

**The Conservation Ecology of the Nile Crocodile
(*Crocodylus niloticus*) at Ndumo Game Reserve in
North Eastern KwaZulu-Natal and the Rio Maputo
Floodplain in South Eastern Mozambique.**

Peter Calverley

Submitted in fulfillment of the academic requirements for the degree of
Doctor of Philosophy

in the Discipline of Zoology

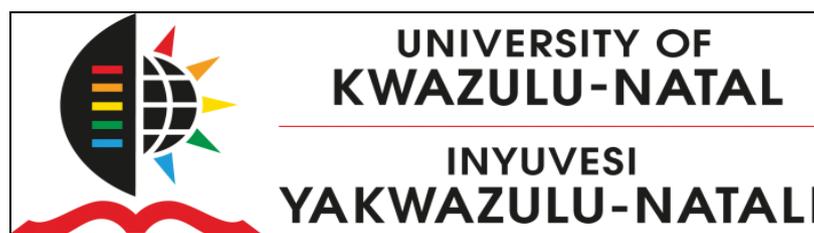
School of Life Sciences

College of Engineering, Agriculture and Science

University of KwaZulu-Natal

Pietermaritzburg

2013



ABSTRACT

Up until 1969 Nile Crocodiles (*Crocodylus niloticus*) were considered as vermin in South Africa and were actively persecuted throughout the country. In an effort to re-establish viable populations within protected areas in Zululand a restocking program was initiated in the late 1960's and early 1970's. Ndumo Game Reserve (NGR) in north eastern KwaZulu-Natal was one of the reserves involved in the restocking program and the Nile Crocodile population in the reserve increased from a minimum absolute abundance of 348 (SE \pm 3.39; N = 3) in the early 1970's to a minimum absolute abundance of 992 (SE \pm 58.70; N = 4) in the 1990's. However, in recent years there has been some concern that the NGR Nile Crocodile population may be on the decline, initiating the current investigation into the ecology and conservation of the NGR population.

We examined changes in relative abundance using aerial survey data from 1971 – 2009. The precision and accuracy of population estimates was affected by water level, season, aircraft type and the use of different observers. A correction factor was applied to survey data and the current NGR Nile Crocodile population is estimated at an absolute abundance of 846 (\pm 263).

Distribution data from the aerial surveys were also used to examine habitat use over the last 40 years and revealed that Nile Crocodiles were not evenly distributed in NGR and that crocodiles favoured the Phongola over the Usuthu floodplain systems. NGR is characterised by a floodplain mosaic landscape and crocodile distributions between the various habitat patches were influenced by landscape physiognomy and composition as well as connectivity and corridor quality. Anthropogenic disturbances influenced the functionality of the floodplain landscape negatively with impacts on habitat use and connectivity.

To quantify the effects of environmental conditions on crocodile habitat use we conducted 40 diurnal counts at Lake Nyamithi between 2009 and 2012 and related changes in crocodile numbers here to temperature, rainfall and water level. Crocodile density in Lake Nyamithi was significantly and negatively related to average maximum ambient temperature and numbers increased in the lake over the cool, dry winter season. Water level and rainfall had strong but not significant ($p > 0.05$) negative influence on crocodile density in Lake Nyamithi. Environmental variables influenced different size class of Nile Crocodiles differently and the density of crocodiles in the 1.5 – 2.5 m Total Length (TL) size class were significantly influenced by rainfall and average minimum monthly temperature.

Movement patterns of 49 Nile Crocodiles between 202 – 472 cm total length (TL) were followed over 18 months using mark-resight ($n = 36$), radio ($n = 10$) and satellite ($n = 3$) telemetry. The duration of radio transmitter attachment (131 days, $SE \pm 11.35$) was significantly related to TL and reproductive status. Satellite transmitters stopped functioning after 15 ($SE \pm 12.53$) days and home range was calculated for 7 crocodiles ranging in size from 202 cm TL – 358 cm TL. Sub-adults (1.5 - 2.5 m TL) occupied smaller, more localized home ranges than adults (> 2.5 m TL). Home ranges overlapped extensively suggesting that territoriality, if present, did not cause Nile Crocodiles to maintain spatially discrete home ranges in NGR during the dry season. A single large scale migration event occurs every year between October and November whereby the majority of the NGR crocodile population leaves the reserve and enters the Rio Maputo floodplain in adjacent Mozambique and only return in April/May.

Nesting effort (19 – 21 %) in NGR was comparable to other populations of Nile Crocodile in southern Africa. Nests are completely destroyed by floods once every 10 years and predation rates may range from 20 – 86 % per year.

In addition to aerial surveys, nesting surveys and movement studies crocodiles ($n = 103$) were caught opportunistically to collect demographic data on population structure. The population structure of Nile Crocodiles in NGR is currently skewed towards sub-adults and adults suggesting an aging population that may decline naturally in the future. This could be due to low recruitment levels in NGR that are not able to sustain the artificially high population size created by the restocking program. Sex ratios were skewed towards females in the juvenile and sub-adult size classes and towards males in the adult size class while the overall sex ratio was even between males and females.

It is predicted that the NGR Nile Crocodile population will decline in the future and that this decline should be considered as a natural process. However, the rate of decline will be accelerated at an unnatural speed and to an unnatural extent due to poaching, uncontrolled harvesting and destruction of nesting habitat within NGR. Based on the findings of the current study, management recommendations for the conservation of the combined NGR – Rio Maputo Nile Crocodile population were made. It is important that further research takes place in the Rio Maputo floodplain in Mozambique to better quantify the nesting ecology of the NGR Nile Crocodile population and to identify possible threats facing Nile Crocodiles in this region.

PREFACE

The data described in this thesis were collected in the Republic of South Africa from February 2009 to November 2012. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg campus, under the supervision of Professor Colleen T. Downs.

This thesis, submitted for the degree of Doctor of Philosophy, in the College of Engineering, Agriculture and Science, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and other than having been upgraded from a Master of Science into a Doctorate has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



.....
Peter Calverley

January 2013

I certify that the above statement is correct...



.....
Professor Colleen T. Downs

Supervisor

January 2013

COLLEGE OF ENGINEERING, AGRICULTURE AND SCIENCE

DECLARATION 1 - PLAGIARISM

I, Peter Calverley, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a. Their words have been re-written but the general information attributed to them has been referenced
 - b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.
5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.



Signed:

Peter Calverley

January 2013

COLLEGE OF ENGINEERING, AGRICULTURE AND SCIENCE

DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1

Calverley, P & CT Downs

HABITAT USE OF NILE CROCODILES IN THE PHONGOLA, USUTHU AND RIO MAPUTO FLOODPLAINS: A NATURALLY PATCHY ENVIRONMENT

Author contributions:

PC conceived paper with CTD. PC collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

Publication 2

Calverley, P & CT Downs

MOVEMENT AND HOME RANGE OF NILE CROCODILES IN NDUMO GAME RESERVE, SOUTH AFRICA

Author contributions:

PC conceived paper with CTD. PC collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

Publication 3

Calverley, P & CT Downs

POPULATION DYNAMICS OF NILE CROCODILES IN NDUMO GAME RESERVE, SOUTH AFRICA

Author contributions:

PC conceived paper with CTD. PC collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

Publication 4

Calverley, P & CT Downs

**THE PAST AND PRESENT NESTING ECOLOGY OF NILE CROCODILES IN
NDUMO GAME RESERVE, SOUTH AFRICA: REASON FOR CONCERN?**

Author contributions:

PC conceived paper with CTD. PC collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

ACKNOWLEDGEMENTS

I would like to thank fellow croc researchers and friends Xander Combrink, Jonathan Warner and Garreth Champion for all their help and support in the field. Ezemvelo KZN Wildlife is thanked for permission and support of the project. In particular I would like to thank Ferdi Myburgh for his tireless work and enthusiasm as well as Clint Halkett-Siddal. Without these two gentlemen the project would not have been possible. The staff at the Ndumo Conservation Office, Cynthia Sithole and Gugu Xulu in particular, are thanked for their kind assistance. Taryn Bigwood is thanked for facilitating our operations in Zululand, for help with GIS and for being a fantastic friend. Brice Gijssbertsen and Ruth Howison are also thanked for all their help with GIS.

