were allocated to one of six categories; 0-1 km, 1-2 km, 2-3 km, 3-4 km, 4-5 km and > 5 km and proportions were determined representing the% daily movement for each crocodile per movement category. For crocodiles that were tracked over seasons, we calculated the proportion of daily movements within each season according to the six categories. These were analysed using RMANOVA. Statistical analyses were conducted in Statistica 7.1 (Tulsa, Ok, USA). Results are presented as means ± standard error (S.E.) (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.8 Biotelemetry

We fitted GPS-satellite transmitters (African Wildlife Tracking) linked to a GSM (Global System for Mobile Communication) download system to Nile Crocodiles in Lake St Lucia (Combrink 2014, Combrink et al. in prep. c,d,e).. We attached transmitters to adult males (n = 7), adult females (n = 9), and sub-adults (n = 3). Units were subcutaneously secured with orthopaedic stainless steel to the nuchal rosette on the mid-dorsal surface of the neck (Appendix 5 for a description of the transmitter attachment procedure). We defined adult Nile Crocodiles as ≥ 2.5 m (TL) and sub-adults ≥ 1.5 m and < 2.5 m (TL) (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.9 Home range analyses

We used nonparametric kernel density estimation (Worton 1989) to estimate utilisation distributions and home ranges of Nile Crocodiles in Lake St Lucia (Combrink 2014, Combrink et al. in prep. c,d,e). All analysis were conducted using ABODE (Laver 2005), a kernel home range estimation for ArcGIS. The 95% home range was contoured at 95% of the volume of the density surface and the core-use area was calculated using Horner and Powell's (1990) statistical clumping core analysis to provide an objective delineation of core-use areas and not some arbitrary defined probability cut-offs (e.g. 50% utilisation distribution). We used a biweight kernel, and the least-squares cross-validation (LSCV) was used for selecting the optimum bandwidth or smoothing parameter, which was fixed (as oppose to adaptive). Data was standardised to unit variance, which meant that h_{ref} was calculated from the standardised dataset (Laver 2005) (Combrink 2014, Combrink et al. in prep. c,d,e). We conducted random asymptote analysis in ABODE to confirm that the sampling duration covered the full behavioural repertoire exhibited by each crocodile and to determine the minimum number of location estimates required to have a specific confidence in the sample. We furthermore conducted sequential asymptote analysis in ABODE to identify temporal dispersal events or significant sallies (Laver 2005). Nile Crocodiles are semi-aquatic animals that spend most of their lives in or at the waters' edge (Cott 1961), utilising distinct ecological boundaries or topographical features. Home range estimates (95% utilisation distribution) that include areas outside the lake, channel or stream boundaries were removed through scrutinisation high resolution orthophotographs of the study area in ArcGIS 9 (Combrink 2014, Combrink et al. in prep. c,d,e).

Crocodilians spend a considerable proportion of their life submerged and seasonal variation in the submerge-emerge ratio has been recorded for the American Alligator (*Alligator mississippiensis*) (Woodward and Marion 1978, Bugbee 2008) and Nile Crocodiles (Combrink 2014, Combrink et al. in prep. a,b).. We calculated day/night and monthly submerged-emerged ratios of Nile Crocodiles using GPS-satellite transmitters and found significant temporal variation (Combrink 2014, Combrink et al. in prep. a,b), a potential bias in home range analysis. We subsequently corrected our dataset with the highest monthly diurnal (Feb. = 0.58) and nocturnal submergence ratio (June = 0.44), removing 35 380 from the original 55 173 observations (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.1.10 Area-use temporal profiles

We constructed area profiles reflecting individual Nile Crocodile temporal use of the major topographic areas of the Lake St Lucia lake system (Combrink 2014, Combrink et al. in prep.

c,d,e). These profiles visually reflected the extent and variation of movements between these areas during their tracking duration (Combrink 2014, Combrink et al. in prep. c,d,e).

2.3.2 Ndumo Game Reserve

2.3.2.1 Capture

All Nile Crocodiles capture in NGR took place in Lake Nyamithi (Fig. 2.2, 2.8, Calverley 2013, Calverley and Downs 2015a). During winter the deepest part of the lake is on average 2.8 m deep while the average depth of the lake is 0.98 m (Dutton 1971). The shallow nature of the lake and high density of crocodile favour noosing as a capture technique described in Hutton and Woolhouse (1989). Crocodiles were approached at night from a 3.5 m aluminum boat powered by a 35 hp Mercury motor (Fond du Lac, WI). Individuals were spotted using two 1 000 000 candle power Coleman spotlights (Golden, CO) powered by a Deltec deep cycle 12V battery (Johannesburg). A 3S-183 cm Thompson self-locking steel snare was positioned around the animal's neck using a 3 m length of aluminum pole to which it was attached using Duct tape and pulled tight. Once pulled tight, the snare locked in place and became detached from the aluminum pole and the crocodile was retrieved using 12 mm nylon ski rope which was attached to the snare via a lock-gate karabiner (Calverley 2013, Calverley and Downs 2015a).

At NGR Nile Crocodiles that submerged upon approach of the boat were often spotted under the clear water and harpooned as described in Webb and Messel (1977) (Calverley 2013, Calverley and Downs 2015a). Harpooned crocodiles were then pulled to the surface and noosed as described above. Harpooning was only initiated in 2012. During 2012, in order to be more selective and to capture during the day heavy duty angling equipment was used to catch crocodiles. A barbless treble hook set in lead was cast over a crocodile seen swimming or floating in the lake. The line was then reeled in with the intention of hooking the crocodile on the neck or side. When 'fishing' from the shore it is sometimes necessary to wade out and secure the neck of the crocodile with a noose as described above as the crocodile uses its feet to dig into the substrate, or is too big to reel in. It was therefore necessary to fish for crocodiles from a boat where close proximity to the individual was achieved without having to enter the water. If the crocodile dug in, the boat was pulled towards the crocodile by reeling in. Once positioned above the crocodile, it was either noosed if the head or tail broke the surface or was harpooned. Fishing necessitated the use of heavy angling equipment so a Penn Power Stick rod (Philadelphia, USA) with a large coffee grinder reel was used (Finn Norr Offshore, USA) with 400 m 80 lb braided fishing line which was attached to 200 lb Marlin monofilament nylon (Calverley 2013, Calverley and Downs 2015a).

Regardless of capture technique all captured Nile crocodiles at NGR were taken ashore for morphometric measurements, then uniquely scute notched for permanent long-term identification and fitted with a unique sequence of coloured tags for short-term visual identification before being released (Calverley 2013, Calverley and Downs 2015a). A unique colour coded sequence of three standard livestock plastic ear-tags were attached to three vertical tail scutes by drilling a single hole through each scute and securing each tag with two cable ties. A location of the capture site was recorded using a Garmin Vista® CX Global Positioning System (GPS) (Kansas, USA). Animals fitted with radio and satellite transmitters took on average 50 min to process while those being scute notched and tagged took on average 20 min to process (Calverley 2013, Calverley and Downs 2015a).

Figure 2.8 Nile crocodile in Ndumo Game Reserve prior to capture (Calverley unpublished data).

2.3.2.2 Transmitter attachment

VHF transmitters (150 MHz) were fitted to 10 Nile Crocodiles of varying size and sex in NGR (Calverley 2013, Calverley and Downs 2015a). Transmitters were attached between the four nuchal scutes on the nuchal plate; seated between the four vertical scutes, secured using cable ties which ran through holes drilled into the four vertical scutes and using dental acrylic (Vortex) to mould around and under the transmitters to strengthen the platform of attachment(Calverley 2013, Calverley and Downs 2015a).

Three satellite transmitters supplied by African Wildlife Tracking (Pretoria, South Africa) were fitted to Nile Crocodiles in NGR; two in 2011 and one in 2012(Calverley 2013, Calverley and Downs 2015a). Following mixed success with the method used with radio transmitters, satellite transmitters were attached using the method described by Brien and Webb (2010) for satellite transmitters. Transmitters were placed between the four nuchal scutes and were attached to the nuchal shield using stainless steel wire (1 mm) which ran under the nuchal plate and through attachment tubes in the transmitters. Dental acrylic was then molded around the transmitter, incasing the stainless steel wires. Our method differed from Brien and Webb (2010) in that the subject was physically and not chemically immobilized and the nuchal area was anesthetized by injecting a local anesthetic, 2% lignocaine hydrochloride (Bayer, Isando, South Africa), under the nuchal shield (Calverley 2013, Calverley and Downs 2015a).

2.3.2.3 Radio and satellite tracking

Thirty one tracking excursions were undertaken from March to November 2009 in NGR (Calverley 2013, Calverley and Downs 2015a). After November 2009 radio transmitters were no longer be located due to detachment or movement of crocodiles into Mozambique and out of range of the receiver and antennae. Search time varied from individual to individual and not all radio tagged crocodiles were located on all tracking excursions. Radio-tagged animals were located using an Alinco DJ-X10 receiver (Tokyo, Japan) attached to a unidirectional YAGI antenna and their location recorded using a Garmin Vista® CX GPS. Movement patterns of Nile crocodiles with satellite transmitters were followed remotely by accessing the AWT website (http://www.awt.co.za/). Recording intervals were initially set for every 8 h, were displayed on Google Maps and were available as GPS co-ordinates (Calverley 2013, Calverley and Downs 2015a).

2.3.2.4 Mark-resight

Between March 2009 and November 2010 diurnal counts were carried out at Lake Nyamithi, NGR, for mark-resight observations (Calverley 2013, Calverley and Downs 2015a). A vehicle was driven around the 9.5 km periphery of the lake with an average search time of 2 h 53 min. Date, time and duration of survey as well as weather conditions were recorded. Minimum and maximum temperature, humidity and rainfall data were collected at NGR Head Office 5 km SE of Lake Nyamithi. Identification and location of tagged Nile crocodiles were recorded using a Garmin Vista GX GPS. By 2011 some or all of the coloured tags fitted to crocodiles had either dislodged or were indiscernible due to a covering of mud or algae. Permission was not granted to attach further tags to crocodiles by EKZNW as it was deemed that a representative amount of the population had been tagged (Calverley 2013, Calverley and Downs 2015a).

2.3.2.5 Statistical analyses

Seaman and Powell (1996) found that the kernel method with cross validation as a smoothing factor was the most accurate method of estimating home range. Additionally, using the fixed kernel method for estimating home range and least-squares cross-validation (LSCV) to calculate the smoothing factor provides the most accurate and least biased estimates (Seaman et al. 1999). However, while fixed kernels density estimates (KDEs) provide the most accurate fit (Worton 1989), minimum convex polygons (MCPs) most closely follow Burt's (1943) definition of home range. Furthermore, MCPs have been used to calculate crocodilian home range due to the robustness of this method when dealing with autocorrelated data (Rootes and Chabreck 1993, Kay 2004a,b). Since some of the data were significantly autocorrelated (Schoener Index < 1.6 > 2.4; Swihart and Slade Index > 0.6) MCPs as well as KDEs were determined for all samples (Calverley 2013, Calverley and Downs 2015a).

The majority of locations achieved through VHF tracking and all of the mark-resight locations at NGR were obtained on the water margin (Calverley 2013, Calverley and Downs 2015a). This can be problematic in sinuous water ways or lakes with large bays or outcrops and where few geographic fixes/locations are available as MCPs and KDEs include large amounts of terrestrial habitat that is not used by the crocodile. River Channel Area (RCA) and Mid-Stream Linear Distance (MSLD) have been used to calculate Nile crocodile home range when the number of fixes is low or the terrain makes other methods unsuitable (Brien et al. 2008). However, in NGR crocodiles make use of lacustrine and riverine habitat so RCAs and MSLDs would not provide appropriate home range estimations for the portion of time spent in pans or lakes. As a comparison it was decided to manually draw our own MCPs using shore lines and river banks as boundaries between locations that were on shorelines. Using this method terrestrial habitat was not included in calculating home range.

Nile crocodiles with more than 10 radio fixes were selected for analysis (n = 8; mean fixes = 17 ± 1.27). Seaman et al. (1999) suggest a minimum of 30 geographic fixes are required when using LSCV for smoothing in the fixed kernel method, while 100-300 fixes may be necessary before an asymptote is reached using MCP analysis. However, Hutton (1989) found that the home range of Nile crocodiles < 2.2 m could be defined in 20-25 fixes while breeding females required 35-45 fixes radio fixes in a seasonal river in Zimbabwe. However, Nile crocodiles are notoriously hard to monitor using radio telemetry mostly due to transmitter attachment or operation failures (Swanepoel 1999, Botha 2005, Strauss et al. 2008). This combined with the seasonal occupation of NGR by Nile crocodiles (Pooley 1969) our number of radiolocations, although lower, should provide a reasonable estimate of home range during the dry season when crocodiles are mostly restricted to Lake Nyamithi.

Home range size was estimated using the Home Range Extension (Rodgers and Carr 1998) for ArcMap 9.3.1 (ESRI, Redlands, California, USA). Fixed KDEs were used to calculate 95, 90 and 50% polygons using LSCV as the smoothing factor. Similarly, fixed mean MCPs were constructed for 95, 90 and 50% contours. One way ANOVAs were run in STATISTICA 7.0 (Statsoft Inc, Tulsa, USA) to determine any significant differences in home range size between male and female, and breeding and non-breeding Nile crocodiles in the dry season. One-way ANOVAs were suitable in determining the effect of a single categorical independent variable (sex or reproductive status) on the home range of Nile crocodiles (Calverley 2013, Calverley and Downs 2015a).

A simple regression was run as a general linear model (GLIM) to check for significant influences of length (TL) on home range size of Nile crocodiles in NGR (Calverley 2013, Calverley and Downs 2015a). GLIM ANOVAs were run to test for differences in home range estimates produced by the KDEs, MCPs and manually drawn polygons. All mean values were presented as mean ± standard error. Significance was assessed at a p value of 0.05.

In this study transmission failure was taken as a sign of attachment failure unless the individual was spotted with a transmitter attached after transmission failure. In both cases the date of last radio fix or visual sighting with the transmitter attached was taken as the day of detachment. One way ANOVAs were run to determine any significant relationships between transmitter longevity and sex. A simple regression was run as a Generalized Linear Model (GLIM) to check for significant influences of TL on transmitter longevity (Calverley 2013, Calverley and Downs 2015a).

2.3.3 Pongolapoort Dam

2.3.3.1 Capture

We caught a number of Nile Crocodiles in Pongolapoort Dam using three commonly used methods hand grabs (used for juveniles), pole-noosing at night with spotlights and a baited spring-trap (Champion 2011, Champion and Downs in prep. a,b). Sex determination was only done for crocodiles of adequate size (n = 15), using the cloacal probing technique (Leslie 1997). This field technique did not allow for the accurate sexing of juveniles or small sub-adult animals (Champion 2011, Champion and Downs in prep. a,b).

2.3.3.2 Broad scale crocodile distribution patterns

We conducted boat surveys mapping the distribution and related habitat used by different size classes of Nile Crocodiles in the northern section of Pongolapoort Dam during the morning hours, on days when weather conditions promoted basking (Champion 2011, Champion and Downs in prep. a,b). A total of 80 h of boat surveys were completed between May 2009 and July 2010, using a 4.5 m aluminium boat powered by a 30 hp outboard motor (Hamamatsu, Japan). Surveys were conducted along predetermined routes of approximately 15 km. The survey boat would travel close to the shore line wherever possible (50 m) at approximately 25 $km.h^{-1}$. Accessibility to a number of areas was occasionally limited, dependent on water level of the dam or the presence of aquatic weed (*H. verticiiata*). With certain areas not being possible to survey, the use of these areas by each crocodile size class could not be determined, however suggestions were made about the probable use of these areas. During surveys, once a crocodile was sighted the boat would be slowed down or stopped if need be and the size class, location and distance to nearest neighbouring crocodile noted. Size class allocation was related to probable life stage, such as juvenile (> 1.2 m), sub-adult (1.2-2.5 m) and adult (> 2.5 m)(Champion 2011, Champion and Downs in prep. a,b).

2.3.3.3 Crocodile capture and radiotracking

From April 2009 to November 2009, we captured Nile Crocodiles (> 2 m) in the northern section of Pongolapoort, using previously described techniques (Champion 2011, Champion and Downs in prep. a,b). Active capture took place at night, preferable on or near new moon phase, using the aluminium boat. Crocodiles were identified by their eye shine in a spotlight. When sufficiently close, a 3 m pole was used to slide an attached standard self-locking 3S-72” Thompson steel snare over the crocodile’s head and then closed around its neck. The snare was attached to 50 m of rope and the crocodile was given rope to fight, away from the boat. After the initial fight, a suitable place on the shore was used to beach the boat and pull the crocodile onto land. The crocodile’s eyes were then covered with a towel to calm the animal, and the jaws were cable tied shut as a precaution. Two people then simultaneously sat on the crocodiles back, subduing it. The jaws were taped closed using duct-tape as a further jaw restraint. Capture location and time was recorded. The animal was then assessed which included morphometric measurements, gender determination, scute clipping (Leslie, 1997), tagging and possibly transmitter attachment. The crocodiles were sexed through cloacal cavity examination. The VHF radio transmitters were attached to the four major nuchal scutes of the neck. A 5 mm hole was drilled through the ridge of each nuchal scute and the transmitter attached using cable-ties and Vortex dental acrylic. Transmitters were encased in plastic casings (50 mm x 20 mm x 80 mm) for protection, with a 250 mm aerial protruding out the back of the box. The tracking of the crocodiles fitted with transmitters was done using a Yogi directional antenna and Alinco wide band receiver (DJ-X10, Japan)(Champion 2011, Champion and Downs in prep. a,b).

We used a spring trap to target very large male Nile Crocodiles that were too wary to catch using the active capture snaring method (Champion 2011, Champion and Downs in prep. a,b). The trap was set up on the waters' edge, and consisted of a "T" piece base, with an attached spring made of three vehicle feather springs attached end to end. One end of the spring was attached to the "T" piece, with the other end had a large sliding noose attached. The sliding noose was tied using 50 mm dynamic climbing rope. The spring was bent over and held in place by a trigger mechanism. The trigger mechanism was attached, using nylon rope, to a bait ball at the base of the "T" piece frame. The sliding noose would be held open across the access point to the bait ball using collected tree branches. Thorny vegetation was then packed around the trap structure to prevent other scavengers from accessing the bait and triggering the trap prematurely. The rope forming the sliding noose was anchored independently of the trap to a fixed structure such as a large tree. The crocodile would enter through the open access point, taking hold of the bait ball and attempting to drag the bait back to the water would spring the trap. As the trap was sprung the sliding noose would tighten around the crocodile's midriff, just behind the front legs. The spring would ensure the rope and noose remained taught, not allowing the crocodile to escape. Traps were usually set up early in the morning, as fast as possible in order to minimize human presence in the area and the associated disturbance. The trap would be checked, from a distance using binoculars, twice daily for captured crocodiles or the premature springing of the trap. Once a crocodile was captured, the capture team would pull the crocodile up onto the bank using the already attached climbing rope. The crocodile would then be subdued and processes as with active captured crocodiles (as above) (Champion 2011, Champion and Downs in prep. a,b).

2.4 Nesting ecology

Effective methods for conducting Nile Crocodile nest site surveys include aerial surveys, ground surveys and surveys from the water (Combrink 2004). We used all three of these methods in this study (Champion 2011, Calverley 2013, Combrink 2014).

2.4.1 Lake St Lucia

2.4.1.1 Historical data: 1959 to 2008

Theses, reports, memorandums, nest recording sheets and published literature, both scientific and popular, were used to obtain historical information on Nile Crocodile nesting at Lake St Lucia from 1959 to 2008 (Combrink 2014, Combrink et al. in prep. f,g).

2.4.1.2 Aerial surveys (2008/9 to 2011/2)

Lake St Lucia Nile Crocodile aerial nesting surveys were conducted in Jan. or early Feb. during the 2008/9 to 2011/12 nesting seasons (Combrink 2014, Combrink et al. in prep. f,g). We used a fixed-wing (two-seater) Microlight aircraft on 1 Feb. 2009, two fixed-wing (two and four-seater) aircraft on 24 Jan. 2010 and a two-seater motorised paraglider on 9 Jan. 2012. Crocodiles often nest near freshwater seeps in small open areas within Swamp Forest (Combrink & Warner, pers. obs.), but such nests are often missed during the foot survey due to concealment from the survey observer's field of view (Combrink 2014, Combrink et al. in prep. f,g).

2.4.1.3 Foot, boat and kayak surveys (2008/9 to 2012/3)

Foot, boat and kayak surveys were conducted as part of the annual EZKZNW Lake St Lucia Nile Crocodile nest monitoring programme each summer from 2009 to 2013 (Combrink 2014, Combrink et al. in prep. f,g). The duration of these surveys varied 15-20 days and all known nesting areas were searched. Once a nest was encountered, a GPS point was recorded and the surrounding area was searched for the female. If present, her position relative to the nest (i.e. on the nest, near the nest or in the water) was noted and her size estimated. If she had a transmitter on or if caudal tags were visible, the colours were recorded and if possible, the scute notch recorded for identification. Nest localities and survey routes were plotted on a digital aerial map in ArcView 9.3 ESRI, Redlands, USA. Mean ± standard error are reported (Combrink 2014, Combrink et al. in prep. f,g).

2.4.2 Ndumo Game Reserve

2.4.2.1 Nest data collection

We divided NGR into two major regions with seven sub-regions for the nest surveys as described by Pooley (1982) with an additional two sub-regions covering the new courses of the Usuthu and Phongola rivers, both of which have diverged subsequent to earlier studies (Calverley 2014, Calverley and Downs 2015b). The reason for this was to demarcate NGR according to different subhabitats in particular related to soil type and proximity to a water source (either river or pan), in order to determine if the number of nesting sites differed according to these factors. The regions and sub-regions were as follows:
Region 1- The Usuthu floodplain and associated pans: Sub-region 1- The Usuthu River as it enters NGR, including Shokwe Pan, to the bifurcation point of the new and old courses. Sub-region 2- The old course of the Usuthu River to the confluence with the Phongola river in the

north eastern corner of NGR. Sub-region 3- The new course of the Usuthu River from the bifurcation point from the old course through (and including) Banzi Pan to the confluence with the Phongola river in the north eastern corner of the reserve (Calverley 2014, Calverley and Downs 2015b).

Region 2- The Phongola floodplain and associated pans: Sub-region 4- The original course of the Phongola river, from the confluence with the Usuthu River upstream to the bifurcation point with the old course. Sub-region 5- Lake Nyamithi. Sub-region 6- The old course of the Phongola river from its bifurcation to the confluence with the Usuthu River, flows through swamps and marshland. Sub-region 7- The main course of the Phongola river, from where it enters the reserve to the point of bifurcation of the new and old courses. Sub-region 8- The new course of the Phongola river from the bifurcation point of the old course to the confluence with the new course (Calverley 2014, Calverley and Downs 2015b).

2.4.2.2 Nest surveys

At NGR egg laying normally occurs from the early November to early December followed by hatching between the late January and late March (Pooley, 1969, Calverley 2014, Calverley and Downs 2015b). We initiated Nile Crocodile nest surveys in NGR on foot on an annual basis from mid-December and throughout the study period assuming that all active nests would have already been present at the onset of the survey. We used local knowledge of the EKZNW game rangers and historical records of nesting sites to investigate historical nesting sites and the possibility of consecutive seasonal use, a phenomenon which has been widely reported (Taylor and Blake 1986, Hartley 1990, Combrink 2004, Shacks 2006) but poorly validated. In addition we did follow up surveys on foot after aerial surveys to examine and confirm nesting sites identified, and searching for any undiscovered nests within the area (Swanepoel et al. 2000, Combrink 2004). We were not granted permission from the park authority (EKZNW) to search for nests by probing potential nesting sites with rods and could have resulted in nests not being discovered (Calverley 2014, Calverley and Downs 2015b).

Once we found a crocodile nest in NGR, we recorded the geographical location using a hand held Garmin eTrex® Vista Cx global positioning system – GPS and allocated it to a sub-region (1-8) (Calverley 2014, Calverley and Downs 2015b). We revisited nest sites on three separate occasions spanning six weeks to determine successful hatching, record predation and other reasons for recruitment failure such as flooding, trampling by large herbivores or nest abandonment. We recorded factors important to nesting ecology such as substrate, slope, distance to water, height above water, slope, exposure to sunlight, and distance to nearest nest. We were not granted EKZNW permission to open nests to check eggs as the smell from the eggs and disturbance may attract nest predators such as Water

Monitor Lizard. We relied on egg shells from hatching or predation to verify suspected nests. In the event that these were not visible after the hatching season (February to March) it was decided to dig up suspected nest sites to check for eggs and to confirm a nest (Calverley 2014, Calverley and Downs 2015b).

We classified substrate of the nest site in NGR into three types as described by Pooley (1969): Finely sorted silt found along the old course of the Phongola river (sub-region 6); Rocky type soils in boulder outcrops along the southern shore of Lake Nyamithi (sub-region 5) and black clay/alluvial silt along the main course of the Phongola river (sub-region 7) (Calverley 2014, Calverley and Downs 2015b). When the distance to water was greater than 20 m, we calculated the distance by taking a GPS waypoint at the nest and another at the water's edge and measuring the distance between the two points. We used a tape measure for distances less than 20 m. We estimated height above water. We then calculated the slope using the cotangent of the distance to water over height above water and converted into degrees (Swanepoel et al., 2000). We measured distance to nearest nest with a tape measure where possible or by measuring distance between GPS waypoints created at each nest where dense vegetation or long distances rendered the tape measure ineffectual (Calverley 2014, Calverley and Downs 2015b).

We used four camera traps in NGR set up at nesting sites in an effort to record nest site attendance by the female and to identify possible nest predators (Calverley 2014, Calverley and Downs 2015b). All cameras were placed so as not to impede access to the nest by females or predators and were attached to tree stumps or naturally occurring vegetation where possible. Where this was not possible cameras were attached to two 100 cm x 10 cm fencing standards which we hammered into the soil (Calverley 2014, Calverley and Downs 2015b).

2.4.2.3 Historical nesting data

The first ground based Nile Crocodile nest surveys were conducted annually in NGR by Pooley from 1967-1974 (EKZNW records unpublished data, Calverley 2014, Calverley and Downs 2015b). Nests known by park rangers previous to initial surveys were investigated and their location mapped. From 1967-1974 any nesting activities sighted by NGR staff during foot and boat patrols were reported and recorded. During this period identified nesting sites were allocated a serial number and marked on a 1: 12,000 topographical map of NGR. Subsequently nesting sites were revisited each breeding season and checked for continued use. Additional data collected at these nesting sites included height above and distance to water, soil type and evidence of predation or flooding. Nest surveys were again carried from 1988-1990 (EKZNW records unpublished data). Surveys were initiated in January annually with the Phongola floodplain walked on foot where accessible. Areas of higher elevation which were unlikely to be inundated by floods were given particular attention. NGR game scouts from Polwe Camp searched the eastern part of the Phongola floodplain while areas of the Phongola river inaccessible by foot were patrolled by boat (Calverley 2014, Calverley and Downs 2015b).

2.4.2.4 Aerial survey for nests

We did an aerial nesting survey in NGR on the 31 January 2010 (Calverley 2014, Calverley and Downs 2015b). High water levels due to the flooding Usuthu River and unprecedented water releases from Pongolapoort/Jozini Dam flooded almost all of the available nesting sites in the reserve at this time. Nonetheless, a full aerial survey was carried out. A Cessna Bushbaby two seater aircraft was used with two observers seated longitudinally. The right window was opened to facilitate counting and the aircraft flown in such a manner that all counting was done on this side. A Garmin GPS plotted the route flown by creating waypoints at 50 m intervals. Weather conditions were good for a nest survey with clear skies and good visibility. The ambient temperature was 28°C and it was expected that nesting females would be visible lying up next to their nests and not concealed while cooling off in nearby deep water. There was a negligible north easterly wind of 10 knots. The survey was conducted at an average speed of 120 kph at an elevation of 70-90 m agl. The survey lasted 45 min (Calverley 2014, Calverley and Downs 2015b).

2.4.2.5 Ground surveys

We did terrestrial Nile Crocodile nest surveys from mid-December through to March in the 2009/2010 and 2011/2012 nesting seasons at NGR (Calverley 2014, Calverley and Downs 2015b). We investigated historical nesting sites and searched for new sites. We carried out foot surveys in the early morning, between 05h00 and 10h00, so that fresh tracks left by nesting females were easy to spot and not concealed by other animal tracks (Hartley, 1990). In addition EKZNW Game Rangers actively searched for nests mapping their survey routes using a Garmin Vista GPS. Routes from all the GPS's were then downloaded onto a Patrol Management System (PMS) which superimposed the routes onto a GIS map of the reserve. In this way it was ensured that all potential nest sites were patrolled. In addition Nile Crocodile nests were located by walking along the shoreline of the major water bodies within NGR and searching for signs characteristic of nesting behaviour such as distinct pathways between the nest and the water, the nest itself being conspicuous as a patch of bare sand, the crocodile guarding the nest being disturbed and rushing into the water and where nesting over successive seasons left debris and shell fragments identifying nesting sites (Taylor and Blake 1986, Calverley 2014, Calverley and Downs 2015b)).

2.4.2.6 Boat survey

During the 2009/2010 Nile Crocodile nesting season at NGR we used a single boat survey to search for nests in otherwise inaccessible parts of the Phongola river (Calverley 2014, Calverley and Downs 2015b). River surveys covered 6.5 km over 2 h using a 3.5 m aluminum boat with a 40 hp motor. No nests were found using this method in 2009/2010 and this section of the reserve was searched on foot in the dry season in 2011 (Calverley 2014, Calverley and Downs 2015b).

2.4.3 Pongolapoort Dam

No previous documentation of number of Nile Crocodile nesting females or nest site localities at Pongolapoort Dam was available (Champion 2011, Champion and Downs in prep. a,c). As a result we carried out surveys to identify general nesting areas. After the nesting areas were identified, detailed information on actual number of current nests, as well as size classes of nesting females and environmental parameters associated with individual nest site selection were obtained. A number of surveys were conducted each month from August 2009 to February 2010, using a combination of methods to achieve these objectives (Champion 2011, Champion and Downs in prep. a,b).

2.4.3.1 Aerial surveys

We conducted a single aerial survey of the north western section of Pongolapoort Dam on the morning of 23 November 2010, during favourable weather conditions, using a AS350 Ecureuil Helicopter (Squirrel) (Champion 2011, Champion and Downs in prep. a,b). This survey team consisted of 4 observers, including the pilot and a scribe. The survey commenced at 10h00 and finished at 11h00, covering 25 km. During this survey a total crocodile count was obtained (Champion 2011), noting distribution, size classes and probability of nesting sites. Probable nesting sites/areas were identified by either atypical basking behaviour, such as unusual basking site selection or odd diffuse basking clusters, or by visuals of nesting depressions or actual eggs of only partially covered nests. The survey route included the river inlet (N2 road Highway Bridge to Railway Bridge), as well as the dam sections 3 and 4 as described elsewhere (Champion 2011). The remaining sections, including the main body of the dam (sections 1, 5-17) were not surveyed due to the high financial cost associated with this method of survey and the low likelihood of nest sites in these sections with unsuitable habitat (Champion 2011). Once a possible nesting area was identified from the air and its geographical location noted using a global positioning system (GPS, Etrex, Kansas, USA), it was later confirmed by a follow-up foot survey (see below) (Champion 2011, Champion and Downs in prep. a,b).

2.4.3.2 Foot surveys

Foot surveys to determine numbers and localities of Nile crocodile nest sites consisted of 2-3 observers who walked along the water-line as closely as possible, however some water-line areas were inaccessible and had to be circumnavigated (Champion 2011, Champion and Downs in prep. a,b). En route any paths possibly created or used by crocodiles were investigated. Areas around well-known basking sites or possible historical nesting sites (various pers. comm.) were more intensively examined for evidence of nesting sites and number of nests within these areas determined by walking them extensively while on a foot survey. When searching for individual nests, a nest's presence was often made known by a fleeing crocodile with observers approach. The exact nest site was often identified by an indent or signs of soil disturbance, accompanied by imprints where the crocodile had been laying near/on the nest. The geographical position of nests was obtained using a GPS (Champion 2011, Champion and Downs in prep. a,b).

In order to minimize disturbance at the Nile Crocodile nesting areas, we spent minimal time there, with the aim to merely confirm the number of nests, their locations and if possible the size class of the nesting females (Champion 2011, Champion and Downs in prep. a,b). Historical nesting sites from prior breeding seasons were also noted if discovered. These were usually identified by the presence of old egg fragments which may take a number of years to decompose fully (Leslie 1997). Female crocodiles were occasionally observed on nests from a distant vantage point with minimal, if any, disturbance. This allowed for a non-bias opportunity to observe the nesting females presence and behaviour at the nest. Each area was not intensively walked more than twice during the breeding season to minimize disturbance. Further measurements and recordings were delayed and only taken at the end of the nesting season (post-hatching) to further minimize disturbance. All parameters measured at each nest were environmental (approach distance from water, exit distance to water, height above water, substrate type, distance to nearest neighbouring nest and vegetation cover). Each nest was assigned a disturbance rank where 0/3 was very low, 1/3 was low, 2/3 was moderate and 3/3 was frequently disturbed. In addition, the probability of discovering previously overlooked nests was expected to be greater after hatching. During these post-hatching measurements attempts were made to estimate hatching success and determine levels of predation at various nesting areas. Due to the flash flooding and resultant destruction of all nests along the river sections and alteration of the river banks, some environmental parameters for some of the nests were approximations made from photographic records. A commonly included parameter in many past studies was height above water. However, in this study it was not included, as the river level fluctuated dramatically with sporadic summer rains and the dam level constantly rose with the onset of summer rains in the upstream catchment area (Champion 2011, Champion and Downs in prep. a,b).

As some of the dam's Nile Crocodiles had been caught, tagged for unique identification and fitted with radio-transmitters (Champion 2011, Champion and Downs in prep. a,b), these were monitored hourly for 24 h each month for several months and any reproduction related data collected presented here. Other crocodiles had been previously caught and were uniquely identifiable from their individual colour-coded tail scute tags assisted in determining presence of males and or females at the respective breeding areas (Champion 2011, Champion and Downs in prep. a,b).

We made a number of opportunistic observations of Nile Crocodile reproduction were made and recorded during surveys and visits to the respective breeding areas and in particular from various vantage points overlooking these during the breeding season (August-February) (Champion 2011, Champion and Downs in prep. a,b). A number of mass basking areas were identified as been used year round, however at only one was opportunistic observations made on courtship and mating events. This mass basking area was referred to as Buffalo Bend (27°22'47.05" S, 31°50'44.43" E). A second area identified as a "communal" nesting site and referred to a Causeway Bend (27°23'22.74" S, 31°50'25.10" E) was also monitored regularly. At all these, observations were made and any mating and/or courtship behaviour, as well as threat displays and aggressive interactions between Nile Crocodiles recorded (Champion 2011, Champion and Downs in prep. a,b).

2.5 Nest effort

Nest effort, or reproductive frequency, is the proportion of mature females in the population that are nesting each year (Combrink 2014, Combrink et al. in prep. f,g). It is an important parameter to estimate as it provides information on the reproductive segment of the population and might reveal other factors (e.g. rainfall, nutrition, social pressure) affecting reproduction. We calculated nest effort (E) of Nile Crocodiles using a method described by Chabreck (1966) and adapted by Leslie (1997) for use at Lake St Lucia, NGR and Pongolapoort Dam (Champion 2011, Calverley 2013, Combrink 2014).

$$N = \frac{X}{A \times F \times E}$$

N = population estimate

X = nest estimate

E = nest effort or reproductive frequency (i.e. proportion of mature females nesting)

A = proportion of mature animals in the population, i.e. no. of mature crocodiles / sample size

F = proportion of females in the mature population, i.e. no. of mature females / number of mature crocodiles

We estimated the population N from winter aerial surveys. To account for visibility bias we estimated diving and detectability bias (Champion 2011, Calverley 2013, Combrink 2014).

At Lake St Lucia we calculated X based on summer nest surveys, multiplied by 1.1 as we estimate that 10% of the nests are missed during the survey (Combrink 2014, Combrink et al. in prep. f,g). We used F = 0.5049, the female to male ratio determined in the capture study. We estimated the sub-adult component of the population based on size estimates obtained during 10 spotlight surveys to be 19.86%. Although the study included capture data from 2009-2012, we included 1982 to 2013 nest and aerial survey data (EKZNW, unpublished data) for comparative purposes. Years where nest and aerial surveys were not conducted or incomplete, were excluded from the analysis then solved the equation for E (Combrink 2014, Combrink et al. in prep. f,g). At NGR N was calculated as total population or absolute abundance counts (Calverley, 2013; Calverley and Downs 2014a, 2015a), X from nesting surveys while A and F were calculated through capture activities (Calverley, 2013; Calverley and Downs 2014a, 2015a).

2.6 Re-use of nest-sites

Pooley (1969) suggested that Lake St Lucia Nile Crocodiles were returning to the same nesting grounds every year due to the presence of old crocodile egg fragments at nest-sites (Combrink 2014, Combrink et al. in prep. f,g). Fawcett (1987b) initiated a system of nest marking during the 1986/87 survey, and identified 63 nest-sites that year, but nest tagging was discontinued in subsequent years. Consequently, in order to quantify the apparent re-use of nest-sites at Lake St Lucia, we marked the position of each nest found during the 2011 survey with a numbered aluminium tag, and secured it to the nearest tree. If the closest tree were more than 3 m away, we used a metal dropper pole sunk into the soil (Combrink 2014, Combrink et al. in prep. f,g).

2.7 Use of burrows

We recorded Nile Crocodile burrowing behaviour at Lake St Lucia. Burrows associated with nesting activities were noted during nest surveys (Combrink 2014, Combrink et al. in prep. f,g).

2.8 Identification of nesting females

2.8.1 Scute marking

We captured nesting Nile Crocodile females during the nesting season and each female was uniquely marked by clipping the caudal verticils with a sharp knife using a numbering system based on Australia's Queensland Parks and Wildlife Service (Kay 2004, Champion 2011, Calverley 2013, Combrink 2014, Combrink et al. in prep. f,g).

2.8.2 Colour-coded caudal tags

We attached 36 x 58 mm colour-coded flexible plastic tags (TAGEM, Ramsay Engineering) during the nesting season to nesting Nile Crocodile females. A sequence of first three, then later four, colour-coded tags was used to uniquely mark each female and tags were attached to both side of the tail, usually the first three or four single caudal verticils (Champion 2011, Calverley 2013, Combrink 2014, Combrink et al. in prep. f,g).

Figure 2.9 Nile Crocodile tag marking used.

2.9 Crocodile health

When we captured Nile Crocodiles morphological measurements were taken. We marked each individual uniquely by scute clipping and fitting of coloured caudal tags (Champion

2011, Calverley 2013, Combrink 2014, Warner in prep.a). In addition we took urine and blood samples. Analyses of blood, serum and urine from Nile Crocodiles were conducted specifically for crocodile nutritional, environmental contaminant, and epidemiological analyses to construct health/nutrition indexes of wild crocodiles, analyses of bioaccumulation of environmental pollutants.

Nile Crocodile urine (n = 39) was analysed for the following: creatinine mmol/L, calcium mmol/L, phosphate mmol/l, calcium/creat ratio, magnesium mmol/L (ref: L 0.86-9.54), uric acid mmol/L, sodium mmol/l, potassium mmol/l, chloride mmol/L, urea mmol/l and osmolality mOsm/kg (ref: mOsm/kg H20 On average fluid intake: 300-900 (Lancet Laboratories, Pretoria) (Warner et al. in prep. b). Urine samples were also analysed for dichlorodiphenyltrichloroethane (DDT) (University of Pretoria) (Warner et al. in prep. c).

Urine samples from Nile Crocodiles (n = 11) in Lake St Lucia exposed to lead sinkers were assessed using semi-quantitative full scan analysis with ICP-MS with values reported as µg/L (ppb) (Analytical Toxicology Laboratory Services, George) for the following: Li, Be, Na, Mg, Al, P, S, Cl, K, Ca, Sc, Ti, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, As, Se, Br, Sr, Mo, Ru, Rh, Pd, Ag, Cd, Sn, Sb, I, Ba, Yb, Lu, Os, Ir, Pt, Au, Hg, Tl, Pb, Bi, Th, U (Warner et al. in prep. d). The samples were suitably diluted in aqueous nitric acid and compared to a 32 element standard solution (2.5-200 µg/L) utilizing various internal standards. Although not as accurate as direct standard comparison in which a calibration curve is created for each element, the semi quant scan method applied here allows one to get an overview of the elemental profile of each sample so that differences can be more easily highlighted. Control standards containing V, Cr, Mn, Fe, Co, Ni, Cu, Zn, Cd, Tl and Pb (1.0 mg/L) were analysed among the samples to monitor quantitative accuracy. All reporting limits for the controls were within set parameters (90-110%), demonstrating the accuracy of this method (Warner et al. in prep. d).

In March 2012 we excavated a wild Nile Crocodile nest at Lake St Lucia that had been abandoned by the mother and examined the eggs.

We got permission from EKZNW to perform necroscopies (n = 4) on emaciated Nile Crocodiles in Lake St Lucia (Warner et al. in prep. e).

We analysed scute and blood samples from Nile Crocodiles captured using isotope analysis. Time series isotope analysis of crocodile claws was also conducted (Warner et al. in prep. f). Tissues for isotopic analyses were degreased in a 2:1 chloroform:ethanol mixture and dried overnight at 70^{o}C (Woodborne et al. 2012). Samples were reacted with a 1% HCl solution to remove any trace of carbonates, rinsed to pH neutral in distilled water and dried overnight at 70^{o}C (Woodborne et al. 2012). Analyses were performed on homogenised whole samples and on a time series of samples taken from the dorsal aspect of the crocodile claws extending from the base to the tip of the claw (Woodborne et al. 2012). Claw samples were cleaned by boiling in distilled water during the extraction process but were not further pre-treated (Woodborne et al. 2012). Carbon and nitrogen isotope analyses were undertaken on 0.5-1.0 mg aliquots, while sulphur isotope analyses required 5 mg aliquots (Woodborne et al. 2012). Analyses are currently in progress.

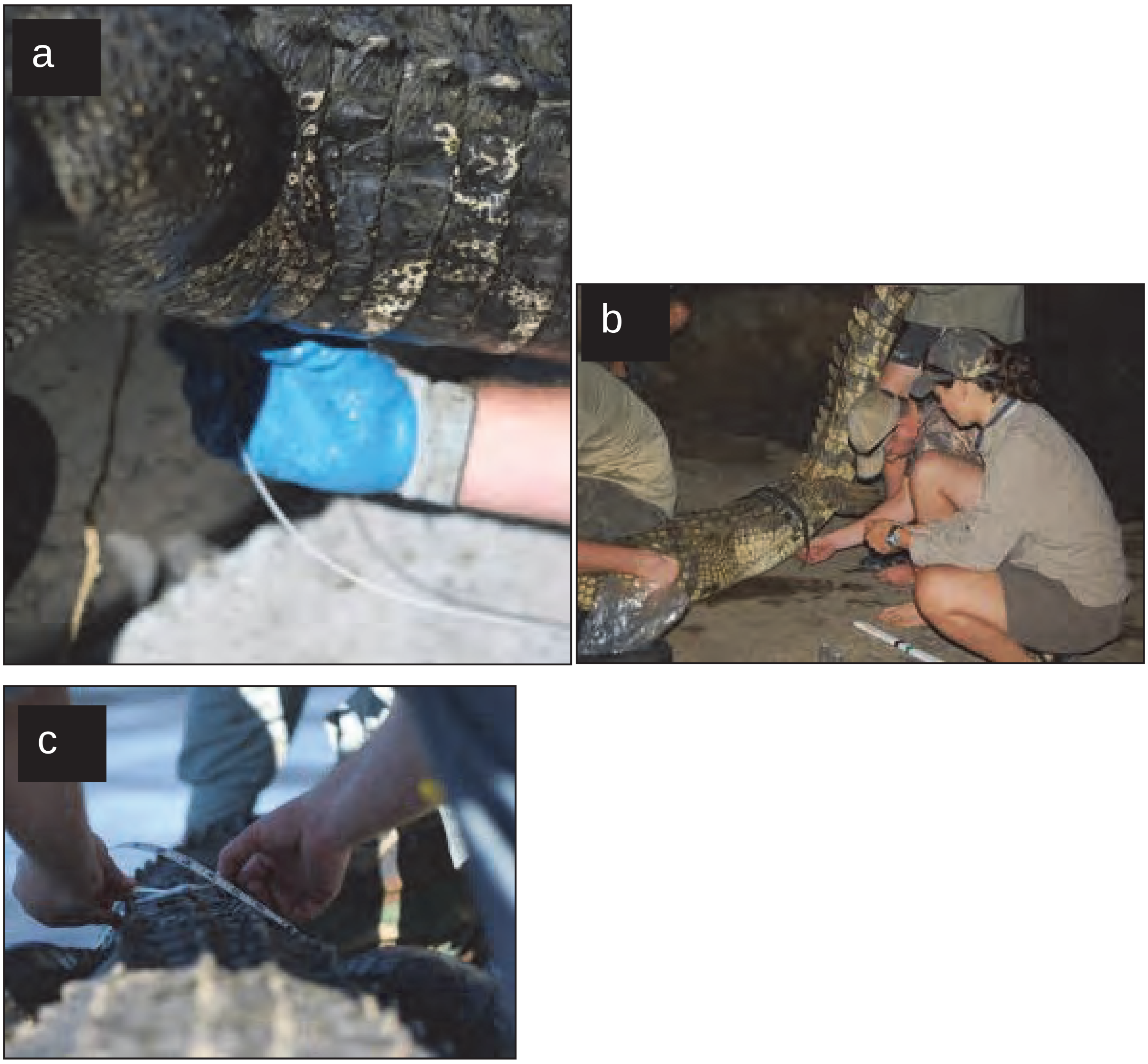


Figure 2.10 Collecting a. urine and b-c. morphological measurements from a captured Nile Crocodile (Warner unpublished data).