To my supervisor Professor Colleen Downs thank you for making this project possible and thank you for the academic and financial support. I would also like to thank Dr. Ricky Taylor for his input into the project.

Mark Kempen from the Department of Water Affairs is thanked for supplying water level data. Mazda Wildlife is thanked for supplying a vehicle for the project. The Hans Hoheisen Charitable Trust kindly provided money for transmitters. The University of KwaZulu-Natal and Water Research Commission are thanked for providing financial assistance. The Bateleurs, and pilots Paul Dutton, Donovan Barton-Hobbs and Chris van den Berg are thanked for conducting aerial surveys. Cliff Dearden is thanked for his assistance with VHF transmitters.

To my family and Jenny Preiss, thank you so much for all the support. Bill and Di thank you for looking after me in Pietermaritzburg during the write up of this thesis. Anne and Louis Botha, thank you so much for accommodating me as well. To all my friends who showed an interest in the project and helped out with capture activities, thank you very much it made a world of difference. A special thanks to Dr. Bruce Finnemore for donating electronic equipment and tags for the mark-resight studies.

TABLE OF CONTENTS

ABSTRACT	i
PREFACE	iv
DECLARATION 1 – PLAGIARISM	v
DECLARATION 2 – PUBLICATIONS	vi
ACKNOWLEDGEMENTS	viii
TABLE OF CONTENTS	x
CHAPTER 1: GENERAL INTRODUCTION	
1.1 STUDY ORGANISM	1
1.1 Nile Crocodiles in Africa	2
1.1.2 Nile Crocodiles in South Africa	4
1.2 AIMS AND OBJECTIVES	7
1.3 STUDY AREA	9
1.3.1 Location	9
1.3.2 Historical Information	10
1.3.3 Ecology of the study area	11
1.3.4 Climate	11
1.3.5 Geology and Geomorphology	12
1.3.6 Hydrology	13
1.3.6.1 Phongola River and floodplain	13
1.3.6.2 Usuthu River and floodplain	14
1.3.6.3 The Maputo River (Rio Maputo) and floodplain	15
1.4 CONCLUSION	16
1.5 REFERENCES	17
ANNEX 1 – ETYMOLOGY	31
 CHAPTER 2: HABITAT USE OF NILE CROCODILES IN THE PHONGOLA, USUTHU AND RIO MAPUTO FLOODPLAINS: A NATURALLY PATCHY ENVIRONMENT	
2.1 ABSTRACT	32
2.2 INTRODUCTION	33

2.2.1 Spatial distribution patterns and the question of scale	33
2.2.2 Landscape as a unit of spatial scale	33
2.2.3 Habitat use of Nile Crocodiles	35
2.2.4 Distribution records of Nile Crocodiles in Ndumo Game Reserve	37
2.3 METHODS	38
2.3.1 Study Site	38
2.3.1.1 Usuthu River	39
2.3.1.2 Phongola River and floodplain	39
2.3.1.3 Lake Nyamithi	40
2.3.1.4 The Maputo River (Rio Maputo) and floodplain	41
2.3.2 Methods	41
2.3.2.1 Diurnal counts	42
2.3.2.2 Stratification of the study site	43
2.3.2.3 Aerial Surveys	43
2.3.3 Statistical analyses	44
2.3.3.1 Between systems and within systems	44
2.3.3.2 Lake Nyamithi	45
2.4 RESULTS	45
2.4.1 Distribution of abundance of Nile Crocodiles between river systems	45
2.4.2 Distribution of abundance of Nile Crocodiles within river systems	46
2.4.2.1 Usuthu River system	46
2.4.2.2 Phongola River System	47
2.4.2.3 Lake Nyamithi	48
2.5 DISCUSSION	49
2.5.1 Environmental conditions influencing habitat use	49
2.5.1.1 Lake Nyamithi and the influence of temperature	49
2.5.1.2 Water level and rainfall	52
2.5.2 Ontogenetic changes in environmental conditions influencing habitat use	53
2.5.3 Distribution of abundance from a landscape perspective	54
2.5.3.1 Landscape complementation	54

2.5.3.2 Landscape composition and physiognomy	55
2.5.3 The Rio Maputo floodplain	58
2.6 CONCLUSION	59
2.7 ACKNOWLEDGEMENTS	61
2.8 REFERENCES	61
LIST OF FIGURES	68
TABLE	69
FIGURES	70
ANNEX 2	80
CHAPTER 3: MOVEMENT AND HOME RANGE OF NILE CROCODILES IN NDUMO GAME RESERVE, SOUTH AFRICA	
3.1 ABSTRACT	81
3.2 INTRODUCTION	82
3.3 METHODS	86
3.3.1 Study site	86
3.3.2 Capture techniques	87
3.3.3 Transmitter attachment	89
3.3.4 Radio tracking activities to estimate home range	90
3.3.5 Mark-resight	91
3.4 STATISTICAL ANALYSES	91
3.4.1 Home range	91
3.4.2 Transmitter attachment longevity	93
3.4.3 Statistical analysis	94
3.5 RESULTS	94
3.5.1 Catching and transmitter fitting	94
3.5.2 Morphometrics	95
3.5.3 Radio tracking to show movements	95
3.5.4 Mark-resight	98
3.5.5 Home range	99
3.5.6 Transmitter attachment longevity	99

3.6 DISCUSSION	100
3.6.1 Telemetry	101
3.6.2 Movement patterns – within seasons	102
3.6.3 Movement patterns – between seasons	103
3.6.4 Home range	106
3.6.5 Territoriality	107
3.7 CONCLUSION	109
3.8 ACKNOWLEDGEMENTS	109
3.9 REFERENCES	110
LIST OF FIGURES	117
FIGURES	118
TABLE	121

CHAPTER 4: POPULATION DYNAMICS OF NILE CROCODILES IN NDUMO GAME RESERVE, SOUTH AFRICA

4.1 ABSTRACT	129
4.2 INTRODUCTION	130
4.3 METHODS	132
4.3.1 Study site	132
4.3.2 Historical data	132
4.3.3 Aerial surveys	133
4.3.4 Correction factors	135
4.3.5 Stratification	137
4.3.6 Capture techniques	137
4.5 RESULTS AND DISCUSSION	138
4.5.1 Aerial surveys	138
4.5.2 Population growth	138
4.5.3 Population stabilisation	140
4.5.4 Sex ratios	141
4.6 CONCLUSION	143
4.7 ACKNOWLEDGEMENTS	144

4.8 REFERENCES	145
LIST OF FIGURES	150
TABLES	151
FIGURES	154
CHAPTER 5: THE PAST AND PRESENT NESTING ECOLOGY OF NILE CROCODILES IN NDUMO GAME RESERVE, SOUTH AFRICA: REASON FOR CONCERN?	
5.1 ABSTRACT	157
5.2 INTRODUCTION	158
5.3 METHODS	161
5.3.1 Study area	161
5.3.2 Sub-division of the study area	161
5.3.3 Nest surveys	162
5.3.4 Historical nesting data	165
5.3.5 Aerial surveys	166
5.3.6 Ground surveys	166
5.3.7 Boat survey	167
5.3.8 Estimates of Nile Crocodile nesting effort	167
5.3.9 Statistics	168
5.4 RESULTS	168
5.4.1 Nest surveys	168
5.4.2 Nest success	170
5.4.3 Characteristics of nesting sites	171
5.4.4 Nesting effort	172
5.5 DISCUSSION	173
5.5.1 Location of nesting sites	173
5.5.2 Nesting effort	173
5.5.3 Availability of suitable nesting habitat in NGR and the spatial clumping of nests	174

5.5.4 The availability of fresh water and burrows	176
5.5.5 Availability of prey items	177
5.5.6. Nursery habitat	178
5.5.7 Communal nesting – limited habitat hypothesis	180
5.5.8 Communal nesting – reduced predation hypothesis	181
5.5.9 Historical nesting – cultural and genetic inheritance hypothesis	183
5.5.10 Nesting outside of Ndumo	184
5.6 CONCLUSION	185
5.7 ACKNOWLEDGEMENTS	185
5.8 REFERENCES	186
LIST OF FIGURES	192
FIGURES	193
TABLE	197
 CHAPTER 6: MANAGEMENT IMPLICATIONS FOR THE NDUMO GAME RESERVE NILE CROCODILE POPULATION	
6.1 INTRODUCTION	198
6.2 RECOMMENDATIONS	199
6.4 CONCLUSION	208
6.5 REFERENCES	209
 CHAPTER7: CONCLUSIONS	
7.1 CONCLUSIONS	213
7.2 REFERENCES	216

CHAPTER 1

General Introduction

1.1 STUDY ORGANISM

The Nile Crocodile (*Crocodylus niloticus*), taxonomy and etymology summarized in Annex 1, is one of 23 extant crocodylian species of the sub-order Eusuchia, first appearing in fossil record in the Cretaceous period some 150-65 million years ago (Leslie, 1997). The Eusuchians, or modern day crocodiles consist of the Family Crocodylidae which is in turn made up of three sub-families: the Crocodylinae, the Alligatorinae and the Gavialidae. Crocodylians are found throughout (but are not restricted to) the tropics between the Tropic of Cancer (23° 26' north of the Equator) and the Tropic of Capricorn (23° 26' south of the Equator) in a variety of habitats including rivers, lakes, fresh water swamps, artificial impoundments, estuarine and brackish water environments in Africa, Asia, Australia and the Americas (Leslie, 1997; Botha, 2005). The African continent is home to three crocodylian species all of the sub-family Crocodylidae namely; the African Dwarf Crocodile (*Osteolaemus tetraspis*), the African Slender-snouted Crocodile (*Mecistops cataphractus*) and the Nile Crocodile (*Crocodylus niloticus*) (Blake, 2006).

Nile Crocodiles occur throughout most of Africa while the Slender-snouted and Dwarf Crocodiles are found only in the equatorial rainforest belt of central and western Africa (Eaton, 2010; Shirley, 2010). The wide spread distribution of Nile Crocodiles in Africa combined with the economic importance of the animal in the leather trade has resulted in the Nile Crocodile being studied extensively in recent years (Botha et al., 2010) and it is by far the most biologically well known of the African crocodiles (Ross, 1998). However, less than half of the 42 countries where Nile Crocodiles occur have some indication of population status with 30% of these

countries having a severely depleted population, 60% a somewhat depleted population and only 10% a population which is not depleted (Ross, 1998; Botha, 2005). Generally Nile Crocodile populations have been compromised in western Africa while southern and eastern Africa are home to secure populations with a moderate need for population recovery (Ross, 1998). This is largely due to the majority of scientific research focused on Nile Crocodiles taking place in southern and eastern Africa (Table 1). However in recent years there has been a broadening in focus with the Crocodile Specialist Group (CSG) convening meetings and promoting much needed crocodile research in West and Central Africa.

1.1.1 Nile Crocodiles in Africa

The natural geographic range of the Nile Crocodile transcends sub-Saharan Africa extending northwards into Egypt and eastward to Madagascar. Localized extinctions in the eponymous Nile River and delta at the turn of the 18th century, in the Comoros and Algeria in the early 19th century and in Israel in the early 20th century have done much to reduce this range (Leslie, 1997; Ross, 1998). Over the last century hunting and poaching for hides, reduction and degradation/pollution of suitable aquatic habitat and extirpation due to perceived and real threats to humans, livestock and wildlife has resulted in severe population reduction of Nile Crocodiles through much of their remaining natural range (Gans and Pooley, 1976; Jacobsen, 1984; Hocutt et al., 1992; Botha et al., 2011; Combrink et al., 2011; Wallace et al., 2011; Woodborne et al., 2012; Bourquin and Leslie, 2012; Wallace et al., 2013). On a global scale, the listing of *C. niloticus* as a Threatened species by the International Union for Conservation of Nature (IUCN) and the ensuing protection against hunting and/or poaching arguably helped stop population collapse within protected areas while the establishment of sustainable hide production through

legal crocodile ranching and farming made illegal harvesting of hides from wild populations unprofitable (Jacobsen, 1984; Child, 1987; Ross, 1998). Regulation in trade by the Convention on International Trade in Endangered Species of Wild Fauna and Fauna (CITES) and marketplace changes (conservationism, globalization and liberalization, fashion trends) resulted in a shift from the exploitation of wild specimens to an increased reliance on the more consistent supply of higher quality skins from captive reared animals (MacGregor, 2002). As a result Nile Crocodile populations have recovered throughout much of their former range and viable populations can now be found in Botswana, Ethiopia, northern Kenya, Malawi, South Africa, Zambia and Zimbabwe (Leslie, 1997).

However, recovering crocodile populations come at a cost. Conflict between humans and crocodiles (Human Crocodile Conflict or HCC) is on the increase globally and can be attributed to recovering crocodile populations coming into increasing contact with humans or increased encroachment of humans on crocodile habitat (Aust et al., 2009; Wallace et al., 2011). For example in the United States recovery of Alligator populations due to protection initiated in the 1970's has resulted in an increase in human-alligator encounters (Langley, 2005). Recovering *C. porosus* populations in Australia have resulted in an increase in HCC as well (Letnic and Connors, 2006). However HCC is most severe in Africa with Nile Crocodiles accounting for more human fatalities than any other species of crocodile in the world (Wallace et al., 2011). In some African countries Nile Crocodiles account for the majority of all wildlife related mortalities (Child, 1987; Dunham et al., 2010). In many areas controlling HCC has taken priority over previous management activities such as ranching or harvesting quotas and trophy hunting (Fergusson, 2010).

1.1.2 Nile Crocodiles in South Africa

The historical range of the Nile Crocodile in South Africa includes every major river and estuary on the eastern seaboard of the country extending as far south as the Eastern Cape (Pooley, 1982). However, populations are now restricted to the northern and eastern portions of the country between the Limpopo River in the north and the Tugela River in the south (Branch, 1998; Combrink, 2004; Van Vuuren, 2011). The spread of agricultural activities in the early 20th century resulted in an increase in unfavorable habitat transformations within this range while an influx of firearms associated with the Anglo-Zulu, Anglo-Boer and ultimately the First and Second World Wars resulted in significant population declines due to extirpation (Pooley, 1982). Between the 1940's and 1960's in particular, hunting and poaching for hides and eradication programs due to perceived and real threats to humans, livestock and wildlife resulted in severe population reduction of Nile Crocodile numbers through much of the remaining geographic range (Gans and Pooley, 1976; Hocutt et al., 1992; Ross, 1998; Combrink, 2004; Botha, 2005).

The Reptiles Protection Ordinance was introduced in 1968 and instituted in 1969, prior to which Nile Crocodiles were viewed as vermin and actively persecuted throughout South Africa (Pooley, 1969). Nile Crocodile were no longer 'fair game' and permits had to be obtained in order to hunt animals on state land, although land owners could destroy animals themselves or give written permission for others to do so on their property (Pooley, 1982). From an international perspective the Nile Crocodile was listed as Threatened in the IUCN Red List lending weight to conservation efforts and garnering public awareness and support for protection of the species. In 1975 the Nile Crocodile appeared in Appendix I of CITES aimed at reducing illegal harvesting though restricting trade in their skins. The South Africa population of Nile Crocodiles was transferred to Appendix II of CITES with an export quota in 1992, and Appendix

II for ranching in 1995, allowing legal production of crocodile skins (Kievit, 2000). Protection given by national laws, international trading regulations and indirectly through the establishment of competitive crocodile farming saw population recoveries throughout much of South Africa (Hocutt et al., 1992; Ross, 1998).

However, in recent years the crocodile populations in several South African rivers and lakes have undergone severe setbacks (Branch, 1998; Botha et al., 2011; Combrink et al., 2011; Ferreira and Pienaar, 2011). Legislation has done little to protect crocodile habitat in the face of increasing agricultural and industrial development and crocodile numbers continue to decline due to water pollution and habitat transformation (Ashton, 2010; Van Vuuren, 2011; Woodborne et al., 2012). Crocodile husbandry introduced in the 1990's is based exclusively on captive breeding in South Africa placing little economic value on crocodile habitat outside of protected areas.