Figure 2.11 Collecting a. blood, b. weighing, c. urine samples and d. morphological measurements from a captured Nile Crocodile (Warner unpublished data).

3 RESULTS: NILE CROCODILE IN LAKE ST LUCIA

3.1 Distribution and relative abundance

3.1.1 Aerial surveys

The mean St Lucia sub-adult and adult Nile Crocodile count from 2009 to 2013 was 722 ± 35.6 (range: 113-819, Combrink 2014, Combrink et al. in prep. a). Overall, less crocodiles were counted in June 2013 (616) compared with June 2009 (819). The June 2011 (760) and 2012 (745) counts were similar, but more compared with the 670 Nile Crocodiles observed in June 2010 (Fig. 3.1, Combrink 2014, Combrink et al. in prep. a). Nile Crocodiles were distributed throughout most of the lake system, albeit at low densities. By far the largest concentration was recorded south of the lake, in the Narrows (192 ± 55.8) and Potters Channel, a dredged extension of the Narrows (167 ± 25.2). On average, 448.0 ± 54.1, or 62.1% of individuals, were concentrated in the Greater Narrows (Combrink 2014, Combrink et al. in prep. a), reaching a high of 82.1% in 2010, in less than 2.0% of the entire lake system. Crocodiles were also recorded in South Lake (117.2 ± 26.9; 16.2% of mean total) and 87.2 ± 22.5 in North Lake (12.1% of mean total), of which 70.8% (62 ± 14.9 Nile Crocodiles) were found in Tewati Bay, a ~25 ha bay along the eastern shoreline fed by fresh seeping groundwater. Remaining parts of the system accounted for < 10% of individuals, with areas containing, on average, > 30 Nile Crocodiles restricted to three freshwater shoreline seepage areas: Dead Tree Bay/Jubangoma (39 ± 10.9), Lake Bhangazi (31 ± 9.2) and Catalina Bay (32 ± 5.3). Very few Nile Crocodiles were found in the extreme north or south, or in False Bay (Combrink 2014, Combrink et al. in prep. a).

We recorded temporal variation in Nile Crocodile densities, consistent with previous findings (Pooley 1982b, Leslie 1997). As expected, more Nile Crocodiles were observed in June (winter basking behaviour), e.g. 670 in 2010 compared with 113 in Jan. (summer) 2011, when most Nile Crocodiles were in the water and less visible or submerged (Combrink 2014, Combrink et al. in prep. a). Water temperature data support this; mean daily water temperature (10:00 to 14:00) varied significantly between winter (June 17.0 ± 0.1°C) and summer (Nov. 25.7 ± 0.2°C, Jan. 27.4 ± 0.1°C) (Combrink 2014, Combrink et al. in prep. a). We counted less Nile Crocodiles during winter south of the lake (Greater Narrows) in 2013 (245) compared with 2012 (435) or 2009 (518). More individuals were observed in North Lake in 2013 (115) compared with 25 in 2010 and 68 in 2012 (Combrink 2014, Combrink et al. in prep. a).

The large proportion of Nile Crocodiles recorded south of the lake from 2009 to 2012, resulted in large basking congregations during winter (Combrink 2014, Combrink et al. in prep. a,b). Exceptionally large congregations of > 200 individuals were counted in the

Narrows and Potters Channel. Large basking formations in North Lake in 2003 (Tewati Bay = 192, Selly's Lakes = 203 and Fani's Island = 99) dispersed as the north and central parts of the lake dried out subsequently (Combrink 2014, Combrink et al. in prep. a). We noted changes between years in the size and location of Nile Crocodile basking congregations in the Narrows due to changing water levels (Combrink 2014, Combrink et al. in prep. a). Elevated (and cold) water levels during the 2010 winter flooded parts of a large 2009 basking area (199 Nile Crocodiles) just south of the Mphathe Stream confluence. Crocodiles moved north to Potters Channel, and basking crocodiles increased from 111 (2009), 163 (2010) to 261 and a density of 372.9 crocodiles km^{-1}, in 2011 (Combrink 2014, Combrink et al. in prep. a).

3.1.2 Diving bias during aerial surveys

The mean Nile Crocodile emergence/submergence ratio during the day (10:00-14:00) was 0.8 ± 0.04, which differed significantly throughout the year (Combrink 2014, Combrink et al. in prep. a,b), with most Nile Crocodiles (93.7 ± 0.04%) emerged in June during winter and least (58.4 ± 0.05) in Feb. during summer. June was the coldest month with mean water temperature 17.0 ± 0.1°C, and air temperature 18.6 ± 0.2°C (Combrink 2014, Combrink et al. in prep. a,b). We noted a strong inverse correlation ($r = -0.95$) between water temperature and diurnal crocodile diving behaviour (Combrink 2014, Combrink et al. in prep. a,b).

The 3.0-3.5 m size class of Nile Crocodile was most often emerged (85.6 ± 0.03%) with 2.5-3.0 m Nile Crocodiles the least (80.7 ± 0.02%), but these differences were not significant (Combrink 2014, Combrink et al. in prep. a,b). June to Aug. were the months with least variation in diving behaviour between size classes, with all sizes spending very little time submerged during the day (mean = 6.4 ± 0.8% submerged). From Nov. to Feb. there was a marked divergence in the diurnal diving behaviour of different sized Nile Crocodiles, with > 4 m crocodiles being submerged most, followed by 2.0-2.5 m, then 2.5-3.0 m while 3.0-3.5 m individuals were emerged most often during a summer's day (Combrink 2014, Combrink et al. in prep. a,b).

3.1.3 Spotlight surveys

Spotlight counts ($n = 10$) in the Narrows between June 2009 and June 2012 revealed temporal variation in Nile Crocodile density, with the lowest figure in Jan. 2011 (2.2 crocodiles km^{-1}) and the highest (10.27 crocodiles km^{-1}) in July 2010 (Combrink 2014, Combrink et al. in prep. a,b). We corrected spotlight counts for diving bias (Combrink 2014, Combrink et al. in prep. a,b) resulting in a range of 2.98-15.91 Nile Crocodiles km^{-1}. Water depth determined the most northern start/end point of each survey and this had a considerable effect on the length of the survey transect. Low water levels (0.47 m, measured at St Lucia bridge) during the first survey on 19 June 2009 restricted the survey to 11.1 km, but as water depth increased to 0.82 m in the Narrows on 4 July 2011, we were able to extend the survey route to 20.3 km. The highest count was made in July 2010 when it was possible to include a large basking area just south of the Mphathe Stream confluence (129 Nile Crocodiles counted during the previous month's aerial survey, Combrink 2014, Combrink et al. in prep. a,b). During the June 2009 spotlight survey, water depth was not sufficient to include the Mphathe Stream confluence area, which might have increased the encounter rate. Increased water levels in July 2011 (0.80 m) allowed the Mphathe Stream confluence area to be surveyed, but the high water level flooded the Mphathe Stream confluence area used the previous years and crocodiles moved north into Potters Channel in search of dry basking areas. The July 2011 encounter rate (11.98 crocodiles km^{-1}) was lower compared with the previous year (15.91 crocodiles km^{-1}), but it was possible to survey only 1.2 km (i.e. 50%) of Potters Channel before it became too shallow (Combrink 2014, Combrink et al. in prep. a,b). The largest basking congregation along Potters Channel was at the northern tip, which was too shallow to be included in the survey. It was not possible to survey the entire Potters Channel in a boat at night due to the shallow nature of the channel and impenetrable stands of *P. australis* in some areas. Dense stands of *P. australis* along the banks also prevented night foot surveys (Combrink 2014, Combrink et al. in prep. a,b).

3.1.4 Diving bias during spotlight surveys

The mean emergence/submerge ratio of Nile Crocodiles during the night (18:00-02:00) was 0.55 ± 0.04%, which differed significantly throughout the year (Combrink 2014, Combrink et al. in prep. a,b). Most crocodiles (66.1 ± 0.05%) were emerged in Jan. (summer) and least (43.5 ± 0.04%) during winter in June, with a strong positive correlation ($r = 0.93$) between water temperature and nocturnal emergence behaviour (Combrink 2014, Combrink et al. in prep. a,b). We recorded size-related variation in nocturnal diving behaviour, with smaller Nile Crocodiles spending less time emerged than larger crocodiles, i.e. sub-adults (2.0-2.5 m) spent significantly less time emerged (46.0 ± 0.03%) compared with crocodiles > 4 m (61.5 ± 0.04%). Nocturnal diving behaviour for different size-classes showed least variation during May, Sept. and Jan., with all crocodiles spending least time submerged in Jan. (34.0%). Nov. was the month with most variation between the sizes classes (Combrink 2014, Combrink et al. in prep. a,b).

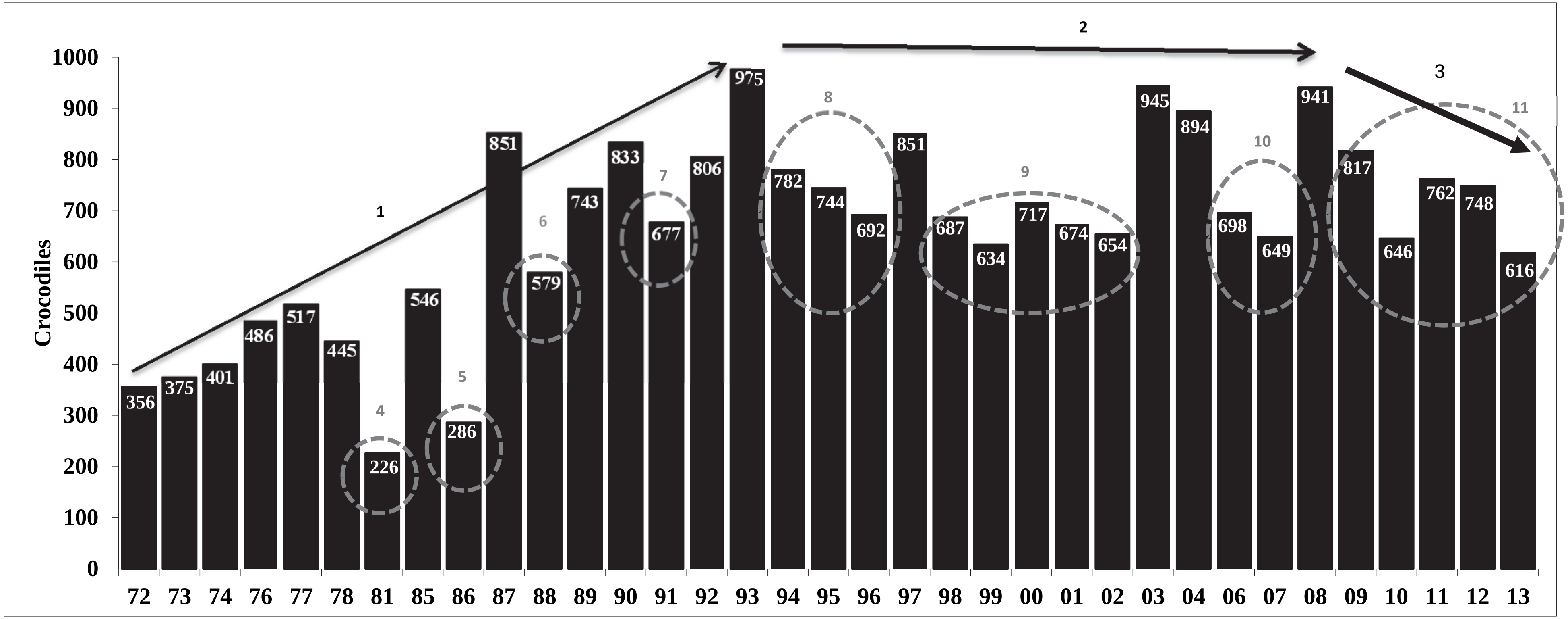


Figure 3.1 Adult and sub-adult Nile Crocodiles counted during aerial surveys at the Lake St Lucia Estuarine system: 1972-2013. Arrow (1) indicates a 13.0% growth from 1972-1993. Arrow (2) indicates an apparent stabilisation phase, and arrow (3) a notable decline (From Combrink 2014, Combrink et al in prep. a,b).

3.1.5 Population estimate

During the simultaneous double count on 13 June 2013, 373 Nile Crocodiles were counted by both airplanes, 244 only by the Cessna that flew anticlockwise around the lake and 115 only by the Bushbaby, flying clockwise (Combrink 2014, Combrink et al. in prep. a,b). We corrected the raw count figures for diving bias using the diurnal June correction factor of 1.0627 (Combrink et al. in prep. a,b). This resulted in 396 crocodiles counted by both Cessna and Bushbaby, 259 crocodiles only from the Cessna and 122 only from the Bushbaby. We estimated the 2013 sub-adult and adult population for St Lucia at 858 crocodiles (variance = 171.87, s = 13.11, S.E. = 0.02, CV = 1.5%; Combrink et al. in prep. a,b; Fig. 3.2). We used the simultaneous aerial count results to obtain a detectability bias correction factor, i.e. 858 / 656 = 1.31. After correcting for observer/detectability bias, the 2009 to 2013 mean population was estimated at 1005 ± 137 Nile Crocodiles, 95% C.I. (Combrink et al. in prep. a,b). Using these correction factors we estimated the St Lucia Nile Crocodile population since 1972 (Combrink et al. in prep. a,b).

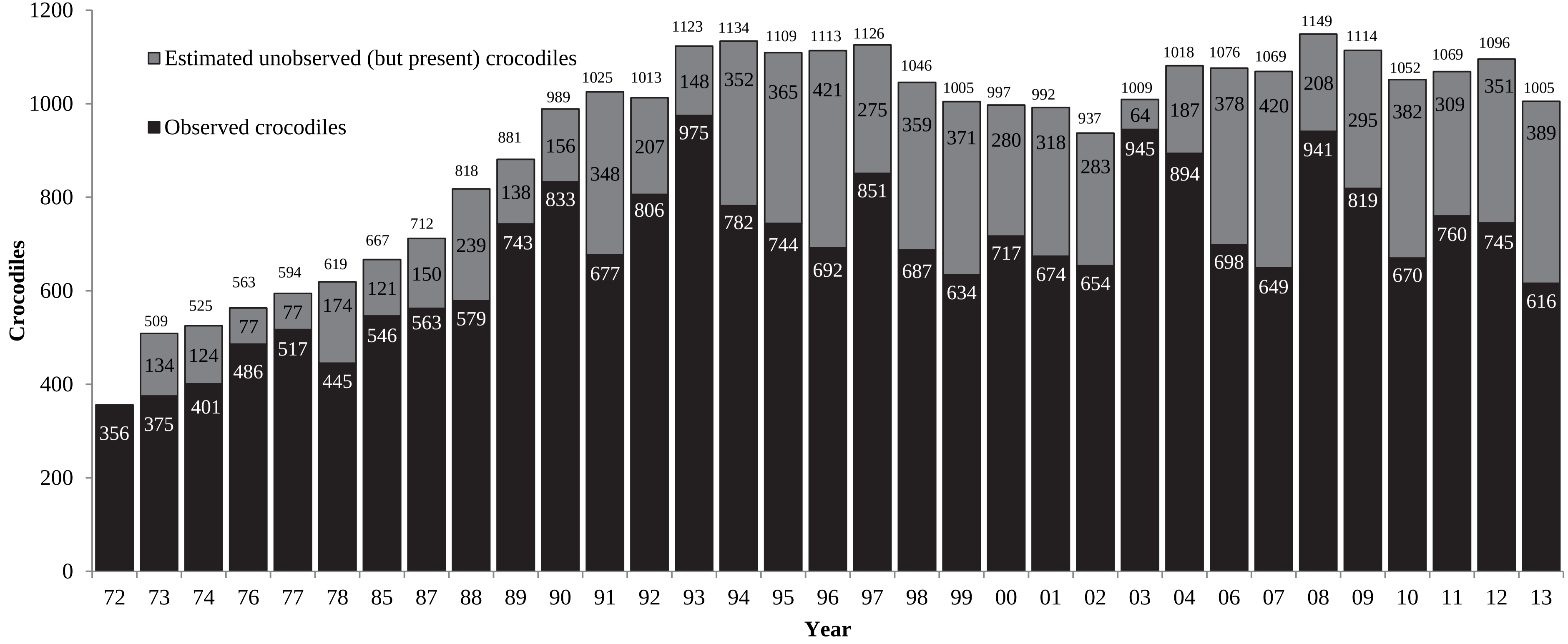


Figure 3.2 Estimated Nile Crocodile population at Lake St Lucia, based on diving and detectability bias correction factors. Black bars represent raw count data, grey bars represent submerged bias and observer/detectability bias, and the figure on top of each bar represents the 5 year mean estimate (from Combrink 2014, Combrink et al. in prep. a,b).

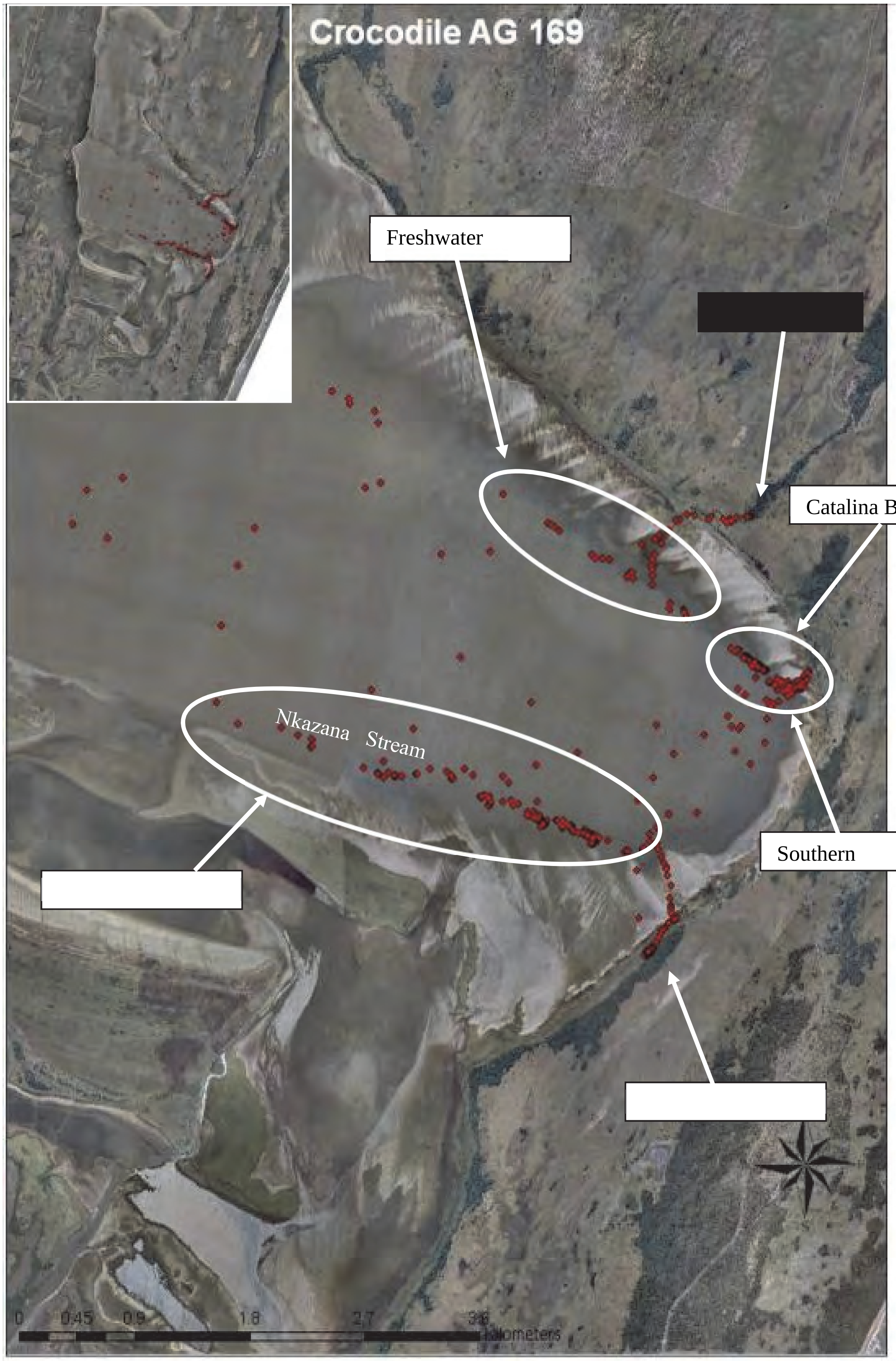


Figure 3.3 Example of Nile Crocodile movement at Lake St Lucia (from Combrink 2014, Combrink et al. in prep. a,b, Combrink unpublished data).

3.1.6 Transmitters

We attached 20 transmitters to 19 Nile Crocodiles from 16 Sept. 2009 to 3 March 2011 in the Lake St Lucia estuarine system (Combrink 2014, Combrink et al. in prep. c,d). Female 447 never entered the GSM network to download data. The mean field data days per transmitter was 397 ± 61, range: 50-1111. The mean GPS fixes per transmitter was 3129 ± 457, range: 491-9063. We have knowledge of a single transmitter (AG 301) which became detached from a crocodile after 535 days. Three transmitter-fitted crocodiles have been recaptured to date, 297, 555 and 1070 days subsequent to transmitter attachment. None of the recaptured animals showed any sign of infection at the attachment site (Combrink 2014, Combrink et al. in prep. c,d).

3.2 Activity levels

3.2.1 Diel pattern

The overall activity level (proportional displacements > 20 m, irrespective of the length of the displacement) of Nile Crocodiles at Lake St Lucia was 41.0%, and it differed significantly throughout the day (Combrink 2014, Combrink et al. in prep. c,d). After a period of low activity (30%) during late morning (10:00 to 14:00), activity increased to 36% during the afternoon (14:00 to 18:00) and continued to increase to a maximum of 46% during the early evening (18:00 to 22:00). Between 22:00 and 02:00 activity decreased slightly to 45%, continued to decrease to 44% from 02:00 to 10:00. Lake St Lucia Nile Crocodiles displayed a bimodal activity pattern with low activity (< 37%) from 10:00 to 18:00 and high activity (> 44%) from 18:00 to 10:00 (Combrink 2014, Combrink et al. in prep. c,d). The overall activity level for adult males was 44%, non-nesting females 51%, nesting females 35% (excluding the nesting summer season = 42%) and sub-adults 30%. Activity levels of adult males, non-nesting and nesting females differed significantly throughout the day, but temporal variation for sub-adults was not significant (Combrink 2014, Combrink et al. in prep. c,d).

3.2.2 Monthly variation

We found a significant positive correlation between Nile Crocodile monthly activity and water and air temperatures, with water temperature correlating slightly stronger than air temperature (Combrink 2014, Combrink et al. in prep. c,d). Crocodiles were > 50% active from Jan. to April when water and air temperatures were high, peaking in March (58.8%). From April to June crocodile activity reflected the sharp decline in air and water temperatures which reached a minimum of 18.3°C in June and July. Minimum overall activity level (27.9%) was recorded in August when the largest difference between mean water and air temperature was recorded, suggesting that the relative difference between water and air temperature was a more important predictor of inactivity than water or air temperature *per se*. The sharpest increase in crocodile activity occurred between Aug. (27.9%) and Sept. (46.9%). Subsequent to a marginal activity decreased during Oct., activity levels increased again for Nov. and Dec., as did water and air temperatures (Combrink 2014, Combrink et al. in prep. c,d).

Non-nesting Nile Crocodile females (n=3) were most active among all crocodiles and activity peaked in Jan. (82%), decreasing to 72.2% in Feb (Combrink 2014, Combrink et al. in prep. c,d). Nesting females (n=4) also showed a decrease from Jan. to Feb., but at very low activity levels due to nest guarding activities. Conversely, both adult males (n=7) and sub-adult (n=3) activity increased from Jan. to Feb., with sub-adult activity reaching a maximum in Feb. (73.5%) which was the highest recorded activity of all crocodiles for that month (Combrink 2014, Combrink et al. in prep. c,d). Adult male Nile Crocodile activity peaked in March (68.3%) and after March all, except nesting females, decreased in activity with sub-adults the lowest in June (18%), and adult males and non-nesting females in July (28.7% and 27.1% respectively). Activity levels of nesting females increased sharply from Feb. (20.9%) while nest guarding to a maximum of 63.1% in April during the post-nesting period (Combrink 2014, Combrink et al. in prep. c,d).

The activity of all Nile Crocodiles increased sharply from Aug. to Sept., apparently in response to a similar sudden increase in water temperature from 19.5°C to 22.3°C (Combrink 2014, Combrink et al. in prep. c,d). All crocodiles, except nesting females, displayed a somewhat lower activity level during Oct. while nesting females continued to increase, reaching a second annual peak in activity during Oct. before activity decreased towards Dec. due to nesting. Sub-adult activity increased very sharply from 25.0% in Oct. to 60.1% in Nov (Combrink 2014, Combrink et al. in prep. c,d).

3.2.3 Seasonal variation

There was a significant seasonal effect on Nile Crocodile activity and as expected they were least active during winter (31%) with the lowest activity level (17%) recorded during late morning (10:00 to 14:00) in winter (Combrink 2014, Combrink et al. in prep. c,d). Spring activity (41%) was comparable with mean annual activity (41%), but during summer activity was considerably higher (45%), with crocodiles being most active in autumn (52%). The highest recorded activity period was early evening (18:00 to 22:00) in autumn (58%, Combrink 2014, Combrink et al. in prep. c,d). The diel activity rhythm of Nile Crocodiles throughout the seasons followed a similar pattern with crocodiles being least active during late morning, followed by increased activity during the afternoon, peaking during the early evening. Thereafter activity levels stabilised or decreased slightly until there was a sudden decrease in activity during late morning (Combrink 2014, Combrink et al. in prep. c,d). Seasonal variation in activity levels for Nile Crocodile adult males, non-nesting and nesting females and sub-adults were all significant, with crocodiles most active in summer and least active in winter, except nesting females (Combrink 2014, Combrink et al. in prep. c,d). Nesting females were most active in autumn (57%) and least active during the summer nesting period (26%, Combrink 2014, Combrink et al. in prep. c,d).

3.2.4 Mean daily movement (MDM)

Summary data for the 19 Nile Crocodiles tracked from 16 Sep 2009 to 20 Oct. 2012 in the Lake St Lucia estuarine system including overall levels of activity (%), mean, median and largest daily movements, number of data points, field transmitter days and days moved > 20 m and > 100 m are shown Combrink 2014 and Combrink et al. in prep. c,d, Fig. 3.3, 3.4, 3.5).

We found a positive correlation between Nile Crocodile size and MDM (Combrink 2014, Combrink et al. in prep. c,d). MDM of crocodiles at St Lucia was 1244 ± 161 m and there was a significant difference between crocodiles (Combrink 2014, Combrink et al. in prep. c,d). Female 601 (293 cm TL) moved the longest daily distances (2854 ± 66 m, median 2331 m) and Male 533 (204 cm TL), a sub-adult and smallest individual in the study, the shortest (213 ± 94 m, median 97 m, Combrink 2014, Combrink et al. in prep. c,d). The largest individual, Male 520 (413 cm TL from the Mphathe Stream) MDMs were the longest (2178 ± 247 m, median 1996 m) of adult males, and Male 501 (316 cm TL) MDMs the shortest (906 ± 235 m, median 469 m, Combrink 2014, Combrink et al. in prep. c,d). However, they were both tracked for a relative short duration, 50 and 55 days respectively. Considering the five adult males tracked for more than 200 days, the MDMs of Male 504 from Lake Bhangazi was the highest (1936 ± 75 m, median 1587 m) and Male 121 from Catalina Bay the lowest (1592 ± 110 m, median 493 m). The MDMs of adult males (1712 ± 34 m, n = 7) were the highest of all crocodiles, did not differ significantly from adult nesting females (1606 ± 36, n = 4), but were significantly different from adult non-nesting females (919 ± 46 m, n = 4) and sub-adults (294 ± 52 m, n = 3, Combrink 2014, Combrink et al. in prep. c,d). Sub-adult MDMs were significantly different from each other (Combrink 2014, Combrink et al. in prep. c,d). The largest, Female 534 (212 cm TL), moved the most (334 ± 18 m, median 270 m), followed by Male 503 (208 cm TL, 311 ± 82 m, median 156 m). The smallest study animal, Male 533 (204 cm TL), made the shortest movements (213 ± 22 m, median 97 m) (Combrink 2014, Combrink et al. in prep. c,d).

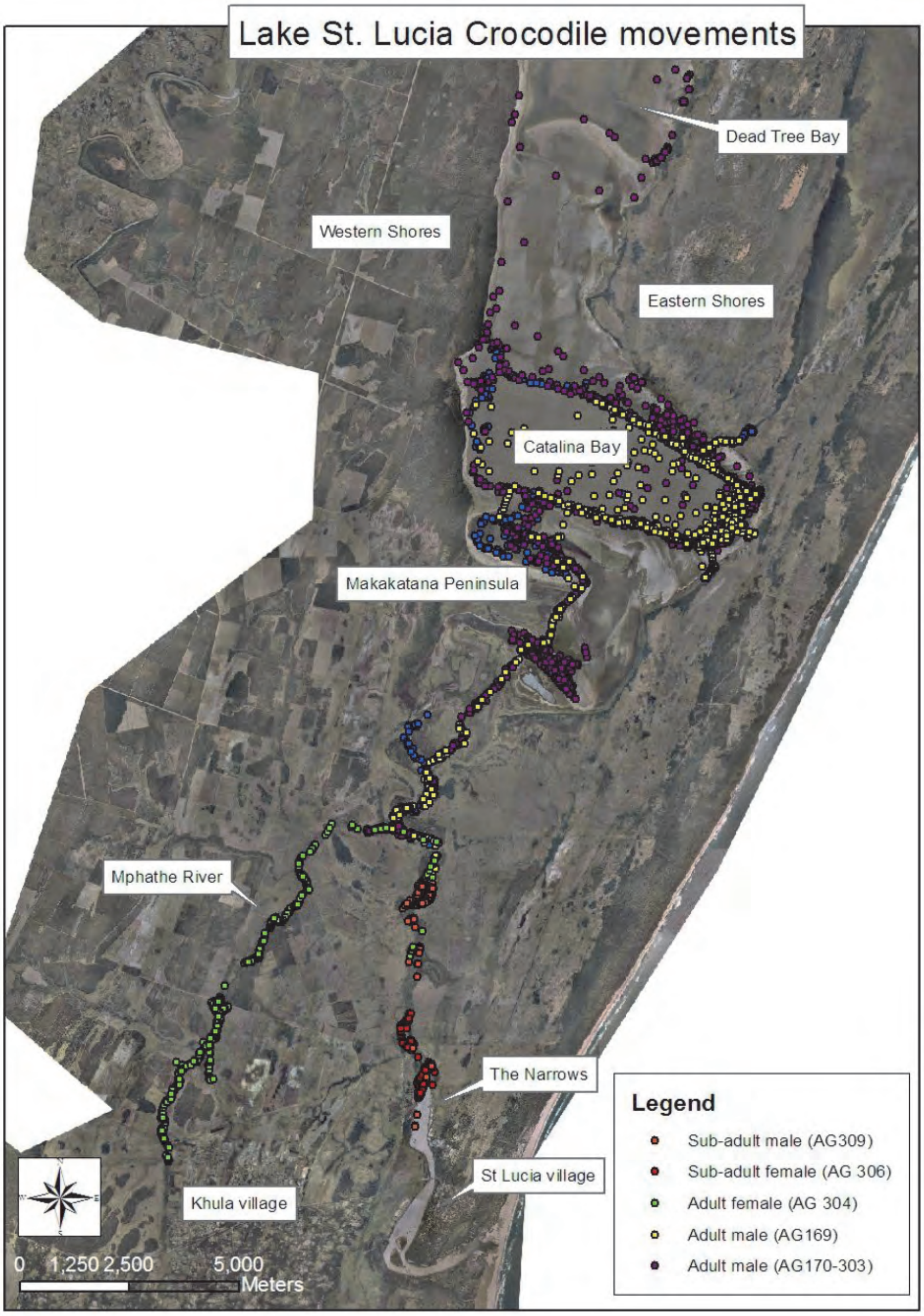


Figure 3.4 The movements of a sub-adult male (orange) and female (red) crocodile compared with a number of adults (green, yellow and purple). Male and female sub-adults are very sedentary compared with adult crocodiles at Lake St Lucia (from Combrink 2014, Combrink et al. in prep. a,b, Combrink unpublished data).

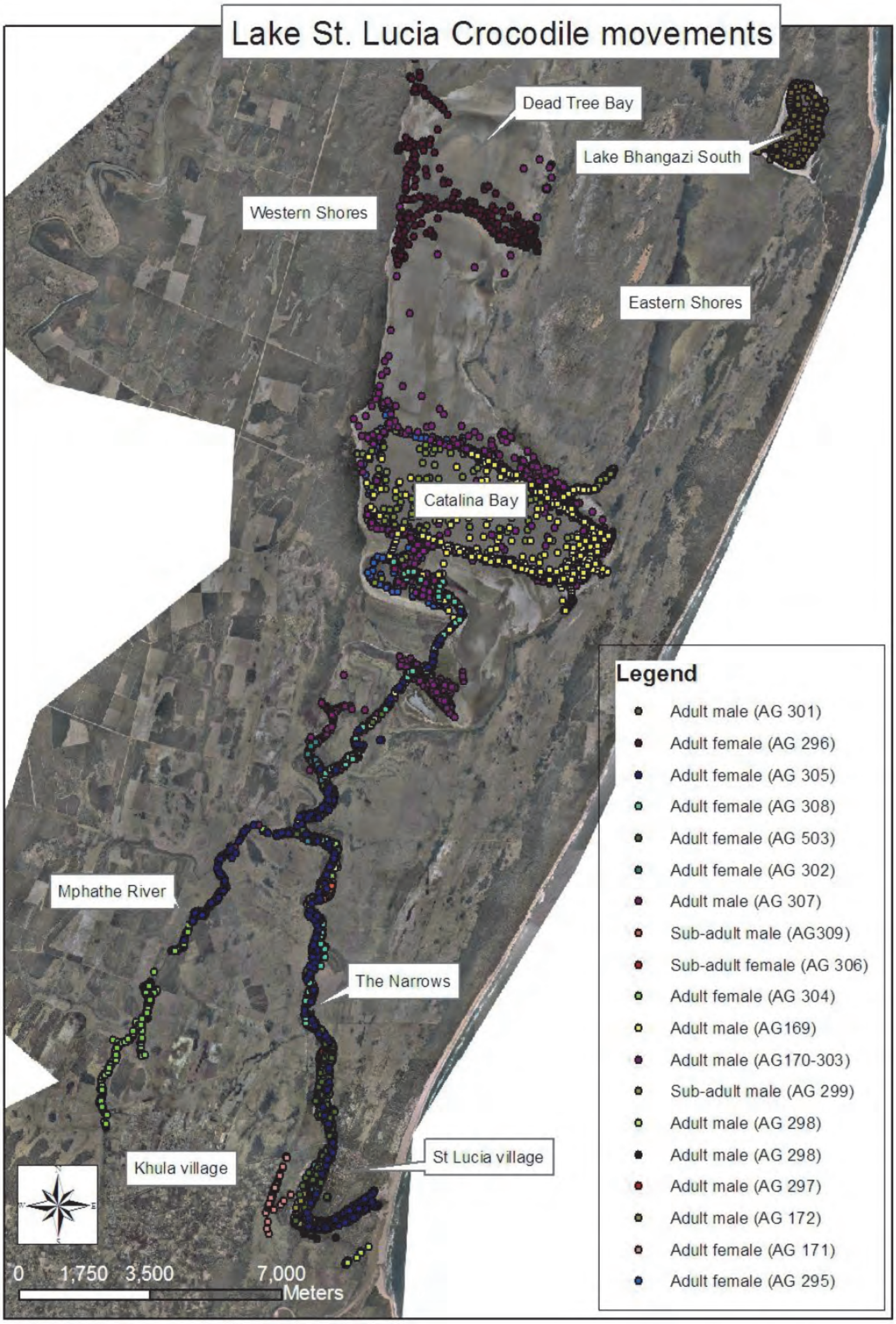


Figure 3.5 The movements of adult and sub-adult crocodiles at Lake St Lucia. Adults are a lot more active than previously suggested. Even though crocodiles frequented hypersaline areas for extensive periods, regular visits to freshwater areas were a key requirement (from Combrink 2014, Combrink et al. in prep. a,b, Combrink unpublished data).

3.2.5 Diel movement patterns

The diel movement pattern of Nile Crocodiles showed a definite rhythm and movements per time period differed significantly throughout the day (Combrink 2014, Combrink et al. in prep. c,d). Crocodiles moved the least (115 ± 5 m) during late morning 10:00-14:00, increased movement (174 ± 6 m) during the afternoon 14:00-18:00, and peaked (289 ± 6 m) during the early evening (18:00-22:00). Between 22:00-02:00 movements decreased somewhat (258 m ± 6 m) and stayed relatively constant during the early morning hours (02:00-06:00: 247 ± 6 m and 06:00-10:00: 243 ± 6 m) before a sharp decline in the late morning (Combrink 2014, Combrink et al. in prep. c,d).

The diel MDM pattern of Nile Crocodile adult males and nesting females showed much higher variability and a preference for nocturnal movements compared with non-nesting females and especially sub-adults (Combrink 2014, Combrink et al. in prep. c,d). Sub-adults moved significantly less without any preference to a particular time period. Nesting females made significantly longer movements than adult males during very early morning, afternoon and early evening, but adult males moved significantly more during the late morning (Combrink 2014, Combrink et al. in prep. c,d). Non-nesting females moved significantly less than adult males and nesting females throughout 24 h, except during late morning, but movements were not significantly different to nesting females (Combrink 2014, Combrink et al. in prep. c,d).

There was a general pattern that Nile Crocodiles confined to narrower and structurally complex parts of the system such as Mphathe Stream and the Narrows had a lower MDM (Combrink 2014, Combrink et al. in prep. c,d). Crocodiles in main Lake St Lucia and Lake Bhangazi were making longer daily movements (such as 1086 m for a 402 cm male in a ~61 ha section of the Narrows, 1935 m for a 406 cm male in a ~220 ha freshwater lake, 444 m for a 270 cm non-nesting female along a 4.5 km freshwater stream and 1222 m for a 240 cm non-nesting female in the Narrows and Catalina Bay) (Combrink 2014, Combrink et al. in prep. c,d).

3.2.6 Diurnal and nocturnal movements

Overall, Nile Crocodiles moved significantly more at night (753 ± 12 m) than during the day (554 ± 12 m, (Combrink 2014, Combrink et al. in prep. c,d)). Both females (706 ± 16 m at night; 509 ± 16 m in the day, and males (808 ± 17 m at night; 607 m ± 17 m in the day) moved more at night (Combrink 2014, Combrink et al. in prep. c,d).

Adult Nile Crocodiles moved significantly more at night (864 ± 13 m) than during the day (625 ± 13 m, Combrink 2014, Combrink et al. in prep. c,d). Adult males and females were significantly more mobile at night compared with the day (nocturnal male movement 981 ± 21 m; diurnal male movements 728.1 ± 20.66; adult females' nocturnal movements 776 ± 17 m, diurnal movements 547 ± 17 m). In contrast sub-adults moved significantly more during the day (161 ± 7 m) than at night (133 ± 7 m) (Combrink 2014, Combrink et al. in prep. c,d).

3.2.7 Monthly movements

Overall, the monthly MDMs of Nile Crocodiles differed significantly throughout the year (Combrink 2014, Combrink et al. in prep. c,d). We also found considerable temporal variation between the different crocodile groups. Water temperature significantly correlated with mean monthly crocodile movement, and the correlation was stronger for sub-adults than adults (Combrink 2014, Combrink et al. in prep. c,d).

Sub-adult Nile Crocodile MDMs per month were longest in Feb. (534 m), while adult males and non-nesting females' MDMs per month were the highest in March, 2302 m and 1461 m respectively (Combrink 2014, Combrink et al. in prep. c,d). After March all crocodiles, except nesting females, daily movements decreased with each month and sub-adults and adult males moved least in June (148 m and 1094 respectively), non-nesting females in July (431 m) and nesting female in Aug. (704 m). The mobility of nesting females were severely restricted during the nest guarding period (Dec. to Feb., Combrink 2014, Combrink et al. in prep. c,d).

Nesting Nile Crocodile female movements increased rapidly subsequent to the nesting period, reaching a maximum of 2531 m during May, most likely to improve condition before winter (Combrink 2014, Combrink et al. in prep. c,d). Thereafter mobility decreased sharply, reaching a low in Aug. The MDM of all crocodiles, except sub-adults, increased between Aug. and Sept. while sub-adults remained the same before a continued increase from Oct. to Feb (Combrink 2014, Combrink et al. in prep. c,d).

3.2.8 Seasonal movements

There was a significant seasonal difference in the MDMs of Nile Crocodiles (Combrink 2014, Combrink et al. in prep. c,d). The longest movements were made in autumn (1730 ± 59 m), followed by summer (1449 ± 34 m) and spring (1351 ± 49 m), while crocodiles least mobile during winter (948 ± 41 m). Tukey HSD post-hoc analysis revealed that movements during summer were significantly longer than winter movements. Spring mobility was significantly less than autumn, while winter movements were significantly lower than all other seasons (Combrink 2014, Combrink et al. in prep. c,d).

Nesting Nile Crocodile females were most mobile during autumn (2529 ± 95 m), which was significantly more than all other crocodiles (Combrink 2014, Combrink et al. in prep. c,d). Movements of nesting females during summer and winter and summer and spring were not significantly different, but spring movements (1597 ± 81 m) were significantly more than winter (1135 ± 66 m). The movements (MDM) for adult males during autumn (1938 ± 95 m), spring (1754 ± 76 m) and summer (1920 ± 54 m) were not significantly different, but winter (1290 ± 67 m) was significantly less. Adult non-nesting female movements during autumn (938 ± 134 m), spring (960 ± 122 m) and summer (1094 ± 75 m) were not significantly different, but movements during winter (610 ± 95 m) were significantly less. Sub-adults were significantly less mobile than all other crocodiles throughout the year. Sub-adult movements during winter (135 ± 95 m) and summer (398 ± 84 m), summer and spring (241 ± 117 m), and winter and autumn (282 ± 147 m) were significantly different, but mobility between autumn and spring, autumn and summer, and spring and winter were not significantly different (Combrink 2014, Combrink et al. in prep. c,d).