On the contrary, Nile Crocodiles pose a significant threat to the livelihood and livestock of people living in rural areas dependent on rivers and lakes for water and when discovered crocodiles nests and eggs are readily destroyed (McGregor, 2005; Aust et al., 2009; Combrink and Taylor, 2009; Wallace et al., 2011). The only economic benefit in these areas comes from the informal market where crocodile products such as blood, fat and organs are sought after in the indigenous medicine or 'muthi' trade (Combrink and Taylor, 2009). Unsurprisingly viable populations exist exclusively within formally conserved areas such as the Kruger National Park, Lake St. Lucia, Pongolapoort Dam and Ndumo Game Reserve (NGR) where they are regarded as tourist attractions (Leslie, 1997; Combrink, 2004; Champion, 2011).

However, crocodiles are becoming increasingly appreciated in the role they play as indicators of ecosystem health (Botha, 2005; Yoshikane et al., 2006; Rainwater et al., 2007;

Poletta et al., 2008; Poletta et al., 2009; Botha, 2010; Stoker et al., 2011). Nile Crocodiles are apex aquatic predators that are considered essential in maintaining the structure and function of aquatic ecosystems through selective predation on fish species, recycling of nutrients and maintenance of wetlands in times of drought (Bourquin, 2008). As such Nile Crocodiles are considered keystone species in aquatic ecosystems where they occur (Ashton, 2010). For example, Whitaker and Whitaker (1979) found that freshwater ecosystems and fisheries in India declined following the removal of crocodiles while fisheries in Uganda were also reported to decline after the official eradication of Nile Crocodile in the 1950's (pers comms Richard Ferrugson). In the Everglades, Alligator (*Alligator mississippiensis*) holes provide important refuge for numerous other aquatic organisms (Liu et al., 2012). Unfortunately there are only a handful of studies that have investigated the role that crocodiles play as apex predators in aquatic ecosystems.

When one considers the potential (and as yet largely un-quantified) roles that crocodiles may play in aquatic ecosystems it becomes of great concern that previously secure Nile Crocodile populations within protected areas are on the decline. Kruger National Park holds the largest population of Nile Crocodiles in South Africa and recently faced a population decline of well over 200 animals over one and a half years due to a pansteatitis epidemic (Osthoff, 2010). The ultimate cause is undoubtedly industrial and agricultural development and ensuing pollution of the Olifants River prior to entry into the reserve (Ashton, 2010; Ferreira and Pienaar, 2011). The Loskop Dam (also on the Olifants River) crocodile population has declined from 25 in 2007 and consists of just 4 individuals today (Botha et al., 2011) also due to a pansteatitis epidemic (Woodborne, 2012). Lake St. Lucia, the second largest population in South Africa is currently facing a population decline due to increased salinity levels associated with ongoing drought

exacerbated by the divergence of fresh water rivers out of the estuary for agricultural purposes (Pooley, 1982; Leslie, 1997; Whitfield and Taylor, 2009). The Lake Sibaya Nile Crocodile population has dropped from over 100 in 1990 to just 7 in 2009 (Combrink et al., 2011). In 2009 concern was raised that the Ndumo Game Reserve (NGR) population was declining however reasons for the decline were not known, stimulating the current study to authenticate the decline in population size and to determine reasons for the decline.

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). 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.

1.2 AIMS AND OBJECTIVES

Conservation biology makes use of an increasingly integrative approach in the protection and management of biodiversity, adopting appropriate principles and experiences from basic biological fields such as genetics, economics and ecology (Meffe and Carrol, 1997). Ecological study forms an integral part of conservation biology and involves the scientific study of the distribution and abundance of organisms as well as the interactions that determine distribution and abundance (Townsend, 2003). In this study we examined the ecology of the Nile Crocodiles over a two year period at NGR in order to collect data on a suite of environmental and ecological

factors and through scientific process aid in the conservation of the species. The following aims were identified at the outset of the project:

1. Determine the NGR Nile Crocodile population status. Relate the current population size to previous estimates in order to determine any trends in population change and the success of restocking programs initiated in the late 1960's
2. Determine the population age structure and sex ratios of Nile Crocodiles to predict future changes in population size.
3. Determine the home range of Nile Crocodiles in NGR in order to understand the spatial requirements and hierarchical status of individuals.
4. Map the present distribution of Nile Crocodiles in NGR and compare past distribution patterns to the present, with particular reference to changes in habitat.
5. Examine movement patterns in order to discover any morphological and geomorphological factors influencing habitat use.
6. Investigate the nesting ecology of Nile Crocodiles in NGR with particular reference to habitat use, nesting effort and recruitment.
7. Identify habitat used by the NGR Nile Crocodile population outside of the reserve.
8. Provide timely and informed suggestions as to the future management and conservation of the NGR Nile Crocodile population.

To achieve these aims the study was divided into four core areas covered in four separate chapters; Chapter 2 Spatial Ecology and Habitat Use; Chapter 3 Population Dynamics; Chapter 4 Reproductive Ecology and Chapter 5 Nesting Ecology. None of these components are mutually

exclusive as each component is interrelated with the next. These interrelations and their implications are discussed in Chapter 6, Management Implications for Nile Crocodiles in Ndumo Game Reserve. Chapter 7 is a concluding chapter and summarises the findings of the study. The current chapter, Chapter 1, serves as an introduction to the study area, the study organism and the approach of the study. As the chapters are prepared as stand alone manuscripts some repetition has been unavoidable.

1.3 STUDY AREA

NGR is a relatively small Ezemvelo KZN Wildlife (EKZNW) reserve in North Eastern KwaZulu-Natal (Pg. 67 Fig. 1, Chapter 2) and is one of the oldest game reserves in South Africa. Proclaimed in 1924 as a sanctuary for the Hippopotamus (*Hippopotamus amphibius*) the 10000ha reserve inadvertently conserves ideal Nile Crocodile habitat and supports South Africa's third largest Nile Crocodile population (Pooley, 1982; Combrink, 2004). NGR is a pioneer in Nile Crocodile research in South Africa and studies conducted here by Anthony Pooley from 1962 - 1982 form a foundation upon which further research of the species has been based.

1.3.1 Location

NGR is situated in the Mozambique Coastal Plain between the latitude 26°50' to 26°54' South and longitude 32°09' to 32°21' East. The reserve is an elongated trapezoid in shape with the longest axis lying east to west (Fig. 1, Chapter 2). 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 (Fig. 1, Chapter 2). The confluence

of these two major river systems in the north east corner of the reserve and the flat nature of the Mozambique Plain conspire to inundate large tracts of the reserve during times of high rainfall forming one of the largest floodplain systems in South Africa (Pooley, 1982).

1.3.2 Historical information

Historical accounts of traders, hunters and explorers suggest that in the past the Phongola, Usuthu and Rio Maputo floodplains surrounding Ndumo were well populated with Nile Crocodiles although no exact numbers are known (Sandwith et al., 1997). However, Nile Crocodiles were viewed as vermin with a reward of ten shillings (about R1.00) per head and three pennies (about 2.5 c) per egg (Pooley, 1982). In the Phongola floodplain (1880's) and later the Usuthu River (1900's) poisoned bait (strychnine) was used to harvest Nile Crocodiles with yields of up to 150 animals per month (Pooley, 1982). The Phongola River and floodplain continued to be intensively hunted from Jozini to the NGR border, as did the Usuthu River from Swaziland alongside NGR to the Mozambique border up until 1969 when protection was finally afforded through the Reptiles Protection Ordinance (Pooley, 1982). At this stage Swaziland offered no protection to Nile Crocodiles while Mozambique initiated protection in the southern portion of the country bordering on South Africa in 1967. In the Mozambique Bulletin No. 17, series 1 (1967) protected crocodiles under 1.5 m in length while no crocodile could be hunted whatsoever during September to March (Pooley, 1982). Nile Crocodile populations failed to re-colonise areas outside of NGR in South Africa after protection was awarded in 1969, largely due to anthropogenic disturbances and transformation of riverine habitat (Pooley, 1982). Today NGR houses the remnants of a much larger population which has been extirpated in the Phongola and Usuthu Rivers and floodplains outside of the reserve while the southern portions of the Rio

Maputo floodplain in Mozambique is thought to house a viable Nile Crocodile population (Fergusson, 2010).