3.2.9 Daily movements per distance category

We investigated daily movements of Nile Crocodiles per distance category as an additional indicator of movement. On average, most crocodiles (61.0 ± 5.7%) moved < 1 km per day, 16.7 ± 2.3%, 1-2 km, 10.0 ± 1.8% 2-3 km, 5.2 ± 1.1% 3-4 km, 3.0 ± 0.7% 4-5 km, and 4.0 ± 1.0% > 5 km per day (Combrink 2014, Combrink et al. in prep. c,d).

The proportion of daily movements differed significantly between Nile Crocodile adult males, non-nesting females, nesting females and sub-adults (Combrink 2014, Combrink et al. in prep. c,d). Adult non-nesting females made significantly more movements in the 0-1 km category per day (67.7 ± 8.1%) compared with adult males (44.9 ± 6.1%), but daily movements of non-nesting and nesting females (59.2 ± 7.8%) were not significantly different. Almost all (96.4 ± 9.0%) daily movements of sub-adults were < 1 km per day, significantly more than all other crocodiles (Combrink 2014, Combrink et al. in prep. c,d).

The proportions of Nile Crocodile movements in the 1-2 km category were similar for adult males (22.1 ± 2.6%) and non-nesting females (20.3 ± 3.5%) with nesting females somewhat less (13.5 ± 3.5%) and sub-adults significantly less (2.6 ± 4.0%). Adult males made the longest daily movements > 1 km but < 5 km, as nesting females proportionally made most movements > 5 km (7.5 ± 1.5%). Only 5.2% of non-nesting females were > 3 km per day, compared with nesting females’ 17.6% (Combrink 2014, Combrink et al. in prep. c,d).

Transmitter longevity of 11 Nile Crocodiles were sufficient for seasonal comparisons (Combrink 2014, Combrink et al. in prep. c,d). Mean transmitter days (n = 18) was 437 ± 89, range: 50-1486. Mean GPS-observations per crocodile was 3357 ± 667, range: 491-11088. We have knowledge of a single transmitter which became detached after 535 days. Crocodiles were captured throughout the lake and feeder streams as well as Lake Bhangazi, a freshwater waterbody ~5.8 km east of Lake St Lucia (Combrink 2014, Combrink et al. in prep. c,d).

Initial GPS-schedules were set to record a point-locality every hour, but this schedule was subsequently changed to 12 points in 24 h and finally to every 4 h. Prior to analysis, GPS-schedules were standardised to a 4 h sequence (Combrink 2014, Combrink et al. in prep. c,d).

3.2.10 Seasonal partitioning

The coldest mean weekly temperature was 16.8°C, and the warmest 28.7°C, range 11.9°C (Combrink 2014, Combrink et al. in prep. c,d). We partitioned seasonal temperature variation into three thermal bands of 4.0°C, i.e. a warmer "summer" band (> 24.7°C) corresponding with the following dates: 8 Nov. to 7 April (151 days), a cool "winter" band (< 20.8°C) from 22 May to 30 Aug. (102 days) and two transitional thermal bands (20.8°C to 24.8°C) "autumn" and "spring", from 8 April to 21 May (44 days) and 1 Sept. to 7 Nov. (68 days) respectively. Movement analysis was reported in daily mean and median values, allowing for comparisons between unequal length seasons. Home range analysis included only the summer and winter (Combrink 2014, Combrink et al. in prep. c,d).

3.3 Home range

3.3.1 All crocodiles

Adult Nile Crocodiles displayed a significantly greater home range (adults 418.3 ha; sub-adults 22.9 ha) and core-use area (adults 103.3 ha; sub-adults 9.0 ha) compared with sub-adults (Combrink 2014, Combrink et al. in prep. e,f). Random asymptote analysis for Male 110, Male 121, Female 125, Male 500 and Female 503 indicated that all Nile Crocodiles reach an asymptote consistently within 5% of the final home range size, after a mean of 490 ± 105 S.E. observations (fixes) or 81.7 days of tracking, based on the 6 observations per 24 h transmitter schedule (Combrink 2014, Combrink et al. in prep. e,f).

At Lake St Lucia, we found a significance difference in home range size of adults (418.3 ha) and sub-adults (22.9 ha, Combrink 2014, Combrink et al. in prep. e,f). Core-use areas (adults = 103.3 ha, sub-adults = 22.9 ha) also differed significantly. Adult male home range was much larger (713.1 ha) and biologically significantly different than adult females (400.8 ha). Seasonal differences were not significant for size or sex, but the median home range of adult males were twice as large in summer compared with winter. Adult female and sub-adult median winter home range were slightly larger in winter compared with summer (Combrink 2014, Combrink et al. in prep. e,f).

3.3.2 Adult males

Adult male Nile Crocodiles occupied a median home range of 713.1 ha, and core-use area of 81.5 ha (Combrink 2014, Combrink et al. in prep. c,d). Three size-related patterns of home range behaviour emerged; transient (< 3 m TL), topographically confined (3.5-4 m TL) and territorial (> 4 m TL). We found a strong inverse correlation between home range size and crocodile size, for adult males (Combrink 2014, Combrink et al. in prep. e,f).

3.3.3 Transient home range (< 3 m TL)

Male 111, the smallest adult male (295 cm TL), moved 2311.6 km during the 1344 tracking days (MDM = 1856 ± 60 m; Combrink 2014, Combrink et al. in prep. e,f). His mean annual home range size during the four years was 1378.8 ± 248.8 ha, the largest of all adult males. He displayed extensive interannual home range variation, both in size and distribution, doubling from 702.0-1449.7 ha from the first to the second year, and increased from 1462.9-1901.0 ha from the third to the fourth (n = 249 days) year. Temporally, his annual home ranges shifted latitudinally, from the Narrows (south of the main lake) to Catalina Bay (southern lake) and Dead Tree Bay (central lake). This transient behaviour was expedited by increased water levels from Jan. 2011, re-linking Catalina Bay and Dead Tree Bay (Combrink 2014, Combrink et al. in prep. e,f).

3.3.4 Topographically confined home range (3.5-4.0 m TL)

The home ranges of Male 110 (350 cm TL) and Male 121 (392 cm TL) were 713.1 ha and 860.2 ha respectively, considerably smaller than Male 111 (1378.8 ± 248.8 ha; Combrink 2014, Combrink et al. in prep. e,f). Their home ranges were mainly restricted to Catalina Bay with 121's main basking area on the southwestern shoreline and 110s on the southeastern shoreline (Combrink 2014, Combrink et al. in prep. e,f). Both males journeyed from Catalina Bay, but at different times of the year. Male 110 moved 13 km south down the Narrows during the last two weeks of April, coinciding with the annual Striped Mullet (*Mugil cephalus*) migration (Whitfield and Blaber 1979). He spent most of the time at two large winter basking congregations. Male 121 journeyed 14 times from his core-use area along the southwestern shoreline to the Nkazana Stream, a small perennial stream flowing into Catalina Bay in the northeast. In total, he utilised the stream 49.5% of the time. The mean salinity of Catalina Bay during the tracking period was 51.9 ± 2.5 psu and both crocodiles established core-use areas at fresh water sources, Male 110 mainly used shoreline seepage pools while Male 121 used the Nkazana Stream (Combrink 2014, Combrink et al. in prep. e,f).

3.3.5 Territorial behaviour (> 4 m TL)

Home ranges of the two largest adult male Nile Crocodiles, Male 500 (200.5 ha) and Male 504 (121.2 ha), were significantly smaller compared with adult males < 4 m (Combrink 2014, Combrink et al. in prep. e,f). These large males were most active and mobile of all males ((Combrink et al. in prep. e,f), and their mean daily movements (MDM) were significantly more compared with other adult males. Elevated mobility within a small home range, suggested territorial maintenance behaviour (Combrink 2014, Combrink et al. in prep. e,f).

Male 504 was restricted to Lake Bhangazi, a ~200 ha freshwater waterbody ~5.8 km east of Lake St Lucia. He moved on two occasions, three days and 14 days respectively, south through a connecting stream to the adjacent Mfabeni swamp, following good rainfall and stream flow (Combrink 2014, Combrink et al. in prep. e,f).

3.3.6 Season

Although Nile Crocodile home ranges and core-use areas exhibited large seasonal variation, they were not significantly different (Combrink 2014, Combrink et al. in prep. e,f). Home range was twice as large in summer (747.2 ha) compared with winter (294.0 ha). Core-use areas were 130.5 ha in summer compared with 75.1 ha in winter (Combrink et al. in prep. e,f). Variation (i.e. interquartile range) of home ranges and core-use areas were much larger during summer compared with winter (Combrink et al. in prep. e,f)

Male 500 (> 4 m TL) journeyed during winter on three separate occasions to large basking congregations (Combrink 2014, Combrink et al. in prep. e,f). These journeys were between June and August, which coincides with the period when Nile Crocodile males have viable sperm (Kofron 1990).

3.3.7 Adult females

Adult Nile Crocodile females occupied a median home range of 400.8 ha, and core-use area of 106.9 ha (Combrink 2014, Combrink et al. in prep. e,f). Home ranges of Female 531, 601 and 515 were restricted mostly to the Narrows channel and were quite similar in size (range:

357-426 ha; Combrink 2014, Combrink et al. in prep. e,f). Female 514 occupied the smallest home range (37.0 ha), mainly upstream from a weir in the Mphathe stream. Female 125, which nested along the Nkazana Stream, occupied the largest home range, 1988.7 ha, utilising large sections of Dead Tree Bay, Catalina Bay and the Narrows (Combrink 2014, Combrink et al. in prep. e,f).

Female 531, the smallest adult (240 cm) in the study, occupied a large home range of 426 ha (Combrink 2014, Combrink et al. in prep. e,f). She utilised her core-use area 76% of the time and embarked on five journeys, 25 days on average. The three journeys during the 2011 winter were to sites of known basking congregations in the Eastern Forks and Potters Channel (Combrink, pers. obs.), possibly for courtship and mating. She stayed the following summer in her core-use area and during 2012 autumn moved to Catalina Bay for 64 days (Combrink 2014, Combrink et al. in prep. e,f).

The home range of Female 449 was severely restricted during her first year when Dead Tree Bay was almost completely dry and she utilised a 21.6 ha freshwater refuge area along the shoreline (Combrink 2014, Combrink et al. in prep. e,f). The water level in the bay increased at the end of her first tracking year after 725 ml of rain in Dec. 2010 and Jan. 2011 (Ezemvelo, unpublished data), which led to an increased home range the second year of 745.2 ha (Combrink 2014, Combrink et al. in prep. e,f).

3.3.8 Season

Home ranges of adult females showed no seasonal variation (summer = 190.5 ha; winter = 198.0 ha), but core-use areas were larger in winter (79.3 ha) than summer (52.2 ha) (Combrink 2014, Combrink et al. in prep. e,f). Home ranges and core-use areas showed little variation (i.e. interquartile range) both during summer and winter (Combrink 2014, Combrink et al. in prep. e,f)).

3.3.9 Sub-adults

Nile Crocodile sub-adults occupied a median home range of 22.9 ha, and core-use area of 9.0 ha (Combrink 2014, Combrink et al. in prep. e,f). Male 533, the smallest sub-adult (204 cm TL) and study animal, occupied the smallest home range (18.4 ha), in the Narrows. He made four short journeys south, on average 1.3 days and 270 m in duration. His habitat preference was vegetated shallow areas adjacent to the main deep channel. He favoured the eastern shoreline (87.4% of observations) over the western shoreline (12.6% of observations) Male 533 was least mobile (MDM = 213 m) with an activity level of 36.1% (Combrink 2014, Combrink et al. in prep. e,f).

Female 534, the largest sub-adult (212 cm), occupied a home range of 22.9 ha in the Narrows (Combrink 2014, Combrink et al. in prep. e,f). She displayed three distinct periods during the tracking duration of 405 days. At first, she exclusively utilised a section in the south. At the onset of winter she moved north and used a number of sites along both the western and eastern shoreline. She continued using them during the next four months, during winter and early spring. She maintained connectivity with the southern area through continuous movement. During late spring, she moved back south. She stayed in this area until the transmitter stopped working 198 days later, never returning to the northern area. Her activity level of 52.7% was considerably more than the mean (44.6 ± 3.6%) activity level for St Lucia Nile Crocodiles and she also had the highest MDM of 333 m of any sub-adult (Combrink 2014, Combrink et al. in prep. e,f).

Male 503 (208 cm) occupied the largest home range (118.4 ha) of all sub-adults (Combrink 2014, Combrink et al. in prep. e,f). He mainly used two areas, a large winter area (~1.1 ha), and ~910 m south a second area (~0.5 ha) consisting of a vegetated shallow area adjacent to the main channel. He also used a third area (~0.3 ha) where the Narrows fork, ~2.7 km north for one week. During late spring, he moved ~8.9 km down the Narrows to the Honeymoon Bend area. His home range in this area was much larger compared with the northern areas (~5.2 ha), staying in this area for the remainder of his tracking duration. Mean daily movement increased to 239 m coincident with warmer summer water temperatures (Combrink 2014, Combrink et al. in prep. e,f).

3.3.10 Season

Home ranges (summer = 16.2 ha; winter = 18.2 ha) and core-use areas (summer = 5.9 ha; winter = 5.7 ha) of Nile Crocodile sub-adults suggested no seasonal variation, but low sample size prevent comparison (Combrink 2014, Combrink et al. in prep. e,f).

3.4 Reproduction

3.4.1 Historical data: 1959 to 2008 – nest surveys

Pooley (1982a) investigated Nile Crocodile nest behaviour at Lake St Lucia from 1959 to 1978 (Fig. 1; Combrink 2014, Combrink et al. in prep. g,h) and the main focus of this work was Otoneni-Ngema, the largest nesting area situated in the north western corner of the Eastern Shores wilderness area (Pooley 1969). He described three other major nesting areas during the sixties and seventies; i.e. the Mkhuze Swamps at the northern tip of the lake, Ndhlozi Pan, situated at the northern tip of Ndhlozi Peninsula and the Mfolozi and Msunduzi River confluence, just south of the St Lucia estuary. Seven smaller nesting areas, i.e. Selley's Lakes, Fani's Island, Tewati Bay, Dead Tree Bay, Nkazana Stream, Mphathe Stream confluence with the Narrows and the western shoreline of the Narrows (Fig. 1) were also identified (Pooley 1982a). Time and manpower constraints limited survey efforts during this era to areas with known nesting activities (Fawcett 1987a, Combrink 2014, Combrink et al. in prep. g,h).

Since the 1985/1986 nesting season, surveys became more structured and standardised and annual maps with nest distribution were recorded for most years (Combrink 2014, Combrink et al. in prep. g,h). However, as a result of the extent of the lake system and the limited number of participating staff, the main focus continued to be the known nesting areas only, monitoring the relative abundance, density and distribution of known nests (Taylor and Blake 1986, Fawcett 1987a, Pullen 1988, Leslie 1997, Robertson 1998, 2001, Greaver 2002, 2003, Dickson 2008, Combrink 2014, Combrink et al. in prep. g,h h).

In an effort to expand survey effort beyond the known nesting areas, especially incorporating suitable, but unsurveyed nesting areas, aerial counts were conducted in 1993 and 1994 (Anderson 1993, 1994, Combrink 2014, Combrink et al. in prep. g,h) and numerous nests, mostly from known areas, were recorded from the air. It is possible for an experienced observer to locate a crocodile nest from the air, but the probability of detection is inversely correlated with aircraft speed (Parker and Watson 1970). Therefore, slow flying aircraft, e.g. helicopters, are ideal, but often impractical due to the amount of time required and associated costs implications (Combrink 2014, Combrink et al. in prep. g,h).

The use of GPS technology has improved the recording accuracy of nest-sites found during surveys (Combrink 2014, Combrink et al. in prep. g,h). Leslie (1997) was the first to use a GPS at St Lucia to record the position of each nest during the 1996/7 nesting season. Despite accuracy limitations due to selective availability (degraded signal effected by US military), the maximum error of 50-80 m was a considerable improvement of the pre-GPS era. In 2000, selective availability was discontinued and accuracy improved to ~5 m under optimal circumstances (Combrink 2014, Combrink et al. in prep. g,h).

3.4.2 Historical data: 1959 to 2008 – relative nest abundance and distribution

The results of Nile Crocodile nest surveys since 1982 are shown in Fig. 3.6 (Combrink 2014, Combrink et al. in prep. g,h). Some years represent incomplete surveys and are indicated with white bars. Hatching success for 1984 (1983/84 nest season) was possibly zero as virtually all nests were flooded by Tropical Cyclone Domoina (Taylor and Blake 1986). Nile Crocodiles do not nest throughout the entire lake system, but select and utilise specific areas which they often re-use (Pooley 1969, Combrink et al. in prep. g,h)). New nests are infrequently recorded (Ezemvelo unpublished data, Combrink, pers. obs.). Refer to a comparison of historical nest recorded by Pooley as well as in the recent past (1982 to 2008,

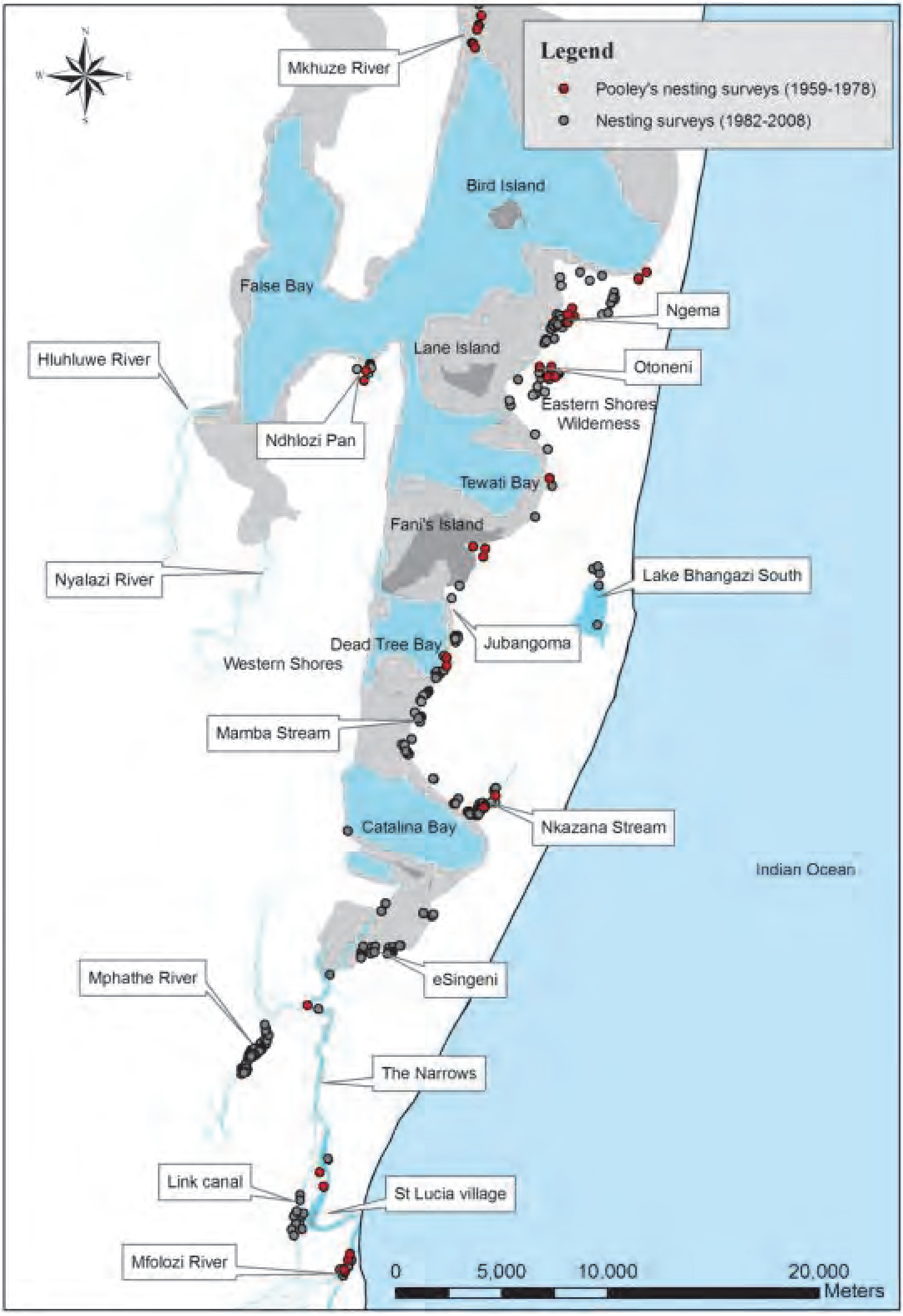


Figure 3.6 Nile Crocodile nest records by Pooley (1959-1978) and more recent (1982-2008) at Lake St Lucia (from Combrink 2014, Combrink et al. in prep. f).

Figure 3.7 Nile Crocodile nests recorded at the St Lucia estuarine system from 2008/9 to 2012/13 (from Combrink 2014, Combrink et al. in prep. f).

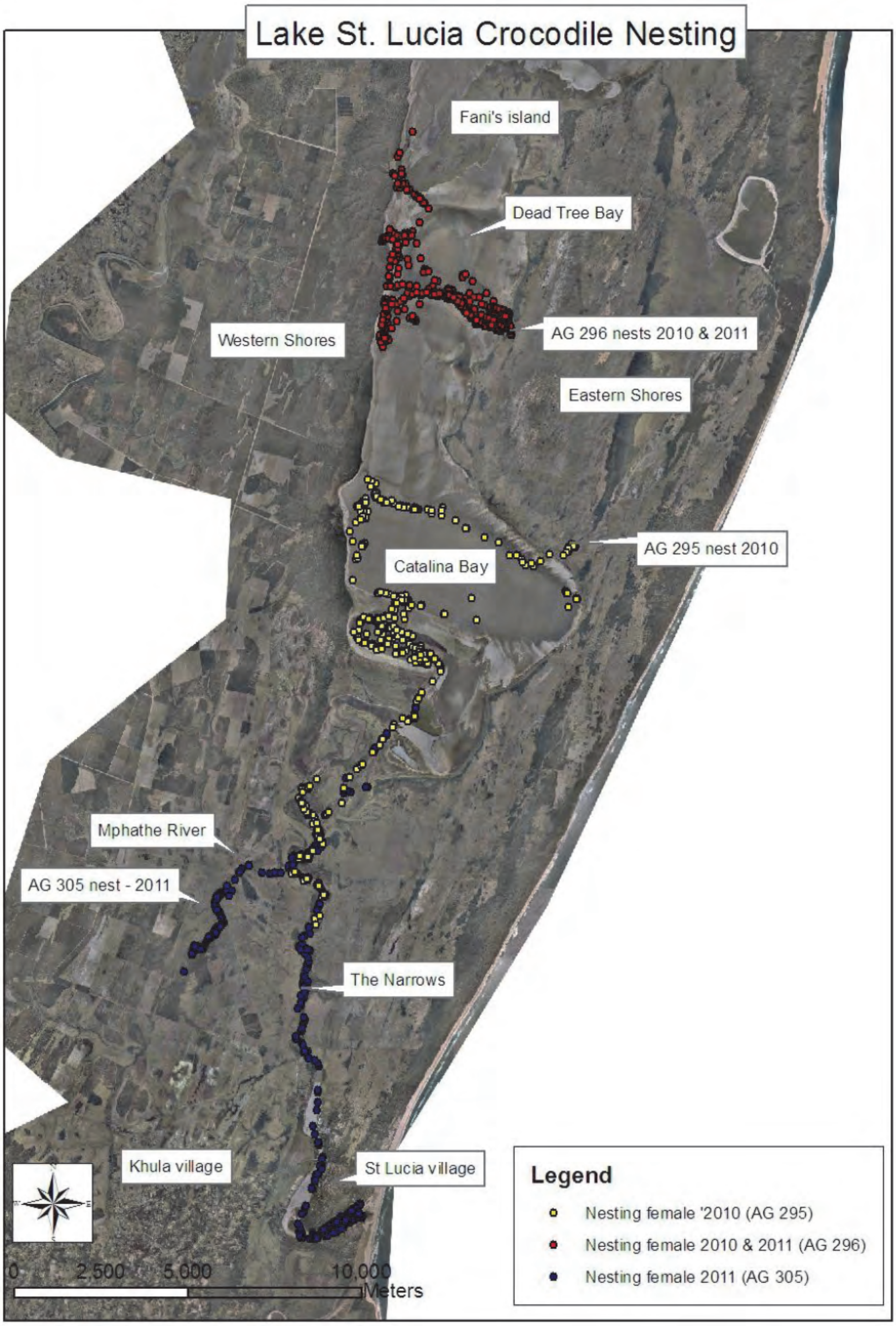


Figure 3.8 The nesting sites and post-nesting movements of three breeding females at Lake St Lucia. Females displayed extensive movement away from the nesting areas during the non-breeding season if conditions were favourable, i.e. deep enough water to facilitate movement. Female AG 296 were restricted to a freshwater refuge during the 2010 non-breeding season when the adjacent lake were extremely shallow and hypersaline (from Combrink et al. unpublished data).

3.4.3 Aerial nest surveys (2008/9 to 2011/12)

Six possible new Nile Crocodile nest-sites were recorded on 1 Feb. 2009 (Combrink 2014, Combrink et al. in prep. g,h, Fig. 3.7). Four potential nests were observed in the Dead Tree Bay area, all in small open areas surrounded by thick forest that would have been impossible to detect during a foot patrol. Two possible new nests were recorded in the Catalina Bay area, one ~500 m north of the Nkazana stream inflow and one ~1.3 km south of the Catalina Bay public jetty. Nest-sites were also observed at Nkazana Stream, the Forks area in the Narrows and the Mphathe Stream (Combrink 2014, Combrink et al. in prep. g,h. g,h). During the aerial survey (Jan. 2011) nine nests were counted in total. Extensive potential nesting areas, especially in the Tewati Wilderness Area, were covered but no nesting activities recorded. During a paraglider survey we covered the area from Jubangoma to Mamba Stream, to a point ~2.6 km further south. The survey distance was ~20 km and the duration 66 minutes. Thirteen nests or likely nest-sites were identified from the air and eight nests were confirmed during a subsequent foot patrol. A number of possible nest-sites recorded from the paraglider above the forest canopy, especially in the Jubangoma area, could not be located on foot, as a result of the dense closed canopy forest, and subsequent lack of navigation with the GPS (Combrink 2014, Combrink et al. in prep. g,h).

The paraglider seems to be a very effective method in locating crocodile nest-sites, especially over terrain where a conventional foot survey would be impractical, e.g. open patches surrounded by forest (Combrink 2014, Combrink et al. in prep. g,h). It also has the ability to cover extensive ground, but at a sufficiently low speed (5 to 40 km^{-1}) to observe nests. Another advantage of using the glider is that wetland and swamp forest margins, where crocodile nests are often encountered, could be surveyed more safely, as Hippopotamus and African Buffalo (*Syncerus caffer*) are often found in these habitats. The low and slow flying capabilities, combined with relative small area required for departure and landing, makes the glider an ideal aerial platform to locate crocodile nests for the air. Despite these advantages, the glider should not replace the conventional foot survey, but could successfully be used as an additional survey tool. The only disadvantage is the inability to fly in wind of more than 30 km^{-1} (Combrink 2014, Combrink et al. in prep. g,h).

3.4.4 Foot, boat and kayak surveys (2008/9 to 2012/13)

Ezemvelo surveys recorded 29, 80, 32, 61 and 60 nests during the 2008/09 to 2012/13 nesting seasons, over 14 areas at Lake St Lucia (Combrink 2014, Combrink et al. in prep. g,h). Nest densities were overall low and only three areas revealed more than five nests, on average, i.e. the Mphathe Stream (mean 18.2 ± 5.62), eSingeni (mean 12.6 ± 2.01) and

Nkazana Stream (mean 7.8 ± 1.39). The highest count of 80 nests is lower compared with the average of 102.9 ± 7.17 nests for the 21 year period prior to the St Lucia estuary mouth closure and drought (1982 to 2002) and the 29 nests in 2009 was the lowest nest count for Lake St Lucia ever recorded. The average nest count since the onset of the drought (2003 to 2011) was 53.2 ± 5.55 nests. All nests were associated with nearby freshwater and therefore no nesting was recorded in the Eastern Shores Wilderness area, as seasonal pans and wetlands were still dry. During the 2013 nesting survey two nests were recorded along the Eastern Shores shoreline, one at Ngema (Combrink 2014, Combrink et al. in prep. g,h).

Since 2007 we recorded increased fluctuations between successive years (i.e. 49, 73, 29, 80, 32, 61, Fig. 3.7), as oppose to a more stable period from 2003 to 2007 (i.e. 54, 54, 49, 49), (Fig. 3.6, Combrink 2014, Combrink et al. in prep. g,h). Furthermore, in the four years prior to the drought and mouth closure (1999 to 2002), the average nest count was 110.5 ± 11.18 nests. This decreased to 52.0 ± 1.87 nests for the first four years since the drought and estuary mouth closure (2003 to 2007). In March 2007, the sea broke through the estuary mouth due to Cyclone Gamede. Seawater flowed in for weeks before the mouth closed naturally during August 2007, with the lake approximately 75% full and salinities throughout at that of seawater (Cyrus et al. 2010). We presume that the massive influx of seawater linking the three remaining isolated water bodies of the (mostly dry) lake, combined with the six months of re-connectivity with the sea (i.e. healthy open estuary) led to improved feeding opportunities for Nile Crocodiles. The following nesting season (2007/08) nesting increased to 73 nests, 80 nests were recorded for the 2009/10 season, which decreased to 60 nests recorded in 2011/12. We expect that improved nutrition resulted in the higher number of females nesting in 2008, but as females seldom nest in consecutive years (Kofron 1990), there was a decrease in 2009 but a high proportion of females once again nested in 2010 (Combrink 2014, Combrink et al. in prep. g,h).

3.4.5 Changes in nest distribution and relative abundance: 1982 to 2013

Nile Crocodiles at Lake St Lucia generally prefer to re-use the same nest areas (Pooley 1969, Combrink 2014, Combrink et al. in prep. g,h). However, during the past three decades there have been dramatic changes in the relative abundance and distribution of nests at St Lucia, seemingly determined by human disturbance, illegal killings, water coverage and the availability or lack of freshwater (Combrink 2014, Combrink et al. in prep. g,h).

Human disturbance (reed harvesting, small scale agriculture, fishing and burning) at the confluence of the Mkhuze River and Lake St Lucia resulted in the abandoning of all nesting since 1989 (Combrink 2014, Combrink et al. 2013, in prep. g,h). This used to be a major nesting area during the 1960s and 1970s with an estimated 20 nests per year (Pooley

1982b). Human disturbance, combined with illegal killings of nesting females (Leslie 1997) south of the St Lucia estuary (Mfolozi River, Backchannels and Link Canal), resulted in a decline from an average of 28.8 ± 2.80 nests (1982 to 1989) to 0.70 ± 0.26 nests (2002 to 2013, Combrink 2014, Combrink et al. in prep. g,h). The decline in nest numbers adjacent to North Lake from 31.8 ± 4.49 nests (1982 to 2002) to 2.6 ± 1.28 nests (2003 to 2013) was seemingly due to the drought (2003 to 2012) and subsequent drying out of the entire North Lake, with only a few small areas of freshwater seepage along the shoreline (e.g. Tewati Bay, Combrink 2014, Combrink et al. in prep. g,h).

The declines in South Lake and eSingeni (1990 to 2002 and 2003 to 2013) were apparently reflecting the general nesting decline during the drought and the Mphathe Stream was the only area where nesting activities increased, most probably as a result of the availability of fresh water required by guarding females and hatchlings in the post incubation period (Combrink 2014, Combrink et al. in prep. g,h). The overall trend the last three decades was a contraction away from disturbance and persecution in the north and south of the lake towards the more protected and disturbance free eastern shoreline from eSingeni wetland to Sengwana Point. During the recent drought, nesting activities were concentrated at freshwater sources along the eastern shoreline and Mphathe Stream on the Western Shores. In 2013 a nesting female was killed at eSingeni, highlighting the need for management to increase patrols in even seemingly secure core areas of the Park (Combrink 2014, Combrink et al. in prep. g,h).

3.4.6 Nest effort

Estimates of Nile Crocodile nest effort at Lake St Lucia varied from 56.4% (1987) to 6.9% (2009) over the 32 year period with a mean of 22.9 ± 2.63% (Combrink 2014, Combrink et al. in prep. g,h). The two best predicting factors for nest effort were the dynamic interaction between food availability and rainfall (Combrink 2014, Combrink et al. in prep. g,h). Abundant feeding opportunities apparently resulted in a higher proportion of reproductive females during a particular year while restricted food availability (e.g. indirect effect due to estuary mouth closure and less fish entering the lake or direct effect during severe droughts when lake level contracts while becoming hypersaline at the same time) had the opposite effect. A high proportion of reproductive females should result in high nest effort, but only when abundant freshwater sources are available. Females selected nest-sites close to freshwater (streams, ephemeral pans or wetlands) for hydration during nest guarding as well as to ensure a nursery area for hatchlings. If spring rainfall (Sept. and Oct.) was late, or below average, some females arrested reproduction possibly by reabsorbing developing egg follicles (Combrink 2014, Combrink et al. in prep. g,h).

We estimated Nile Crocodile nest effort since 1982 and indicated mean lake salinity values for the two months preceding nesting, as well as annual rainfall (Combrink 2014, Combrink et al. in prep. g,h). The first two years (1981/82 and 1986/87 nest surveys) were the highest ever recorded. This might have been due to general low levels of disturbance and illegal killings and good food availability, especially Striped Mullet (*Mugil cephalus*) and low lake salinities, especially in 1987 (Combrink 2014, Combrink et al. in prep. g,h).

The next period of elevated Nile Crocodile nest effort was from 1996 to 2002, again during high rainfall low lake salinities (Combrink 2014, Combrink et al. in prep. g,h). Subsequently to that and during the recent drought with periods of hypersalinity, nest effort decreased to record low levels. During the recent drought the estuary mouth was closed for almost the entire period. It seemed likely that the status of the estuary mouth (i.e. open or closed) had an indirect effect (open mouth facilitate healthy estuarine functioning and increased food abundance) on nest effort (Combrink 2014, Combrink et al. in prep. g,h). The mean nest count prior to estuary closure (1982 to 2001) in 2002 was 103.07 ± 7.7 nests, while during the period when the estuary mouth was closed (2003 to 2012) nesting significantly decreased to 53.6 ± 5.92 nests (Combrink 2014, Combrink et al. in prep. g,h). In March 2007 the estuary reconnected to the sea for six months and nesting increased from 49 (pre-mouth opening) to 73 (post-mouth opening) nests (Combrink 2014, Combrink et al. in prep. g,h).

3.4.7 Physical properties of nest-sites

Throughout the Nile Crocodile range, suitable nesting areas appear to be remarkably similar. Important features consist of well-drained soils, access to fresh water, adequate exposure to sunlight, nest elevation above nearby rivers or streams and adequate cover for the guarding female (Cott 1961, Modha 1967a, Pooley 1969, Swanepoel et al. 2000, Botha 2005, Combrink 2014, Combrink et al. in prep. g,h). While these fundamental nest habitat requirements are present and well documented at all recorded nesting areas at Lake St Lucia (Fawcett 1987, Leslie 1997), the macro-level heterogeneity of nesting habitats within a single population is possibly unique. This includes nests close to seasonal pans several kilometres from the main lake, on river islands, along the lake shoreline, in close proximity of freshwater seeps, streams and rivers, on elevated levees created by dredger operations and adjacent to or surrounded by swamp forests (Combrink 2014, Combrink et al. in prep. g,h).

3.4.8 Use of burrows

We recorded Nile Crocodiles using burrows at five localities, eSingeni (two), Nkazana Stream (19), Mamba Stream (two), Dead Tree Bay (six) and False Bay Park (one) and recorded the use of the burrows with camera traps (Combrink 2014, Combrink et al. in prep. g,h). All localities, except Mphophomeni Pan (in False Bay Park), are known nesting areas and we have observed nesting females entering nearby burrows when disturbed. At Nkazana Stream, nine burrows are associated with nest-sites, and two burrows at eSingeni, Mamba Stream and Dead Tree Bay have been used by nesting females during the nesting season. In all areas, burrows were excavated where the adjacent water, e.g. stream (Nkazana) or freshwater seepage (eSingeni, Mamba Stream and Dead Tree Bay) was too shallow to facilitate adequate cover for the nesting female. Burrows possibly serve as important microhabitats for female thermoregulation as burrow temperatures are more stable than ambient temperatures in summer. Crocodile burrows are used by males and females during the non-nesting season, and different individuals have been observed using the same burrow over time (Combrink 2014, Combrink et al. in prep. g,h).

Pooley (1962) described burrowing behaviour by Nile Crocodiles in the banks of the Mkhuze River during the drought of 1960 and anecdotal information from game guards of similar behaviour in the same river during previous droughts (Pooley 1982a, Combrink 2014, Combrink et al. in prep. g,h). The only anecdotal information of crocodile burrowing behaviour at Lake St Lucia previously described was a burrow recorded in Sept. 1977 at the edge of a pan in an area north of the lake. The entrance of the burrow was ~1 m in diameter and there was signs of a crocodile track leading into the burrow (Pooley 1982a, Combrink 2014, Combrink et al. in prep. g,h).

3.4.9 Identification of nesting females

We captured 12 nesting Nile Crocodile females on or adjacent to their nest-site during the 2009/10 nesting season (Combrink 2014, Combrink et al. in prep. g,h). Additional five mature females were caught (22 Oct. and 19 Nov. 2009) in the Nkazana Stream, a known nesting area at the onset of the nesting season and the following year (23 Oct. 2010) a female in the Mphathe Stream. A tagged nesting female, colour code OOB was recorded next to her nest during the 2013 survey along the shoreline of Catalina Bay, adjacent to the Nkazana Stream. She was captured in the Nkazana Stream on 6 May 2009, 1317 days before the re-sighting, and fitted with coloured plastic caudal tags. The tags were in good condition with minimal fading of colour and little algae coverage (Combrink 2014, Combrink et al. in prep. g,h).

Scute marking and attaching colour-coded caudal tags were effective methods for unique identification of female Nile Crocodiles (Combrink 2014, Combrink et al. in prep. g,h). Not wanting to cause additional disturbance, we did not return to check on the tagged females, so the likely tagging effect on the animal's nesting behaviour was not noted. However, all females that were fitted with caudal tags and transmitters, returned to their respective nests to continue with nest guarding activities (Combrink 2014, Combrink et al. in prep. g,h). When nesting females can be uniquely identified and re-sighted in subsequent years, important biological and ecological spatial and temporal information such as reproductive frequency, growth, body condition and changes in nest-site usage can be recorded and monitored (Combrink 2014, Combrink et al. in prep. g,h).

Figure 3.9 Female Nile Crocodile at nest at Lake St Lucia (from Combrink 2014, Combrink et al. in prep. f).

3.4.10 Reuse of nest-sites

During the 2009 Nile Crocodile nesting survey, 11 nest-sites (38%) were reused (Combrink 2014, Combrink et al. in prep. g,h). In 2011, 24 nest-sites (30%) were reused, 13 from 2009. During the Jan. 2011 survey 20 of the 26 nest-sites, 77%, were reused, five from 2010 and three from 2009. During the 2012 survey 46 of the 58 nests were reused, a total of 79%. Ten nests were from 2011, 23 from 2010 and four from 2009 (Combrink 2014, Combrink et al. in prep. g,h).

A 2.6 m Nile Crocodile female that was captured and tagged in Nov. 2009 was recorded on her nest 390 m downstream in 2010 (Combrink 2014, Combrink et al. in prep. g,h). This nest-site was unused in 2011 but she nested again in 2012 at the exact same nest-site. At eSingeni an untagged female nested in 2011 on a nest-site used by a tagged female in 2010. This confirms that occasionally different females are using the same nest-site. Similar behaviour was observed at Dead Tree Bay in 2012 where a female nested on the same nest-site used in 2011 by a different (transmitter) female. At the Mphathe Stream camera traps recorded two different females using the same nest in 2010 and 2012. Female 449 was captured on her nest in 2010 at Dead Tree Bay and she continued to nest the following year again, 73 m from her previous nest-site (Combrink 2014, Combrink et al. in prep. g,h).

3.5 Human crocodile conflict

The Nile Crocodile is an apex aquatic predator of the Lake St Lucia estuarine system. Situated at the southern tip of the St Lucia estuary is the small town of St Lucia, a popular eco-tourist destination with waterborne activities that include boat based “Hippo and Crocodile tours”, guided kayaking trips on the estuary and fishing both in the estuary and along the coastline. Furthermore, local inhabitants living adjacent to the estuary in the south and Mkhuze swamps in the northwest, interact on a daily basis with water and other natural resources from rivers flowing into the lake. Invariably, this shared space has led to a number of crocodile attacks on people and tourists.

3.5.1 Killing of crocodiles

Since the arrival of the first Europeans with firearms, Nile Crocodiles at St Lucia were killed by professional hunters, missionaries, soldiers and traders for skins and fat, and to safeguard their families and livestock (Pooley 1982b). Despite proclaiming Lake St Lucia a protected area in 1897 (Pooley 1973b), Nile Crocodiles were considered vermin (Pooley 1976) outside of officially proclaimed areas and the killing of crocodiles justified, especially in rivers feeding into Lake St Lucia. Records exist of crocodiles killed with dynamite in the Hluhluwe River (Pooley 2013) while a number were killed, at least once, in the northern parts of the lake during an air-to-ground firing exercise by the SADF Catalina aircraft operating in the area from 1942-1944 (Pooley 1982b).

In 1957 a young boy of European origin, ignored official warnings and swam unsupervised in False Bay. He was fatally attacked and the public reacted calling for the extermination of all crocodiles in Zululand (Pooley 2013). The Natal Parks Board (NPB) responded by employing a professional hunter to exterminate crocodiles near campsites, jetties and other public places (Pooley 1982e), but he resigned after a few months. In total, 67 crocodiles were shot by him and other NBP staff (Pooley 2013). The introduction of the Reptiles Protection Ordinance No. 32 of 1968 brought an official end to the "sanctioned" killings (Pooley 1982a).

3.5.2 Illegal killing of crocodiles, post 1968

However, the killing of Nile Crocodiles continued by local people, using "simple but highly effective traps and snares" (Pooley 1971), (Fig. 3.10 and 3.11a, b), fuelled by a demand for organs used for medicinal (Cott and Pooley 1971, Pooley 1973a, b, Pooley 1976, Blake and Jacobsen 1992) purposed and witchcraft (Pooley 1982b). In the late 1980s Blake (1989) noted that "poaching would appear to be a bigger threat to crocodiles in Natal that was considered in the past" and mentioned evidence of organised illegal killings for trade in crocodile products by traditional healers (Blake 1989). Leslie (1997c) noted that 20 female crocodiles were snared and killed while nesting, and a number of clutches of eggs removed from the Link canal area of Lake St Lucia in 1996. The killing of female crocodiles on nesting sites were also recorded in 2013 (Fig.3.11b, c) at St Lucia (Combrink and Robertson 2013) and 2014 at Lake Sibaya (Z. Dlamini, pers. comm., Fig. 3.11 d, e) and in 2011 the carcass of a Nile Crocodile was found at St Lucia, caught with a baited steel hook (Combrink 2011), (Fig. 3.11f). On 5 January 2013 three sections of a crocodile carcass washed ashore close to the Mfolozi mouth at St Lucia (Fig. 3.12a, b). It was evident that the crocodile was illegally killed, cut into at least three sections and the tongue removed as well, presumable for Muthi purposes.

A survey of the Faraday traditional medicine market in Johannesburg found that 69% of all traders sold Nile Crocodile products, including skin, scull, osteoderms, lower jaws bones and eggs (Whiting et al. 2011).

3.5.3 Attacks on humans

Even though Nile Crocodiles are responsible for more human fatalities than any other large animal in Africa (Hutton and Loveridge 1999, Lamarque et al. 2009), crocodile attacks at Lake St Lucia and surrounds are relative rare and well documented (24 attacks from 1950-2012, S. Pooley, pers. comm.), unlike the situation in numerous other African countries. While some attacks are without provocation, crocodiles are attracted to jetties or slipways as a result of fish cleaning activities or illicit feeding by some tourists (Taylor et al. 2007). Policy procedure (Ezemvelo KZN Wildlife Board Policy on Crocodilians 3.4 of 1997) stipulates the “capture and relocation of a problem crocodile elsewhere” following “conflict with legitimate human interests”. However, as removed animals are not visibly marked, no information is available on the likelihood of their return to the capture location. In order to test the Nile Crocodile’s homing behaviour over a considerable distance, we caught a 2.7m female on 1 May 2012 with known home range (previously caught and fitted with transmitter on 23 October 2010) in the Mphathe Stream and released her 40.3 km (straight line distance) north, the same day. She returned to the exact same pool captured after 136 days (Combrink et al. 2013, in prep. e).

3.5.4 Boat mortalities

We recorded two mortalities, in 2009 (Fig. 3.12 c) and 2012 (Fig. 3.12 d) which were suspected to be the result of high speed impacts by boats on the estuary. Given the number of boat-trips on the estuary (seven concession boats as well as some privately owned boats), the impact is low.

3.5.5 Gillnets

Nile Crocodile mortality from gillnets are widely reported throughout Africa (Hutton 1984, Loveridge 1996, Kyle 1999, Botha 2005a, Combrink et al. 2011, Calverley and Downs 2014a), and it is especially smaller individuals entangled in gillnets that drown or are killed. Numerous large crocodiles were captured in the Narrows section of the St Lucia system from 2009-2012 in order to remove parts of gillnets, normally attached to the tail section or head (Fig. 3.12e).

Figure 3.10 A number of photographs of a snared crocodile caught at Lake St Lucia. The cut made by the snare was very deep, especially on the side of the neck and except for a small area (~20cm) on the ventral side; the skin was cut completely through. Based on morphometric analyses, the 298cm female appeared to be in really good condition. Even though the snare must have been terribly uncomfortable and probably caused severe pain, apparently she was still able to feed. Alternatively, she might have been snared at the start of the cool dry season (e.g. May 2011) and during this time her reduced metabolism prevented major loss in body condition. We administered Necrospray (purple colour on the last photo) to all affected areas prior to her release (Combrink 2014, Combrink et al. unpublished data).

Figure 3.11 A number of photographs illustrating (a) snared crocodile in Msunduzi River, (b) snares found at a nest site, (c) the head of a crocodile killed at a nesting site, (d, e) dead crocodile at nest site covered by leaves with eggs destroyed and (f) baited hook found inside crocodile carcass at St Lucia (X. Combrink unpublished data).

Figure 3.12 A number of photographs illustrating (a, b) tail and mid-body sections of a Nile Crocodile killed in Mfolozi River, (c) tail section of a crocodile killed possibly by collision with a boat, (d) crocodile with large section of tail missing also the likely collision of boat, (e) crocodile with gillnet rope through its mouth (X. Combrink unpublished data).

4 RESULTS: NILE CROCODILE IN NDUMO GAME RESERVE

4.1 Population estimate

From January 1967 to November 1974, 1257 hatchling Nile Crocodile were released as part of a restocking program in the NGR (Pooley 1982, Calverley 2013, Calverley and Downs 2014a,b,c). The first phase of the restocking program saw hatchlings (produced during the 1967-1968 season) reared for two to three years; thereafter, 700-800 individuals were released. The second phase saw roughly 500 hatchlings (produced during the 1969-1970 season) released into the reserve between 1972 and 1974 (Calverley 2013, Calverley and Downs 2014a,b,c).

Aerial surveys carried out in the 1970s and 1980s using the same observers, aircraft, and pilot provided the estimates of population size with the lowest standard errors (estimators of precision), whereas surveys in the 1990s with different observers had larger variation. Our surveys conducted in 2009, where water level, season, observers, and aircraft varied, yielded the highest SE values (Calverley 2013, Calverley and Downs 2014a,b).

Relative abundance of Nile Crocodiles in the NGR increased from the 1970s (272 ± 1.5; 1971-1973) to the 1980s (507.7 ± 3.7; 1985-1988), and again in the 1990s (774.8 ± 22.9; 1990-1994)(Calverley 2013, Calverley and Downs 2014a,b). After the initial large increase of 1990, the population within the reserve increased evenly year by year, until 1994 when the population decreased (Calverley 2013, Calverley and Downs 2014a).

All Nile Crocodiles captured at the NGR (n = 103) ranged from 92.6-472 cm in total length (TL), with a mean (± 1 SD) TL of 230.5 ± 71.0 cm (Calverley 2013, Calverley and Downs 2014a). The NGR has a lower proportion of juveniles (13%) compared with sub-adults (39%) and adults (48%; Table 2). At the NGR, sex ratios were biased toward females in the juvenile (80.0%) and the sub-adult age (63.0%) classes (Table 2). Adult sex ratios, however, were biased towards males (64.7%). Average sex ratio across all size classes was even (50.6:49.4% female:male). The intercept of equal sex ratios occurred within the 251-350 cm size class at ± 310 cm (Calverley 2013, Calverley and Downs 2014a).

During this study we observed 15 Nile Crocodiles in Lake Nyamithi with snares around their necks (Calverley 2013, Calverley and Downs 2014a). These individuals were large (TL > 280 cm), and possibly represent a small proportion of snared individuals (those managing to break free from traps by snapping the snare cable) (Calverley 2013, Calverley and Downs 2014a).

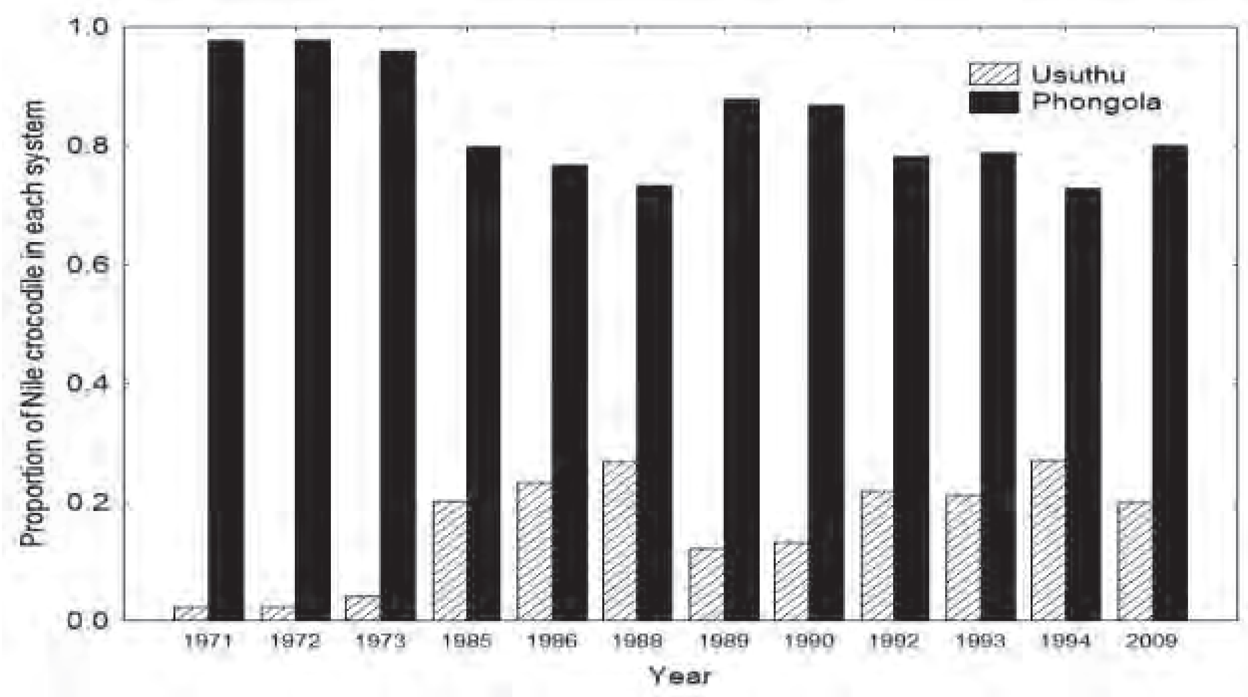


Figure 4.1 Proportion of Nile Crocodiles counted in the Usuthu and Phongola river systems from 1971-2010 in the Ndumo Game Reserve (from Calverley 2013, Calverley and Downs 2014a).

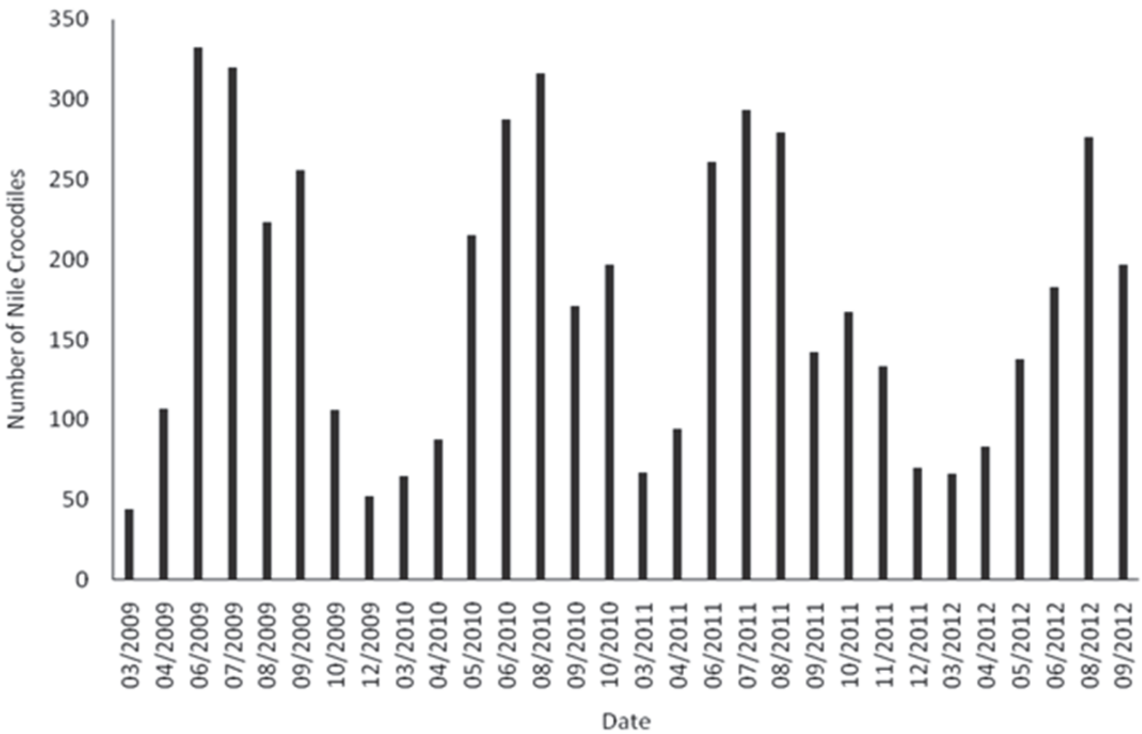


Figure 4.2 The monthly change in abundance of Nile Crocodiles at Lake Nyamithi in Ndumo Game Reserve from 03/2009-08/2012 (from Calverley 2013, Calverley and Downs 2014b).

4.2 Habitat use

4.2.1 Between-River Distributions

Nile Crocodiles were unevenly distributed between the two major river systems of the NGR, with more individuals occupying the Phongola system than the Usuthu system during the respective winter seasons from 1971-2009 (Calverley 2013, Calverley and Downs 2014b). There was no correlation between the area of habitat available in each system and total number of crocodiles counted indicating different carrying capacities for the two systems (Calverley 2013, Calverley and Downs 2014b). The Usuthu system held a minimum of 6 crocodiles in 1971 and a maximum of 202 in 1994, while the values for the Phongola system were 258 (1973) and 693 (1993), respectively. The proportion of crocodiles found in each system remained relatively constant (but not significantly so) over consecutive count years, despite increases in population size in each system from 1971-2009 (Calverley 2013, Calverley and Downs 2014a,b).

The proportion of crocodiles counted within each system (Phongolo and Usuthu) remained constant from 1985-2009 and was unrelated to changes in total population size during this period (Calverley 2013, Calverley and Downs 2014a,b). The only changes in the proportion of crocodiles occurred when the crocodile density was low (1971-1973), and when one river system experienced flooding while the other did not (1989). Excluding the counts of the 1970s, the Phongola system on average accounted for 79% of the NGR Nile Crocodile population and the Usuthu system for 21% from 1985-2009 (Fig. 4.1) (Calverley 2013, Calverley and Downs 2014b).

4.2.2 Within-River Distributions

Historically Lake Banzi and Shokwe Pan accounted for the majority of the Usuthu crocodile population with less than 1% found in the Usuthu River over the last 25 years (Calverley 2013, Calverley and Downs 2014b). This relationship has persisted since 1988 to 2012 with Banzi having a greater proportion of crocodiles over the years (Calverley 2013, Calverley and Downs 2014b). During our survey efforts, a greater proportion of Nile Crocodiles were observed in Lake Banzi (~75%) than in Shokwe (~25%) and the Usuthu River (Calverley 2013, Calverley and Downs 2014b).

Since 1971, the majority (61%) of Nile Crocodiles in the Phongola system were found in the floodplain during the winter period, when the surveys took place (Calverley 2013, Calverley and Downs 2014a,b). There was a difference in the number of Nile Crocodiles counted in the Phongola floodplain compared with Lake Nyamithi from 1971-2009. The proportion of crocodiles counted in the Phongola floodplain and Lake Nyamithi remained relatively constant and distinct from one another. Unusually, in 2009 the majority (69%) of the counted crocodiles were observed in Lake Nyamithi (Calverley 2013, Calverley and Downs 2014b). From 2009-2012, the number of crocodiles counted in Lake Nyamithi changed throughout the year, increasing from 61 ± 5.5 in March to 306 ± 13.5 in July. The mean number of individuals then oscillated around 273 ± 13.5 in August, dropping to 192 ± 24.3 in September 2009 and to 61 ± 1.4 by December (Fig. 4.2, Calverley 2013, Calverley and Downs 2014b).

Nile Crocodile relative abundance in Lake Nyamithi was negatively related to mean maximum monthly ambient temperature (Calverley 2013, Calverley and Downs 2014b). Rainfall and water level appeared to exert negative effects on the relative abundance of crocodiles in Lake Nyamithi, but the relationships with these variables were not significant (Calverley 2013, Calverley and Downs 2014a).

The number of crocodiles observed in each size class typically peaked between June and August (austral winter) of each year (Calverley 2013, Calverley and Downs 2014b). When delineated into different size classes, environmental variables had an effect on the number of crocodiles counted only in the 150-250 cm size class. The minimum average monthly temperature and rainfall both exhibited negative relationships with the number of crocodiles between 150-250 m TL counted over the 2 years (Calverley 2013, Calverley and Downs 2014a).

4.3 Catching and transmitter fitting

The majority of Nile Crocodiles captured (82%) were caught using the noosing technique. Twelve crocodiles (9%) were caught using the harpoon method and six crocodiles were caught using angling equipment (4%) (Calverley 2013, Calverley and Downs 2015a). This does not indicate the efficacy of the different capture methods, as harpooning and angling equipment were only introduced in 2012 while noosing was used throughout the study. No crocodiles were caught using baited traps. Between March and May 2009, 10 Nile crocodiles caught were fitted with radio transmitters at Lake Nyamithi. This consisted of seven males between 234-358 cm TL and three females between 202-281 cm TL (Calverley 2013, Calverley and Downs 2015a). Between March 2009 and November 2010 a further 88 crocodiles where caught and fitted with coloured tags for mark-resight, of these 45 were females between 100 cm and 319.4 cm and 43 were males between 84.3 cm and 472 cm (Calverley 2013, Calverley and Downs 2015a).

4.4 Radio tracking to show movements

Between March 2009 and November 2009 thirty one radio tracking excursions were undertaken (Calverley 2013, Calverley and Downs 2015a). Not all 10 individuals were located during a particular excursion and the highest number of fixes for an individual over this period using radio telemetry was 23 for a 202 cm (TL) female. The fewest number of radio locations was 5 for a 259 cm (TL) male who ranged widely throughout the floodplain, often out of range of the VHF signal. The average number of fixes for the telemetered crocodiles was 17 (SE ± 1.27). From December onwards no signal could be obtained for the radio tagged crocodiles (Calverley 2013, Calverley and Downs 2015a).

In NGR in winter Nile Crocodiles movements for individuals ≤ 202 cm TL were mostly restricted to Lake Nyamithi (Calverley 2013, Calverley and Downs 2015a). Larger individuals spent the majority of their time within the lake but made numerous and extensive forays into the Phongola floodplain and to the new course of the Usuthu River below Banzi Pan, returning to Lake Nyamithi thereafter (Calverley 2013, Calverley and Downs 2015a). Only one of the telemetered Nile Crocodiles captured in the Phongola system ventured into the Usuthu River system or Banzi Pan (Calverley 2013, Calverley and Downs 2015a).

4.5 Mark-resight

Between March 2009 and October 2010, 27 mark-resight exercises were carried out at Lake Nyamithi (Calverley 2013, Calverley and Downs 2015a). After October flooding of the lake made accessibility impossible. In total 131 observations of 37 tagged Nile Crocodiles were made with a highest re-sighting of 10 for an individual and a mean of 3.4 ± 0.42 for 37 re-sighted individuals. Mark-resight results did not produce enough locations to run home range analyses but did add to (n = 17) data on radio tracked Nile Crocodiles once transmitters had fallen off. No marked individuals were observed in NGR during the summer months partially due to the inaccessibility of Lake Nyamithi because of high water levels and the majority of crocodiles leaving the lake to enter the floodplain and possibly Mozambique (Calverley 2013, Calverley and Downs 2015a)..

4.6 Home range

Only home range estimated using KDEs showed significant relationships between home range size and TL of Nile Crocodiles (Calverley 2013, Calverley and Downs 2015a). Core home range, 90% and 95% home range estimates were significantly related to TL (Calverley 2013, Calverley and Downs 2015a). Adult Nile crocodiles occupied larger home ranges (2200.7 ± 373.45 ha) than sub-adults (419.4 ± 466.77 ha) for the 95% polygons (Calverley

2013, Calverley and Downs 2015a). 3a). Core area (50% polygon) used by adults was also larger (510.4 ± 98.90 ha) than sub-adults (2.4 ± 3.26 ha) (Calverley 2013, Calverley and Downs 2015a).

On average core home range use (50% polygon) of sub-adult Nile crocodiles (n = 4) formed 19.9% of the 95% kernel estimation (e.g Hutton 1987) while those of adult Nile Crocodiles (n = 4) formed 24% of the 95% kernel estimation (Calverley 2013, Calverley and Downs 2015a). Ninety percent home range polygons of sub- adult Nile crocodiles (n = 4) formed 77.3% of the 95% kernel estimation and 95% home range polygons of adult Nile Crocodiles (n = 4) formed 79.0% of the 95% kernel estimation (Calverley 2013, Calverley and Downs 2015a).

4.7 Transmitter attachment longevity

Radio transmitters (n = 10) lasted on average 131 (SE ± 11.4) days on Nile Crocodiles in NGR before becoming dislodged or failing to transmit (Calverley 2013, Calverley and Downs 2015a). Duration of transmitter attachment/life was significantly related to size (TL). Nine of the ten transmitters were dislodged between August and November which coincided with the onset of the breeding season in NGR (Calverley 2013, Calverley and Downs 2015a). Four transmitters were recovered, two of which had visible bite marks. Transmitters were found still embedded in the dental acrylic and with the cable ties still attached. Cable ties had not broken on any of the transmitters and attachment failure was due to poor bonding between the acrylic and the nuchal plate and the cable ties wearing through the four ventral scutes. For example, Crocodile 150.196 gave ample opportunities for observation on cable ties pulling through the scutes until only one cable tie was holding the transmitter in place. Soon after the transmitter was dislodged completely and recovered. From these observations it was clear that the dental acrylic did not bond to the nuchal plate from the outset Satellite transmitters lasted on average 15 days (SE ± 12.5, n = 3) on Nile crocodiles in NGR. No transmitters were recovered (Calverley 2013, Calverley and Downs 2015a).

4.8 Nest surveys

Nile Crocodile nesting surveys in NGR during the late 1960s and late 1980s showed that the majority of nesting sites occurred along the old Phongola river course (sub-region 6; Calverley 2013, Calverley and Downs 2015b). The river has subsequently diverged and now runs along the eastern boundary of the reserve (sub-region 8). During the course of the current study no nests were found along the new river course and at least two historical nesting sites were abandoned due to increased anthropogenic disturbance (Calverley 2013, Calverley and Downs 2015b).

In 2009/2010 prime historical nesting sites along the old course of the Phongola river were not used (Calverley 2013, Calverley and Downs 2015b). The lack of nesting activity here could be attributed to the change in the Phongola river's main course altering the nesting landscape or to increasing anthropogenic disturbances in this part of the reserve that we observed (Calverley 2013, Calverley and Downs 2015b).

In January 2010, we found four nests along the western periphery of the Phongola floodplain in Sub-region 6 (Calverley 2013, Calverley and Downs 2015b). Although these nests were in historical nest sites, they were considerably further inland (west) due to high water levels. We found two nests at historical nesting sites on the south eastern shore of Lake Nyamithi (Sub-region 5) in both 2009/2010 and 2011/2012 surveys. We found one nest along the banks of the main course of the Usuthu River (Sub-region 2) in March 2010. This is the first time a nest has been found along this river course. We found three new nesting sites on the new course of the Usuthu River in the region of Diphini Hide (Sub-region 3) in 2011/2012. Nesting sites were not always used in consecutive seasons, and successive nesting surveys result in additional nesting sites being discovered (Calverley 2013, Calverley and Downs 2015b). We found a new nesting site on the banks of the Balamhlanga stream in 2010 as it enters Lake Nyamithi. The nest site contained four active nests and one active burrow which we observed was used by at least one female and numerous hatchlings (Calverley 2013, Calverley and Downs 2015b).

4.9 Nest success

Historical abandonment of five Nile Crocodile nests at Lake Nyamithi due to disturbance associated with increased motor vehicle activity was documented (Pooley 1969, Calverley 2013, Calverley and Downs 2015b). Also historical predation was documented with Water Monitor as the primary predator of crocodile eggs during surveys from 1962-1969 in NGR (Pooley 1969). Predation pressure during this time usually effected less than 20% of nests (Pooley 1969). During the 2009/2010 survey two nests found at Lake Nyamithi were abandoned and predated by Water Monitor. It is not clear if disturbance to the nest sites from the nearby road or natural predation had led to the abandonment of these nests. Nor is it clear whether the nests were first abandoned then predated. However, it is likely that disturbance increases the frequency of nest predation as the female crocodile is usually driven off the nest allowing predators an opportunity to raid the nest. In 2011/2012 two nests were found in this area, however only one was predated. The unpredated nest was closely guarded by a 2.8 m female who refused to move from the nest site, emitting a warning hiss to researchers who approached too closely (Calverley 2013, Calverley and Downs 2015b).

Three of the four nests attended by female Nile Crocodile in the western periphery of the floodplain showed signs of predation but were subsequently submerged by flooding, thus it was not possible to quantify the levels of predation (Calverley 2013, Calverley and Downs 2015b). The fourth nest in this area was considerably closer to the water and was flooded prior to discovery. This nest was not predated after flood waters subsided neither did it hatch. Consequently predation affected 86% of nests in NGR for the 2009/2010 season. All nests were ultimately abandoned either due to predation (86%), flood damage (71%) or a combination of the two. Consequently, there was zero recruitment from the seven Nile Crocodile nests located in NGR over the 2009/2010 breeding season (Calverley 2013, Calverley and Downs 2015b).

Conversely, none of the nine nests found in 2011/2012 were flooded and 66% were predated (Calverley 2013, Calverley and Downs 2015b). Three nests hatched successfully, however it was not possible to estimate how many hatchlings actually emerged. One of the nests that hatched showed signs of predation prior to hatching and the female was not observed at the nesting site. However, a fresh body print was visible on the nest indicating that she had recently been in attendance (Calverley 2013, Calverley and Downs 2015b).

Camera traps located at four nest sites during the 2011/2012 season were unable to detect female Nile Crocodile despite them being in attendance of the nest (Calverley 2013, Calverley and Downs 2015b). Images of potential nest predators captured nests that were predated included the Cape Porcupine (*Hystrix africaeaustralis*) and the Vervet Monkey (*Chlorocebus aethiops*). Numerous signs of Water Monitor presence and predation of the nests were present but not captured by the camera traps (Calverley 2013, Calverley and Downs 2015b).

4.10 Characteristics of nesting sites

The characteristics of the nesting sites are summarized in Calverley (2013) and Calverley and Downs (2015b). Nile Crocodile nests were found in lacustrine and riverine habitats in NGR and in a variety of substrates including; red rocky soils in a boulder bed outcrops, in white sandy soil and in alluvial silt/clay. Nests were anything from 1-3 m above water level and up to 25 m from the water's edge (Calverley 2013, Calverley and Downs 2015b).

4.11 Nesting effort

We ran a correlation matrix to determine any relationships between date, nesting effort and numbers of nests found in NGR over the last 50 years (Calverley 2013, Calverley and Downs 2015b). When nesting effort (*E*) was calculated using winter estimations of total population size (N_w), a significant decrease ($P = 0.001$) in the nesting effort of Nile Crocodile in NGR from over 20% in the 1960s to just over 5% in 2010 and 6% in 2012 was found (Calverley 2013, Calverley and Downs 2015b). This was a function of an increasing Nile Crocodile population size with time, while the number of nests remained constant (Calverley 2013, Calverley and Downs 2015b). The number of nests found within NGR has stayed relatively constant over the years, while the population has increased threefold resulting in a much lower nesting effort *E* with time if winter absolute abundance data (N_w) were used. However, when *E* was calculated using the lower *N* measured during summer (N_s) *E* was calculated as 18-22% and no significant difference in *E* was found from the 1960s to the present (Calverley 2013, Calverley and Downs 2015b).

4.12 Human crocodile conflict

NGR poses a unique challenge to the conservation of Nile Crocodiles for a number of reasons. It is one of the four breeding areas of Nile Crocodiles in South Africa (Calverley 2013). Although proclaimed as a protected area in 1924, NGR continued to house members of the Mathenjwa and Tembe communities up until the early 1940s. These people were displaced under the pretence that they would be returned to the reserve once the tsetsi fly (*Glossina fuscipes fuscipes*) problem in the reserve had been resolved (Meer 2010). This of course did not happen, however, controlled harvesting of resources (low impact fishing and reed collection for the building purposes) within the reserve was allowed. The complex relationship between the reserve and the neighbouring community in the Mbangweni Corridor has meant that conservation in NGR has become an increasingly contested and contentious issue (Meer 2010). Disgruntled community members with filial links with those evicted from the reserve in 1947, as well as individuals seeking opportunities for economic gain removed the eastern boundary of NGR in 2008 (Meer 2010). The removal of the eastern boundary fence has resulted in unprecedented access to areas east of the Phongola floodplain but still within NGR. Increased levels of anthropogenic disturbance in this previously secluded area of the reserve may have a significant influence on the future of the Nile Crocodile population (Figs 4.3, 4.4, Calverley 2013). These concerns are based on the following:

- NGR field rangers discovered three crocodile deaths due to snaring in 2009 (Calverley 2013).
- A further 15 crocodiles were observed with snares around their necks in Lake Nyamithi during the course of this study presumably collected in the Phongola or Rio Maputo floodplain (Calverley 2013).
- Cultivation of crops and harvesting of trees and reeds has been observed in the Phongola floodplain within Ndumo Game Reserve (Calverley 2013).
- Illegal and extensive fishing practices (gill netting) were observed in the Phongola floodplain within Ndumo Game Reserve (Calverley 2013).
- Snares have been frequently recovered from the Phongola floodplain within Ndumo Game Reserve (Calverley 2013).
- The recent divergence of the Usuthu River has left the northern boundary exposed. Coupled with the removal of the eastern boundary fence in 2008, which has not been replaced to date (01/2013), illegal access to the reserve has increased (Calverley 2013).
- Consequently poachers can easily enter and exit the reserve. An indication of this is the loss of over 50% of the NGR White Rhino (*Ceratotherium simum*) population to poaching since the onset of this project (Calverley 2013).
- These factors together with the current political climate surrounding the reserve are reasons for concern for the reserve (Calverley 2013).

The implications of these anthropogenic effects for the NGR Nile Crocodile population are not good (Calverley 2013). In other African countries increased competition for scarce resources has brought crocodiles and man closer together resulting in an increase in the occurrence of crocodile attacks on humans and livestock and crocodiles are considered to be serious problem animals (McGregor 2005). However, the threat also extends to crocodile populations and generally increases in direct proportion to the proximity and density of human populations (Ross 1998). To mitigate threats to both humans and crocodiles a Human Crocodile Conflict (HCC) management plan needs to be drafted. Drawing from the current study we highlight the following occurrences in the western portion of the Phongola floodplain threatening to the NGR Nile Crocodile population:

- The illegal poaching of live animals
- The destruction of riverine vegetation and unsuitable agricultural activities
- Competition for food resources
- Anthropogenic disturbance at nesting sites (Calverley 2013).

Figure 4.3 Example of a Nile Crocodiles snared in Ndumo Game Reserve during 2009-2010 showing injury to the animal (from Calverley 2013).

Figure 4.4 Anthropogenic disturbances in Ndumo Game Reserve during 2009-2010 affecting habitat used by Nile Crocodiles (from Calverley 2013).

5 RESULTS: NILE CROCODILE IN PONGOLAPOORT DAM

5.1 Aerial count

The aerial count of the entire Pongolapoort Dam in winter 2010 recorded a total of 134 Nile Crocodiles (> 1.2 m) along the shoreline (Champion 2011, Champion and Downs in prep.a,b). The majority of crocodiles were found in the Northern half of the dam with high densities in the narrow north western sections (Champion 2011, Champion and Downs in prep.a,b). A total of 27 crocodiles were observed on the south western bank of the main dam from the most southern point (27°31'28.85"S 31°59'47.22"E) of the dam to the start of transect 5, southern entrance to the narrow section (27°22'11.73"S 31°55'59.58"E), 94 crocodiles seen in the narrow section up to the Railway Bridge (27°22'11.73"S 31°55'59.58"E to 27°22'14.64 S 31°51'20.03" E), and 13 crocodiles seen in the Northern section of the main dam, including the Swaziland section (27°20'56.77"S 31°55'30.02"E to 27°17'43.69"S 31°57'02.83"E). During the survey of the entire eastern shore of the main dam no crocodiles were observed (27°17'43.69"S 31°57'02.83"E to 27°31'28.85"S 31°59'47.22"E) (Champion 2011, Champion and Downs in prep.a,b).

The helicopter survey in November 2009 of the northern section of Pongolapoort Dam recorded 126 Nile Crocodiles, 17 juveniles, 25 sub-adults and 83 adults (Champion 2011, Champion and Downs in prep.a,b). Of these, 48 were observed in the upper inlet section of the river, between the N2 highway Bridge (27°23'40.24"S 31°49'36.29"E) over the Phongola river up to and including Buffalo Bend (27°22'47.05"S 31°50'44.43"E, Fig. 1). In the lower inlet section below Buffalo Bend to the Railway Bridge (27°22'10.81"S 31°51'22.49"E) 18 crocodiles were observed. A further 49 crocodiles were observed on the western bank of the narrow section between the Railway Bridge and Cliff End (27°21'45.81"S 31°53'40.16"E, Champion 2011, Champion and Downs in prep.a,b). After switching banks to Houseboat Bay (27°21'25.72"S 31° 53'15.34"E) and travelling back towards Railway Bridge (Fig. 2), another 11 crocodiles were recorded (Champion 2011, Champion and Downs in prep.a,b).

5.2 Spotlight survey

The large-scale spotlight survey on 30 October 2009 recorded 170 Nile Crocodiles over three sections (Champion 2011, Champion and Downs in prep.a,b); 29 in section 1 (northern section in South Africa of main dam), 116 in section 3 (both banks between railway bridge and Inkwazi Lodge) and 25 in section 4 (southern bank from Inkwazi Lodge to southern exit of narrow section). Transects 2 (northern bank from Inkwazi Lodge to EZKZNW camp site) and 5 (southern exit of narrow section to midpoint on western bank of main dam 27°25’43.60”S 31°56’04.45”E) were not completed due to equipment failure and the apprehending of illegal gill-net fishermen, respectively. The inlet river section was also not included as it was inaccessible, too shallow to navigate by boat. During this survey 75 observed crocodiles were identified as juveniles (< 1.2 m), 4 as sub-adults (1.2-2.5 m) and 4 as adults (> 2.5 m) (Champion 2011, Champion and Downs in prep.a,b).The remaining 87 observed crocodiles were recorded as “eyes only” (Champion 2011, Champion and Downs in prep.a,b). The survey done on 12 June 2010 recorded 219 crocodiles over 6 transects, 60 crocodiles in the river section, 29 in section 1 , 39 in section 2, 66 in section 3, 12 in section 4 and 24 in section 5 (Champion 2011, Champion and Downs in prep.a,b). A total of 16 juveniles were recorded, 13 sub-adults and 31 adults (Champion 2011, Champion and Downs in prep.a,b). The remaining 159 observations were recorded as “eyes only” (Champion 2011, Champion and Downs in prep.a,b).On a smaller scale spotlight survey of section 3 on the 25 November 2009, 113 crocodiles were recorded. 43 juveniles (< 1.2 m), 31 sub-adults (1.2-2.5 m) and 24 adults (> 2.5 m) were identified. The remaining 15 crocodiles were recorded as “eyes only” (Champion 2011, Champion and Downs in prep.a,b).

5.3 Day boat survey

A number of day boat surveys were done during the study period (Champion 2011, Champion and Downs in prep.a,b). The highest number of the juvenile size class was recorded during one of these surveys. The highest number of juveniles recorded was 116 on the 22 October 2009, during a 3 h survey including sections 2, 3, 4 and the river inlet up to Buffalo Bend (Champion 2011, Champion and Downs in prep.a,b). There had recently been the annual mass water releasing (late September 2009), dropping the water level and exposing an unvegetated, muddy shoreline. Juveniles were easily spotted, as they basked high up on the back (approximately 10 m from the water line) and could be seen fleeing to the water on approach. This unusual basking behaviour may have been a result of lower bank, covered in wet cold mud, not allowing crocodiles of small body size to efficiently attain the thermoregulatory requirements during basking. Smaller crocodiles would therefore travel further from the water’s edge in search of drier land (Champion 2011, Champion and Downs in prep.a,b).

5.4 Survey compilations

The highest number of each size class of Nile Crocodile was recorded using different survey methods (Champion 2011, Champion and Downs in prep.a,b). The highest juvenile count (n = 116) was recorded using a day boat survey (22 November 2009), the highest sub-adult count (n = 31) was recorded during a spotlight survey (25 November 2009), and the highest number of adults counted (n = 82) was recorded during the helicopter survey (23 November 2009). The total population is therefore a minimum of 229 individuals (Champion 2011, Champion and Downs in prep.a,b). The exact number is most likely considerably higher as surveys under estimate numbers as a result of observer and visibility bias (Games 1994, Ferreira and Pienaar 2011).

5.5 Sex ratio

A total of 32 Nile Crocodiles were captured at Pongolapoort Dam during the study period; 4 using a baited spring-trap, 17 hand grabs and 11 crocodiles using a pole noose (Champion 2011, Champion and Downs in prep.a,b). 17 crocodiles were small juveniles (all “hand grabs”) and of an insufficient size for sexing using the particular field method. The other 15 were large enough to sex. A total of 7 females and 8 males were confirmed, resulting in a sex ration of 0.88:1 females to males (n = 15). All crocodiles caught using baited traps were male (n = 4), 27% of total number of animals caught (Champion 2011, Champion and Downs in prep.a,b).

5.6 Historical changes in impoundment and crocodile habitat use

The Pongolapoort Dam level for the 12 years after construction remained very low, fluctuating from 1.5% capacity in 1972, up to 21% capacity in 1975, a 23 m difference in height (van Vuuren 2009, DWAF 2010, Champion 2011, Champion and Downs in prep.a,b). This minor water impoundment would still have dramatically altered the environment, changing available basking areas and flooding any previous used nest sites. The fluctuations in dam surface area from 500 ha at 1.5% capacity to 4 800 ha at 21% capacity, resulted in changes in shoreline characteristics and would also have forced changes in distribution of any crocodiles still present in the gorge (Champion 2011, Champion and Downs in prep.a,b).

In early summer of 1983/84 the Pongolapoort Dam was at 8.5% capacity (Champion 2011, Champion and Downs in prep.a,b). In January 1984 a large-scale flood occurred as a result of Cyclone Domoina (Rossouw 1985). The flooding resulted in record level peak flow (1600 $m^3.s^{-1}$) of the Phongola river, with 700 mm of rainfall falling over the catchment area, above the dam (van Vuuren 2009). The dam level rose from 8.5% capacity in January 1984 to 82.1% capacity by February of the same year (DWAF, 2010). This equated to a surface area increase of the impoundment from 2 800 ha to 11 800 ha, resulting in hundreds of hectares of previously un-flooded land becoming submerged. This was the second and most extreme major habitat disturbance experienced by the Nile crocodiles in the system after the dam construction (Champion 2011, Champion and Downs in prep.a,b).

After the Domoina floods, the impoundment maintained a more stable water level, between 1984 and 1991 (Champion 2011, Champion and Downs in prep.a,b). From 1991 (75% capacity) the area experienced drought conditions and the dam level dropped to 30% capacity in 1993, a resultant drop of 15 m in height (Champion 2011, Champion and Downs in prep.a,b). The drought period ended in late 1995, when another flood event occurred, raising the dam level from 38% early December 1995 to 90% in January 1996, a 12 m increase in height (Champion 2011, Champion and Downs in prep.a,b). The timing of this flood, post nest laying and pre-hatching would most likely have resulted in the flooding of any established nest sites. The sudden and substantial shift of shoreline would once again have changed the dynamics of associated microhabitats (Champion 2011, Champion and Downs in prep.a,b).

Annual variations in water height from 1996 to 2002 were relatively stable in comparison with earlier years, with less than 4 m fluctuation in mean annual water height (Champion 2011, Champion and Downs in prep.a,b). These years remain the highest maintained level in the dam's history thus far, with percentage capacity maintained above 90% (Champion 2011, Champion and Downs in prep.a,b). In the summer of 2001 large-scale flooding occurred over most of the eastern regions of southern Africa (Mwaka et al. 2003). This was the first time that the dam reached and exceeded 100% capacity (Champion 2011, Champion and Downs in prep.a,b). As a result of the already high capacity of the Pongolapoort (> 90%) prior to this flooding, there was minimal change in water level in meters, > 2 m change in annual mean water level. This would therefore have had less of an impact on the changing shoreline locality or possible dynamics of shoreline around the entire dam, such as previous flood events. The impact on the river inlet was however substantial, with the Phongola river bursting its banks, flooding all areas identified as nesting sites in 2009 and 2010 (Champion 2011, Champion and Downs in prep.a,b, Rippon pers. comm.). The flooding also greatly changed the shape of the inlet channel and its banks, as well as changing the shape of the dam where the inlet enters the dam (C. Rippon pers. comm.). During this period this area was already seen to contain the majority of Pongolapoort Dam Nile crocodile population and contained nesting sites (M. Thomas pers. comm.). The bursting of the Phongola river banks in 2001 would therefore most likely destroyed the majority if not all nesting sites located in these sections, as was seen in 2009/2010 nesting season (G. Champion pers. obs. 2010, Champion 2011, Champion and Downs in prep.a,b).

In 2002 the mean annual percent capacity of Pongolapoort Dam was dropped as a result of management decisions (Mwaka et al. 2003). The flooding and over-flow from the dam in 2001 has caused substantial damage downstream, most noticeable in Mozambique (Mwaka et al*.* 2003, Champion 2011, Champion and Downs in prep.a,b).

A further environmental change which has occurred in Pongolapoort Dam is a result of the introduction of an alien invasive aquatic weed, *H. verticillata* (Champion 2011, Champion and Downs in prep.a,b). The seasonal changes in water level prevent the weed from maintaining mats near the water's edge. Instead these mats are found a number of meters off shore, dependent on water depth. This creates a channel of weed free water between the bank and the mat which may create an important habitat component for small crocodiles (Champion 2011, Champion and Downs in prep.a,b).

Seasonal distribution patterns and associated broad habitat use

Pongolapoort Dam experienced seasonal changes in habitat traits as a result of changes in water level through the year (Champion 2011, Champion and Downs in prep.a,b). In brief areas of Pongolapoort Dam shoreline not seasonally flooded were well grazed by game species, leaving a grazing lawn along most of the dam shoreline (Champion 2011, Champion and Downs in prep.a,b). As the water level dropped (late September), a newly exposed lower shore line developed which had thick, muddy banks with little or no vegetation (Champion 2011, Champion and Downs in prep.a,b). As these banks dried out a number of plant species colonized the sediment deposit and a successional shift took place, with taller grass species later dominating the banks until the water level rose once more raising the shoreline (Champion 2011, Champion and Downs in prep.a,b). This resultant dynamic change in shoreline changed habitat characteristics temporally, which in effect affected changes in crocodile distribution and abundance (Champion 2011, Champion and Downs in prep.a,b).

In Pongolapoort Dam, juvenile Nile Crocodiles were seen to be predominantly solitary, with no communal basking groups of juveniles identified (Champion 2011, Champion and Downs in prep.a,b). Juveniles were most common along well vegetated banks and areas with high densities of aquatic weed, which appeared to provided safe refuge (Champion pers. obs.). Juveniles and sub-adults were often seen in the shallows hunting during dusk. Basking sites of juveniles and sub-adults appeared to be informal with any structure or opening in vegetation being used including small sand patches (< 1 m), exposed logs and weed mats (Champion 2011, Champion and Downs in prep.a,b). Sub-adults crocodiles appeared in a wide array of habitats, with no apparent preference. Sub-adults appeared to have a shifting habitat preference as they increased in size, with smaller individuals mostly solitary and inconspicuous preferring vegetated habitats, similar to juveniles. The larger sub-adults (> 2 m) were seen basking in clusters on open banks, occasionally with a single larger crocodile present. Definitive movement patterns could not be determined for either juvenile or sub-adult size classes as they favoured vegetated habitats and therefore the ability to spot individuals and accurately survey distributional trends varied seasonally (Champion 2011, Champion and Downs in prep.a,b).

Adult Nile Crocodiles in Pongolapoort Dam were often found to have preferred basking sites, characterised by low vegetated banks with high sun exposure and a nearby deep water channel as an escape route (Champion 2011, Champion and Downs in prep.a,b). A definite seasonal change in distributional pattern was observed during the study period. During the winter months (May-July) the majority of adult crocodiles were observed between Buffalo Bend and Inkwazi Lodge (Champion 2011, Champion and Downs in prep.a,b). Major basking clusters were located in most major bays, including Croc Bay and Hissing Bay. In August, the onset of the breeding season there was a mass movement of crocodiles into the inlet section, with the highest density of crocodiles located at Buffalo Bend (Champion 2011, Champion and Downs in prep.a,b,c). At the end of the September 2009, the Tiger Fish Bonanza was held, the largest Tiger fishing competition in the southern hemisphere. During this time of high disturbance crocodiles still present in the dam sections, became very shy and wary. It is expected that the crocodiles remained in hidden, highly vegetated areas. After the fish competition, the mass water release from Pongolapoort Dam took place, dropping the water level by 2 m within a week. The inlet section became shallow, with few deep channels and a number of exposed mud flats on which adult crocodiles congregated (Champion 2011, Champion and Downs in prep.a,b). A large number of adult crocodiles still congregated at Buffalo Bend during this time. In November the first summer rains raised the river level, changing the water colour and basking site availability for adult crocodiles. Most of the crocodiles migrated upstream of Buffalo Bend with only a few remaining behind (Champion 2011, Champion and Downs in prep.a,b). The crocodiles that moved upstream spent the remainder of the summer months there basking on open sandy banks. Some females selected nesting sites here and guarded their nests (Champion 2011, Champion and Downs in prep.a,b).