1.3.3 Ecology of the study area

NGR lies within the Maputoland Centre of Endemism and is an internationally recognised Important Birding Area (IBA) home to over 420 bird species. Thirty five of these bird species are considered nationally threatened and are included in the South African Red Data Book of which nineteen are waterfowl dependent on the floodplain (Kyle and Marneweck, 1996). The Phongola River system has the greatest diversity of fresh water fish species in South Africa with 50 species, two of which are in the South African Red Data book (Kok, 1980). In 1997 NGR was listed in the Directory of Wetlands of International Importance (Ramsar Site No. 887) (Sandwith et al., 1997). NGR is also home to 10 reptile species in the South African Red Data book including the Nile Crocodile (Sandwith et al., 1997).

1.3.4 Climate

NGR is situated in the central Tongoland sector of the Mozambique Coastal Plain and although 400km south of the Tropic of Capricorn, the extremely low relief (80 m a.s.l.) and the effects of the warm Mozambique current passing 70km off shore sustain a Tropical Savannah and Dry Forest climate (Sandwith et al., 1997). NGR has a hot, humid tropical climate with seasonal summer rainfall and a dry winter season.

Annual rainfall is around 630-640 mm with the majority of precipitation falling in the form of summer thunderstorms in mid to late summer (November to March) (Wadeson, 2006). However, rainfall patterns can be highly erratic with un-seasonal floods occurring as late as June

and annual precipitation falling below 500 mm during dry years (Sandwith et al., 1997). Rainfall frequently comes from the south west (Sandwith et al., 1997).

Relative humidity is high during summer, exceeding 70% between November and February resulting in heavy dew during this period. Evaporation rate is also very high (particularly between August and April) resulting in dense morning valley mists which are intensified by cold air drainage off the Lebombo range on to the plain at night resulting in heavy dew with occasional light showers (Sandwith et al., 1997).

Daily maximum temperature may exceed 40° C in summer, while an annual mean of 22.9°C (09:00 air temperature) prevails (Wadeson, 2006). Climatic tolerability for humans shows 'acute to serious' discomfort levels from December to March with only a brief period from mid-June to late July falling in what is considered the 'comfortable' range (Heeg and Breen, 1982).

The climatic zone can be classified as Bush - Steppe climate i.e. an arid zone due to a mean annual temperature above 19° C and the low seasonal rainfall with dry winter seasons (Sandwith et al., 1997). Wind direction is predominantly north-east in the dry season and south to south-west during the wet season. During the wet season winds of high velocity (up to 51.5 km h⁻¹) but short duration may be experienced during thunder storms (Sandwith et al., 1997).

1.3.5 Geology and Geomorphology

The majority of NGR is low lying with an average altitude of 30 m a.s.l ranging from 18 m in the floodplain to 170 m on Ndumo Hill (Sandwith et al., 1997; Wadeson, 2006). Geologically, the area is comprised of cretaceous beds which produce saline groundwater overlain with alluvium and tertiary sediments (Wadeson, 2006). Ndumo Hill consists primarily of red sands and slopes gently towards the Phongola floodplain in the east to north east and the Usuthu River and floodplain in the north to north

west. The majority of the rather flat area between Ndumo hill and the Usuthu consists of reddish sandy clay (6316 ha), as does the western area of the reserve (648 ha). Between Ndumo Hill and the Phongola floodplain is roughly 1151 ha of sandveld composed of undulating pallid sands at an altitude of 30 m followed by grey compacted coarse sandy clay (Sandwith et al., 1997).

1.3.6 Hydrology

NGR conserves two major river systems; the Usuthu River flows east to west along the northern boundary of the reserve while the Phongola River and floodplain runs from south to north through the eastern portion of the reserve (Fig. 2, Chapter 2). These two rivers meet in the north eastern corner of the reserve and together inundate over 40% (4047 ha) of the reserve during the wet season. During the average dry season roughly 15% of the surface area of the reserve is covered by water in the form of 12 permanent pans and the two river courses. However, while the floodplain may be inundated for several weeks or even months of the year, it may not be fully inundated for several consecutive seasons (Sandwith et al., 1997).

1.3.6.1 Phongola River and floodplain

The Phongola River descends steeply through 7700 km² of catchment area in the Mpumalanga Province of South Africa exiting the Lebombo Mountain range in KwaZulu-Natal at Jozini through the Pongolapoort Dam. Immediately hereafter the river encounters the flat Maputoland coastal plain depositing finely sorted sediment in a 100 km x 3 km strip forming the Phongola floodplain. Upon entering NGR the main course of the river bifurcates forming an old and a new course (Fig. 2, Chapter 2). 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 (*Hippopotamus amphibius*) pathways which traverse the floodplain linking all of these courses with one another as well as with permanent and ephemeral pans. Lake Nyamithi by definition is a pan, not a lake but is known as Lake Nyamithi and has been referred to as such in previous studies. We therefore refer to Nyamithi as Lake Nyamithi in this study.

The major pans in the Phongola floodplain include Lake Nyamithi and Polwe Pan. The largest permanent pan in the Phongola floodplain is Lake Nyamithi (157 ha).

1.3.6.2 The Usuthu River and floodplain

The catchment area of the Usuthu River (16 967 km²) spans three countries namely South Africa (Mpumalanga Province), Swaziland, and to a lesser extent Mozambique (Wadeson, 2006). After exiting Swaziland through a gorge in the Ubombo mountain range the Usuthu immediately encounters the flat Mozambique coastal plain creating a reduced flow rate, depositing sediments in a floodplain composed mostly of sandy alluvium (Wadeson, 2006).

Due to extensive flooding in 2000 and sedimentation the main course of the Usuthu has bifurcated flowing southward into the reserve and through Banzi Pan, the largest Pan in Ndumo (270 ha, Fig. 2, Chapter 2). The new course of the Usuthu meets the old course of the Phongola in the region of Bakabaka Pan and the main course of the Phongola in the north eastern corner of the reserve. The original course of the Usuthu only flows during summer months when rainfall in the catchment area elevates the water level sufficiently.

1.3.6.3 The Maputo River (Rio Maputo) and floodplain

For the purposes of this study and for comparison to previous studies we refer to the origin of the Rio Maputo as the junction of the Pongola and Usuthu Rivers just north of the eastern boundary of NGR. There are no tributaries that join the Rio Maputo along its 135km journey from this junction to the ocean at Maputo Bay to the north-west. The catchment area is therefore a combination of those described for the Usuthu and Pongola Rivers. Approximately 10km downstream from the junction is the only and largest lake (Lake Pandejene) in the Rio Maputo Floodplain. The lake is joined to the main course of the Rio Maputo through a side channel of the river during periods of high water levels in summer (JMRBWRS, 2008) and through a swampy area for the rest of the year (Kramer, 2003). Downstream of Pandjene the river meanders through a shallow valley about 2 to 5km wide and itself has a width of 50 -100m with numerous bends and steep banks (Kramer, 2003). The river only starts to widen out in the vicinity of Salamanga 95km downstream and 40km from the mouth where the width is from 2 to 8km wide. The eastern shore of the river is protected by the Maputo Special Reserve and is characterized by extensive Mangrove forests and brackish tidal lakes adjacent to both sides of the main channel.

The extremely low gradient of the river ($<1:3000$) results in tidal influence on water levels 65 – 70 km inland and salt water intrusion as high up as Salamanga (40km inland) (Kramer, 2003). According to the Department of Water Affairs (DWA) the habitat integrity of the Maputo floodplain from the confluence of the Pongola and Usuthu downstream to the zone of tidal influence is placed in the “B” category: “largely natural with few modifications” and

that although “a small change in natural habitats and biota may have taken place but the ecosystem functions are essentially unchanged” (JM RBWRS, 2008).

Historical records suggest that several small dykes were constructed in the Rio Maputo between Salamanga and Lake Pandejene for irrigation purposes, but evidence of these is no longer visible and they were more than likely destroyed in either the 1984 or 2000 floods (Kramer, 2003). The 2000 floods in some ways have helped restore connectivity within the floodplain system (Kyle, 2002). Along with the construction of dykes extensive drainage canals were excavated in the Rio Maputo floodplain by Portuguese colonists to drain the floodplain for agricultural activities (Kramer, 2003). These are still in evidence today and presumably influence the hydrology of the floodplain.