5.7 Crocodiles fitted with VHF radio transmitters

Due to logistic difficulties capture of Nile Crocodiles and attachment of transmitters at Pongolapoort Dam was delayed (Champion 2011, Champion and Downs in prep.a,b). However, 9 crocodiles were eventually captured and fitted with transmitters, ranging in size from 2.12-4.3 m. 5 of the 9 transmitter crocodiles were females (2.81-3.06 m), of which 4 were observed at Buffalo Bend during breeding period and one was later identified on a nest at the Causeway Bend (Champion 2011, Champion and Downs in prep.a,b). The 4 males fitted with transmitters (2.12-4.3 m) showed varying degrees of movement, with the larger crocodiles moving less both in frequency and distance (Champion 2011, Champion and Downs in prep.a,b). The largest of the transmitter crocodiles, a 4.3 m male, was the last fitted with a transmitter and moved from Hissing Bay (capture site) to the Buffalo Bend, where he remained for the duration of the breeding season (Champion 2011, Champion and Downs in prep.a,b). During this time all transmitters became detached, with the longest attachment lasting nearly 4 months and the shortest only 6 weeks (mean $\pm$ SE attachment days 76.9 $\pm$ 26.4 days). (Champion 2011, Champion and Downs in prep.a,b).

Figure 5.1 Aerial photo showing the *Hydrilla verticillata* weed mats found a number of meters off shore in the Pongolapoort Dam, creating a channel of weed free water between the bank and the mat which may create an important habitat component for small crocodiles (from Champion 2011).

5.8 Mating and courtship

The Buffalo Bend basking area (Fig. 2.3) for Nile Crocodiles was a large island located on the inner corner of a river bend at the dam inlet of the Phongola river (Champion 2011, Champion and Downs in prep. c). The 2009 Nile Crocodile mating season commenced during August, when numbers of crocodiles using this basking area increased from 13 (observation July) to 75 (observation August) i.e. a 577% increase in numbers. These crocodiles were mainly in the 3-4 m size class (85%) with a single large dominant male of

4.5 m present (Champion 2011, Champion and Downs in prep. c). This male was the only one observed mating during repeated surveys at this time. He was observed performing aggressive displays towards other crocodiles in the water as well as occasionally chasing a number of smaller crocodiles of unknown genders from the basking site. Presence of a number of tagged crocodiles with unique colour-coded tags attached to their tail scutes (Champion 2011, Champion and Downs in prep. c) confirmed that although the largest male appeared dominant, there were a number of other smaller males present, included two tagged males of 3.4 m and 3.0 m. During this period there were also a number of previously tagged adult females present at the basking area, some of which had travelled from their usual basking areas to Buffalo Bend (Champion 2011, Champion and Downs in prep. a,b,c). While others of these were commonly found in the area prior to the mass congregation/aggregation in August 2009 (Champion 2011, Champion and Downs in prep. c).

Two tagged adult female Nile Crocodiles with VHF radio transmitters attached arrived at Buffalo Bend during this period (Champion 2011, Champion and Downs in prep. c). These females, both 3 m in length, were observed during 24 hour observational sessions, moving further up river periodically at night and returning before morning to this basking area. At this time of year the water was clear and the river above Buffalo Bend was still very shallow (< 30 cm), except for a very thin channel along the outer edge which was slightly deeper (approximately 1 m). With the arrival of the first rains in early November, the river rose considerably and water colour changed dramatically to brown as a result of sediment run-off into the river. With the resulting rise in river level, Buffalo Bend basking area was greatly reduced in size and the once large long island was reduced to a number of small islands. Within two days of the dramatic change, the large numbers of crocodiles previously based there dispersed. The majority of these crocodiles moved upstream from Buffalo Bend, some being re-sighted, during the helicopter survey (23 November 2009), as high as the N2 road highway bridge that crosses the Phongola river 7 km upriver from Buffalo Bend in an area previously unpopulated by adult crocodiles during the winter months (Champion 2011, Champion and Downs in prep. c).

5.9 Nest sites and nesting

Three general communal Nile Crocodile nesting areas at Pongolapoort Dam were identified in the 2009/2010 breeding season (Champion 2011, Champion and Downs in prep. c). These areas are referred to as “Croc Bay” (27°22’42.90” S 31°52’27.93” E), “Cliff Ledges” (27°23’33.19” S 31°51’26.58” E) and “Causeway Bend” (27°23’22.74” S, 31°50’25.10” E) (Fig. 2.3). The reproductive index, proportion of actual females nesting to the total females with the potential to reproduce, of 0.73 was high in relation to other large populations in South Africa (Champion 2011, Champion and Downs in prep. c).

5.9.1 Croc Bay

Croc Bay was located in Section 3 of the dam, on the southern bank between Inkwazi lodge and the railway bridge (Champion 2011, Champion and Downs in prep. c). This was the largest bay in the section and was well protected against wind. The bay consisted of a large bowl bay, with a second narrow curved bay extending off the back of the larger bay. The small narrow bay has steep banks and clay substrate with a high gravel load. Here a number of old nesting depressions were located, scattered with degrading egg fragments, suggesting that the area had been used in prior breeding seasons for nesting. Only two nests (7% of total nests found) were identified here during the 2009/2010 season, one located on a well-used animal path and another at the base of a cliff, very near the water edge (Champion 2011, Champion and Downs in prep. c).

The nest located on the game path was approximately 8 m from the water edge and 3 m above the water surface, at about the 100% full capacity mark of the dam (Champion 2011, Champion and Downs in prep. c). The associated female was an estimated 3 m long. The nest site had no nearby shade for the female to rest in during the heat of the day. The nest site was on bare soil, but surrounded by weeds of approximately 50 cm in height, with *Parthenium hysterophorus,* the alien invasive plant, being the dominant species (Table 1). As the nest was located off a game path, it was allocated a disturbance level of “3/3” (very frequent). This path was used daily by a number of game species as a water access route. On 12 December 2009 at 10h00, a large Water Monitor was observed digging up the nest, stealing an egg and fleeing to a nearby shrub thicket. Once the egg was consumed, the lizard would return and steal another. Predation on the nest continued for a number of days until the nest was completely raided with no eggs remaining. It is uncertain whether the initial lizard, responsible for opening the nest, consumed all the eggs or whether a number of lizards were responsible for raiding the complete clutch. At no time during this period was the nesting female present during the nest raids and once the nest had been opened, no attempt to recover it was made by the female. After the nest was predated, the nesting female was not seen at the nest site again (Champion 2011, Champion and Downs in prep. c).

The Nile Crocodile nest sites at the base of the cliff (27°22’42.90” S 31°52’27.93” E) were on shallow, hard soil, which appeared to only form as a result of sediment wash off down the cliff face (Champion 2011, Champion and Downs in prep. c). It was 2 m from the water edge and only 0.5 m above the water surface on a small ledge. It was considerably below the dam’s 100% full capacity mark. The nest was not observed prior to predation and it is assumed that predation happened soon after the eggs were laid, as the eggs were not covered sufficiently with soil once laid. The nesting female associated with this nest was the smallest of the observed breeding females during the 2009/2010 breeding season, estimated at 2.8 m. The site had no nearby shade but was very near the water, which would offer protection during the heat of the day. Due to this site's locality it was only accessible by water and therefore was allocated a "0/3" (very low) disturbance value, as no large game or people could reach it. However, this female abandoned the nest soon after it had been predated and few observations were made regarding her behaviour around the nest (Champion 2011, Champion and Downs in prep. c).

These two Nile Crocodile nest sites were approximately 30 m from one another (Champion 2011, Champion and Downs in prep. c). No interactions between the two nesting females were witnessed, nor were any other Nile crocodiles seen in the inner bay during this time, even though the large outer bay was used year round as an established basking site, with a number of crocodiles residing there (Champion 2011, Champion and Downs in prep. c). Consequently both nest sites at Croc Bay failed early in the season as a result of predation by Monitor Lizards (Champion 2011, Champion and Downs in prep. c).

5.9.2 Cliff Ledges

The Cliff Ledges Nile Crocodile nesting area (27°23'33.19" S 31°51'26.58" E) was located along the inlet section of the river, 500 m upstream of the favoured basking and courtship site "Buffalo Bend" (Champion 2011, Champion and Downs in prep. c). A high proportion of the ledges were inaccessible as the site backed onto high cliffs, with a number of rock protrusions which extended out of the cliff face, into the river creating wall like obstructions from either side. This area was only accessible from the water or an arduous climb down a cliff face. This protected area was given a disturbance level of 0/3 (very low). The soils on the ledges appear to have accumulated as a result of the both culluvial and fluvial deposits, resulting in shallow clay sediment, with varying gravel loads (Champion 2011, Champion and Downs in prep. c). The area contained the highest number of identified nest sites, with a total of 19 sites (68% of total nests found) identified during an aerial survey by helicopter. The nests were all located on the outer bend of the river. Nine sites were visited during a later foot survey. The remaining ten sites were either inaccessible or unfound during the foot survey. Four of the nine nests visited (during the foot survey) fell outside the inaccessible ledge area and could be easily accessed by following the bank alongside the river. Two of these nests were down-stream of the cliffs and two upstream. The locality of the nests outside the protected ledges resulted in easier access and a higher disturbance frequency, allocated a 2/3 (moderate disturbance) as large game, especially African Elephant

(*Loxodonta africana*), frequented the area whilst feeding on riverside vegetation and accessing water (Champion 2011, Champion and Downs in prep. c).

Although, during the helicopter survey, a high number of Nile Crocodile nests were found along the less accessible ledges only five nests were reached and verified by foot (Champion 2011, Champion and Downs in prep. c). During the aerial survey, on approaching the cliffs, a high number of crocodiles were seen fleeing off the ledges into the river. These ledges seemed noticeably atypical with regards to areas usually selected for basking, both with respect to the ledge's physical characteristics and the diffuse basking pattern observed (Champion 2011, Champion and Downs in prep. c). On closer observation a number of nesting sites were identified, some already opened and predated, others visible as they were inadequately covered. During the aerial survey just after 10h00 a 3 m female crocodile was seen dropping her entire clutch of eggs, with no attempt to excavate or clear a nesting area (Champion 2011, Champion and Downs in prep. c). The over 45 eggs were dropped directly onto a patch of flattened grass. On the helicopters approach the female made no attempt to flee into the water, but remained next to the mound of eggs. She showed no response to the helicopter presence, even with the wind and sound disturbance the helicopter created whilst hovering over the site. Later a foot patrol found the site, where all eggs had been destroyed by predators including Monitor Lizards. The various ledges were separated by the rock protrusions, each ledge accommodating a various number of nests. Nests along the ledges were in close relation to one another, with the mean distance between nearest neighbouring nests being 5 ± 2.4 m (n = 9). Mean length of female crocodiles nesting on the ledge was 3.1 ± 0.1 m (n = 9) (Champion 2011, Champion and Downs in prep. c).

A network of pathways was visible from the air, leading from less demanding access points from the water, up onto the ledges towards apparent Nile Crocodile nesting sites (Champion 2011, Champion and Downs in prep. c). Return pathways (escape routes) into the water, ran straight towards the water, directly off the steep banks, making clear slide marks. These pathways showed a definite circular pathway to and from the nest sites, with the approach path usually being considerably longer than the departure. Distance from nest to water varied from 3 to 40 m, with a mean direct distance from nest to water of 9.8 ± 12.0 m (n = 9) (Champion 2011, Champion and Downs in prep. c).

Of concern was the high abundance of alien invasive plants along the ledges where the Nile Crocodile nests were (Champion 2011, Champion and Downs in prep. c). The two main dominant species included *P. hysterophorus*, which surrounded seven of the eight nests along this area and *Chromolaena odorata*, which created a number of dense thickets along the foot of the cliff and was in close proximity of five of the nine nests. It was however noted that these *C. odorata* thickets were used as shade refuge by a number of crocodiles nesting on the ledges. The shading effect of surrounding vegetation on nests was not quantified in this study (Champion 2011, Champion and Downs in prep. c).

5.9.3 Causeway Bend

The Causeway Bend Nile Crocodile nesting area (Fig. 2.3) was just below a washed out causeway, located 500 m downstream of the N2 road highway bridge, where it crosses the Phongola river and 1.5 km upstream of the dam (Champion 2011, Champion and Downs in prep. c). This crocodile nesting area, with 7 nests (25% of total nests found), was the furthest up the inlet from the dam of the three identified nesting sites (Champion 2011, Champion and Downs in prep. c). However, it must be noted that crocodiles were seen above this point. The area above the highway was however not surveyed for nests because of logistic constraints. Nest sites were identified on both sides of the river at Causeway Bend, five on the inner bank of the bend (river left) and two on the outer bend (river right). Inner and outer banks were dissimilar to each other in environmental characteristics (Champion 2011, Champion and Downs in prep. c).

The outer bank was similar to the Cliff Ledge Nile Crocodile nesting area, with a ledge backing onto a cliff and inaccessible except by water (Champion 2011, Champion and Downs in prep. c). These nests here were therefore allocated a disturbance level of 0/3 (very low). The soils were shallow, formed through colluvial and fluvial deposits. Both weeds *P. hysterophorus* and *C. odorata* were dominant plant species surrounding the site. In contrast, the inner bank consisted of a large sandy beach, surrounded by *P. australis* reed beds. Here the soil substrate was uniform river sand, with a very low gravel load. This area had few alien invasive plant species, and no *P. hysterophorus* or *C. odorata* evident (Champion 2011, Champion and Downs in prep. c). As a consequence of its isolation and infrequent visitation by other animals or humans and the surrounding reed bed which formed a protective barrier around, this nesting area was allocated a disturbance level of 1/3 (low). Nests were in close proximity to one another with mean distance to nearest neighbouring nest 5.7 $\pm$ 1.7 m (n = 7). Distance to water from each nest varied considerable though, as nests were scattered in a circular fashion. The two nests on the outer bank were near the water, both 3m from the ledge edge. The inner nests were all further, with a mean distance of 14.6 $\pm$ 10.9 m (n = 5) (Champion 2011, Champion and Downs in prep. c). Mean length of nesting females was higher than the mean length of nesting females at the other nesting areas. These females were also observed spending a large proportion of time at their nest sites. The nesting area had a number of shade refuges that females would use during the heat of the day. Nests on the outer bank were not visited and could only be observed during the aerial survey. Therefore very little observational data was obtained for these sites. The inner bank nesting sites however were visited on two occasions by foot survey and easily viewed on a number of occasions from a high vantage point, which created no disturbance for the nesting females during observations. All of the nests on the inner bank were well buried and no form of predation was apparent at any of these nesting sites. During one of the foot surveys to the inner this site, a number of nest sites from prior breeding seasons were identified by the presence of old degrading egg fragments (Champion 2011, Champion and Downs in prep. c).

On 10 January 2010 the Phongola river had a major flash flooding, with highest river levels recorded since the 2000 floods (Champion 2011, Champion and Downs in prep. c). The flash flood resulted from major rainfall over the entire catchment area above the Pongolapoort Dam, flooding all tributaries and the Phongola river itself. The Phongola river burst its banks and flooded all nest sites along the inlet section (i.e. all nest sites described above). The flood waters transformed and reshaped the whole inlet section of the river into the dam, erasing past basking areas and creating others in new areas. The recruitment for the 2009/2010 Nile Crocodile breeding season was estimated to be zero. However, there were unverified reports of a few hatchlings being spotted in the inlet section during February 2010 either suggesting the possibility of a nest hatching prior to the flooding or a nest site in another area being successful (Champion 2011, Champion and Downs in prep. c).

Despite the apparently low recruitment in the 2009-2010 Nile Crocodile breeding season numbers of juvenile crocodiles were observed showing that they are having reproductive success, all be it annually variable (Champion 2011, Champion and Downs in prep. c, Summers unpublished data).

Figure 5.2 Nile Crocodiles congregating at Buffalo Bend, Pongolapoort Dam in August (from Champion 2011, Champion and Downs in prep. a, Champion unpublished data).

Figure 5.3 Female Nile Crocodile seen on the cliff ledges, laying a clutch of eggs, with no apparent attempt to dig a nest or cover the eggs after laying (from Champion 2011, Champion and Downs in prep. a).

5.10 Human crocodile conflict

Pongolapoort Dam possesses a unique situation in which the whole dam is surrounded by protected. It is one of South Africa's largest man-made water bodies, and is surrounded by several game reserves (state, and/or privately owned and managed) (Champion 2011). For this reason, human wildlife conflicts are not as common as Ndumo Game Reserve and Lake St Lucia. A case of a Nile Crocodile being caught in an illegal fishermen's gill net was noted in 2014, however the crocodile did manage to free itself (Summers pers. obs.). Due to the size of Pongolapoort Dam, one cannot be sure how many Nile crocodiles are lost to illegal netting each year, and this needs to be quantified. Regular boat and foot patrols should be implemented to reduce chances of crocodiles being lost in this manner.

Pongolapoort Dam is also a popular Tiger fishing destination, which draws in boating and fishing enthusiasts from all over the country. There are a few sites where people can launch their boats from, and these sites are possible human-crocodile conflict zones. Although no incidences have been reported, there is a chance of future human-crocodile conflicts in these areas. Occasionally fishermen may get to close to crocodiles and the crocodile may push the boat with their noses and hiss, but this is human induced aggression. To reduce the chances of any human-crocodile conflicts, signs at launch sites should be erected, warning people of possible danger.

6 RESULTS: CROCODILE HEALTH IN ZULULAND

6.1 Morphological measurements

When we captured Nile Crocodiles morphological measurements were taken. We marked each individual uniquely by scute clipping and fitting of coloured caudal tags (Champion 2011, Calverley 2013, Combrink 2014, Warner in prep. a). More than 200 Nile Crocodiles were caught and measured in the different study sites and also at Lake Sibaya and Kosi Bay. Morphological data for Nile Crocodiles captured are summarised in Warner et al. (in prep. a).

6.2 Urine

Urine samples from Nile Crocodiles in Lake St Lucia, NGR and Pongolapoort Dam analyses are shown in Table 6.1.

Table 6.1 Lake St Lucia, NGR and Pongolapoort Dam Nile Crocodiles urine analysis (Warner et al. in prep. b).

Parameter	n	Mean	Minimum	Maximum	SD
CREATININE mmol/L	38	1.3013	0.58000	17.3900	2.68109
CALCIUM mmol/L	38	0.7382	0.42000	3.4800	0.56348
PHOSPHATE mmol/l	38	7.7742	0.20000	53.8600	9.79724
Calcium/Creat ratio	22	73.8182	1.00000	101.0000	45.43403
MAGNESIUM mmol/L (ref: L 0.86-9.54)	38	0.4711	0.01000	14.6600	2.37058
URIC ACID mmol/L	38	0.1426	0.03000	0.8000	0.19620
SODIUM mmol/l	38	74.3947	6.00000	131.0000	37.71339
POTASSIUM mmol/l	38	5.8684	1.00000	21.0000	3.71390
CHLORIDE mmol/L	38	48.4474	13.00000	124.0000	19.84221
UREA mmol/l	38	0.7632	0.00000	6.0000	1.32408
OSMOLALITY mOsm/kg (ref: mOsm/kg H20 On average fluid intake: 300-900	39	168.8205	75.00000	269.0000	44.81945

Urine samples from Nile Crocodiles (n = 11) in Lake St Lucia exposed to lead sinkers were assessed using semi-quantitative full scan analysis with ICP-MS (Analytical Toxicology Laboratory Services, George) for the following: Li, Be, Na, Mg, Al, P, S, Cl, K, Ca, Sc, Ti, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, As, Se, Br, Sr, Mo, Ru, Rh, Pd, Ag, Cd, Sn, Sb, I, Ba, Yb, Lu, Os, Ir, Pt, Au, Hg, Tl, Pb, Bi, Th, U. The analyses of these data are in progress (Warner et al. in prep. d).

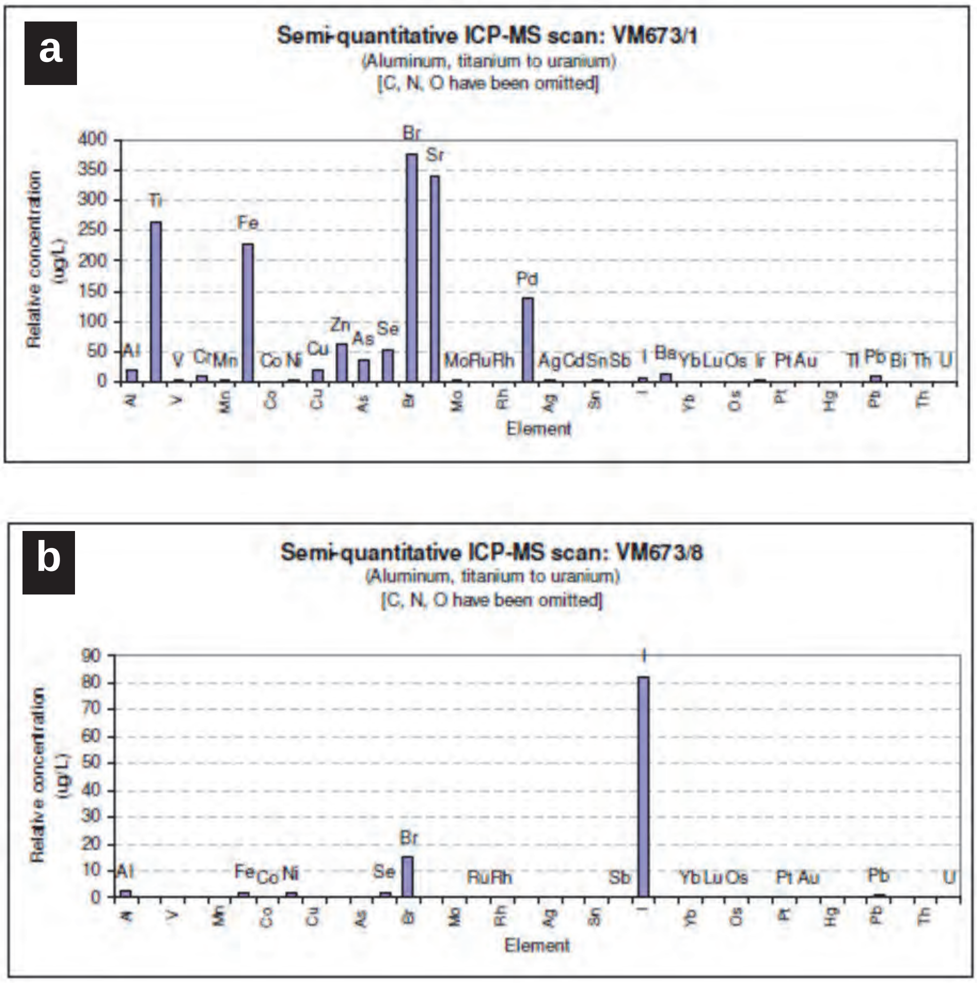


Figure 6.1 Examples of Nile Crocodile urine analysis for a. Crocodile OBO and b. Crocodile 94. (Warner et al. in prep. d).

6.3 DDT

Urine DDT analyses are still in progress and the final results pending (Warner et al. in prep. c).

6.4 Necroscopies

Permission was obtained to perform necroscopies on Nile Crocodiles that were emaciated in Lake St Lucia. The first crocodile was undertaken in 2011 (Fig. 6.3) (Warner et al. in prep. e). Significant Pb concentrations were found in the tissues of emaciated dead crocodiles (Croc 1 (liver): 3.0 mg/kg; Croc 2 (liver): 5.7 mg/kg) (Warner et al. in prep. e). Blood and kidney Pb concentrations were high in Croc 2 and lead sinkers were found in the stomach cavity necroscopy (Warner et al. in prep. e).

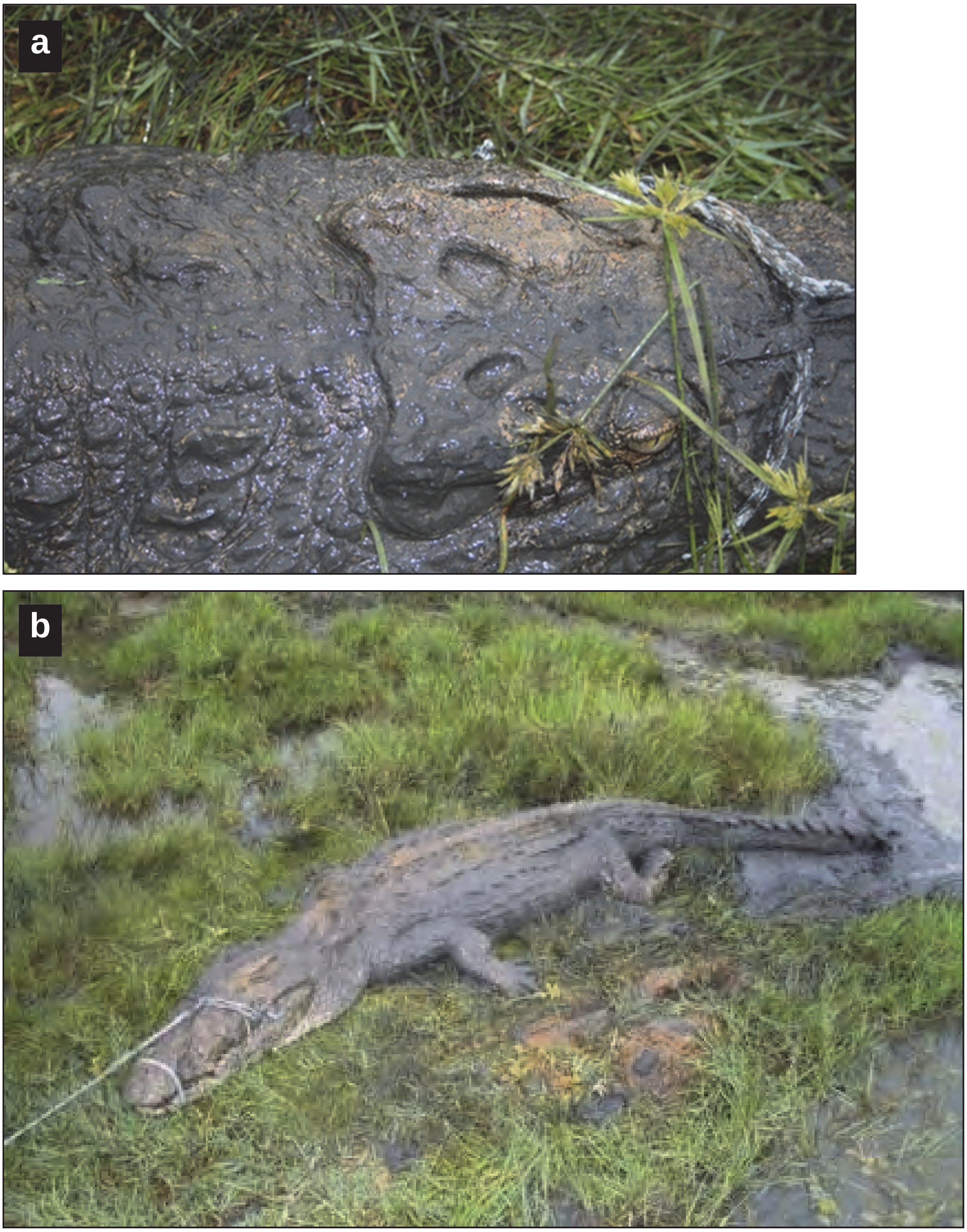


Figure 6.2 Emaciated Nile Crocodile in Lake St Lucia used for a necroscopy (Warner et al. in prep. e).

Figure 6.3 Necroscopy performed on a Nile Crocodile at Lake St Lucia.

In September and October 2013 a female Nile Crocodile (Fig. 6.5) was observed in poor condition. Its condition deteriorated and it was found dead on 13 October 2013 (32.40940 -28.35895) in the Narrows, 150m north of Dredger Harbour, Lake St Lucia (Warner et al. in prep. e). Its total length was 2790 mm, and snout vent length (SVL) 1603 mm. The cause of death was unknown. She was very emaciated and lost almost all her teeth, so the most likely cause of death is starvation due to old age. Based on the appearance of her skin, she looked very old. We caught this female more than one year ago and removed a transmitter fitted in 2009. In 2012 she was still in good condition and increased in length since initial capture in 2009. However, her tail girth did decrease somewhat. Based on measurements at the time of her death, she has shrunk considerably, even on the SVL measurement.

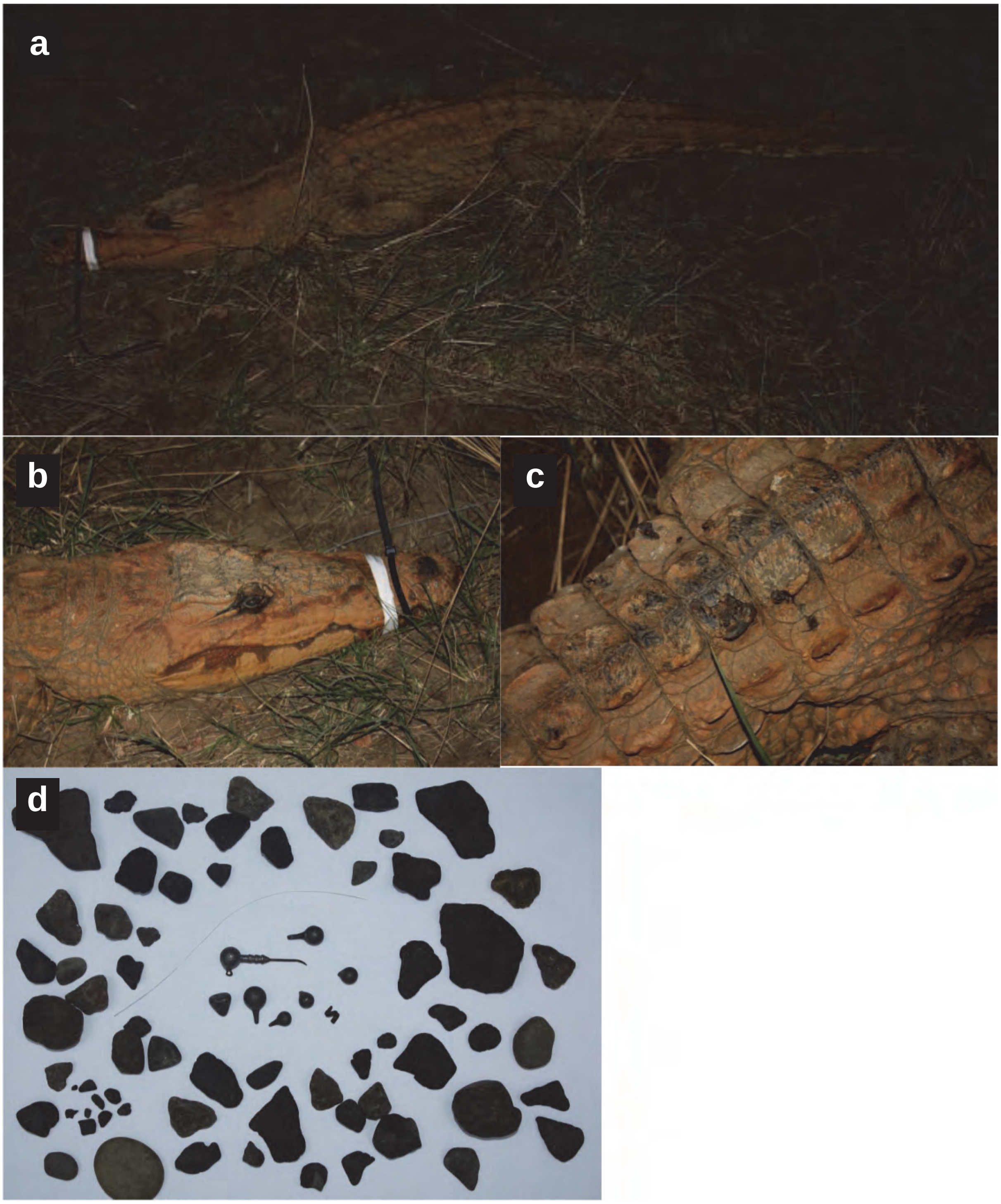


Figure 6.4 Nile Crocodile that died in the Narrows, Lake St Lucia 2013 where a-c. taken 21 days before the crocodile died. It was evident that she was in very bad condition; and d. the stomach was completely empty, except for 66 gastroliths (3-49 mm), 6 drop shot, one small sinker, one hair (139 mm) and the remains of a coil spring (6 mm) (Warner et al. in prep. e).

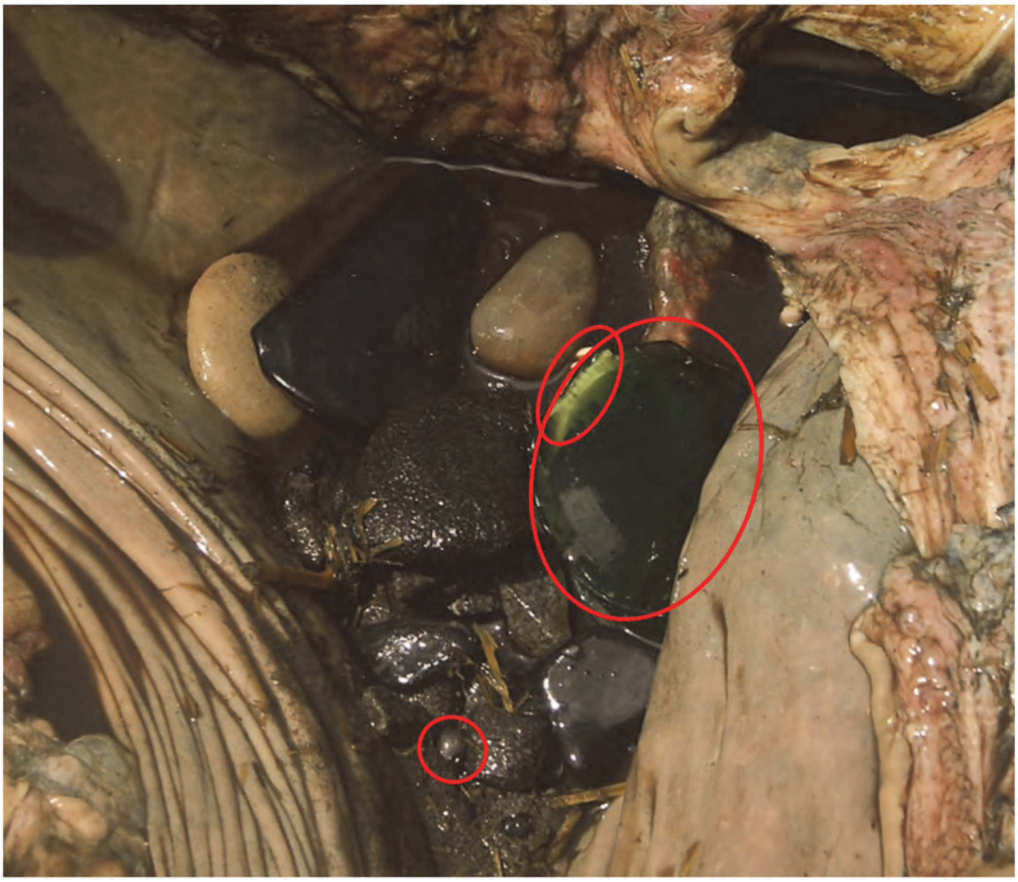


Figure 6.5 Foreign bodies in the gastrointestinal tract of a dead Nile Crocodile at Lake St Lucia (Warner et al. in prep. e).

A third Nile Crocodile (406cm male) that was dissected at Lake St Lucia following its death also had foreign bodies in its gastrointestinal tract (Fig. 6.5). In the stomach, we found stones, lead sinkers, swivels, glass pieces and a spark plug (Fig. 6.5). The crocodile also had a large fishing hook imbedded in it lower jaw, as well as two other smaller fishing hooks in his tongue (Warner et al. in prep. e).

6.5 Eggs

In March 2012 we excavated a wild Nile Crocodile nest at Lake St Lucia that had been abandoned by the mother and examined the eggs. Of the 32 eggs, 7 were rotten (all on the bottom layer). One of the hatchlings was born with two bottom jaws (both with the normal two rows of teeth (Fig. 6.2, Warner et al. in prep. d.)

Figure 6.6 Nile Crocodile hatchling born with two bottom jaws (March 2012, Lake St Lucia) (Warner et al. in prep.d.).

Figure 6.7 Nile Crocodile skeleton found in Nkazana Stream, Lake St Lucia.

6.6 Isotope analyses

Isotope analyses of scutes and blood are still in progress and the final results pending (Warner et al. in prep. f).

6.7 Crocodiles in the rest of Zululand

Lake Sibaya is one the smaller Nile Crocodile populations in Zululand. In the 2009-2013 aerial surveys estimates were lower (7-21) than recent estimates of 90-134 Nile Crocodiles (Combrink et al. 2011). There was major disturbance to the available Nile Crocodile habitat and evidence of trapping of Nile Crocodile (Fig. 6.4, Combrink and Warner unpublished data).

Figure 6.8 Nile Crocodile habitat at Lake Sibaya a-c. affected by anthropogenic disturbance and d. a crocodile trap at Lake Sibaya with a freshly killed dog used as bait (Combrink and Warner unpublished data).

Kosi Bay has few Nile Crocodiles (Combrink and Warner unpublished data). Here there is nesting disturbance as well as effects from fishermen (Fig. 6.5). Other localities with relatively small Nile Crocodile populations in northern Zululand are Muzi Pan, uMkhuze Nsumo Pan, uMkhuze swamps, Ithala (Bivane River, Phongola river) and Hluhluwe-iMfolozi (Combrink and Warner unpublished data). Muzi Pan and the uMkhuze swamps are severely affected by disturbances from cattle and people (Fig. 6.6, Combrink and Warner unpublished data). Other localities with relatively small Nile Crocodile populations in southern Zululand are the Tugela River (affected by siltation from sugarcane, heavy anthropogenic inputs), Amatigulu/Inyoni Rivers and Estuary, Umtunzini, and Enseleni River (affected by agriculture, afforestation) (Combrink and Warner unpublished data).

Figure 6.9 Disturbance to the Kosi Bay system by fishermen (Combrink and Warner unpublished data).

7 DISCUSSION

7.1 LAKE ST LUCIA

7.1.1 Distribution and relative abundance

The Lake St Lucia estuarine-lake system is a fluctuating and highly dynamic environment, subjected to a magnitude of external abiotic drivers (Whitfield 2013, Combrink 2014, Combrink et al. 2013, in prep. a,b). Nile Crocodiles at St Lucia seemingly have the ability to adapt to such changes. Factors influencing their distribution include physical variables such as adequate water depth for cover and locomotion (Combrink 2014, Combrink et al. 2013, in prep. a,b), courtship and mating activities (Pooley 1982b), thermoregulation (buffering for winter air temperatures at night and heat sink during summer), low salinity, life history variables such as reproductive (nesting) status, size (juveniles are excluded from the main lake), food availability and areas free from anthropogenic disturbance (Pooley 1982b, Leslie 1997, Combrink 2014, Combrink et al. 2013, in prep. a,b).

Historical data showed a mean increase of 13.0% per annum from 1972 to the early 1990s, stabilising thereafter (Combrink 2014, Combrink et al. 2013, in prep. a,b). The fluctuation in raw counts after 1993 seemingly reflected variation in optimal and sub-optimal counting conditions due to biases, rather than actual changes in the population. The count index seem to reflect an inverse relationship between high lake levels and observed crocodiles, as crocodiles disperse from the lake when full to adjacent wetlands, increasing visibility bias (e.g. 1994, 1995, 2007, 2011 to 2013). When lake levels decrease, crocodiles return to the lake, are more exposed and easier to observe from the air, especially during winter (Combrink, pers. obs.). However, during the recent drought (2003 to 2011) when most of the lake basin completely dried out, counting conditions again deteriorated as some individuals moved from the lake to freshwater seepages, swamp forests, *P. australis* reedbeds and burrows (Combrink et al. 2013), increasing visibility bias (Combrink 2014, Combrink et al. 2013, in prep. a,b).

7.1.2 Aerial surveys

Aerial Nile Crocodile counts have been conducted at St Lucia since 1972, and remains the most efficient method to cover the ~600 km survey area, of which large areas is too shallow for boat-based counts (Combrink 2014, Combrink et al. 2013, in prep. a,b). The results emphasised the importance of aerial surveys in June, when water temperatures are at a minimum and crocodiles are most visible during the day while basking. During the study period (2009-2013) up to 82.1% of crocodiles were recorded south of the lake, in the Greater Narrows area. This ~27 km channel never dried out, unlike the main lake where more than

90% was exposed and dry in 2006 (Whitfield and Taylor 2009). Salinities in the Greater Narrows were low due to freshwater intrusion from the Mfolozi River, with suitable water depth for cover, courtship and mating, deep cool water during summer for thermoregulation, more fish relative to the main lake (Cyrus and Vivier, unpublished data) and dense shoreline stands (*P. australis*) providing shelter (Combrink 2014, Combrink et al. 2013, in prep. a,b).

Some Nile Crocodiles did not move south but were restricted to freshwater seepage areas along the eastern shoreline, e.g. Tewati Bay or utilised freshwater arteries within swamp forest adjacent to the shoreline, often associated with burrows (Combrink 2014, Combrink et al. 2013, in prep. a,b).

The number of Nile Crocodiles south of the lake peaked in 2010, but good rainfall (> 700 mm) in Dec. 2010 and Jan. 2011 resulted in a reconnection of previously isolated waterbodies and decrease in salinity. Crocodiles responded by moving north, and the 2013 count showed a 44% decrease from the Greater Narrows and 69% increase in South Lake and North Lake (Combrink 2014, Combrink et al. 2013, in prep. a,b).

7.1.3 Diving bias during aerial and spotlight surveys

Our data illustrated temporal variation of Nile Crocodile emergence behaviour, related to water and air temperatures (Combrink 2014, Combrink et al. 2013, in prep. a,b). Increased water and air temperatures from Oct. to Jan. (spring to summer) resulted in decreased emergence behaviour during the day and increased emergence at night, peaking in Jan. (66.1%). Diurnal and nocturnal emergence behaviour was similar in Jan. and March and the lowest diurnal emergence recorded in Feb. From March (early autumn) onwards, as temperatures decreased, we saw an increase of diurnal emergence behaviour and a decrease in nocturnal emergence until diurnal emergence peaked in June (93.7%). Aerial and spotlight surveys should be planned around these diving proportions to maximise the sightability of crocodiles during the day and night (Combrink 2014, Combrink et al. 2013, in prep. a,b).

7.1.4 Spotlight surveys

Temporal variation in Nile Crocodile density in the Narrows was mainly a function of winter congregations, dependent on the availability of elevated (i.e. dry) basking areas. Basking congregations formed in the northern Narrows (Mphathe River northwards) as water levels increased in 2011 (Combrink 2014, Combrink et al. 2013, in prep. a,b). From Nov. onwards, the encounter rates of spotlight counts decreased as basking congregations disperse and crocodiles seemingly moved south down the Narrows, north into Catalina Bay as well as up the Mphathe Stream. Six crocodiles fitted with GPS-satellite transmitters confirmed movements between the Narrows and the Mphathe Stream and one crocodile between the Narrows and the Mfolozi River (Combrink 2014, Combrink et al. 2013, in prep. a,b).

Spotlight surveys are not the preferred Nile Crocodile survey technique at St Lucia (Combrink 2014, Combrink et al. 2013, in prep. a,b). The lake is too shallow, even during normal lake levels to adequately cover the ~400 km shoreline (Taylor 2006) with numerous submerged sandbanks, as well as an additional ~200 km shoreline of islands, streams, rivers and channels. However, spotlight counts may provide important information on the size component of crocodiles within the survey transect, which are not recorded during aerial surveys. Nonetheless, it is generally not possible to estimate the size of each crocodile as some individuals are wary and dive before the boat can approach close enough. Those individual are classified as EO "Eyes Only" (Messel 1977). There seems to be a positive correlation between the size of a crocodilian and its wariness and therefore likelihood to dive before a size estimate is possible (Bayliss et al. 1986, Woodward and Moore 1993). The proportion of EO crocodiles recorded in the Narrows ranged between 33.3-74.3%, which is high compared with EO ratios for other Nile Crocodile populations, e.g. Flag Boshielo Dam 3.3% (Botha 2005), Okavango Delta 17.0% (Bourquin 2007), 28.0% at Lake Sibaya (Combrink et al. 2011) and Lake Bhangazi 7.3% (Combrink, unpublished data). The reasons for the elevated EO level in the Narrows might be a combination of wariness and habitat factors. The shallowness of the survey transects and impenetrable submerged macrophytes (S. pectinata) *colonising extensive shoreline areas, often prevented* the boat to approach a crocodile close enough for a size estimate (Combrink 2014, Combrink et al. 2013, in prep. a,b).

The 19.9 ± 2.9% mean sub-adult component was comparable with 16.0% in the Panhandle of the Okavango Delta (Bourquin 2007), 21.6% in Flag Boshielo Dam (Botha 2005), 27.4% at Jozini Dam (Champion 2011) but considerably lower than 39.0% in Lake Nyamithi at Ndumo Game Reserve (Calverley and Downs 2014a) (Combrink 2014, Combrink et al. 2013, in prep. a,b). The Narrows is connected to the Mphathe Steam, the largest nesting area (mean = 18.2 ± 5.6 nests) during the study period (Combrink 2014, Combrink et al. 2013, in prep. a,b). Although not possible to estimate, it is suspected that a large proportion of these hatchlings will (as hatchings, yearlings or juveniles) disperse downstream into the Narrows, facilitated by strong flow subsequent to localised rainfall events. We predict a high survival rate of these young crocodiles due to dense shoreline vegetation lining the banks of the Mphathe Stream and Narrows, providing shelter and apparent food abundance such a small fish, amphibians and insects (Combrink 2014, Combrink et al. 2013, in prep. a,b).

The mean Nile Crocodile juvenile component of 6.6 ± 2.0% was considerably less compared with other populations in southern Africa, such as 13.0% in Lake Nyamithi at Ndumo Game Reserve (Calverley and Downs 2014), 43.5% in the Panhandle of the Okavango Delta (Bourquin 2007), 17.7% in Flag Boshielo Dam (Botha 2005) and 38.1% at Jozini Dam (Champion 2011) (Combrink 2014, Combrink et al. 2013, in prep. a,b). We suspect that some juveniles were included in the 49.4 ± 4.8% EO component, especially as they often prefer very shallow water on the land-water interface which was very difficult to reach by boat or too far to estimate size. We suspect the majority of the EO component was adults. Only 24.1 ± 4.4% of size-recognisable crocodiles were recorded as adults, but this size class, especially larger individuals, are more wary and often dive before a size estimate is possible (Messel et al. 1981, Montague 1983, Platt and Thorbjarnarson 2000, Stirrat et al. 2001, Botha 2005, Fukuda et al. 2013, Combrink 2014, Combrink et al. 2013, in prep. a,b).

7.1.5 Population estimate

There is a paucity of data regarding historical distribution and densities of crocodiles in the lake system, but early reports suggested it harboured a large population (Pooley 1982c, Combrink 2014, Combrink et al. 2013, in prep. a,b). Since the arrival of the first European explorers in Zululand, Nile Crocodiles were hunted and killed as vermin as well as for skins in the post-war period until the 1968, but very few factual records exist regarding the extent of this persecution. The introduction of the Reptiles Protection Ordinance No. 32 of 1968 brought an official end to the killings (Pooley 1982a). Pooley released 486 individuals (5-18 months) in Lake St Lucia from 1967 to 1976 (Pooley 1980). No information exists regarding their survival rates, but given the low crocodile density at the time, survival were probably high and these introductions most likely contributed to the recovery of the St Lucia population (Combrink 2014, Combrink et al. 2013, in prep. a,b).

Survey data of Nile Crocodiles indicated an increase of 13.0% per annum from 1972 to the early 1990s (Combrink 2014, Combrink et al. 2013, in prep. a,b). This equals the maximum estimated rate of increase (13%) of a typical Nile Crocodile population (Craig et al. 1992). It appears that the population have stabilised since the early 1990s, possibly as a result of density dependent mechanisms (e.g. intraspecific predation), low reproductive frequency, illegal killings, habitat transformation in the north and south of the lake, and disturbance, especially at nesting grounds (Combrink 2014, Combrink et al. 2013, in prep. a,b).

Lake levels strongly influence visibility of Nile Crocodiles during aerial counts with fewer crocodiles observed during high lake levels or when large parts of the lake has dried up, as was the case during the height of the recent drought (Combrink 2014, Combrink et al.

2013, in prep. a,b). The 2013 population estimate using the double-count method was conducted under high lake levels, and despite using correction factors to account for observer/detectability and diving bias, the result (858 crocodiles) should be seen as an underrepresentation due to visibility bias. Although the count data from 2008 to 2013 indicate a substantial declining trend, after correcting for diving and observer bias, the five year mean population estimate of 2013 (1005 ± 138 crocodiles 95% C.I.) is comparable with the 2003 estimate (1009 ± 219 crocodiles 95% C.I.), the first year of the drought (Combrink 2014, Combrink et al. 2013, in prep. a,b). This highlights the importance of using correction factors for population estimates as well as the apparent resilience of sub-adult and adult crocodiles during prolonged drought conditions. Visibility/vegetation bias remained unquantified as mark-recapture efforts were unviable due to extensive shoreline vegetation in the Narrows, making it impossible to re-sight coloured tagged crocodiles. Water level indicators were installed in the lake in 2013, allowing for the incorporation of lake levels during crocodile counts as a covariate in the population estimate (Combrink 2014, Combrink et al. 2013, in prep. a,b).

The present study is unique in that we report on the largest number of Nile Crocodiles fitted with satellite transmitters (n = 18), the highest number of locational fixes per unit (n = 9063) and individual crocodile (n = 11088), and the greatest longevity of a satellite transmitter on a crocodilian to date (n = 1486 days) (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). GPS-satellite transmitters, despite initial high setup costs, are the ideal method to remotely monitor crocodile movements and activity. Battery longevity or premature failure seems to be the main limitation preventing datasets of > 5 years in the field, which will likely improve as battery technology continues to improve. This will furthermore allow the inclusion of hatchling and juvenile crocodiles in GPS-satellite movement studies, where transmitter dimensions and subsequent battery longevity and costs are currently a limitation (Combrink 2014, Combrink et al. 2013, in prep. c,d).

7.1.6 Activity levels

The paucity of literature describing crocodilian activity levels reflects the difficulty in obtaining detailed spatial information of this aquatic predator, often in very remote and inaccessible areas (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). The overall temporal pattern confirms elevated nocturnal activity levels for Nile Crocodiles. However, during summer when water temperatures are high, the clear distinction between nocturnal and diurnal activity levels became diffused (Combrink 2014, Combrink et al. 2013, in prep. a,b,c,d,e).

Nile Crocodiles were bimodally active at Lake St Lucia with a period of low activity (< 37%) from 10:00-18:00 and high activity (> 44%) from 18:00-10:00 (Combrink 2014, Combrink et al. 2013, in prep. a,bc,d,e). Diel activity levels varied significantly and the seasonal variation in activity patterns was seemingly an interchange between water and air temperatures and solar radiation. Crocodiles were least active during winter with very little activity from 10:00-18:00, coinciding with winter basking behaviour (Combrink, pers. obs., Downs et al. 2009). Crocodiles returned to the water at night to escape the cool air temperatures with subsequent increased activity, especially during early evening when body temperatures are still elevated from basking (Combrink 2014, Combrink et al. 2013, in prep. a,b,c,d,e). During summer when water temperatures were high, crocodiles were not reliant on solar radiation to elevate body temperatures and therefore seldom came ashore to bask, with an associated subsequent decrease in activity variance throughout the day (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Variation in monthly Nile Crocodile activity followed changes in water and air temperatures, except for nesting females (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Their activity levels were strongly influenced by nest guarding activities, resulting in decreased activity during the summer nest period, followed by a rapid increase in post-nesting activity, possibly to improve condition, as water temperature decreased towards winter (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Brien et al. (2008) investigated activity levels for Estuarine Crocodiles (*Crocodylus porosus*) in a 8.7 km long, permanent, non-tidal, freshwater billabong in northern Queensland, Australia, during the winter dry season. They found an overall mean activity level of 31.2% for nine Estuarine Crocodiles, comparable with 30.5% for Nile Crocodiles during the (dry) winter season at St Lucia (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Both studies found increased activity levels during late afternoon and early evening, but whereas the activity level of Estuarine Crocodiles seemed to decrease after midnight, activity levels of Nile Crocodiles only decreased at the onset of mid-morning basking. Nile Crocodiles appear more inactive during the day in winter compared with the Estuarine Crocodile, but caution must be applied when comparing the two studies as Brien et al. (2008) used VHF technology (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Hutton (1989) investigated the frequency of diurnal movements (i.e. activity) of Nile Crocodiles at Lake Ngezi, a high altitudinal (1220 m) artificial impoundment in Zimbabwe (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). On average, 17.0% of Nile Crocodiles moved > 20 m during the day (n = 12). Nile Crocodiles at Lake St Lucia were considerably more active with 92.0% moving > 20 m during the day, and 65.6% > 100 m (n = 18) (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). It must be noted that this is an overall figure and based on the aforementioned seasonal variation, one can expect winter activity levels at St Lucia to be considerably lower. It is not clear what time of the year the activity levels were determined at Ngezi, but it was most likely during winter or spring. The high altitude of Lake Ngezi, and resultant cool air and water temperatures especially in winter, are likely to be a determinant in the reported low Nile Crocodile activity. Nonetheless, the Ngezi sample size was small (mean of 10 days per crocodile) and data collected using VHF telemetry, so comparisons must be interpreted with caution (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

In this study non-nesting Nile Crocodile females were most active (50.9%) of all crocodiles, followed by adult males (44.5%) and nesting females (35.2%), with sub-adults considerably less active (29.9%) (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Nesting behaviour had a major effect on nesting female activity and when the summer (nesting season) was excluded, activity increased to 42.0% (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Nile Crocodile adults generally displayed the same temporal pattern, being most inactive during late morning followed by increased activity during the afternoon which increased even further and peaked during the first part of the evening (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). During late evening activity levels stabilised, with adult male and non-nesting female activity decreasing somewhat in the early morning hours, and increased activity for adult non-nesting females. Activity levels of all adults decreased sharply from early to late morning (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Conversely, sub-adults displayed almost no variance in their diel activity pattern. Activity levels of adults and sub-adults were significantly influenced by season. Adult males were most active in summer, non-nesting and nesting females during autumn, while the most inactive season was winter. Nesting females were equally inactive during the cool winter season and the nesting summer season. Sub-adults displayed remarkable differences in activity between the seasons. During winter (13.8%) and spring (17.9%) they were almost completely inactive, while during summer they were more active (62.9%) than adult males (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Brien (2008) recorded activity level of the Estuarine Crocodile during winter (cool dry season). Adult males were more active (45.3% and 44.8%) compared with this study (mean 36.6%), but they found a similar trend for a single sub-adult (22.7%) compared with 13.8% for this study (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Winter activity levels of Estuarine Crocodile (mean 31.3%) were similar to mean winter Nile Crocodile levels in this study (30.5%). Both studies recorded an adult female as the most active individual during winter, with Estuarine Crocodiles (51.5%) and Nile Crocodiles (60.9%) (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.7 Mean daily movement

The absence of literature describing detailed crocodilian movements reflects the lack of crocodilian field studies using satellite-based transmitter technology with sufficient (≥ 6) positions captured daily (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). However, a number of VHF studies have investigated crocodilian movement (Joanen and McNease 1972, McNease and Joanen 1974, Hutton 1989, Hocutt et al. 1992, Kay 2004, Botha 2005, Brien et al. 2008, Calverley 2010, Champion 2011, Calverley 2013) and have provided valuable information on broad movement patterns. Unfortunately, most studies were of relative short duration and the very nature of VHF tracking precludes data collection at the frequency resolution required to detailed movement analysis. This has limited the possibility for direct comparisons among and within species, nonetheless broad differences within and between species is informative and valuable (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Overall, MDM of Nile Crocodiles in the Lake St Lucia system was 1244 ± 161 m, but differences amongst crocodiles were significant (Combrink 2014, Combrink et al. 2013, in prep. c,d,e), highlighting the importance of tracking a large number of study animals in crocodilian studies (Kay 2004). Sex, size and reproductive state were the most important predictors of daily movements, but topographical features and water coverage were also important. Adult males were most mobile, but not significantly more than nesting females. Non-nesting females were significantly less mobile and the mobility of sub-adults was severely restricted (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Sub-adults Nile Crocodiles were confined to specific shallow and vegetated habitats adjacent to the main and much deeper channel of the Narrows (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). They seldom ventured into deep water of the main channel possibly due to predation risk by larger crocodiles (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Of the three sub-adults, the smallest individual was the least mobile while the largest sub-adult made the longest daily movements. Habitat features, such as topography, affected adult movements as well. There was a general pattern that crocodiles confined to narrower and structurally complex parts of the system such as Mphathe Stream and the Narrows had a lower MDM, while crocodiles in main Lake St Lucia and Lake Bhangazi were making longer daily movements. Large parts of Lake St Lucia were completely dry for the first part of this study period. With increased rainfall and freshwater input from the Mfolozi River, water levels increased, which led to a range expansion of some crocodiles into previously dry parts of the lake, resulting in increased daily movement (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Kay (2004) found MDM of Estuarine Crocodile adult females in the lower Ord estuary, northern Australia, much lower (<1 km) compared with this study, but movements might have been restricted due to possible nesting activities in summer (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). The maximum daily movement recorded by a female was 10 100 m compared with 14 507 m for a Nile Crocodile (Female 601) in this study (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). This was also considerably more than the previously recorded Nile Crocodile daily movement of 2 900 m at Lake Ngezi, Zimbabwe (Hocutt et al. 1992). Adult male Estuarine Crocodile movements (1578 m, range 600-3300 m) were somewhat less but related to movements in this study (1708 m, range 905-2178 m). The maximum daily movement recorded for a male (4.3 m) Estuarine Crocodile was 23 300 m moving downstream, and it was possible that a current or tidal effects could have facilitated the high rate of movement (Kay 2004). Read (2007) recorded a maximum daily movement of 30 400 m for a 4.5 m Estuarine Crocodile in the ocean homing back to its capture location. This movement rate was only possible due to Estuarine Crocodiles adopting behavioural strategies to use the momentum of favourable surface currents. This strategy required very little active swimming, reduced the daily energy budget and facilitated increased dispersing potential (Campbell et al. 2010). The maximum daily movement for Nile Crocodiles recorded in the Lake St Lucia system was 17 389 m by a 2.7 m female, also homing back to its capture location (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Brien et al. (2008) investigated movement for adult male and female Estuarine Crocodiles in an 8.7 km long, permanent, non-tidal, freshwater billabong in Lakefield National Park, northern Queensland, Australia, during the winter dry season (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). He found considerable smaller daily movements compared with the lower Ord estuary and this study. Overall MDM for Estuarine Crocodile were substantially less than the current study. Furthermore overall maximum (winter) daily were considerably less than our winter movements for Nile Crocodiles. Brien et al. (2008) argued that the rather restricted movements of Estuarine Crocodile were not surprising as other species have also known to exhibit smaller movements in topographically constrained habitats (Horner and Powell 1990, Minns 1995, Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.8 Diurnal and nocturnal movements

Cott (1961) noted that Nile Crocodiles is nocturnally aquatic, but Hutton (1989) was able to determine the extent of behavioural differences between diurnal and nocturnal movements at Lake Ngezi. Overall, the mean nocturnal movement at Ngezi was 660.0 m, somewhat less than the 752.5 m for this study (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

However, Nile Crocodiles at Lake Ngezi were seemingly much less active during the day (73.16 m) compared with this study (554.02 m), while most Ngezi crocodiles moved > 20 m on less than 40% of days (Hutton 1989). At St Lucia crocodiles moved > 20 m 92.0% of days and > 100 m 65.6% of days. Hutton (1989) noted that juveniles at Ngezi were more strictly nocturnal compared with adults. At St Lucia sub-adults were significantly more active during the day. We suggest this may be a temporal intraspecific predation avoidance strategy and equates to ecological separation of sub-adult and adults. Cott (1961), Graham (1968) and Hutton(1989) noted ecological separation between juveniles and adults, and we propose a similar dynamic at St Lucia, at least in the Narrows where sub-adults were tracked (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.9 Seasonal movements

A number of crocodilian studies have attributed differences in seasonal movements, for the most part, to changes in temperature (Chabreck 1965, Joanen and McNease 1972, Goodwin and Marion 1979, Hutton 1989, Kay 2004, Combrink 2014, Combrink et al. 2013, in prep. c,d,e). At St Lucia water temperature significantly correlated with mean monthly Nile Crocodile movement, and the correlation was stronger for sub-adults than adults. At Lake St Lucia, crocodiles were most mobile during autumn and females were also most active during autumn. Adult males were equally mobile in summer (1920.17 ± 54.33 m) and autumn (1937.53 ± 95.07 m). Nesting female mobility peaked subsequent to the three month nest guarding period, possibly due to searching of optimal feeding opportunities before winter. American Alligator (*Alligator mississippiensis*) adult males were most active during summer (MDM = 855 m) with almost no movements during winter at the den site (Joanen and McNease (1972). Daily movements (4000 m) for adult male Estuarine Crocodile during summer were high (Kay 2004), with movements during winter (1300 m) similar to winter movements for St Lucia adult males (1290.2 ± 66.63 m). It appears the temperate distribution of the American Alligator has a restrictive effect on winter mobility whereas Estuarine Crocodile and Nile Crocodile are relatively more active during winter, with Nile Crocodiles at St Lucia often undertaking long journeys to winter basking congregations (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.10 Total daily movements

Despite the MDM of 1244 ± 161 m for Nile Crocodiles at St Lucia, 61% of total daily movements were < 1 km per day (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Adult males proportionally made much longer movements than non-nesting females per day, more than twice in the 2-3, 3-4 and 4-5 km categories and more than 20 times for movements > 5 km per day. These longer journeys might be related to territorial maintenance behaviour of large males. Nesting females proportionally made most movements > 5 km, of which most occurred subsequent to the nesting period. It is likely that these long movements were in search of optimal feeding opportunities prior to winter, as well as re-establishing home ranges after a three month absence. Sub-adults were less active, moving > 2 km per day on less than 1% of the days. We suspect this behaviour is a strategy to minimise intraspecific predation. Sub-adults for the most part avoided open water in the Narrows, staying in densely vegetated shallow water adjacent to the main channel (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

The absence of literature describing detailed crocodilian movements reflects a lack of crocodilian field studies utilising satellite based transmitter technology with sufficient daily GPS capture rates (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Two recent field studies on Estuarine Crocodile using satellite transmitters (Read et al. 2007, Campbell et al. 2013) revealed valuable spatial information, but at low temporal scale of ~two positional fixes per day, which were sufficient for the objectives of the respective studies. However, this study highlights the need for more crocodilian field studies recording detailed spatial and temporal data, which would allow for comparison across population and crocodilian species allowing for a more complete interpretation of their biology, ecology and life history (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.11 Conceptual framework

A general conceptual framework for movement ecology was outlined by Nathan et al. (2008). They proposed three basic components related to the individual, i.e. internal state, navigation capacity and motion capacity, and a fourth component referring to external factors affecting its movement (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Arrows indicated the direction of impact and the subsequent movement path feeds back to the internal and external components. We have presented a simplified conceptual framework for Nile Crocodile movement in the Lake St Lucia estuarine system (Combrink 2014, Combrink et al. 2013, in prep. c,d,e), based on these principals. The most important external factors consisted of the physical environment or habitat and the diel and seasonal influence of water and air temperature. This affected the internal state, i.e. “why move”, of the individual crocodile as a result of three factors: nutrition, reproduction and social aspects. The internal state influenced both motion capacity and navigation capacity. The motion capacity consisted of swimming, overland walking if surface water was unavailable and in extreme circumstances and for very short distances, galloping. Navigation capacity, i.e. “where to move", consisted of hatchling dispersal from the natal area and juvenile and small sub-adult dispersal to the main lake. Nest site selection, territorial maintenance behaviour and homing instinct all were part of navigation capacity. The actual movement path was a dynamic interplay of the external and internal factors affecting movement, the navigation capacity and motion capacity (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Despite being the largest and most widely distributed of all African crocodilians, covering 42 range states (Fergusson 2010), surprisingly little published research of Nile Crocodile home range behaviour are available (Hutton 1989, Hocutt et al. 1992, Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Furthermore, all home range studies suffered from low observations per study animal, a consequence of the difficulty in tracking crocodilians using VHF-technology as well as low transmitter longevity. Seasonal data were limited to four individuals (Hutton 1989), limiting comparisons between studies (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.12 Adult males

Virtually no home range data is available for adult male Nile Crocodiles (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). A large male (410 cm TL) in Flag Boshielo Dam occupied a home range of 28 ha, (Botha 2005), considerably smaller compared with the two "territorial" males in this study (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Flag Boshielo Dam is much smaller (surface area = ~1 285 ha) than Lake St Lucia (~35 000 ha) and smaller crocodilian home ranges have been reported in topographically constrained habitats (Brien et al. 2008). Botha (2005) recorded winter movements of a large male to a basking area, possibly related to breeding, similar to Male 500 in this study (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Campbell et al. (2013) described two discrete behavioural space-use strategies of male Estuarine Crocodiles during the breeding and nesting season in the Wenlock River (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). They found that "nomadic" males (3.81 ± 0.08 m TL) did not display a stable total (95% UD) home range but travelled extensively, comparable with Male 111, while "site-fidelic" males (4.17 ± 0.14 m TL) were characterised by a stable home range within discrete sections of the river, comparable with the larger males (110, 121 and 500) in this study (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Campbell et al. (2013) found Estuarine Crocodile maintained larger home ranges and core-use areas compared with Nile Crocodiles in this study (905 ± 80.7 ha and 410 ± 36.7 ha compared with St Lucia Nile Crocodiles 713.1 and 81.5 ha respectively). Overall, Estuarine Crocodile males were more mobile (MDM 4156 ± 884 m) compared with

Nile Crocodile males in this study (1701 ± 60 m), but this may have been facilitated by tidal current flow (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Kay (2004) found his smallest Estuarine Crocodile male (253 cm TL) in the Ord River occupied the largest mid-stream linear range (87 km) which did not stabilise at the end of the study, similar to transient Male 111 (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). His largest male (434 cm) was most mobile (3300 ± 6500 m S.D.), a trend also noted for St Lucia males, but at much higher rates sustained by current flow (Kay 2004). Ord River Estuarine Crocodile males did not appear to be site fidelic to any particular section of river, but the low number of observations per study animal (mean = 32) preclude more complete understanding (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.13 Adult females

Adult females occupied biologically significant smaller home ranges compared with adult males, and they were generally less variable (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). It furthermore seemed that habitat and topography might be a significant factor limiting home range size. Generally, females in the main lake (125 and 449 during her second year) maintained larger home ranges than females mainly restricted to the Narrows (531, 601 and 515) and Female 514, restricted to the small Mphathe Stream, occupied the smallest home range. During the drought Female 449's home range was concentrated within a small freshwater refugia, but as lake levels increased, she moved from the shoreline into the bay, significantly increasing her home range (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). We suspect that import resources such as freshwater seepage areas, preferred hunting/feeding areas and basking/mating sites (especially during winter), are spatially more dispersed in the main lake, compared with the Narrows, which seemingly facilitates larger home ranges (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). The absence of home range size differentiation between summer and winter could be attributed to winter movements to basking/mating areas of all females, except Female 449, and restricted space use in summer on the nest for four nesting females (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.14 Sub-adults

Home range and core-use areas of sub-adult Nile Crocodiles at St Lucia was significantly smaller than adults (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). All transmitter-fitted sub-adults were captured in the Narrows and they were very habitat specific, partial to shallow, well vegetated areas adjacent to the deep channel and strictly territorial with no overlap between neighbouring sub-adults (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

Hutton (1989) found small and localised home ranges of 10 ha (100% isopleth) at Lake Ngezi for Nile Crocodiles < 2.2 m, considerably smaller than the 22.9 ha median home range of the present study (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). His findings that large sub-adults abandoned their home ranges and moved throughout much of the available habitat were not recorded at St Lucia. Nonetheless, the sub-adults in this study were possibly still too small to disperse, although exploratory behaviour was recorded for Female 531, a small (240 cm) adult (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). Calverley (2013) recorded somewhat smaller sub-adult total home ranges (15.2 ± 10.8 ha) in a Lake Nyamithi of Ndumo Game Reserve than this study (22.9 ha median). Brien et al. (2008) recorded the home range for a sub-adult male Estuarine Crocodile (171 cm) during winter at Seven Mile Waterhole. His home range was 1.2 ha and core-use area 0.1 ha, much smaller than this study's median home range and core-use area of 18.2 ha and 5.9 ha respectively (Combrink 2014, Combrink et al. 2013, in prep. c,d,e). The MDMs of sub-adult Nile Crocodiles at St Lucia (199 ± 17 m) were also higher compared with the Seven Mile Waterhole Estuarine Crocodile male (137 m) as well as the maximum daily movement (Nile Crocodile = 2023 m, Estuarine Crocodile 1075 m) (Combrink 2014, Combrink et al. 2013, in prep. c,d,e).

7.1.15 Nesting

The Nile Crocodile population at the Lake St Lucia estuarine system represents the most southern viable nesting population throughout the species' range (Combrink 2014, Combrink et al. in prep. f,g). It is also the largest estuarine nesting population and largest recorded and possibly most stable (i.e. unaffected by flooding) nesting population in South Africa. Although some aspects of Nile Crocodile reproductive ecology at Lake St Lucia were investigated from 1959 to 1978 (Pooley 1982a), nest surveys have been conducted since the 1980s, making it one of the longest monitored Nile Crocodile populations in Africa. The mean number of nests recorded at St Lucia from 1982 to 2013 was 76.19 ± 6.42 (Combrink 2014, Combrink et al. in prep. f,g). Historically, large nesting areas were distributed from the very north of the system next to the Mkhuze River, along the eastern shoreline, Mphathe Stream, and the Link canal, Backchannels and Mfolozi River in the very south. Increased anthropogenic disturbance and habitat transformation north and south of Lake St Lucia resulted a shift in nest distribution, contacting towards the protected eastern shores (Combrink 2014, Combrink et al. in prep. f,g).

Below average rainfall led to the closure of the estuary mouth in 2002 (Combrink 2014, Combrink et al. in prep. f,g). Prolonged low rainfall from 2002 to 2011 with no freshwater input from feeder streams led to the lake drying out, with nest effort at record low levels (6.9% and 8.0% in 2009 and 2011 respectively). Most nests were recorded at the Mphathe Stream and freshwater seepage areas along the eastern shoreline. The mean nest count prior to estuary mouth closure (1982 to 2001) was 103.07 ± 7.7 nests, while during the period when the estuary was closed (2003 to 2012) nesting significantly decreased to 53.56 ± 5.92 nests (Combrink 2014, Combrink et al. in prep. f,g).

Since 2011 rainfall patterns have normalised, the estuary was relinked to the ocean in 2012 and during the 2013 nest survey some nests were recorded along the Eastern Shores Wilderness area (Combrink 2014, Combrink et al. in prep. f,g). Insights into the abundance and distribution of Nile Crocodile nests and understanding how threats, such as human disturbance, lead ingestion through fishing sinkers or alien invasive plants might affect rates of reproduction, should result in management actions mitigating these consequences (Combrink 2014, Combrink et al. in prep. f,g).

7.1.16 Human crocodile conflict

Since the arrival of first European explorers at St Lucia, Nile Crocodiles were regarded as vermin and exterminated for economic and safety considerations, as well as sport hunting. Legislation and strict protective measures in 1969 finally brought an end to the killings. However, the demand for Nile Crocodile body parts, eggs, blood and fat used in the traditional trade and witchcraft, combined with highly effective capture techniques such as baited snare traps and hooks, are having a negative impact on the population.

Fences separate Nile Crocodiles and neighbouring inhabitants for the most part at Lake St Lucia, but crocodiles might move into connecting rivers and streams utilised by local people. Education campaigns combined by mitigation measures, e.g. boreholes and physical barriers at the water's edge, could minimize attacks on livestock and people. Crocodiles that are attracted to jetties or slipways in designated fishing areas are captured and removed to an area separated by a physical barrier, as a result of their ability to "home" back to the capture location.

7.2 NDUMO GAME RESERVE

7.2.1 Population estimate

When conducting aerial surveys of crocodilians it is important that high levels of accuracy and precision are achieved in order to produce relevant and comparable results (Games 1994, Brown et al. 2004, Calverley 2013, Calverley and Downs 2014a). Precision can be measured by the standard error (SE) surrounding an estimate, with low values for SE indicating high levels of precision (Graham 1987). On the other hand, accuracy is a measure of how close an estimate is to the actual population size (Combrink 2004). Aerial surveys carried out in the 1970s and 1980s using the same observers, aircraft and pilot provided the estimates with the smallest SE values, while surveys in the 1990s with different observers provided larger SE values. Surveys carried out in 2009, where water level, season, observers and aircraft varied, provided the highest SE values. We recommend that future Nile Crocodile surveys in NGR take place during (1) the austral winter, when individuals are more likely to be out of the water basking; and, (2) periods of low water levels, when visibility is less likely to bias results (Combrink 2004; Downs et al. 2008). Furthermore, wherever possible we suggest using helicopters for survey efforts because of their ability to operate safely at lower altitudes and slower speeds, thus facilitating more accurate counts (Combrink 2004, Calverley 2013, Calverley and Downs 2014a).

Relative abundance of Nile Crocodiles in the NGR increased from the 1970s to the 1980s, and again in the 1990s (Calverley 2013, Calverley and Downs 2014a).This increase in population size was likely attributable to the restocking program initiated in the NGR. The crocodiles released in the restocking program would not have been noticed in the first series of aerial counts from 1971-1973 because of their small size, as only individuals having TL > 200 cm are visible from the air (Games 1994). Generally, it takes 14 years for males and 17 years for females to exceed 200 cm in TL (Hutton 1987). Individual growth rates are determined by temperature, resource availability and genetics, however, and it difficult to age crocodiles according to body length after three years of age (Hutton 1987a, Kofron 1990). Based on previous research (e.g., Hutton 1987), we assumed that all hatchlings surviving in the NGR would be visible in aerial surveys 20 yr after their release (Calverley 2013, Calverley and Downs 2014a).

The second series of aerial counts of Nile Crocodiles were initiated in 1985 (M.C. Ward, personal communication, Calverley 2013, Calverley and Downs 2014a). By that time, individuals released in the initial restocking effort would be visible during aerial surveys (having attained sufficient TL), which partially explains the increase in Nile Crocodile population size between 1973 and 1985. The second batch of crocodiles released were expected to reach a TL > 200 cm between 1988 and 1990, likely explaining the second increase in the population size between 1989 and 1990. An improvement in survey method could have further resulted in the increase in yield (M.C. Ward personal communication). Our results should be interpreted with caution, however, as it is unlikely that observer bias alone could account for the increase in crocodile population size (Calverley 2013, Calverley and Downs 2014a).

The Nile Crocodile population at the NGR continued to grow in the early 1990s, until the population decreased in 1994 (Calverley 2013, Calverley and Downs 2014a). The current population size appears to have stabilized since the last survey in 1994. Collected demographic information revealed that the NGR Nile Crocodile population structure is skewed towards adults with juveniles forming the lowest percentage at only 13%, while sub-adults and adults account for 39% and 48% of the population, respectively. This type of population structure could be indicative of a declining population and emphasizes the poor recruitment in the NGR (Calverley, 2013, Calverley and Downs 2014a,b, 2015b). As the population of artificially introduced individuals ages, continued population decline in the NGR should be expected because recruitment levels within the reserve are low (Calverley 2013, Calverley and Downs 2014a,b). The current nesting effort in the NGR is relatively poor, but indicates a self-sustaining population size of 230 individuals (Calverley 2013, Calverley and Downs 2014a,b). A much larger population size might be achieved by securing breeding grounds within the reserve and in the adjacent wetlands of neighbouring Mozambique, and by preventing the illegal harvesting of Nile Crocodiles both inside and outside of the NGR (Calverley 2013, Calverley and Downs 2014a,b, 2015b).

The earlier Nile Crocodile restocking program in the NGR can explain the pattern of population increase detected by the aerial surveys but fails to explain the periods of zero population growth between survey periods (Calverley 2013, Calverley and Downs 2015b). While crocodilian populations can adhere to density dependent methods of population regulation such as cannibalism (Cott 1961, Pooley 1982) and exclusion (Hutton 1989, Richardson et al. 2002), this was unlikely the case in the NGR because periods of population stability in the 1970s and 1980s were followed by increases in population size. Historical data indicate that nesting effort declined as the NGR population has increased (Calverley 2013, Calverley and Downs 2014a). Nesting effort was generally low at 21% (Calverley 2013, Calverley and Downs 2015c) and Pooley (1982) estimated only a 1-2% survival rate of Nile Crocodile past the first year at the NGR. Consequently, the larger population size did not produce increased recruitment, and so it has been unable to sustain the artificially high population size brought about by the restocking program. When compared with other demographic studies on Nile Crocodiles in Africa, the NGR population has a lower proportion of juveniles compared with sub-adults and adults (Calverley 2013, Calverley and Downs 2014a,b, 2015b). We therefore suggest that the restocking program initiated in the late 1960s and early 1970s elevated the NGR population of Nile Crocodile to an artificially high density that was not been sustained by recruitment. Therefore, the NGR population stabilized only temporarily, and will like continue its decrease as the cohorts released in the re-stocking programs age and die (Calverley 2013, Calverley and Downs 2014a,b, 2015b).

Nile Crocodile sex ratios in the NGR were biased toward females in the juvenile and sub-adult age classes, but biased towards males in adults (Calverley 2013, Calverley and Downs 2015b). However, average sex ratio across all size classes was even. The bias among juvenile individuals might be a consequence of sex-biased dispersal (Tucker et al., 1998), whereby juvenile males to disperse further away from nesting sites (located at Lake Nyamithi). Hutton (1987b) found that Nile Crocodiles in Zimbabwe had a female biased sex ratio across all size classes. This was attributed to temperature-dependent sex determination in crocodilians and low nest temperatures (Hutton 1987b). Similarly, Leslie (1997) found a female biased (61.9%) sex ratio in sub-adult and adult Nile Crocodiles at St. Lucia. Bourquin (2008) however, found a male biased sex ratio for yearling and juvenile Nile Crocodiles in Botswana (61.8% and 61.2% respectively), and a slight bias towards females in the adult and sub-adult size classes (54.8% and 55.3% females respectively; Calverley 2013, Calverley and Downs 2015b). Bourquin (2008) attributed the increased females to a higher mortality rate in males due to aggressive male-male competition for reproductive rights (Calverley 2013, Calverley and Downs 2015b).

The even sex ratio at the 310 cm size class could also be a product of incubation temperatures used for during the restocking program at the NGR that favoured neither sex (Calverley 2013, Calverley and Downs 2015b). If this was not the case, we would expect the development of a female biased sex ratio seen in the juvenile and sub-adult size classes to be transmitted through to the adult size class thereafter. Other causes of biased sex ratios throughout size classes might include differential mortality and habitat selection between the different sexes (Thorbjarnarson 1997); only one habitat (Lake Nyamithi) was sampled in the NGR. Nevertheless, the 1:1 sex ratio at the reproductive size class in the NGR must be considered optimal for maximum recruitment, and current sex ratios do not explain poor recruitment within the reserve. This is explained by the seasonal movement of the majority of the NGR population out of the reserve and during the nesting season (Calverley 2013, Calverley and Downs 2015b).

We feel that the restocking of Nile Crocodiles at the NGR has success led to an increased population size for this species (Calverley 2013, Calverley and Downs 2015b).

Continued long term monitoring programs are necessary to follow population trends, however, as crocodiles are long lived animals. For restocking programs to be sustainable, sufficient nesting habitat that is protected needs to be available (Combrink 2004, Calverley 2013, Calverley and Downs 2014b, 2015b).

7.2.2 Environmental conditions influencing habitat use

Variations in spatial abundance are a function of resource availability and conditions (Townsend 2003, Calverley 2013, Calverley and Downs 2014b, 2015b). This may be particularly true for crocodiles where ambient temperature, water levels, season (breeding, nesting), salinity levels, prey densities and disturbance factors all influence habitat use (Pooley 1982, Hutton 1987b, Kofron 1993, Leslie 1997, Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). The amount of solar radiation available for controlling body temperature varies on a spatial and temporal scale (Angilletta et al. 2002) necessitating adaptations in thermoregulation (Grigg et al. 1998). In crocodilians, this is generally achieved behaviourally (Seebacher 1997, Downs et al. 2008) and through habitat selection (Cott 1975). In the NGR, Nile Crocodiles selected Lake Nyamithi as a winter habitat primarily because of the habitat types available. These include basking sites that are protected from human disturbance, exposed to sun and with gently sloping banks in close proximity to deep water (Swanepoel et al. 2000). The seasonal influx of crocodiles into the lake during months of the austral winter has been occurring for at least 50 years, and Lake Nyamithi forms an important winter habitat for Nile Crocodiles in the NGR and possibly the outlying Rio Maputo floodplain (Pooley 1969). This has important management implications for the outlying pans and floodplain in terms of protecting suitable crocodile habitat (Calverley 2013, Calverley and Downs 2014a,b, 2015b).

Reproductively active crocodiles likely benefit from maintaining high body temperatures during winter (Seebacher and Grigg 1997, Calverley 2013, Calverley and Downs 2015b). High temperatures facilitate testicular and ovarian development while also allowing higher levels of activity for intraspecific competition during the early breeding season when mating occurs (Seebacher and Grigg 1997). The large number of Nile Crocodiles observed in Lake Nyamithi over the breeding season identifies the lake as an important breeding habitat within the NGR, and likely for the Rio Maputo population downstream from the reserve. The majority of Nile Crocodiles leave Lake Nyamithi before prior to oviposition (November-December); Pooley (1982) suggested that this migration occurs not only from the lake but from the NGR as well as females will search for suitable nesting habitat in the Rio Maputo floodplain. Because mating has already taken place by this time, we cannot explain the similar pattern of movement exhibited by male crocodiles (Calverley 2013, Calverley and Downs 2015b).

For reptiles, an increase in ambient temperature results in an increased metabolic rate, placing more emphasis on finding food resources than suitable basking habitat (Calverley 2013, Calverley and Downs 2015b). Crocodiles of both sexes thus move away from winter basking sites in search of foraging sites. Swanepoel (1999) and Botha (2005) both reported that crocodiles positioned themselves in habitats were prey items (fish) are naturally concentrated on account of the local topography or hydrology. In the Phongolo River floodplain, numerous pans become isolated from the main river channel during dry winter months and are only reconnected during high water levels in summer triggering mass fish movement into and out of the pans when water levels allow (Heeg and Breen 1982). An estimated 25 of the 35 fish species occurring in the floodplain move between the main channel and the pans/lakes during high water levels (Kramer 2003). Crocodiles are adept at making use of ephemeral prey resources (Webb et al. 1982), and congregate at the outlets/inlets of the pans to feed on the fishes moving in or out of the pans (personal observations). Crocodiles could be moving out of Lake Nyamithi in order to take advantage of seasonal migrations of estuarine fish species such as striped mullet (Leslie 1997), as well as the freshwater fish species of the Phongola floodplain (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b).

The dry season in South Africa coincides with the austral winter, and the ensuing decrease in water levels of the floodplain places emphasis on habitats with permanent bodies of water (Swanepoel 1999, Botha 2005, Calverley 2013, Calverley and Downs 2014b, 2015b). In the NGR, the surface area of the floodplain decreases from roughly 4,200 ha to 1,200 ha (Kyle and Marneweck, 1996) suggesting a significant seasonal change in the amount of habitat available to Nile Crocodiles. Seasonal changes in habitat availability might be exaggerated in the Rio Maputo where the floodplain has been drained for agricultural purposes (Kramer 2003). Furthermore, the largest and only permanent lake in the floodplain (Lake Pandejene, downstream from the NGR) is used heavily for fishing, and disturbance levels for crocodiles are high here. As the Rio Maputo floodplains dry up in winter, crocodiles move into NGR where permanent pans, deep-water channels, and basking sites are abundant and protected (Calverley 2013, Calverley and Downs 2014b).

7.2.3 Ontogenetic factors influencing habitat use

Crocodiles utilize habitats differently according to size and such niche partitioning might help sustain large populations in confined areas through reducing intraspecific competition for resources (Radloff et al. 2012, Calverley 2013, Calverley and Downs 2014b). At Lake Nyamithi, environmental conditions influenced the number of crocodiles in each size class differently (Calverley 2013, Calverley and Downs 2014b). Nile Crocodiles < 150 cm TL were least influenced by seasonal changes in water level, temperature and rainfall. This is most likely because crocodiles in this size class have small, localized home ranges (< 0.1 km^2; Hutton 1989) and Lake Nyamithi (0.17 km^2) encompasses the entire home range. Habitat use of crocodiles in this size class is likely to change within the lake according to environmental conditions and resources, but the number residing in the lake remained relatively constant throughout the year (Calverley 2013, Calverley and Downs 2014a,b).

Relative abundance of Nile Crocodiles in the dispersal size class (150-250 cm TL) was most strongly influenced by minimum monthly temperatures and rainfall, whereas those larger than 150 cm TL were most strongly influenced by rainfall as opposed to water levels (Calverley 2013, Calverley and Downs 2014b). This suggests that, although water levels may facilitate or encourage movement of crocodiles out of and into the pans/lakes in the floodplain, this movement is triggered by season. Larger, reproductively-active Nile Crocodiles responded to seasonal changes in rainfall and not water level as rainfall patterns are related to the onset of the breeding season while water levels are artificially controlled in the NGR from releases from the Pongolapoort/Jozini Dam (Heath and Plater 2010, Calverley 2013, Calverley and Downs 2014b).

7.2.4 Crocodile distribution from a landscape perspective

Water level and temperature alone do not explain why Lake Nyamithi has such a high density of crocodiles compared with other pans within the reserve (Calverley 2013, Calverley and Downs 2014b). Pooley (1982) attributed a similar pattern to the availability of suitable basking sites and abundance of prey items. Adult Nile Crocodiles radio tagged in Lake Nyamithi were found to move in and out of the lake numerous times during the winter season, however, suggesting that they might be supplementing their resource intake by frequenting the Phongola river floodplain (Calverley, 2013). Resource supplementation occurring at the focal patch (Lake Nyamithi) might maintain a population greater than in similar isolated patches (Calverley 2013, Calverley and Downs 2014b). Lake Nyamithi is highly connected in terms of both physiognomy and the biophysical nature of the corridors that facilitate crocodile movement between the various habitat patches making up the Phongola river floodplain (Henein and Merriam 1990, Taylor 1993, Calverley 2013, Calverley and Downs 2014b).

7.2.5 Landscape complementation

More Nile Crocodiles were counted in NGR during the dry season than during the wet season (Calverley 2013, Calverley and Downs 2014a,b). Although high water levels are known to negatively influence crocodile surveys (Montague 1983, Combrink, 2004, Malvasio 2006, Simpson and Mediyansyah 2009) correction factors applied to count data support the pattern of Nile Crocodiles leaving the NGR during the wet season (Calverley 2013, Calverley and Downs 2014a,b).The NGR and the Rio Maputo floodplain form spatially discreet habitat patches that are used by Nile Crocodiles on a seasonal basis. The NGR provides protection, permanent water and favourable thermal environments during the winter when these factors are limited in the Rio Maputo floodplain. The Rio Maputo more than likely provides good foraging and possibly nesting habitat (Swanepoel 1999). Crocodiles access these respective resources by moving between the two habitats. The proximity and connectivity between these resource patches supports a larger population than if these patches were further apart or not as well connected through landscape complementation (Calverley 2013, Calverley and Downs 2014a,b).

Aerial surveys from 1971-2009 showed that Nile Crocodiles were unevenly distributed within the NGR (Calverley 2013, Calverley and Downs 2014a,b). It has been suggested that the Phongola river system has a greater population of Nile Crocodiles than the Usuthu River system because of the differences in landscape composition between the two systems (Pooley 1982, W.S. Mathews, personal communication). The Usuthu River experiences frequent anthropogenic disturbance, and is too shallow with few deep pools to offer protection for Nile Crocodiles, while Lake Banzi has insufficient basking sites to support a large population of Nile Crocodiles (Pooley 1982). The Phongola system likely supports a larger population of Nile Crocodiles, on the other hand, as the Phongola river has a greater diversity and abundance of fish species and Lake Nyamithi has numerous suitable basking sites (Pooley 1982, Calverley 2013, Calverley and Downs 2014a,b).