1.4 CONCLUSION

In conclusion it is important to note the following about the study site. The amount of aquatic habitat available to Nile Crocodiles fluctuates widely on a seasonal basis and is determined by water level in either the Usuthu or Phongola rivers. The catchment areas of these two rivers is some distance from the reserve and localized rainfall has little effect on water levels, and levels may increase dramatically with little or no rainfall having taken place in the reserve. Water levels in the Phongola River are controlled by the Pongolapoort/Jozini Dam and are also not related to rainfall. An annual artificial flood release takes place in late September/early October and completely inundates the floodplain areas within NGR. Although the Phongola and Usuthu rivers meet in the north eastern corner of the reserve, high water levels in either one of these rivers can completely inundate low lying areas of the reserve through back filling and due to the low relief and gradient synonymous with the Mozambique Plain upon

which the reserve is based. The early flooding of the reserve due to the artificial water release in spring can be followed by flooding of the Usuthu due to high rainfall during summer months such that the reserve remains inundated for extended periods of time. Nile Crocodiles are free to move out of NGR into the Phongola, Usuthu or Rio Maputo floodplains and there is evidence suggesting crocodiles do leave the reserve during high water levels in summer. Access to the floodplain is severely hampered during periods of high water levels making field work during this period challenging.

1.5 REFERENCES

- ASHTON, P. J. 2010. The demise of the Nile Crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in South Africa: The case of the Olifants River. *Aquatic Conservation of Marine and Freshwater Ecosystems* 20:489–493.
- AUST, P., B. BOYLE, R. FERGUSON, AND T. COULSON. 2009. The impact of Nile Crocodiles on rural livelihoods in Northeastern Namibia. *South African Journal of Wildlife Research* 39:57–69.
- BISHOP, J. M., AUST, P., COTTERILL, F. P. D. , LESLIE, A. J. AND C. O'RYAN. 2008. Colonizing a desert wetland: Population history of the Nile Crocodile in south central Africa represents a biotic signature from an ancient palaeo-lake. 11th Congress of the European Society of Evolutionary Biology, 20-25 August 2007 Uppsala, Sweden.
- BISHOP, J. M., LESLIE, A. J., BOURQUIN, S. L., AND C. O'RYAN. 2009. Reduced effective population size in an overexploited population of the Nile Crocodile (*Crocodylus niloticus*). *Biological Conservation* 142:2335–2341.

- BLAKE, D. K. 2006. The Nile Crocodile, *Crocodylus niloticus*: Capture, care, accomodation and transportation. Wildnet Africa- Capture and care manual. Pp 1-20.
- BLAKE, D. K., AND J.P. LOVERIDGE.1987. Observations on the behavior of Nile Crocodiles *Crocodylus niloticus* in captivity. *In: Wildlife management: Crocodiles and Alligators*. G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.). Surrey Beatty and Sons, Sydney. Pp 295-300.
- BOTHA, P. J. 2005. The ecology and population dynamics of the Nile crocodile *Crocodylus niloticus* in the Flag Boshielo Dam, Mpumalanga Province, South Africa. MSc thesis. University of Pretoria, Pretoria.
- BOTHA, P.J. 2010, The distribution, conservation status and blood biochemistry of Nile crocodiles in the Olifants river system, Mpumalanga, South Africa, PhD thesis, University of Pretoria, Pretoria.
- BOTHA, H., VAN HOVEN, W. AND L.J. JR GUILLETTE. 2011. The decline of the Nile crocodile population in Loskop Dam, Olifants River, South Africa. *Water SA* 37:103–108.
- BOURQUIN, S. V. 2008. The population ecology of the Nile Crocodile (*Crocodylus niloticus*) in the Panhandle Region of the Okavango Delta, Botswana. PhD thesis. University of Stellenbosch, Stellenbosch.
- BOURQUIN, S. L. AND A. J. LESLIE.2012. Estimating demographics of the Nile crocodile (*Crocodylus niloticus* Laurenti) in the panhandle region of the Okavango Delta, Botswana. *African Journal of Ecology* 50:1-8.
- BRANCH, W. R. 1998. Status of the Nile Crocodile in Natal, South Africa. Unpublished report.

- BROWN, C. J., STANDER, P., MEYER-RUST, R., AND S.MAYES. 2004. Results of a Crocodile *Crocodylus niloticus* survey in the river systems of north-east Namibia during August 2004. Namibia Nature Foundation, Wildlife Science and Lianshulu Lodge.
- CHAMPION, G. 2011. The Ecology of Nile Crocodile (*Crocodylus niloticus*) in Pongolapoort Dam, Northern KwaZulu-Natal, South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.
- CHILD, G. 1987. The management of crocodiles in Zimbabwe. In: Wildlife Management: Crocodiles and alligators (eds G.J.W. Webb, S.C. Manolis & P.J. Whitehead). Surrey Beaty and Sons, Australia.
- CLOUDSLEY-THOMPSON, J. L. 1964. Diurnal rhythm of activity in the Nile crocodile. *Animal Behaviour* 12:98-100.
- COMBRINK, A. S. 2004. Population status of *Crocodylus niloticus* (Nile Crocodile) at Lake Sibaya, Republic of South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X. 2013. Spatial and reproductive ecology and population dynamics of the Nile Crocodile (*Crocodylus niloticus*) in the St Lucia Estuarine system, South Africa. PhD thesis in prep., University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X., J. L. KORRÚBEL, KYLE, R., TAYLOR, R. AND ROSS, P. 2011. Evidence of a declining Nile Crocodile (*Crocodylus niloticus*) population at Lake Sibaya, South Africa. *South African Journal of Wildlife Research* 41:145-157.
- COMBRINK, X., AND R. TAYLOR. 2009. Nile Crocodile aerial survey at Lake Sibaya 26 July 2009. Ezemvelo KZN Wildlife. Unpublished Report.

- COMBRINK, X., WARNER, J. AND DOWNS, C. T. 2013. Crocodiles, p. 332 - 253. *In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. D. D. S. a. R. H. T. Renzo Perissinotto (ed.). Cambridge University Press, Cambridge.
- COTT, H. B. 1961. Scientific results of an enquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London* 29:211-356.
- COTT, H. B., AND A. C. POOLEY. 1971. Crocodiles: The status of crocodiles in Africa. *In: IUCN Conference Paper No. 33*. Vol. 2, Gland, Switzerland.
- DOWNS, C. T., GREAVER, C., AND R. TAYLOR. 2008. Body temperature and basking behaviour of Nile crocodiles (*Crocodylus niloticus*) during winter. *Journal of Thermal Biology* 33:185–192.
- DUNHAM, K. M., A. GHIURGHI, R. CUMBI, AND F. URBANO. 2010. Human–wildlife conflict in Mozambique: a national perspective, with emphasis on wildlife attacks on humans. *Oryx* 44:185-193.
- FERGUSON, R. 2010. Wildlife survey phase 2 and management of human-wildlife conflicts in Mozambique. *In: Survey of Crocodile Populations in Mozambique*. Vol. Part 5. AGRECO G.E.I.E., Brussels, Belgium.
- FERREIRA, S. M. AND D. PIENAAR. 2011. Degradation of the crocodile population in the Olifants River Gorge of Kruger National Park, South Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21:155-164.
- GAMES, I. 1990. The feeding ecology of two Nile Crocodile populations in the Zambezi Valley. PhD thesis. University of Zimbabwe, Harare.

- GAMES, I. 1994. Aerial surveys for monitoring trends and estimating population size of *Crocodylus niloticus* or The theory and practice of aerial survey in Africa. CSG Proceedings, Pattaya, Thailand, 2-6, May, 1994. Crocodile Specialist Group. 1: 245-255.
- GANS, C., AND A. C. POOLEY. 1976. Research on crocodiles? Ecology 57:839-840.
- HARTLEY, D. D. R. 1990. A survey of crocodile nests in Umfolozi Game Reserve. Lammergeyer 41:3-12.
- HEEG, J., AND C.M. BREEN. 1982. Man and the Pongolo floodplain. National Scientific Programmes Unit: CSIR, SANSP Report 56, 1982, pp 129.
- HOCUTT, C. H., J. P. LOVERIDGE, AND J.M. HUTTON. 1992. Biotelemetry monitoring of translocated *Crocodylus niloticus* in Lake Ngezi, Zimbabwe. Journal of Zoology 226:231-242.
- HUTTON, J. M. 1986. Incubation temperatures, sex ratios and sex determination in a population of Nile Crocodiles (*Crocodylus niloticus*). Journal of Zoology (London) 211:143-155.
- HUTTON, J. M. 1987a. Growth and feeding ecology of the Nile Crocodile (*Crocodylus niloticus*) at Ngezi, Zimbabwe. Journal of Animal Ecology 56:25-38.
- HUTTON, J. M. 1987b. Incubation temperatures, sex ratios, and sex determination in a population of Nile Crocodiles (*Crocodylus niloticus*). Journal of Zoology (London) 211:143-155.
- HUTTON, J. M. 1987c. Morphometrics and field estimation of the size of the Nile Crocodile. African Journal of Ecology 25:225-230.
- HUTTON, J. M. 1989. Movements, home range, dispersal and the separation of size classes in Nile Crocodiles. American Journal of Zoology 29:1033-1050.
- HUTTON, J. M., AND J. P. LOVERIDGE. 1999. Resolving conflicts between Nile Crocodiles and man in Africa. The Africa Resources Trust, Cambridge, UK.

- HUTTON, J. M., AND M. E. J. WOOLHOUSE. 1989. Mark-recapture to assess factors affecting the proportion of a Nile Crocodile population seen during spotlight counts at Ngezi, Zimbabwe, and the use of spotlight counts to monitor crocodile abundance. *Journal of Applied Ecology* 26:381-395.
- JACOBSEN, N. H. G. 1984. Distribution and status of crocodile populations in the Transvaal outside the Kruger National Park. *Biological Conservation* 29:191-200.
- KIEVIT, H. 2000. Conservation of the Nile Crocodile: Has CITES helped or hindered? The past, present and future of CITES, the Convention on International Trade in Endangered Species of Wild Fauna and Flora. Edited by J. Hutton and B. Dickson Earthscan Publications Ltd Chapter 8:56-62.
- KOFRON, C. 1989. Nesting ecology of the Nile Crocodile (*Crocodylus niloticus*). *African Journal of Ecology* 27:335-341.
- KOFRON, C. 1990. The reproductive cycle of the Nile Crocodile (*Crocodylus niloticus*). *Journal of Zoology* 211:477-488.
- KOFRON, C. P. 1992. Status and habitats of three African crocodiles in Liberia. *Journal of Tropical Ecology* 8:265-273.
- KOFRON, C. P. 1993. Behavior of Nile Crocodiles in a Seasonal River in Zimbabwe. *Copeia* 2:463-469.
- KOK, H. M. 1980. Ecological studies of some important fish species in the Pongola floodplain. PhD thesis. University of Natal, Pietermaritzburg.
- KRAMER, A. 2003. Managing Freshwater Ecosystems of International Water Resources –The Case of the Maputo River in Mozambique. Working Paper On Management in Environmental Planning 07/2003.

- KYLE, R. 2002. More information from the mark and recapture of fish at Kosi Bay, South Africa. *Koedoe* 45:121-122.
- KYLE, R., and G. MARNEWECK. 1996. Ndumo Game Reserve, South Africa: Information Sheet for the site designated to the List of Wetlands of International Importance. Department of Environmental Affairs and Tourism, Pretoria.
- LANGLEY, R.L. 2005. Alligator attacks on humans in the United States. Ricky L RL Langley · *Wilderness and Environmental Medicine* 16:119-124.
- LESLIE, A. J. 1997. The ecology and physiology of the Nile Crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. PhD thesis. Drexel University, Philadelphia. USA.
- LESLIE, A. J., AND J. R. SPOTILA. 2001. Alien plant threatens Nile crocodile (*Crocodylus niloticus*) breeding in Lake St Lucia, South Africa. *Biological Conservation* 98:347-355.
- LESLIE, A. J., AND J. R. SPOTILA. 2000. Osmoregulation of the Nile crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. *Comparative Biochemistry and Physiology* 126:351–365.
- LETNIC, M., AND G. CONNORS. 2006. Changes in the distribution and abundance of saltwater crocodiles, *Crocodylus porosus*, in the upstream freshwater reaches of rivers in the Northern Territory, Australia. *Wildlife Research* 33:529-538.
- LIU, Z., L.A. BRANDT, D.E. OGURCAK AND F.J. MAZZOTTI. 2012. Morphometric and hydrologic characteristics of alligator holes in Everglades National Park, Florida from 1994 to 2007. *Ecohydrology* DOI: 10.1002/eco.1266 early view.
- LOVERIDGE, J. P. 1996. A review of crocodile management in Zimbabwe. Department of Biological Sciences. University of Zimbabwe, Harare. Unpublished report.

- MACGREGOR, J. 2002. International Trade in Crocodilian Skins: Review and analysis of the trade and industry dynamics for market-based conservation. IUCN/SSC Crocodile Specialist Group; TRAFFIC; International Resource Africa, London.
- MCGREGOR, J. 2005. Crocodile crimes: people versus wildlife and the politics of postcolonial conservation on Lake Kariba, Zimbabwe. *Geoforum* 36:353–369.
- MEFFE, G. K., AND C. R. CARROL. 1997. Principles of Conservation Biology. 2nd Edition. Sinauer Associates Inc. Sunderland, Massachusetts, USA.
- MODHA, M. L. 1967. The ecology of the Nile Crocodile, *Crocodylus niloticus* Laurenti. 1786, on Central island, Lake Rudolph. *East African Wildlife Journal* 5:74-95.
- OSTHOFF, G., HUGO, A., BOUWMAN, H., BUSS, P., GOVENDER, D., JOUBERT, C. C. AND J. C. SWARTS. 2010. Comparison of the lipid properties of captive, healthy wild, and pancreatitis-affected wild Nile Crocodiles (*Crocodylus niloticus*). *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology* 155:64-69.
- POLETTA, G.L., A. LARRIERA, AND P. A. SIROSKI. 2008. Broad snouted caiman (*Caiman latirostris*) growth under different stocking densities. *Aquaculture* 280:264-266.
- POLETTA, G.L., A. LARRIERA, E. KLEINSORGE, AND M. D. MUDRY. 2009. Genotoxicity of the herbicide formulation roundup (glyphosate) in broad-snouted caiman (*Caiman latirostris*) evidenced by the Comet assay and Micronucleus Test. *Mutation Research* 672:95-102.
- POOLEY, A. C. 1969. Preliminary studies on the breeding of the Nile Crocodile, *Crocodylus niloticus*, in Zululand. *Lammergeyer* 10:22-24.
- POOLEY, A. C. 1973. Conservation and management of crocodiles in Africa. *Journal of the South African Wildlife Management Association* 3:101-103.