The landscape physiognomy of the two systems might also partially explain our observed patterns of crocodile distribution (Calverley 2013, Calverley and Downs 2014a,b).The Usuthu system has far fewer potential habitat patches (2) that are far apart in the form of Lake Banzi and Shokwe Pan, while the Phongola system has at least 8 pans that are in close proximity to one another (Calverley 2013, Calverley and Downs 2014b). Successful movement between habitat patches is also determined by the landscape through which an animal must travel, however, and the extent to which a landscape promotes or inhibits movement between resource patches can vary (Taylor 1993, Tischendorf and Fahrig 2000). From a physiognomy perspective, the Usuthu system has poorer connectivity because of the greater distances between the habitat patches found within it, which might result in underutilization of suitable habitat and lower population densities in outlying patches (Calverley 2013, Calverley and Downs 2014a,b). On a biophysical level, the Usuthu River has poorer connectivity due to anthropogenic disturbances along its northern bank and low water levels during winter reducing its quality as a corridor (Henein and Merriam 1990). On the other hand, the Phongola river is deeper with numerous pools, and has a mandatory winter flow rate controlled by the Pongolapoort/Jozini Dam (Heath and Plater 2010). Until recently, the Phongola system also received better protection from anthropogenic disturbances along both banks (Calverley 2013, Calverley and Downs 2014a,b).

Landscape connectivity appears to influence the movement of crocodile between and within the two river systems (Taylor 1993, Calverley 2013, Calverley and Downs 2014b). Our data showed that the proportion of crocodiles between the Usuthu and Phongola systems has stayed the same over the last 50 years despite the physical distribution of crocodiles within each system changing. This pattern supports the contention by M.C. Ward (personal communication) that the population of Nile Crocodiles in the Phongola floodplain tends to fluctuate with the Lake Nyamithi population while the Usuthu-Lake Banzi-Shokwe populations tend to interchange between sub-regions. The recent divergence of the main course of the Usuthu River through Lake Banzi (R. Wadeson, personal communication), however, might serve to increase connectivity not only within the Usuthu system but between the two systems as well. The new course of the Usuthu is characterized by a faster flow rate and numerous vegetative obstructions in the main channel (R. Wadeson, personal communication). An improvement in biophysical connectivity that can be navigated on a large scale by Nile Crocodiles might only be achieved after the channel stabilizes. Such an improvement could support a greater proportion of crocodiles in the Usuthu River system in the future (Calverley 2013, Calverley and Downs 2014b).

The unusually high density of Nile Crocodiles counted in Lake Nyamithi during 2009 might be attributed to inaccuracy associated with fixed wing surveys in the NGR (Pooley 1982, Calverley 2013, Calverley and Downs 2014a,b). This factor along with the fact that crocodiles were more visible, and therefore easier to count, on the banks of Lake Nyamithi, might have skewed the results of the aerial survey in 2009. Alternatively, the removal of the NGR eastern boundary fence in May 2008 has resulted in unprecedented human access and disturbance to areas of the Phongola river floodplain within the NGR (Calverley 2013, Calverley and Downs 2014a,b). Increased levels of disturbance in this previously secluded area of the reserve may be forcing increased numbers of crocodiles to favour Lake Nyamithi over the floodplain, hence contributing to the results of the 2009 survey (Calverley 2013, Calverley and Downs 2014a,b).

7.2.6 The Rio Maputo floodplain

More Nile Crocodiles were counted in the NGR during the dry season than during the wet season. Aerial surveys conducted in the Rio Maputo floodplain indicate that movement out of the reserve starts in November, before water levels start to rise (Pooley 1982, Calverley

2013, Calverley and Downs 2014a,b). Diurnal counts at Lake Nyamithi and telemetry studies (Calverley 2013, Calverley and Downs 2014a,b, 2015a) validate this and suggest movement back within the reserve boundary takes place during April/May. The majority of Nile Crocodiles in the Rio Maputo floodplain are concentrated between the outlet of Lake Pandejene (10 km downstream from the NGR) and Salamanga (an additional 90 km downstream). Lake Pandejene in particular is a fish-rich lake (Kramer, 2003). Crocodile numbers gradually diminish downstream of the lake, likely because salt water intrusion can occur as far inland as Salamanga. From the outlet of Lake Pandejene to Salamanga, the Rio Maputo flows through a slight valley with hills on both sides and steep river banks (Kramer 2003). This area potentially provides suitable nesting habitat (located above the high water mark) for Nile Crocodiles during the summer months. More than likely, an interplay between high concentrations of prey in the Rio Maputo and the proximity of suitable nesting habitat explains the observed pattern of crocodiles leaving the NGR during the summer months. The seasonal changes in water levels (flood waters in summer followed by increasing tidal influence during lower water levels in the winter) would facilitate the movements of crocodiles downstream from, and back into, the NGR (Campbell et al. 2010, Calverley 2013, Calverley and Downs 2014b).

7.2.7 Telemetry

High rates of transmitter loss and detachment in crocodilians have been attributed to intra-specific social interactions, particularly during the breeding season (Strauss et al. 2008). In NGR courtship takes place from early August and into September (Pooley 1982, Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). During this period the majority of transmitters on Nile crocodiles in NGR were dislodged suggesting that courtship and possible mate competition behaviour were the primary cause of attachment failure. Despite larger crocodiles having more pronounced nuchal scutes which form a better attachment location (Franklin et al. 2009), attachment period was negatively related to TL. Although Strauss et al. (2008) postulated that UV exposure may compromise cable tie strength, we found that the reason for dislodgment was the inadequacy of the nuchal scutes as an attachment site. We are in agreement with Strauss et al. (2008) that further attachment methods be investigated such as bone pins into the osteoderms, a better adhesive, or subcutaneous attachment (Kay 2004a, Franklin et al. 2009, Calverley 2013, Calverley and Downs 2015a).

7.2.8 Movement patterns – within seasons

Movement patterns of crocodilians generally constrict during the dry season (Hocutt et al. 1992, Campos et al. 2006, Thomas et al. 2010, Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). Radio transmitters fitted to Nile crocodiles in NGR showed that dry season movements for individuals ≤ 202 cm TL were mostly restricted to Lake Nyamithi. Larger individuals spent the majority of their time within the lake but made extensive forays into the floodplain returning to Lake Nyamithi thereafter. Extensive movements during winter is unusual in crocodiles (Hutton 1989, Hocutt et al. 1992). Lake Nyamithi is well stocked with fish (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b) and crocodiles feed less in winter (Games 1990, Wallace and Leslie 2008) so it is unlikely that movement out of the lake is due to foraging behaviour. Furthermore the lake provides excellent basking habitat (Pooley 1982) with aggregations of up to and exceeding 100 animals in a single locality observed (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). The extensive and repeated movement out of the lake comes at a high energetic cost during winter when ectotherms normally try to conserve energy through behavioural thermoregulation (Downs et al. 2008). Cyclic movement out of Lake Nyamithi did not coincide with the breeding or nesting season so it is unlikely that reproduction is playing a role in these movement patterns. One possible explanation could be rising salinity levels in Lake Nyamithi during the dry season. In summer salinity levels range from 200-900 ppm (parts per million) in a gradient running from the outlet in the east to the inlet in the west (Forbes and Demetriades 2006). However, during winter evaporation exceeds precipitation and combined with intrusion of saline water through ground seepage salinity levels rise to anything from 5,630 ppm in the middle of the lake to 11,290 ppm at the inlet (sea water is 35,000 ppm) (Heeg and Breen 1982). Although Nile crocodiles are considerably more euryhaline than previously thought, periodic access to fresh water is considered essential for survival in saline conditions and osmoregulation is often achieved behaviourally through selection of fresh water habitats (Leslie and Spotila 2000, Combrink 2014). Movement out of Lake Nyamithi and into the fresh water of the Phongola and Usuthu River channels could be a behavioural osmoregulatory response (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b).

7.2.9 Movement patterns – between seasons

Seasonal changes in habitat use of crocodiles is common and often results in seasonal changes in movement patterns (Modha 1967, Pooley 1982, Hutton 1989, Leslie 1997, Swanepoel 1999, Botha 2005, Champion 2011, Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). In winter or during the dry season movements are mostly nocturnal and are focused around basking sites (Hutton 1989). In summer movements are diurnal and are often related to foraging activities. Transmitters did not stay attached or transmit during both the wet and the dry season making it difficult to discuss seasonal changes in movement patterns in NGR. However, following monthly changes in abundance of Nile crocodiles in Lake Nyamithi have shown that numbers drop from a peak of around 400 in July to 60 in November and that numbers only start to increase again in April (Calverley 2013, Calverley and Downs 2014a,b, 2015a). Nile Crocodiles therefore move out of Lake Nyamithi during the wet season and return in the dry season. Total population estimates for the entire reserve over November have shown an absolute abundance of 377 Nile crocodiles in the reserve while the winter estimate is close to 850 (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b) suggesting that this movement is not only out of Nyamithi but out of the reserve as well. A survey of the Rio Maputo in mid-November 2010 showed and absolute abundance of 242 (Fergusson 2010) while a survey conducted by in NGR in early November 2011 yielded only 28 crocodiles over this same area. It is likely that movement out of the reserve and into the Rio Maputo takes place from early November onwards. Some of the crocodiles counted by Fergusson (2010) were as far as 90 km from the reserve and constitute a significant movement which would be the furthest recorded for the species if they originated from the reserve. There is however no direct evidence that this is the case and further telemetric studies would be necessary to quantify the extent of movement between NGR and the Rio Maputo floodplain (Calverley 2013, Calverley and Downs 2015a).

Large-scale seasonal movement or migrations in reptiles are uncommon and are usually attributed to a return to thermal refugia and/or breeding sites as well as seasonal changes in prey availability (Madsen and Shine 1996, Calverley 2013, Calverley and Downs 2015a). Generally crocodilians do not display migratory behaviour although the Nile crocodile may be the exception (Russell et al. 2005) with recent studies showing that both Nile Crocodile and *C. porosus* have homing capabilities (Combrink 2014). Swanepoel (1999) found that Nile crocodiles in KNP move up to 36 km between South Africa and Mozambique on a seasonal basis. Pooley (1982) noted similar movement patterns in NGR where the majority of Nile crocodiles moved between the reserve and the Rio Maputo floodplain in Mozambique on a seasonal basis presumably for nesting purposes. Nile crocodiles are known to return to historical nesting sites which could induce a seasonal migration as suggested by Pooley (Combrink 2014). The movement of Nile crocodiles into NGR from the Rio Maputo floodplain during winter could therefore be for thermoregulatory reasons while the movement out of NGR during the wet season could be related to foraging or nesting requirements since mating takes place within the reserve. However, male and female crocodiles leave the reserve over the wet season indicating that something other than the presence of favourable nesting habitat is triggering movement into the Rio Maputo floodplain. Furthermore, nesting surveys carried out in NGR (Calverley 2013, Calverley and Downs 2014a,b, 2015a) indicated that suitable nesting habitat was not in short supply within NGR and the abundance of juvenile and sub-adult crocodiles in Lake Nyamithi suggest a degree of localized nesting does occur within the reserve (Calverley 2013, Calverley and Downs 2015a).

Crocodiles are highly adept at exploiting ephemeral prey resources such as concentrations of fish (Webb et al. 1982, Calverley 2013, Calverley and Downs 2015a) and where such prey concentrations occur seasonally, large-scale seasonal movement or migration of crocodiles could be expected. Furthermore, crocodiles feed more in summer than winter (Wallace and Leslie 2008) and movement patterns in response to prey densities would more likely take place in summer. There is also evidence that Nile crocodiles undertake large-scale seasonal movements in response to spatial and temporal changes in prey abundance (Leslie 1997). Leslie (1997) suggested that Nile crocodile movement patterns in Lake St Lucia follow the migration patterns of Striped Mullet which do in fact move up the Rio Maputo during summer floods and have been found in pans as high up the river system as Lake Nyamithi (Kyle 2002). In either case moving below the confluence of the Usuthu and Phongola rivers fish concentrations would be concentrated in the comparatively narrow Rio Maputo channel before they enter the extensive floodplain system within NGR (Calverley 2013, Calverley and Downs 2015a).

Crocodiles need to bask for longer durations in winter than in summer (Kofron 1993, Calverley 2013, Calverley and Downs 2015a). Nile crocodiles move from the Rio Maputo floodplain and into NGR to take advantage of undisturbed basking sites such as Lake Nyamithi (Pooley 1982). Densities in Lake Nyamithi peak in June/July which correlates with the coldest time of the year and then drop sharply after mating has taken place in August. Movement from the Rio Maputo into NGR and Lake Nyamithi in particular may be to access undisturbed basking and breeding sites (Calverley 2013, Calverley and Downs 2015a).

7.2.10 Home range

Similar to Hutton's study on Nile Crocodile (Hutton 1989b) and other studies on saltwater crocodiles (Kay 2004b, Brien et al. 2008) no differences in home range between male and females during the dry season were found (Calverley 2013, Calverley and Downs 2015a). Thermal constraints often render ectotherms like crocodiles inactive for colder periods of the year confining them to thermal refugia where they avoid periods of low resource availability (Madsen and Shine 1996). Since both males and females will be equally influenced by thermal constraints it is not surprising that home ranges do not differ during the dry/cool season. Home range of individuals within such thermal refugia would be expected to contract (Webb et al. 1982) and most studies on home range show smaller home ranges during the cool/dry season (Hutton 1989, Kay 2004b, Brien et al. 2008). However, home ranges for Nile crocodiles in NGR during the dry season where larger than those calculated by Hutton during the wet and dry season despite Lake Ngezi having a surface area 3.5 times the magnitude of Lake Nyamithi. This could be due to the topography of the study site (Brien et al. 2008) and the high degree of connectivity in the Phongola floodplain (Calverley 2013) allowing crocodiles to move freely throughout the reserve and the fact that Lake Ngezi is a closed system (Calverley 2013, Calverley and Downs 2015a).

In contrast to Hutton (1989) we found that home range increased with size (TL) and that adult Nile crocodiles (> 2.5 m TL) occupied larger total home ranges than sub adult crocodiles (< 2.5 m TL) (Calverley 2013, Calverley and Downs 2015a). Core areas where sub-adults spent 50% of their time made up a small percentage of their total home range indicating highly localized use of home ranges. Adult Nile crocodiles made use of larger home ranges with core areas constituting a larger percentage of total home range size, indicating more expansive use of home range areas. Generally, sub-adult Nile crocodiles were confined to Lake Nyamithi, while adults ranged widely throughout the Phongola floodplain making use of riverine and lacustrine habitat. The ability and inclination for crocodiles to move long distances between habitat patches is influenced by life history parameters such as size and sex as well as social interactions and predation threats. In Lake Nyamithi sub-adult crocodiles were confined to the shallow inlets of the lake. Both Botha (2005) and Champion (2011) noted changes in the habitat use of Nile crocodile in artificial water impoundments (Calverley 2013, Calverley and Downs 2015a).

Only one of the telemetered Nile crocodiles captured in the Phongola system ventured into the Usuthu River system or Banzi Pan (Calverley 2013, Calverley and Downs 2015a). This validates Ward's (1989) observation that populations within these two systems remain relatively independent of one another. Interestingly the individual in question was located in the new course of the Usuthu after it exits Banzi Pan and may signal greater mixing between the Usuthu and Phongola river populations in the future due to the recent divergence of the Usuthu (Calverley 2013, Calverley and Downs 2015a).

7.2.11 Territoriality

Territorial behaviour has been observed by Nile crocodile in numerous studies (Modha 1967, Pooley and Gans 1976, Garrick and Lang 1977, Swanepoel 1999, Champion 2011, Calverley 2013, Calverley and Downs 2015a, Combrink 2014). However, territoriality as a component of crocodilian movement ecology is becoming increasingly questionable (e.g. Kay 2004b, Brien et al. 2008, Combrink 2014). By comparing the degree of home range overlap territoriality can be investigated. For example Kay (2004b) and Brien et al. (2008) found that home ranges of large male *C. porosus* overlapped extensively, concluding that territoriality was not displayed in their respective study areas contrary to popular belief (Calverley 2013, Calverley and Downs 2015a).

Some studies suggest that if territorial behaviour is displayed by Nile crocodiles, it may be suspended facilitating large-scale movement or migrations at certain times of the year (Swanepoel 1999) as well as aggregations around basking sites during the non-breeding season and at areas of high prey density (Lang 1987) (Calverley 2013, Calverley and Downs 2015a). At NGR home range of Nile crocodiles overlapped extensively during the dry season indicating a lack of territoriality. However, territorial displays or conflicts necessitate that individuals be in close proximity to one another and may be of very short duration (Garrick and Lang 1977). Using the extent of which home ranges overlap as an indication of territoriality may therefore not be a suitable method (Calverley 2013, Calverley and Downs 2015a).

7.2.12 Location of nesting sites

In the past the majority of Nile Crocodile nesting sites in NGR were found on the banks of the main course of the Phongola river (Pooley 1982, Calverley 2013, Calverley and Downs 2015b). The diversion of the main course further east in 2002 has resulted in these historical nesting sites no longer being used. However, crocodile nests have not been found along the new course of the Phongola river and historical nesting sites in this area have been abandoned due to increased anthropogenic disturbance and habitat transformation (Calverley 2013; Calverley and Downs, 2014a,b). All nesting sites were found along the western periphery of the Phongola and Usuthu Floodplains pointing strongly to the deleterious influence the current disturbance in the eastern part of the reserve is having on crocodile nesting activities. The source-sink dynamics implies that conservation of some habitat patches may be more important to the long-term survival of the population as for other crocodilians (Da Silveira and Thorbjarnarson 1999, Platt and Thorbjarnarson 2000, Calverley 2013, Calverley and Downs 2015b).

7.2.13 Nesting effort

Generally, the number of nests in a given area is a function of population size (Graham, 1987) as well as habitat suitability, as defined by nesting requirements of Nile Crocodile (Modha 1967, Pooley 1969, Calverley 2013, Calverley and Downs 2015b). Historical records suggest that the nesting effort of Nile Crocodile in NGR was low considering the population size (Pooley 1969, Ward 1990). That is to say a disproportionately small number of mature breeding females are nesting within the reserve. Low nesting effort (E) in areas of relatively high crocodile density could be an indication of unfavourable nesting habitat (Swanepoel et al. 2000) or excessive disturbance within suitable nesting habitats (Pooley 1982). However, in the past population estimates (N) have been carried out in winter/low water months when Nile Crocodile are most visible while nesting surveys take place in summer months during the peak of the nesting season. In open systems such as NGR crocodile are free to move out of the study area and often do so on a seasonal basis (Pooley 1982). As such in open systems N within a particular study site may vary, particularly between seasons and E can only be accurately calculated using N during summer (Ns). In NGR, E calculated using Ns was higher at 18-22% than E calculated using winter (Nw) at 5-6% (Calverley 2013, Calverley and Downs 2015b). We consider E calculated using Ns to be the true nesting effort of NGR as this describes the percentage of the population of crocodile residing in the reserve during summer that are nesting in the reserve. This has important implications for the calculation of E in other areas where seasonal changes in population size may occur (Calverley 2013, Calverley and Downs 2015b).

While nesting effort in NGR is comparable with other Southern African Nile Crocodile populations such as the Okavango Delta and Lake St Lucia (Leslie, 1997) it is still considerably lower than has been reported in other populations of Nile Crocodile (Bourquin, 2008, Calverley 2013, Calverley and Downs 2015b). Anthropogenic disturbance resulted in the abandonment of at least two historical Nile Crocodile nest sites in NGR and directly resulted in a decrease in nesting effort during the study period. However, unless suitable nesting habitat is severely limited we would expect crocodile to 'make the best of a bad situation' and nest elsewhere in the reserve in the future (Somaweera and Shine 2012b). By far the greatest influence on E within NGR was the number of crocodile leaving the reserve during summer and over the nesting season. The population of crocodile in NGR has tripled since the 1960s but the number of nests found within the reserve has stayed the same. This suggests that the reserve is at capacity with regards to the availability of suitable nesting habitat or at least the accessibility of suitable nesting habitat in relation to other essential resources required by Nile Crocodile over the nesting season (Calverley 2013, Calverley and Downs 2015b).

7.2.14 Availability of suitable nesting habitat in NGR and the spatial clumping of nests

When examining suitable habitat available for crocodile to nest in, it is important to differentiate between that which constitutes a nest and that which constitutes a nest site (Calverley 2013, Calverley and Downs 2015b). Nest sites may contain more than one nest and are often used repeatedly over many seasons/years and by different females (Pooley 1982, Swanepoel et al. 2000). The substrate, slope and vegetation communities are generally the same within a particular nesting site but can vary between different nesting sites as was found in this study. While nests within a nest site may be less than 1 m or more than 100 m apart, nest sites are often separated by many kilometres (Pooley 1982, Swanepoel et al. 2000). As such nests often appear to be clumped in distribution as they are normally found in closer proximity to one another within a nest site then nest sites are to one another. Clumping of nests is often attributed to a scarcity of suitable nesting habitat forcing crocodile to nest in what suitable nest habitat there is (Pooley 1982, Blake and Loveridge 1987, Somaweera et al. 2011). Nile Crocodile nests were clumped in distribution in NGR and several causal factors may behind this phenomenon including availability of prey items, topography, nursery habitat and the availability of fresh water and burrows which need further investigation (Calverley 2013, Calverley and Downs 2015b).

7.2.15 Historical nesting

In NGR numerous nesting sites found in 2009-2012 were previously recorded as nesting sites as early as 1964 (Calverley 2013, Calverley and Downs 2015b). Nile Crocodile are known to re-use historical nesting sites (Graham 1968, Pooley 1969, Combrink 2004, Combrink et al., 2011, 2013, in prep. f,g) and in some instances the female may show strong nest site fidelity using the same site over and over again (Pooley and Gans 1976). However it is unlikely that all the nesting sites discovered in 1964 and re-examined in 2010 and 2012 are being used by the same females today as it is likely that some of the females would be too old to still be breeding or may have died in the interim. It is unlikely that terrestrial nesting parameters are so strict, static, limiting and perceivable to crocodile from the water that the exact same nesting sites should be chosen over 40 years later based purely on the characteristics of the nesting site (i.e. slope, substrate, shading, distance to water etc.). This is particularly true in the continued use of a nest site that contains only one or two nests. However, the continual use of specific nesting sites over long periods of time by reptiles could also be explained through cultural or genetic inheritance of nest site locations or natal homing (Brown and Shine 2007, Calverley 2013, Calverley and Downs 2015b).

7.2.16 Nesting outside of Ndumo

The Phongola river enters NGR through a densely populated area on the western boundary where much of the natural vegetation has been cleared for cultivation and continual disturbance by people and livestock does not provide suitable nesting conditions (Pooley

1969, Calverley 2013, Calverley and Downs 2015b). No Nile Crocodile nests were found nor could the local inhabitants remember nesting incidences along this stretch of the river (Pooley, 1969). Disturbance and agricultural activities within this area are more intense today than they were 50 years ago in Pooley's time (P. Dutton pers. comm.). Similarly we found no Nile Crocodile nests outside of NGR in the Phongola floodplain for the duration of the current study despite extensive boat surveys. The Usuthu River as it enters NGR is similarly plagued by anthropogenic disturbances and there are no records of crocodile nesting here from the 1960s to the present, presumably for similar reasons as those of the Phongola floodplain outside of the reserve (Calverley 2013, Calverley and Downs 2015b).

The Maputo River stems from the confluence of the Phongola and Usuthu Rivers in the north eastern corner of NGR, very soon thereafter flowing northwards out of the reserve (and South Africa) into Mozambique (Calverley 2013, Calverley and Downs 2015b). Previously with the onset of the laying period, the majority of Nile Crocodile of reproductive size leave NGR and enter Mozambique via the Maputo River (Pooley 1969, Calverley 2013, Calverley and Downs 2015b).To conserve the current population of Nile Crocodile in NGR, the nesting ecology of the Nile Crocodile outside of the reserve needs to be investigated and the conservation status of adjacent wetlands in Mozambique highlighted (Calverley 2013, Calverley and Downs 2015b).

7.2.17 Human wildlife conflict

In May 2008, the eastern boundary fence of the NGR was forcibly removed by the neighbouring Mbangweni community (including individuals having filial links to those evicted when the reserve was established in 1947), allowing unprecedented access to the Phongola river and floodplain (Meer 2010, Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). Since then, agricultural activities and resource use in the form of fishing, and reed and wood harvesting take place within the reserve throughout the eastern floodplain from the Phongola river to the fence line (Meer 2010). Poaching activities in the form of snaring and gill netting also take place in this part of the reserve (Calverley 2013, Calverley and Downs 2014a,b).These activities impact on Nile Crocodiles with changes in habitat availability and quality. Increased levels of anthropogenic disturbance in this previously secluded area of the reserve may have a significant influence on the future of the Nile Crocodile population (Calverley 2013, Calverley and Downs 2014a,b, 2015b).

The NGR is home to South Africa's third largest Nile Crocodile (Calverley 2013, Calverley and Downs 2014a,b, 2015a,b). Any future decline in this population might not only be attributed to natural causes, but also because of human persecution, including snaring. We feel it likely that many smaller individuals were snared, and a percentage of larger animals were not able to escape the snares; our methods would have failed to detect both groups of individuals. Management of water releases from the upstream impoundments is also likely to be important, as these events affect numbers and distribution of crocodiles in the NGR. Additionally, viable and historic crocodile nesting habitat within the NGR is being destroyed and is unavailable to crocodiles as illegal resource use and agriculture is taking place within the reserve (Meer 2010, Calverley 2013, Calverley and Downs 2014a,b 2015a,b). The complex relationship between the reserve and the neighbouring community in the Mbangweni Corridor has meant that conservation in the NGR has become an increasingly contested and contentious issue (Meer 2010, Calverley 2013, Calverley and Downs 2014a,b 2015a,b).

7.3 PONGOLAPOORT DAM

7.3.1 Population estimate

No surveys had been conducted to assess the Nile Crocodile population size in Pongolapoort Dam as a whole prior to this study (Champion 2011, Champion and Downs in prep. a,b,c). In prior years portions of the dam (pre and post its establishment) were included in provincial large-scale surveys as Pongolapoort Dam fell over two provincial borders, the former Transvaal (now Mpumalanga) accounted for the northern half of the dam and former Natal (now KZN) which accounted for the southern half (Jacobsen 1991). As the dam crossed provincial boundaries, it also fell under two associated conservation agencies (former Transvaal Conservation Agency and Natal Parks Board) and therefore data on such provincial surveys only included a fraction of the dam on any one survey (D. K. Blake pers. comm.). No official records of crocodile numbers in the southern section (former Natal side) exist as the area was considered to only contain a low number of individual crocodiles, not seen as a self-sustaining viable population (D. K. Blake pers. comm., Champion 2011, Champion and Downs in prep. a,b,c). Former reports on survey results done by Jacobsen (1991) of the upper Phongola river (from Commondale to Pongolapoort Dam) and including the northern dam sections show considerably low numbers of crocodiles. Jacobsen (1991) did an aerial survey of 193 km along the Phongola river in 1981 and in 1989 where he recorded a total of 11 (0.06 per km) and 16 (0.08 per km) crocodiles respectively (Champion 2011, Champion and Downs in prep. a,b,c). It must be noted that the apparent increase from 1980 to 1989 cannot, for a number of reasons, be interpreted as a true increase in crocodile population through reproductive recruitment. Firstly, the survey was done by aerial count and therefore has possibility of error (Games 1994, Ferreira and Pienaar 2011). Secondly, the dam level had changed dramatically between these two surveys (from < 13% in 1980 to 85% in 1989) (Heath and Plater 2010) which would have resulted in more areas being flooded in the northern sections of the dam, possibly allowing crocodiles residing in the dam on the southern (former Natal province) section to move into these newly available areas. Thirdly, as a result of these major increases in water levels it is unlikely that nesting areas would have survived flooding. Jacobsen (1991) described the Phongola river and Dam as generally disappointing with regards to number of crocodiles seen. Jacobsen (1991) also mentioned although his survey did not include crocodiles observed on the former Natal province side in their survey results, a number of larger crocodiles but these were also in low numbers. He also noted that the dam had created a new sanctuary for the potential establishment of a viable crocodile population (Jacobsen, 1991). During the present study the number of Nile crocodiles on the upper Phongola river above the N2 bridge was not determined. There are a number of small weirs, private dams and farming reservoirs along this upper section which may provide potential refuge for crocodiles (G. Champion pers. obs.). These numbers are, however, likely to be low and comprised of sparsely scattered individuals, not representative of a self-sustainable population (various pers. comm., Champion 2011, Champion and Downs in prep. a,b,c).

Detailed interpretation of survey results on crocodilian populations is often difficult because of the number of factors that affect the precision and accuracy of methods used and the dynamics of populations in terms of season and habitat use (Campos et al. 1995, Ferreira and Pienaar 2011, Champion 2011, Champion and Downs in prep. a,b,c). In the current study a minimum total number of Nile crocodiles was determined as a baseline for further surveys and population estimates. This was a consequence of the lack of historical data available, length of the current study and the dynamics of determining crocodile abundance. Estimates of crocodile abundance can vary significantly with time as a result of several reasons (Ferreira and Pienaar 2011, Shirley et al. 2012) highlighting the importance of on-going surveys and the determination of correction factors for improved precision and accuracy of estimates. Although the use of standard correction factors for the various survey techniques used to determine crocodile population estimates, it is now understood that each environment and associated population needs its own correction factors calculated (Combrink 2014 The use of a standard correction factor derived from a separate survey site may lead to greatly biased estimates (Ferreira and Pienaar 2011). There has been a significant increase in the number of Nile crocodiles in Pongolapoort Dam currently compared with the aerial survey results of 1980 (11 crocodiles) and 1989 (16 crocodiles) of the entire upper Phongola river (193 km) including the northern section Pongolapoort Dam (Champion 2011, Champion and Downs in prep. a,b,c). In comparison in 2009, 134 crocodiles (94 recorded in the northern section) were observed in an aerial survey of

Pongolapoort Dam alone. The presence of a range of size classes from 50cm to 4.6 m observed during this 2009/2010 study suggests a healthy population structure. Identification of over 30 nesting sites) during the 2009/2010 further supports the current presence of a viable Nile crocodile population in Pongolapoort Dam (Champion 2011, Champion and Downs in prep. a,b,c).

Other impoundments previously identified to have viable Nile Crocodile populations in South Africa, include Loskop Dam and Flag Boshielo Dam (Jacobsen 1991, Champion 2011, Champion and Downs in prep. a,b,c). Both of these impoundments are located on the Olifants River, a river system that contains the highest number of Nile crocodiles in the country (Ashton 2010). Both of these populations of Nile crocodiles found in these impoundments have been studied, with focus on population trends, movement dynamics and reproductive output (Botha 2005, Botha et al. 2011, Champion 2011, Champion and Downs in prep. a,b,c). Botha's (2005) study of Flag Boshielo Dam Nile Crocodiles showed a viable population (> 210 individuals), with a similar population structure to the current Pongolapoort Dam population structure with a high percentage of juveniles and sub-adults (> 50%). The reproductive effort of the Flag Boshielo population was low in comparison to other South African populations, with 5.3 mean annual nests found in the system (13% reproductive effort). Loskop Dam had an estimated Nile Crocodile population of 32 individuals in 1979 (Botha et al. 2011). Concerns of the decline of crocodile numbers in Loskop Dam were raised in the 1980s (Jacobsen 1984). Spotlight counts in 2010 estimated that only 4 crocodiles remained in the dam (Botha et al. 2011). Two hypotheses have been given for the notable decline of the Loskop Nile crocodile population (Botha et al. 2011). The first suggested that crocodiles were dying as a result of pollution entering the upper catchment area, directly effecting crocodile health as well as poisoning food resources (Ashton 2010, Botha et al. 2011). The second suggested habitat alteration, as a result of raising the dam wall, inundated historically important nesting areas and reducing recruitment (Botha et al. 2011). The inundation of basking sites was also suggested to have possibly decreased the general suitability of the dam for crocodiles and may have also have resulted in individuals moving out of the dam and into the river system (Botha et al. 2011). The current situation in both Loskop and Flag Boshielo Dams is of great concern, with surveys showing continued decreases in population size and reproductive output (Ashton 2010, Botha et al. 2011). The combination of continued environmental stress and contaminant build up in the aquatic food web, resulting in the decline of crocodile numbers in these two impoundments, appears to be a commonality across all populations found in the Olifants drainage system (Jacobsen 1984, Ashton 2010, van Vuuren 2010, Botha et al. 2011, Ferreira and Pienaar 2011). The trends seen in Nile crocodile populations in these impoundments along the Olifants River underlines the lack of protection our aquatic habitats have and further highlights the importance of conserving Nile Crocodile Populations which appear to be in less threatened or degraded environments, such as Pongolapoort Dam (Champion 2011, Champion and Downs in prep. a,b,c).

The preliminary data on sex ratios of Nile Crocodiles of 0.88 females to males in Pongolapoort Dam is not representative of the entire population sex ratio. (Champion 2011, Champion and Downs in prep. a,b,c). Sample size was inadequate as a result of difficulties in catching adult crocodiles, and the need for physical examination for sex determination. There is also a gender bias in one catching technique used with baited spring-traps often favouring large male crocodiles (M. Robertson pers. comm.). Similarly at Pongolapoort Dam all crocodiles caught using baited traps were male, 27% of total number of animals caught. It is therefore suggested that future studies should focus on determining more accurate sex ratios by significantly increasing sample size and thereby reducing any bias effect. Studies with significant sample sizes for sex ratios of other nearby populations of Nile crocodile in St. Lucia Estuary and NGR have shown a very near 1:1 ratio of males to females (Champion 2011, Champion and Downs in prep. a,b,c, Calverley 2013, 2014a, Combrink 2014).

7.3.2 Habitat use

There have been major changes in the last half century in the region now covered by the Pongolapoort Dam (Champion 2011, Champion and Downs in prep. a,b,c). These changes in ecosystem structure and habitat mosaic have resultantly effected the Nile Crocodile population of the area. Prior to the impoundment of the Phongola river, the river was mostly shallow and swift flowing with only occasional seasonal pools, having relatively few crocodiles (Jacobsen, 1991). The gorge or “poort” section, site selected for the construction of the dam wall, contained most of the adult crocodiles which resided in the deeper perennial pools (K. Landman pers. comm.) (Champion 2011, Champion and Downs in prep. a,b,c).

The construction of the Pongolapoort Dam wall resulted in a high disturbance level in this previously isolated and undisturbed gorge (van Vuuren 2009, Champion 2011, Champion and Downs in prep. a,b,c). Once the dam wall construction was completed in 1972, any Nile Crocodiles upstream of the wall would have been isolated from the lower, substantial Nile Crocodile population found in NGR (Calverley and Downs 2014a,b). The wall also significantly changed the river ecosystem by modifying hydrology, morphology and habitat structure as in other impoundments (Zhai et al. 2010). Similarly the impoundment of the Phongola river altered the physical characteristics of the habitats, including continuity, flow distribution organic matter and water temperature as in other impoundments (Zhai et al. 2010). This would have altered the bio-ecological processes of the system further effecting resident animal populations (Heath and Plater 2010), such as the Nile crocodile population.

For example these habitat changes, particularly changing water levels, would result in resource changes that may affect the ecology of Nile Crocodiles, including reproduction. Nile crocodile populations have been shown to establish specific nesting areas, reusing these areas for consecutive years (Pooley 1969, Kofron 1989, Hartley,1990). Fluctuating water levels may result in reproductive failure, either as a result of low water levels, increasing distance from nest to water line decreasing the survivability of nests or as a result of high water levels, flooding nests (Pooley 1969, Botha et al. 2011, Champion 2011, Champion and Downs in prep. a,b,c).

The second and most extreme major habitat disturbance experienced by the Nile crocodiles in the system after the dam construction was a result of Cyclone Domoina (Rossouw 1985, (Champion 2011, Champion and Downs in prep. a,b,c). The rapid landscape remodelling would have affected resident crocodiles with changing dynamics and increased habitat availability with changing resource distribution and density. This would have once again have changed available basking sites and potential nesting sites (Jacobsen, 1991). Jacobsen (1991), during surveys of the upper Phongola river in 1981 and 1989, described the upper Phongola river as generally disappointing with regards to Nile crocodile numbers but mentioned that the impoundment and resultant flooding of surrounding areas post-Domoina, appeared to create a favourable habitat for the establishment of a viable crocodile population (Champion 2011, Champion and Downs in prep. a,b,c).

In 1993 the Pongolapoort Dam level was at 30% because of drought (Champion 2011, Champion and Downs in prep. a,b,c). The large drop in water level would have resulted in a substantial retraction of water line, exposing previously submerged ground, which would almost definitely resulted in changes in shoreline dynamics with regard to crocodile food resources, basking site availability and possibly distribution of favourable habitat types. This would also have disturbed the reproductive ecology of the resident Nile crocodiles, with any previously used nesting areas prior to the drought being a great distance from the water (Champion 2011, Champion and Downs in prep. a,b,c).

Since 1995 the water management policy of the Pongolapoort Dam has attempted to ensure minimal unplanned flood damage to areas below the Pongolapoort Dam, maintaining dam levels around 75% capacity (Heard and Whitley 2009, Champion 2011, Champion and Downs in prep. a,b,c). In order to simulate natural seasonal flooding, which drive numerous ecological processes in the lower Phongola flood plain, there is an annual controlled mass release of water from the Pongolapoort Dam each September (Dickens et al*.* 2008). This release results in an approximate 2 m drop in water level. This pre-rain season release ensures that the effects of summer floods on areas below the dam can be controlled or at least reduced (Dickens et al. 2008). The current water management plan of Pongolapoort

Dam results in a more predictable and less extreme fluctuation of seasonal water level than experienced in the earlier years after dam construction. This management plan has, however, no control on water inlet, with river flow rate and water volume entering the dam determined by rainfall in the above catchment area of the upper Phongola river. This therefore results in this area still being susceptible to natural flood disturbances, which continue to alter and change the inlet section. As this area is used extensively by the Nile Crocodiles in Pongolapoort Dam, notably for breeding, the natural environmental disturbances still have a significant effect on their population dynamics (Champion 2011, Champion and Downs in prep. a,b,c).

A further environmental change was a result of the introduction of an alien invasive aquatic weed, *H. verticillata* in Pongolapoort Dam (Champion 2011, Champion and Downs in prep. a,b,c). This was the first water body in South Africa where this submersed macrophyte was identified (Madeira et al. 2007). First identified in February 2006, it has since become a dominant species along the inlet section and western shoreline of the main dam. Although the weed has been shown to have the potential for economic and environmental damage, there is little evidence of it showing major environmental problems in Pongolapoort Dam as of yet (Madeira et al. 2007). The weed has created thick mats near the shoreline, which become impenetrable by motor boats, clogging up their propellers (Champion pers. obs.). The weed appears to be favoured by many fish species as a protective nursery (C. Rippon pers. comm.). The seasonal changes in water level prevent the weed from maintaining mats near the water's edge (Champion 2011, Champion and Downs in prep. a,b,c).

The adaptability of the Nile Crocodile as a species is shown in the way the population of Pongolapoort Dam, has not only survived through large-scale environmental disturbances and habitat alterations but the population has expanded and formed one of South Africa's significant populations both in size and reproductive success (Champion 2011, Champion and Downs in prep. a,b,c). The high frequency of natural disturbances in riverine ecosystems has likely aided in the adaptability of the aquatic biota in larger scale, anthropogenic caused habitat alterations. Although Pongolapoort Dam levels fluctuated greatly within and between years, the Nile Crocodiles appear to adjust to these changes and successfully persist here (Champion 2011, Champion and Downs in prep. a,b,c).

Fluctuation in water levels causes dynamic changes in the shoreline vegetation species and structure (Peintinger et al. 2007), and shoreline topography (Champion 2011, Champion and Downs in prep. a,b,c). The general distributional pattern of the Nile Crocodiles in Pongolapoort Dam appeared to be driven by two key factors. Firstly, a rank of their ecological objectives was a key factor which changed temporally. These included mating, nesting, feeding, survival or basking. The ranking of these objectives were dynamic, changing as certain objectives become more important and others less. These ecological objectives affected not only distribution but the density at which crocodiles congregated (Kofron 1993). Secondly, the spatial locality of these congregations was a key factor and was determined by habitat/locality which provided for the successful completion of the respective ecological objective concerned. The ranking of ecological objectives and related responses, and consequently changing distribution and habitat use of crocodiles also appeared to differ between different size classes of crocodile (Champion 2011, Champion and Downs in prep. a,b,c). This should be expected as size classes differ greatly in diet, risk of predation, degree of inter-specific competition, or drive to reproduce (Hutton 1987, 1989, Kofron 1990, Wallace and Leslie 2008). The resultant spatial separation of size classes appears to be due to the differences in the ranking of ecological objectives and therefore a difference in perception of what defines a favourable habitat. However, the threat of cannibalism to smaller individuals may also add to the size class separation (Hutton 1989). The majority of Nile Crocodiles were concentrated in the north-west section of the dam, moving upstream and utilizing the Phongola river in summer months while residing in the inlet section during the winter months where there are historical basking sites. Movement of crocodiles upstream of inlets during months of high water appears to be a common occurrence, especially with respect to impoundment based populations (Hutton 1989, Jacobsen 1991, Jacobsen and Kleynhans 1993, Kofron 1993, Swanepoel 1999, Botha 2005, Champion 2011, Champion and Downs in prep. a,b,c).

Transmitter attachment method and resultant longevity has been a problem when studying movement dynamics of crocodilians, with similar results seen in Flag Boshielo Dam and Ndumo Game Reserve (Strauss 2008, Calverley 2013, Calverley and Downs 2014a,b). The tracking of the nine Nile Crocodiles fitted with radio transmitters did not give rise to viable home range or territory predictions at Pongolapoort Dam (Champion 2011, Champion and Downs in prep. a,b,c).

7.3.3 Mating and courtship

During this study dam water level fluctuated (68-81%) with an approximate 2 m vertical difference in water level (Champion 2011, Champion and Downs in prep. a,b,c). The observed aggregation and increase in number of Nile Crocodiles present at Buffalo Bend during the mating season was most likely due to its locality. As this basking site is the last “deep” water, after which the river upstream became shallow and did not appear to offer adequate depth as refuge to large crocodiles. Aggregations of Nile Crocodiles during the mating season have been previously documented (K. Landman pers comm.). Presence of a number of adult males at Buffalo Bend suggested no strict territorial structure, particularly during the mating season. However, the apparent dominance of a single large male suggested a hierarchical system. Smaller males present were not observed mating, however they may have done so opportunistically when the larger male was not present to assert dominance. Movement of some females upriver during night at this time is likely explained as preliminary visits to potential nest sites, as described by Blake and Loveridge (1987). Their movement upstream at night was most likely due to the darkness being perceived as a safe time to traverse the shallow river (Champion 2011, Champion and Downs in prep. a,b,c).

7.3.4 Nest site selection

Croc Bay (Fig. 2.3) appeared to be a previously well used historical Nile Crocodile nesting site, at a time when the dam level was maintained at a far higher level (1996-1998) (C. Rippon pers comm., Champion 2011, Champion and Downs in prep. a,b,c). During these years there appeared to a high number of nesting females at this site (C. Rippon pers comm.). Previously as a result of the higher water levels, the cliffs that are now present were mere ledges, allowing for more nesting sites with close proximity to the water. The disturbance level was much lower, as at high levels the nearby road was unused and game accessed water using different game trails (various pers comm.). The reason for continued use of this area during the 2009/2010 season despite its current unsuitability is unknown and may be related to inexperience or their inability to adapt to unpredictable water levels (Champion 2011, Champion and Downs in prep. a,b,c).

Location of Nile Crocodile nest sites in the inlet section of the main river entering the dam appear to escape the effect of dam level fluctuations and anthropogenic disturbance (Champion 2011, Champion and Downs in prep. a,b,c). These sites appeared to experience conditions similar to nesting sites in other river systems (Graham 1968, Pooley 1982, Leslie 1997, Swanepoel 1999, Botha 2005, Bourquin 2008). Similarly observations made during the 2009/2010 breeding season had similarities with other studies of Nile Crocodile populations in other systems, including open river systems. In particular, congregation in deep pools during the dry season where mating takes place has been documented in some studies of river-based crocodile populations (Kofron 1993, Swanepoel 1999). This can be likened to the use of Buffalo Bend as a mating area, as it was the last deep water before the river became shallow further upstream away from the dam (Champion 2011). Commencement of nesting with the onset of first summer rains has also been documented in other systems, including the major crocodile population at NGR, also on the Phongola river (Pooley 1969). Botha (2005) showed a similar preference of a dam-based Nile Crocodile population to nest in the dam inlet section rather than in the main dam body (Champion 2011, Champion and Downs in prep. a,b,c).

With regard to the great variability in Nile Crocodile nest site selection, Pooley (1969) and Hartley (1990) also recorded variation in soil substrate chosen for nesting, the distance from water, surrounding vegetation cover and distance to neighbouring nests (Champion 2011, Champion and Downs in prep. a,b,c). Pooley (1969) and Kofron (1989) also found that nest depth varied according to substrate type, with coarse river sand allowing for the deeper nests. It is unsure whether the predatory level is related to the depth at which the eggs are buried, with shallower nests possibly being more easily detected through higher levels of scent (from the egg chamber) escaping through the soil. This may explain the high predation level at the Cliff Ledge nesting site while no nests were predated at Causeway Bend. Observations of only partially covered eggs along the Cliff Ledge suggest this may be the case (Champion 2011, Champion and Downs in prep. a,b,c).

Annual recruitment of Nile Crocodiles varies as a result of environmental variability between seasons (Pooley 1969, Kofron 1989, Swanepoel et al. 2000, Champion 2011, Champion and Downs in prep. a,b,c). Total recruitment failure due to flooding is not uncommon and has been documented in a number of studies at various localities (Pooley 1969, Kofron 1989, Swanepoel et al. 2000). Noting the delay of laying in anticipation of the first rains, it is evident that drought periods affect recruitment as well. In the current study fluctuating river levels affected Nile Crocodile recruitment adversely. However, despite the apparently low recruitment in the 2009-2010 breeding season, high numbers of juvenile crocodiles, from prior seasons, were observed (Champion 2011) showing that the Nile Crocodiles were having reproductive success. From the number of nests found in 2009-2010 at Pongolapoort Dam it appears that the Nile Crocodile population has a relatively high potential reproductive out-put although their annual successes may vary greatly because of loss of nests to predation and fluctuating water levels, particularly river inlet. Thus far the population appears to have a high reproductive index of 0.76, when compared with other major crocodile populations in South Africa, such as NGR (0.2, Calverley 2013) and St. Lucia (0.3, Combrink 2014.). However, it appears that there is a paucity of suitable nesting areas with crocodiles sometimes using unsuitable cliff ledges. A further concern is the degree of alien invasive vegetation at several of the nesting areas and its potential negative impact. However with the observation of reproductive effort and high number of juveniles, preliminary assessment currently suggests a healthy population (Champion 2011, Champion and Downs in prep. a,b,c).

7.4 CROCODILE HEALTH

As top predators crocodilians are increasingly being viewed as “sentinel” species for aquatic ecosystems. However the indirect effects are much less understood than direct effects. The

KNP crisis showed that wild crocodiles in South Africa can only tolerate the indirect effects of habitat alteration to a certain extent in terms of environmental contamination. In contrast there are different ecotoxicological issues for Nile Crocodiles in KZN, in particular the concerns relate to the riverine systems in KZN. There are concerns at Lake St Lucia in particular regarding crocodile health. It is recommended that the use of lead for fishing is terminated.

Lake St Lucia, Pongola/Jozini and NGR are major strongholds in KZN for Nile Crocodiles. However, each is a different system (freshwater, estuarine, riverine). Generally numbers are low outside of major protected areas, primarily because of direct human-based threats to crocodiles and available Nile Crocodile habitat. While KZN Nile Crocodile populations are very different, direct threats to crocodile habitat are similar. Indirect threats are not as well known.

8 CONCLUSIONS

Nile Crocodiles (*Crocodylus niloticus*) occur in 42 African countries of which 22 have been scientifically assessed (Ross 1998). The majority of information on the species comes from studies conducted in southern Africa with Botswana and South Africa in particular contributing significantly to Nile Crocodile research in the past twenty years. In South Africa studies have taken place at the Flag Boshielo Dam in Mpumalanga Province (Botha 2005), the Olifants River in Kruger National Park (Swanepoel 1999, Ferreira and Pienaar 2011), Loskop Dam in Mpumalanga (Botha et al. 2011) and in KwaZulu-Natal at Lake St Lucia (Leslie 1997, Combrink, 2004, 2014, Combrink et al. 2013), Lake Sibaya (Combrink 2004, Combrink et al. 2011); NGR (Calverley 2013); and Pongolapoort Dam in KwaZulu-Natal (Champion, 2011). However, while these studies contribute greatly to our scientific understanding of the ecological requirements of Nile Crocodiles as a species, management plans by their very nature need to be site specific and tailored to the challenges facing a particular population (Leslie 1997, Champion 2011, Calverley 2013, Combrink 2014, Warner in prep.).

8.1 Lake St Lucia

Lake St Lucia estuarine system, Africa's largest estuary, contains the largest Nile Crocodile population in a single waterbody in South Africa and possibly the largest estuarine population throughout its range (Combrink 2014). Historically the estuarine-lake system harboured a large and viable crocodile population and large seasonal rivers entering the lake ensured regional connectivity with other populations. Since the arrival of the first European explorers, crocodiles were hunted and killed, until protective legislation in 1968. The lake was restocked from 1967 to 1976 with juvenile crocodiles, responded well and increased up to the early 1990s, stabilising thereafter. The St Lucia Nile Crocodile population have been monitored using aerial surveys for more than 40 years but biological and environmental parameters subject aerial surveys to large and hitherto unquantified biases (Combrink 2014).

By using emerge/submerge ratios from GPS-transmitters attached to Nile Crocodiles, we found that 6.3% of crocodiles were submerged (= invisible) during a winter (June) aerial survey, 33.9% during a summer (Jan.) spotlight survey, increasing to 56.5% in winter (June) (Combrink 2014). Observer bias accounted for 30.7% crocodiles missed by observers from a second airplane during a simultaneous survey in winter (June). We corrected aerial and spotlight counts for these biases and estimate the 2013 adult and sub-adult population at 858 crocodiles and a mean (2009 to 2013) population estimate of 1005 ± 137 crocodiles (95% CI) (Combrink 2014).

During the first decade of the 21st century, the lake-estuarine system experienced a prolonged drought, rivers ceased flowing and more than 90% of the total water area evaporated (Combrink 2014). Most Nile Crocodiles moved to the Narrows, a sufficiently deep and low salinity area south of the lake. However, some crocodiles continued to stay in the central and northern lake, but were dependent on small wetland refugia fed by groundwater seepage along the eastern shoreline and seepage arteries in shoreline swamp forests, often in conjunction with subterranean burrows. Subsequent to 725 mm rainfall in Dec. 2010 and Jan. 2011, lake levels increased and a large proportion of crocodiles moved back to the lake once again (Combrink 2014).

Although raw counts of Nile Crocodiles from 2008 to 2013 indicate a substantial declining trend, after correcting for diving and observer bias, the population estimate of 2013 is comparable with 2003, the first year of the drought (Combrink 2014). This highlighted the apparent resilience of sub-adult and adult crocodiles during prolonged drought events. It furthermore emphasised the importance of correction factors for population estimates, which will also improve the accuracy of future population surveys at Lake St Lucia, allowing for a more effective management response, if required (Combrink 2014).

Despite being the largest, most dangerous and widely disturbed crocodilian in Africa, very little scientific data is available on the spatial ecology and home range behaviour of Nile Crocodiles, with all previous studies focusing on lacustrine or lotic systems (Combrink 2014). Typical of all estuaries, the Lake St Lucia estuarine system is spatio-temporally dynamic as well as the largest estuarine system on the continent. The inherent physical and biological variability was exacerbated by a prolonged drought, followed by rapid restoration of water-levels within the tracking duration of a number of study Nile Crocodiles (Combrink 2014). This resulted in behavioural adaptations in spatial ecology and home range behaviour, reflecting the variability of the physical and biological environment. Asymptote analysis confirmed that the number of observations for most Nile Crocodiles were sufficient to describe their full range of movements, but we recorded transient behaviour of a young adult male, gradually moving northwards subsequent to the restoration of water levels. Adult males revealed a negative correlation between home range size and crocodile size, while adult female home range size were generally more homogeneous. All nesting females displayed an explosive increase in mobility and space-use subsequent to the nesting period, and we hypothesized that this behaviour was in response to a need to increase body condition before the onset of winter. All adult Nile Crocodiles moved during winter to large congregations that formed south of the lake during the drought period (Combrink, pers. obs.). We hypothesized that this was driven primarily by reproductive requirements and not thermoregulatory needs. Since early 2011, lake-water levels were restored, resulting in a decrease of these winter congregations. Sub-adults occupied significantly smaller home range than adults, which were habitat specific. They remained in shallow vegetated areas adjacent to deep water, avoiding the open deep water altogether. It is likely that this limited sub-adult habitat in the Narrows might be an important density regulating mechanism at St Lucia (Combrink 2014).

During the drought large parts of the western, northern and central lake dried out or became hypersaline and too shallow to facilitate crocodile movement (Combrink 2014). Crocodiles either moved south to Catalina Bay where sufficiently deep water expedited movement and other activities (e.g. basking and feeding), providing they had access to freshwater seepage along the eastern shoreline of the bay. Aerial data suggests that most Nile Crocodiles moved even further south to the low salinity Narrows channel. However, some remained in the central region and were restricted to freshwater shoreline seepages areas, or refugia inside swamp forest bordering the eastern shoreline. As water levels increased, former areas were rapidly colonised and movement levels increased. We conclude that size, sex, reproductive status and habitat influenced Nile Crocodile space-use and movements, resulting in complex and varied home range patterns, not surprising given the dynamic nature of estuaries, especially during times of perturbations (Combrink 2014).

The Nile Crocodile population at the Lake St Lucia estuarine system represents the most southern viable nesting population throughout the species' range (Combrink 2014). It is also the largest estuarine nesting population and largest recorded and possibly most stable (i.e. unaffected by flooding) nesting population in South Africa. Although some aspects of Nile Crocodile reproductive ecology at Lake St Lucia were investigated from 1959 to 1978 (Pooley 1982a), nest surveys have been conducted since the 1980s, making it one of the longest monitored Nile Crocodile populations in Africa. The mean number of nests recorded at St Lucia from 1982 to 2013 was 76.19 ± 6.42. Historically, large nesting areas were distributed from the very north of the system next to the Mkhuze River, along the eastern shoreline, Mphathe Stream, and the Link canal, Backchannels and Mfolozi River in the very south. Increased anthropogenic disturbance and habitat transformation north and south of Lake St Lucia resulted a shift in nest distribution, contacting towards the protected eastern shores (Combrink 2014).

Below average rainfall led to the closure of the estuary mouth in 2002. Prolonged low rainfall from 2002 to 2011 with no freshwater input from feeder streams led to the lake drying out, with nest effort at record low levels (6.9% and 8.0% in 2009 and 2011 respectively) (Combrink 2014). Most nests were recorded at the Mphathe Stream and freshwater seepage areas along the eastern shoreline. The mean nest count prior to estuary mouth closure (1982 to 2001) was 103.07 ± 7.7, while during the period when the estuary was closed (2003 to 2012) nesting significantly decreased to 53.56 ± 5.92 nests (Combrink 2014).

Since 2011 rainfall patterns have normalised, the estuary was relinked to the ocean in 2012 and during the 2013 nest survey some nests were recorded along the Eastern Shores Wilderness area (Combrink 2014). Insights into the abundance and distribution of Nile Crocodile nests and understanding how threats, such as human disturbance, lead ingestion through fishing sinkers or alien invasive plants might affect rates of reproduction, should result in management actions mitigating these consequences (Combrink 2014).

8.2 Ndumo Game Reserve

Nile Crocodiles were not evenly or randomly distributed in NGR (Calverley 2013). Winter distribution patterns over the last 40 years have remained similar, with the greatest relative abundance of crocodiles was found in lacustrine habitat with suitable basking sites and permanent deep water. Crocodiles were found to move frequently between habitat patches; where suitable patches were closer together and well connected with good corridor quality, crocodile density was highest (Calverley 2013).

Temperature is likely an overriding environmental factor influencing crocodile density indicating that thermoregulatory requirements influence habitat selection in winter. However, environmental variables influence different size classes of crocodile differently indicating that the way in which individuals react to environmental conditions is influenced by size. The majority of the NGR Nile Crocodile population leaves the NGR and enters the Rio Maputo floodplain over the summer months – a pattern that was first observed 50 years ago (Calverley 2013). We conclude that the Rio Maputo floodplain contains certain resources critical to sustaining the current crocodile population. Research into what these resources are and how best to safeguard them is considered essential for the long term viability of the NGR population of Nile Crocodiles (Calverley 2013).

Studying the movement patterns of Nile crocodiles in NGR has contributed to understanding the role that the reserve plays in the conservation of the greater NGR-Rio Maputo Nile crocodile populations (Calverley 2013). The reserve acts as a winter refuge and spring breeding site for an estimated 846 crocodiles which also inhabit the Rio Maputo during summer months. Interestingly crocodiles are not satisfied to remain within particular basking loci and range widely throughout the floodplain during winter. Movement out of the reserve and into the Rio Maputo is thought to be in response to seasonal concentrations/migrations of prey items and starts in November. Nile crocodiles then move back into NGR as water levels in the floodplain contract in May. As the Rio Maputo is more important for Nile crocodiles, especially their the recruitment into the NGR than vice versa (Calverley 2013), it is strongly recommended that the Rio Maputo or at least parts of it that are important as breeding sites receive formal protection or at least compatible land use activity (Calverley 2013).

The distribution of Nile Crocodile nesting sites in NGR has changed due to changes in the hydrological landscape and due to anthropogenic disturbances and habitat transformation at historical nesting sites (Calverley 2013). The amount of nests has remained relatively constant over the last 50 years despite drastic population increases due to restocking programs. This is because seasonal movement patterns of Nile Crocodile in response to prey resources outside of the reserve coincide with the nesting season and the majority of the NGR population nest outside of the reserve in the Maputo River Floodplain. The selection of suitable nesting site in NGR may therefore also depend on prey densities as well as nest site characteristics such as the availability of suitable nursery habitat for hatchlings and access to deep water or burrows. Historical nesting sites have been used for over 50 years and could be attributed to natal homing or cultural inheritance (Calverley 2013).

8.3 Pongolapoort Dam

The Nile Crocodile population in Pongolapoort Dam following the impoundment of the Phongola river appears to have increased based on minimum total numbers counted and number of juveniles, both suggesting successful reproductive recruitment and population viability (Champion 2011). It is unlikely that the population increase was as a result of immigration from surrounding areas as the dam wall is a substantial barrier between the dam and the lower crocodile population of NGR some 70 km downstream. The high number of crocodiles found through all size classes, juveniles to large adults, also suggests that this population has been increasing for a number of years and has a sustainable breeding population (Champion 2011). Future studies should aim at determining a population index, in order to monitor any changes in the Pongolapoort Dam Nile crocodile population and allow comparison with other populations (Ferreira and Pienaar 2011). The positive status of this population is of great importance as many other populations in South Africa are currently under threat as a result of habitat degradation through pollution. Continued monitoring of the Nile crocodile population in Pongolapoort Dam is required to determine if the impoundment continues to support a viable population and determine accurate and precise population estimates (Champion 2011).

Although Pongolapoort Dam levels fluctuate greatly within and between years, the Nile Crocodiles appear to adjust to these changes and successfully persist here (Champion 2011). The majority of the crocodiles were concentrated in the north-west section of the dam, moving upstream and utilizing the Phongola river in summer months while residing in the inlet section during the winter months where there are historical basking sites. The current management of water levels by the Department of Water Affairs and Forestry appears to have no noticeable negative effects on the Nile Crocodile population in Pongolapoort Dam. The maintenance of this water level management paradigm may promote further nesting in the dam itself as levels are perceived as more predictable, however this may not be the case. However, infrequent flooding of the inlet river affects nesting of crocodiles (Champion 2011).

As mentioned Pongolapoort Dam was completed in 1972 on the Phongola river (Champion 2011). The section of river incorporated into the dam supported a relatively low number of Nile crocodiles prior to dam completion (Jacobsen 1984) and these were mainly found in the gorge section prior to impoundment. The construction of the dam resulted in a complete habitat change, as rising dam levels flooded areas previously used by crocodiles and made new areas available (Champion 2011). Such drastic habitat change may be equated to the relocation of the crocodile population. The impoundment changed food availability and distribution patterns (Ward 1998), as well as shifting available basking and nesting areas. Consequently Nile crocodile home range and territory parameters, communal courtship sites and available nesting areas were affected (Botha 2010). Since the establishment of the dam in 1972, its water level has fluctuated drastically, between 12 to 107% capacity (60 m fluctuation in height at the dam wall), as a result of floods, droughts and changes in management strategies (van Vuuren 2009b). The results of this study may therefore only be relevant for this specific combination of range of water levels and the water management strategy being followed at the time of the study. However, the results will allow for future studies to explore the changes in population dynamics of the Pongolapoort Dam Nile crocodile population in response to changes in the characteristics of the water body they inhabit (Champion 2011).

As a result of human encroachment and habitat destruction there has been a great decrease in suitable Nile Crocodile breeding grounds in general (Pooley 1969; Combrink 2004). Despite the generally negative effects of river impoundments, the Pongolapoort Dam has resulted in the establishment of a relatively large Nile crocodile population, with a considerable reproductive potential (Champion 2011). However, the latter is affected by changing water levels and predation. This underlines the importance of ensuring the consideration of Nile Crocodiles and their breeding grounds in Pongolapoort Dam management plans. Further studies are recommended, specifically focusing on nesting dynamics and seasonal changes in the success of nesting effort, as well as any changes in areas used for nesting (Champion 2011).

8.4 Impact of study

The Nile Crocodile is listed as a threatened (Red Data) species in South Africa as a result of ongoing range contraction and fragmentation due to past hunting and extermination programmes, habitat loss, illegal killings (poaching for muthi, etc.) and disturbance of nesting areas. It is therefore a species of conservation concern and requires special protective measures.

Like all crocodilians, the Nile Crocodile is a wetland flagship species, and as the top predator in aquatic systems is considered to be an important biological indicator of aquatic ecosystem health. The iSimangaliso Wetland Park and Lake St Lucia in particular, is a critical conservation area for wild crocodiles, as it hosts the largest number of individuals in a single water body in South Africa, and is likely to be the largest and most secure population in an estuarine environment throughout the species' range. Lake St Lucia is also one of only three viable wild crocodile populations left in South Africa and the most significant southern breeding population on the continent

Given confirmed and suspected recent die-offs of Crocodilian populations, both within and outside of South Africa, Nile Crocodile merit serious scientific study if the species and its wetland habitats are to be adequately protected and managed. Crocodilians have been appropriately recognized in recent years as "sentinel species" within aquatic ecosystems: if crocodile populations are sick, it is a serious reflection on the health of associated water bodies and other sub-apex organisms in the food web. Mitigation of threats to crocodiles is useful for protection of aquatic habitats at an ecosystem level.

The outputs of this Nile Crocodile programme will benefit the scientific and conservation management communities both nationally and internationally in a number of ways including generation of comprehensive management plans, Nile Crocodile population models, understanding/mitigation of environmental contaminants in Ramsar wetlands in South Africa, and greater overall understanding of Nile Crocodile ecology. The data contribute to developing a national approach to the factors affecting Nile Crocodiles. In addition ecotourism and local people are benefitting from the outputs.

8.5 Conclusion

The only secure populations of Nile Crocodiles in South Africa occur in protected areas. It is therefore essential that within these protected areas Nile Crocodiles are afforded the protection necessary to sustain viable populations. This is achieved by adopting and maintaining monitoring programs that can generate information regarding changes in population size and recruitment. Through these measures informed and timely management actions can be put in place to safeguard the future of Nile Crocodiles in South Africa. However, crocodiles are semi-aquatic animals and have the ability to move freely in and out of fenced conservation areas. Cognisance needs to be taken of this and we need to establish whether the conservation of Nile Crocodile populations residing within protected areas depends on habitat outside of protected areas and the degree of connectivity that is required between these areas. In such scenarios investigations into the habitat use of crocodiles outside of protected areas should be investigated and where possible conservation strategies put in place to mitigate threats to crocodiles and humans alike.

9 RECOMMENDATIONS

It is important to note from the outset that many conservation areas such as Lake St Lucia and NGR have a history of Nile Crocodile monitoring programs that have been used to generate management objectives for Nile Crocodiles in the past (e.g. Mathews, 1994). However, the perceived recovery of Nile Crocodile populations in South Africa (Ross, 1998) has resulted in a cessation of many of these monitoring programs and a lax in the implementation of specific Nile Crocodile management objectives. Outlined below are recommendations for the conservation of the KZN Nile Crocodile population drawn from the current study, existing literature, personal observations and the Integrated Management Plans (IMP).

9.1 Lake St Lucia recommendations

The following recommendations about Nile Crocodile in Lake St Lucia are made:

- Continue with the annual winter aerial counts in June to record the relative abundance of Nile Crocodiles and their distribution (Combrink 2014).
- Lake level monitors have recently been installed in a number of areas. Given the apparent positive correlation between lake level and visibility/vegetation bias during aerial crocodile surveys, lake levels could now be quantified on the day of the aerial count and incorporated as a covariate in future count estimates (Combrink 2014).
- Partition the sub-adult component using photographic/videographic techniques from a slow-flying aerial platform, such as a double-motorised paraglider. The sub-adult proportion in the Narrows was estimated at 19.9 ± 2.9% during spotlight counts, but it would be valuable to validate this figure with data for the entire population (Combrink 2014).
- Quantify the effect of airplane speed and visibility/vegetation bias during high lake levels using a slow-flying aerial platform, such as a double-motorised paraglider. This should preferably be conducted a close as possible to the annual aerial survey and the obtained ratio could be used as an additional “speed” correction factor in future surveys (Combrink 2014).
- The proportion of juvenile crocodiles (non-hatchlings: 0.4-1.5 m, ~1-4 years of age) is unknown at Lake St Lucia (Combrink 2014). They are not observed during aerial surveys due to their size and preference of vegetated habitats. This is an important segment as they represent recruitment and will affect future abundance. Estimate juvenile abundance through a mark-recapture programme by setting traps in nesting and adjacent areas (Combrink 2014).

- As a result of depleting populations and escalating threats, the Nile Crocodile is a threatened and protected species in South Africa, listed as Vulnerable (McLachlan 1978, Jacobsen 1988, Marais 2014, Combrink 2014). The Lake St Lucia estuarine system is host to the largest Nile Crocodile population within a single waterbody in South Africa and is the largest population in the province of KwaZulu-Natal. It is recognised that within the context of conserving a healthy and viable Lake St Lucia ecosystem, a specific management strategy is required for Nile Crocodiles (Taylor et al. 2007) which highlights research as a key objective to underpin management actions (Combrink 2014).
- The general insights provided by this investigation will contribute to a more complete understanding of crocodile biology, ecology and life history (Combrink 2014). Specific information on diel, monthly and seasonal movement and activity levels will contribute to the survey and monitoring programme, a key management function. It will also support the dissemination of aspects pertaining to human-crocodile conflict, an important management component at St Lucia, as tourists and community members almost daily interact with shared natural resources such as water, fishing and reed harvesting (Combrink 2014).
- Public and community education initiatives, another management objective, could incorporate aspects of the study in education programmes such as audio-visual material and posters as part of existing talks and interpretation at the St Lucia Crocodile Centre to stimulate interest in crocodile biology, ecology and conflict mitigation (Combrink 2014).
- Crocodile activity and movements are such integral components of their overall ecology and life history that improved understanding of these aspects will indirectly inform numerous other management actions such as capture of damage-causing crocodiles, protection of key basking and breeding areas, and determining routes of law-enforcement foot and boat patrols at Lake St Lucia (Combrink 2014).
- Nesting Nile Crocodile females, especially those nesting far from water, are particularly vulnerable to illegal killings. The killing in 2013 of a female at eSingeni, the second largest nesting area on the eastern shores during the nesting period, highlighted this threat. Field rangers should patrol the boundary of large known nesting areas for suspicious signs and activity from Nov. to March (Combrink 2014).
- St Lucia Nile Crocodiles tend to re-use the same nest-sites during periods of similar rainfall and salinity, the GPS position of every previously used crocodile nest-site should systematically be checked during surveys (Combrink 2014). As new nests are discovered, they should be added to the database and checked in subsequent years.

Therefore, survey effort should theoretically increase slightly every year. Survey routes will be pre-planned and uploaded on a GPS which will ensure more effective integration of new staff that might not be familiar with the survey area, as well as minimise disorientation or losing direction (Combrink 2014).

- Cybertracker, an integrative GPS information system that records the actual route followed during the survey, also have the capacity to capture GPS locations of nests together with a suite of pre-selected nest parameters should be incorporated as a standard method during nest surveys (Combrink 2014). This will increase efficient capturing of survey effort, a vital aspect of post-survey analysis and interpretation, and will also allow for a post-survey audit, if required (Combrink 2014).
- Each active nest-site should be photographed in order to monitor bush encroachment and the presence of Triffid Weed (Combrink 2014). The presence of Triffid Weed should be recorded and due to their vegetative development and immense seed production, plants must be manually removed on an annual basis, before June/July, prior to flowering and seed dispersal (Leslie 1997, Combrink 2014).
- When a female crocodile is encountered on/next to her nest, her tail section should be photographed for subsequent identification (Combrink 2014). Uniquely identified females that are re-sighted in subsequent years provide important biological and ecological information such as reproductive frequency and nest-site fidelity (Combrink 2014).

9.2 Recommendations for future research at Lake St Lucia

The following recommendations for future research on Nile Crocodile in Lake St Lucia are made:

- One of the key unknown aspects of any crocodile nest monitoring programme is the proportion of present, but unrecorded nests in the population. In order to estimate this ratio we suggest using a double motorised paraglider (Combrink 2014). This survey craft has the ability to operate at speeds as low as 5 km^{-1} at whatever height required, providing a stable aerial platform for improved coverage of all potential nesting habitat. We expect the paraglider to locate more nests compare with the conventional foot survey and this ratio of paraglider count to foot patrol count could serve as a future correction factor (Combrink 2014).

- Mapping of all potential nesting areas, linked to hydrological patterns. This will inform management of important areas during the nesting period and allow researchers to ground truth some of these areas to check if we are missing nests (Combrink 2014).
- Investigate the role and importance of temperature sex determination in wild crocodile nests at Lake St Lucia (Combrink 2014). During incubation the developing embryo is subjected to a number of factors that will determine its survival and consequent contribution to the dynamics of the population. While predation, flooding and nest abandonment are some of the obvious causes of egg mortality, none plays a more important role in the development, body size, frequency of abnormalities, post-hatching growth, survivorship, thermoregulation patterns and sex of the hatchlings than incubation temperature (Hutton 1984, Deeming and Fergusson 1989, Webb and Cooper-Preston 1989, Thorbjarnarson 1990, Combrink 2014).
- Conduct a double shift, pulsed temperature experiment at the St Lucia Crocodile Centre to determine the temperature sensitive period for the Nile Crocodile (Combrink 2014).
- Investigate nest temperature and sex of hatchlings for a number of nests at the St Lucia Crocodile Centre. This will require keeping hatchlings up to an age where that can be sexed with 100% certainty. Leslie (1997) found even at 14 months of age there were obvious males and females but there were also a large number of individuals that showed cliteropenis characteristics of both males and females (Combrink 2014).
- Research and survey activities will result in some degree of disturbance to nest guarding females and the aim is always to minimise the time spent at/near the nest (Combrink 2014). However, the attachment of three transmitters to nesting females as well as setting and checking 19 camera traps at crocodile nests with no evidence of nest abandonment and very little of subsequent predation, suggest the strict policies for crocodile researches at nests could be relaxed to allow for more research activities at wild crocodile nests at Lake St Lucia (Combrink 2014).

9.3 Ndumo Game Reserve and Rio Maputo Nile Crocodile Population recommendations

The following recommendations about Nile Crocodile in Ndumo Game Reserve are made (Calverley 2013):

9.3.1 Annual aerial surveys

It is suggested that annual aerial surveys be re-implemented (Calverley 2013). These surveys should follow historical method and take place during times of low water levels and during winter (July/August). Wherever possible the same observers should be used for consecutive surveys to improve precision and a helicopter should be used for safety reasons and to increase accuracy. The continuation of the crocodile monitoring program initiated by Pooley in 1971 is necessary to follow changes in population size so that timely management decisions can be made. Surveys should be designed to collect data aimed at answering specific questions. Aerial surveys can be used to determine whether the total population is increasing, decreasing or remaining stable and to follow changes in distribution patterns.

- Where financial or logistical constraints may limit the implementation of aerial surveys it is suggested that diurnal surveys take place at Lake Nyamithi on a seasonal basis due to the high density of crocodiles here, easy accessibility and the ability to conduct accurate vehicle based surveys (Calverley 2013).

9.3.2 Annual nesting surveys

Nile Crocodile nesting sites are generally used repeatedly and are biologically sensitive sites that need to be conserved to secure future recruitment of Nile Crocodiles in NGR (Calverley 2013). Nesting surveys initiated in the 1960s were carried out sporadically thereafter and there are no records of any nesting surveys since 1990. Annual nesting surveys of Nile Crocodiles should be implemented to identify key nesting habitat and as a measure of recruitment within the reserve (Calverley 2013). This will help predict future population changes of Nile Crocodiles within NGR (Calverley 2013).

9.3.3 Protection of nesting sites

Nile Crocodile nesting sites located in annual nesting surveys in NGR need to be safeguarded from disturbances (Calverley 2013). Pooley (1982) noted the abandonment of nesting sites at Lake Nyamithi due to the construction and subsequent use of a road running in close proximity to active nesting sites. These nesting sites were used in 2009 but were also abandoned, possibly for the same reasons (Calverley 2013). Where possible, existing roads lying close to historical nesting sites should be diverted to minimize disturbance in these areas. Future developments such as the construction of bird hides, for example, should take cognisance of the location of nesting sites and should not be constructed in these areas. Similarly, the harvesting of natural resources within NGR by the local community such as reed collection and low intensity fishing practices should not be allowed to take place near nesting sites, particularly during the nesting season. Identified nesting sites should be protected from disturbance from walking trails, and under no circumstances should field guides excavate nests to show tourists crocodile eggs. Such practices not only chase female Nile Crocodiles from the nest allowing a window of opportunity for egg predators to raid the nest but may permanently discourage protection of the nest by the female. Excavated nests are also easier for predators such as Nile Monitor Lizards to locate as the scent of the eggs permeates more easily in disturbed sites than if the eggs were left covered (Calverley 2013).

9.3.4 Limit anthropogenic disturbance

Anthropogenic threats to Nile Crocodile populations include; increased pollution of our rivers due to industrial and agricultural development (Ashton 2010, Osthoff 2010, Ferreira and Pienaar 2011), competition for food resources (Leslie 1997), unsustainable harvest of wild populations and/or their eggs for captive ranching (Leslie 1997, Bourquin 2008, Wallace et al. 2011, 2013), destruction of riverine vegetation and unsuitable agricultural practices (Pooley 1969, Botha 2005, Woodborne et al. 2012), destruction of nests and disturbance at nesting sites by humans and livestock (Combrink 2004, 2014), illegal poaching of live animals (Combrink and Taylor 2009; Wallace et al. 2011, 2013) and the divergence of fresh water courses for agricultural purposes (Leslie 1997). These all need be reduced (Calverley 2013).

9.3.5 Competition for food resources

Fish make up an estimated 98% of the diet of juvenile and sub-adult Nile Crocodiles (Games 1990, Calverley 2013). The removal of the eastern boundary fence of NGR in 2008 has increased accessibility to the western portion of the Phongola floodplain resulting in an increase in illegal netting of fish and could constitute a threat to the food resources of Nile Crocodiles. Furthermore, hatchling and juvenile Nile Crocodiles can get caught in fishing nets and drown. However, the illegal harvesting of fish is not only a product of the eastern boundary fence being removed. Poachers are entering the reserve by boat from Mozambique in the north and from South Africa in the east of the reserve. The annexure of the reserve west of the Phongola river does make enforcing law in this section of the reserve more difficult as field rangers positioned here are surrounded by an often hostile community. Rope bridges that field rangers rely on to patrol the eastern portion of the Phongola floodplain have been destroyed and often take months to be fixed. In 2009, members of the Mbangweni community went so far as to kidnap field rangers residing in a field camp in this part of the reserve. The issues surrounding the removal and resurrection of the eastern boundary fence has become a question of politics rather than conservation (Meer 2010). Only when an amicable solution has been reached and the fence resurrected will any protection be offered to any wildlife west of the Phongola river. As it currently stands there are no animals left west of the Phongola river due to poaching activities and disturbance factors. Gill netting is illegal in any river system in South Africa and anti-poaching efforts need to be focused on preventing the continued uncontrolled and unsustainable harvest of fish resources within the reserve. At the very least boats and fishing equipment such as nets need to be confiscated or destroyed and perpetrators prosecuted. The suggestion here is to increase patrols along the eastern periphery of the Phongola floodplain and to enforce laws that protect the fauna and flora of the reserve (Calverley 2013).

9.3.6 The illegal poaching of live animals

Snares as well as crocodile carcasses have been recovered from the eastern part of the Phongola floodplain and it is likely that increased accessibility due to the removal of the boundary fence has resulted in an increase in poaching activities in NGR (Calverley 2013). However, a crocodile poaching syndicate was discovered operating in NGR before the removal of the fence and anti-poaching efforts need to be focused on preventing the snaring of crocodiles. An increase in patrols along the periphery of river channels and water bodies with the specific objective of searching for crocodile snares in particular would help reduce the levels of poaching in NGR (Calverley 2013).

9.3.7 The destruction of riverine vegetation and unsuitable agricultural activities and the resultant destruction of nesting sites

Over 50 ha of land east of the Phongola rivers was estimated to be under cultivation in 2009 (Calverley 2013). At the current rate of destruction very little of the floodplain east of the Phongola will be free from cultivation in one year’s time. Pooley (1969) identified the destruction of riverine vegetation as one of the primary factors causing the decline of Nile Crocodile populations outside of protected areas. Historical nesting sites on Mavilo Hill (Ward, 1990) used as recently as2008 are now adjacent to agricultural fields and areas of the Phongola utilized for fishing. It is therefore strongly recommended that further agricultural development and disturbances be halted in this part of the floodplain in the interim period before the eastern boundary fence is re-erected. Failure to do so could result in a decline of the carrying capacity for Nile Crocodiles in NGR (Calverley 2013).

9.3.8 Identification of nesting sites outside of NGR

There are serious doubts as to whether NGR can support a sustainable Nile Crocodile population without habitat supplementation from neighbouring Mozambique (Calverley 2013). Even at the comparably low density of approximately 270 Nile Crocodiles in the 1970s, the majority of the NGR population left the reserve during summer months presumably to nest in Mozambique (Pooley 1982). The same seasonal movement pattern is evident today and NGR has a low nesting effort of 21%. With the average number of nests found in the reserve from surveys conducted in 1989, 1990 and again in 2009 being only 10, recruitment is predicted to be low. Pooley suggested a 20% predation rate of nests and a 1-2% survival rate of hatchlings in NGR. Simple mathematics shows that of the approximate 450 eggs laid during the average breeding season, only between 4-7 individuals are expected to survive to the age of one year. Less than 50% of these will make it to a reproductive age and only half of which will be females and can be expected to breed only every second season. Taking the optimistic view of a 2% hatchling survival rate NGR is only capable of producing 1 breeding female per year. This does not take into account that all nests are destroyed by flooding at least once every 10 years resulting in zero recruitment. Even if surveys found only half of the nests in NGR recruitment is still un-sustainably low. The future of the NGR Nile Crocodile population therefore lies in Mozambique (Calverley 2013). It is essential that at the very least an investigation into the nesting ecology be undertaken in the Rio Maputo floodplain where the majority of the Nile Crocodiles counted in NGR are thought to nest. The connectivity of these areas also needs to be investigated. This area in Mozambique is under no official protection and it does not serve to become complacent regarding the future security of this essential habitat. With this in light the following recommendations are made (Calverley 2013):

- Current aerial surveys in NGR must extend into the Rio Maputo floodplain to more accurately assess the state of the greater Usuthu/Phongola/Rio Maputo Nile Crocodile population.

- This will necessitate collaboration with Mozambican officials in order to obtain permissions for the surveys.
- The seasonal movement patterns of adult Nile Crocodiles need to be followed using advanced telemetry techniques, such as satellite transmitters, in order to identify the habitat use of crocodiles in the Rio Maputo floodplain with particular reference to nesting sites.
- Boat and or foot patrols will be required to follow up on aerial and telemetry studies to locate and map nesting sites used in the Rio Maputo floodplain
- Using population surveys and nesting surveys a management plan for the Rio Maputo/NGR Nile Crocodile population can be created.

9.3.9 Human wildlife conflict

The potential for human crocodile conflict in the Rio Maputo is massive with an estimated 500 crocodiles leaving the reserve every year over the summer months (Calverley 2013). It is only a matter of time before human populations and crocodiles in the Rio Maputo floodplain converge. Already humans and crocodiles compete for the same resources at Lake Pandejene – fish. An autopsy on a large (4.72 m) male crocodile found in Lake Nyamithi in 2010 produced human remains indicating at least one fatality can be attributed to the NGR Nile Crocodiles. It is strongly suggested that HCC in the Rio Maputo is pre-empted and a strategy to reduce risks at both sides of the human crocodile interface is developed. Habitat transformation in the Rio Maputo floodplain could have severe negative influences on the NGR Nile population as the majority of the population appear to nest in the Rio Maputo floodplain (Calverley 2013).

9.4 Pongolapoort Dam

Aerial and spotlight surveys:

Aerial surveys of Nile Crocodiles in Pongolapoort Dam need to happen twice a year every year to build on baseline data. These aerial surveys need to be backed up by numerous daytime and night time spotlight boat surveys. The daytime spotlight surveys are effective in estimating sizes of crocodiles, whereas nigh time spotlight surveys are effective in estimating crocodile numbers. Annual surveys will aid in getting accurate minimum population counts of Nile Crocodiles in Pongolapoort Dam. This will aid conservation bodies in making important conservation decisions.

Nesting sites:

Annual nesting surveys of Nile Cocodileas in Pongolapoort Dam will add to the database of communal nesting sites, historical nesting sites, and possible recruitment numbers. Nesting surveys also need to be conducted upstream of Pongolapoort Dam. Our understanding of nesting areas upstream of Pongolapoort Dam and in Pongolapoort Dam itself is limited. It is recommended that the conservation bodies conduct annual surveys on nesting ecology and nesting sites, and these areas should be mapped and added to patrol routes to reduce the chance of egg poaching.

Anthropogenic disturbances need to be reduced in areas where there are Nile Crocodile nesting sites. Some of these nests occur on sand roads used by the reserves for game drives. During the nesting season, these roads can be avoided and parallel roads can be used. This will increase the likelihood of hatchling survival.

Key conservation areas:

Pongolapoort Dam has a wide variety of shoreline habitats. Key to Nile Crocodile distributions is the availability of basking sites. The inlet section of Pongolapoort Dam has ideal basking sites, and during the mating season, these basking sites become highly populated with Nile Crocodiles (Champion 2011). The western section, including the inlet section of Pongolapoort Dam should be considered a key conservation area due to the majority of the population if Nile Crocodiles occurring in this area. Foot and boat patrols should be done on a regular basis to make a presence known, and to remove any gill nets or illegal snares. For example, rangers found a three meter crocodile trapped in a gill net on the western shores in 2013 (Summers unpublished data). The crocodile was still alive and it managed to free itself. This highlights the necessity for regular foot and boat patrols.

Use of identification tags for distributional data:

Cattle identification tags are an effective way of identifying Nile Crocodiles by attaching the tags to their tail scutes. During fishing competitions and boat patrols, rangers and fishermen alike could take GPS coordinates of where the crocodiles have been located and submit these coordinates with the identification code to a central location.

Future studies:

To get a better understanding of how best to conserve Nile crocodiles, one needs to address many key issues of their ecology, physiology and behaviour. Scientific studies and historical data could combine to create an effective management plan. Future research ideas are as follows:

- Follow up studies such as Champion (2011), must be done to build a record of population numbers, population structure, spatial and temporal movements and nesting ecology. This will add to baseline data that has been collected.
- Current aerial surveys need to encompass Pongolapoort Dams entire perimeter, including the inlet and if possible, aerial surveys should extend upstream past the N2 bridge. Possible nesting sites and basking areas may be found upstream of the protected Pongolapoort Dam.
- Data of spatial and temporal distributions need to be built on following Champion (2011) study. Fitting crocodiles with GPS transmitters would increase the data collected, and when the transmitter is fitted using the methods described by Brien and Webb (2010) and Combrink (2013), the longevity of the transmitters will be increased. Crocodiles fitted with transmitters may give us a better understanding of how far upstream the Pongolapoort population of Nile crocodile's moves. This may result in reassessment of protected areas.
- Of importance is a nesting survey to estimate recruitment of hatchlings. Pongolapoort Dam has potential to have a high recruitment rate of hatchlings and this need to be researched in more depth. A combination of foot surveys and aerial surveys would best suite nest site identification.
- Farming practices upstream of Pongolapoort Dam have resulted in high volumes of sediment being deposited in the inlet section of Pongolapoort Dam (Calverley 2014, pers. comm.). The effect of deposition on Nile Crocodile ecology needs to be addressed. Areas that are silted up by deposition of sediments may offer basking sites to crocodiles, as well as opening up nesting areas. Research on this may be beneficial to both the conservation body and the farmers upstream of Pongolapoort Dam.
- Basking behaviour and the effect of the thermal environment on crocodiles is another research topic which could be investigated.
- Invasive alien vegetation is a threat in many parts of KwaZulu-Natal. Quantifying the effect and threat of invasive alien vegetation should be a priority research point, as it affects not only Nile Crocodiles, but the ecosystem as a whole.
- The ecotoxicology of Nile Crocodiles is Pongolapoort Dam can be researched to quantify the health of crocodiles as indicators of ecosystem health.
- The use of stable isotope analyses may give an idea of food webs and prey items and abundance.
- Pongolapoort Dam is a popular fishing and safari destination. Evidence of Fish poachers has also been noted. The human wildlife conflict of crocodiles and people

will always be an issue. Understanding how crocodiles and people interact on Pongolapoort Dam is essential in conserving the species. Census and interviews are an effective way of gaining an understanding of human crocodile conflict in Pongolapoort Dam.

9.5 Crocodile health

While KZN Nile Crocodile populations are very different, direct threats to crocodile habitat are similar. Indirect threats are not as well known. Continued monitoring of Nile Crocodile health is recommended. In particular their lead and DDT concentrations should be monitored. It is recommended that use of lead sinkers for fishing is stopped. Fishermen need to be educated about the effects of abandoned line and hooks to Nile Crocodiles as well as other wildlife.

Connectivity is of Nile Crocodiles in KZN is important long term. Currently there is discontinuity of KZN Nile Crocodile populations. The isolated populations/individuals become soft targets (e.g. Lake Sibaya; HiP/iSimangaliso; NGR/PGR). Habitat is suitable in many smaller reserves, but we need know what the critical mass is. Crocodiles undergo extensive movements and need to utilize different habitats throughout their lives, and therefore are exposed to more threats. Populations can tolerate some degree of disturbance, but this is variable dependent on: level of protection, size of area, type of habitat, type and severity of disturbance, resiliency of the species, nest and nesting habitat destruction and intentional killing. The latter two are critical if a population is in decline.

Documenting local extinction in places not adequately protected complex issue. Research and management approaches should by necessity vary among protected areas and habitats or even in single areas: iSimangaliso. We need to know how crocodiles in the rest of Zululand connected to major populations and what is their status and importance.

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