- POOLEY, A. C. 1974. Parental care in Nile Crocodile: A preliminary report on behaviour of a captive female. *Lammergeyer* 21:43-45.
- POOLEY, A. C. 1977. Nest opening response of the Nile Crocodile *Crocodylus niloticus*. *Journal of Zoology, London* 182:17-26.
- POOLEY, A. C. 1982. The ecology of the Nile Crocodile, *Crocodylus niloticus*, in Zululand, South Africa. MSc thesis. University of Natal, Pietermaritzburg.
- RADLOFF, F. G. T., HOBSON, K. A. AND A. J. LESLIE. 2012. Characterising ontogenetic niche shifts in Nile crocodile using stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses of scute keratin. *Isotopes in Environmental and Health Studies* 48:439-456.
- RAINWATER, T. R., T. H. WU, A. G. FINGER, J. E. CAÑAS, L. YU, K. D. REYNOLDS, G. COIMBATORE, B. BARR, S. G. PLATT, G. P. COBB, T. A. ANDERSON AND S. T. MCMURRY. 2007. Metals and organochlorine pesticides in caudal scutes of crocodiles from Belize and Costa Rica. *The Science of the Total Environment* 373:146-156.
- ROSS, J. P. 1998. Crocodiles. Status survey and conservation action plan. 2nd Edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. 8:96.
- SANDWITH, T. S., GOODMAN, P.S, POTTER, D.J., LE ROUX, N.P., DENSHAM, W.D., PORTER, R.N., BOWLAND, A., SCHEEPERS, T., ROBERTS, S., THOMSON, P.J. AND R. TAYLOR. 1997. KZN Nature Conservation Service Protected Area Management Plan. Unpublished internal report.
- SHIRLEY, M. H., DORAZIO, R. M., ABASSERY, E., ELHADY, A.A., MEKKI, M.S. AND H.H. ASRAN. 2012. A sampling design and model for estimating abundance of Nile crocodiles

- while accounting for heterogeneity of detectability of multiple observers. *The Journal of Wildlife Management* 76:966-975.
- STOKER, C., M. R. REPETTI, S.R. GARCÍA, M. A. ZAYAS, G. H. GALOPPO, H. R. BELDOMÉNICO, E. H. LUQUE, AND M. MUÑOZ-DE-TORO. 2011. Organochlorine compound residues in the eggs of broad-snouted caimans (*Caiman latirostris*) and correlation with measures of reproductive performance. *Chemosphere* 84:311-317.
- STRAUSS, M., BOTHA, H. AND W. VAN HOVEN. 2008. Nile Crocodile *Crocodylus niloticus* telemetry: observations on transmitter attachment and longevity. *South African Journal of Wildlife Research* 38:189-192.
- SWANEPOEL, D. J. G. 1996. Identification of the Nile Crocodile *Crocodylus niloticus* by the use of natural tail marks. *Koedoe* 39:113-116.
- SWANEPOEL, D. J. G. 1999. Movements, nesting and the effects of pollution on the Nile Crocodile *Crocodylus niloticus* in the Olifants River, Kruger National Park. MSc thesis. University Natal, Pietermaritzburg.
- SWANEPOEL, D. G. J., FERGUSON, N. S AND M. R. PERRIN. 2000. Nesting ecology of Nile Crocodiles (*Crocodylus niloticus*) in the Olifants River, Kruger National Park. *Koedoe* 43:36-46.
- TOWNSEND, C. R., BEGON, M. AND J. L. HARPER. 2003. *Essentials of Ecology*. Blackwell Science Ltd.
- VAN VUUREN, L. 2011. KwaZulu-Natal : it's man versus croc : conservation. *Water wheel* 10:13-18.
- WADESON, R. 2006. Lower Usuthu River-diversion channel. Unpublished scoping report. Department of Water Affairs and Forestry, Pretoria.

- WALLACE, K. M., AND A. J. LESLIE. 2008. Diet of the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42:361–368.
- WALLACE, K. M., LESLIE, A. J. AND T. COULSON. 2011. Living with predators: a focus on the issues of human–crocodile conflict within the lower Zambezi valley. *Wildlife Research* 38:747-755.
- WALLACE, K., LESLIE, A. J. AND T. COULSON. 2013. Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model. *Journal of Animal Ecology* 82:155-165.
- WHITFIELD, A. K., and R. H. TAYLOR. 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Systems* 19:838-848.
- WHITAKER, R., AND Z. WHITAKER. 1979. Preliminary crocodile survey - Sri Lanka. *Journal of Bombay Natural History Society* 76:66-85.
- WOODBORNE, S., HUCHZERMAYER, K. D. A., GOVENDER, D., PIENAAR, D.J., HALL, G., MYBURGH, J.G., DEACON, A.R., VENTER, J. AND N. LÜBKER. 2012. Ecosystem change and the Olifants River crocodile mass mortality events. *Ecosphere* 3(10):87.
- YOSHIKANE, M., W. R. KAY, Y. SHIBATA, M. INOUE, T. YANAIC, R. KAMATAA, J. S. EDMONDS, AND M. MORITA. 2006. Very high concentrations of DDE and toxaphene residues in crocodiles from the Ord River, Western Australia: an investigation into possible endocrine disruption. *Journal of Environmental Monitoring* 8:649-661.

Table 1. Scientific studies from international peer reviewed journals and theses focused on *Crocodylus niloticus* over the last 50 years.

Author	Year	Country	Research Topic
Cott	1961	Uganda	Ecology and Economic Status
Cloudsley Thompson	1964	Khartoum, Sudan	Diurnal Rhythm
Modha	1967	Kenya	Ecology
Pooley	1969	South Africa	Breeding
Cott and Pooley	1971	Africa	Conservation and management
Pooley	1973	Africa	Conservation and Management
Pooley	1974	South Africa	Parental care
Gans and Pooley	1976	Africa	Research on Crocodiles
Graham	1976	Botswana	Nesting
Pooley	1977	South Africa	Nesting
Jacobsen	1984	South Africa	Distribution and Status
Hutton	1986	Zimbabwe	Age Determination
Hutton	1987	Zimbabwe	Incubation temperature
Hutton	1987	Zimbabwe	Growth and Feeding
Hutton	1987	Zimbabwe	Morphometrics and Size Estimation
Blake and Loveridge	1987	Zimbabwe	Nesting Observations in Captivity
Child	1987	Zimbabwe	Management
Kofron	1989	Zimbabwe	Nesting
Hutton	1989	Zimbabwe	Movement, Home Range, Size Separation
Hutton and Woolhouse	1989	Zimbabwe	Monitoring Crocodile Abundance
Hutton et al.	1989	Zimbabwe	Capture Methods
Kofron	1990	Zimbabwe	Reproduction
Hartley	1990	South Africa	Nest Survey
Games	1991	Zimbabwe	PhD. Feeding Ecology
Kofron	1992	Africa	Status and Habitat
Kofron	1993	Zimbabwe	Behavior
Games	1994	Africa	Aerial Surveys
Swanepoel	1996	South Africa	Identification
Loveridge	1996	Zimbabwe	Management
Leslie and Spotila	1997	South Africa	Threats to breeding
Leslie	1997	South Africa	PhD. Ecology and Physiology
Swanepoel	1999	South Africa	MSc. Ecology
Hutton and Loveridge	1999	Africa	Resolving Conflicts- Crocodiles and Man

Leslie and Spotila	2000	South Africa	Osmoregulation
Swanepoel et al.	2000	South Africa	Nesting ecology
Combrink	2004	South Africa	MSc. Population Status
Brown et al	2004	Namibia	Population Survey
Botha	2005	South Africa	MSc Ecology and Population Dynamics
McGregor	2005	Zimbabwe	Conservation Politics
Blake	2006	NA	Capture
De Toeuf-Boulade	2006	Botswana	Reproductive cycle, sexual size dimorphism
Maciejewski	2006	Botswana	TSD
Shacks	2006	Botswana	Habitat use
Thomas	2006	Botswana	HCC
Wallace and Leslie	2008	Botswana	Diet
Bourquin	2008	Botswana	PhD. Population Ecology
Bishop et al.	2008	South Central Africa	Population History
Strauss et al.	2008	South Africa	Technique
Downs et al.	2008	South Africa	Body Temperature and Basking Behaviour
Bishop et al.	2009	Botswana	Genetic Variation
Aust et al.	2009	Botswana	Human-Wildlife conflict
Botha	2010	South Africa	Disease
Fergusson	2010	Mozambique	Human-Wildlife conflict
Osthoff et al.	2010	South Africa	Disease
Botha et al.	2011	South Africa	Disease
Champion	2011	South Africa	MSc. Ecology
Combrink et al.	2011	South Africa	Population estimate
Ferreira and Pienaar	2011	South Africa	Disease, Population ecology
Wallace et al.	2011	Zambia, Zimbabwe	Human-Wildlife conflict
Bourquin and Leslie	2012	Botswana	Demographics
Shirley et al.	2012	Egypt	Population estimate
Radloff et al.	2012	Botswana	Diet
Woodborne et al.	2012	South Africa	Isotope
Wallace et al.	2013	Africa	Trade
Combrink et al.	2013	South Africa	Ecology
Combrink	2013	South Africa	PhD. Ecology

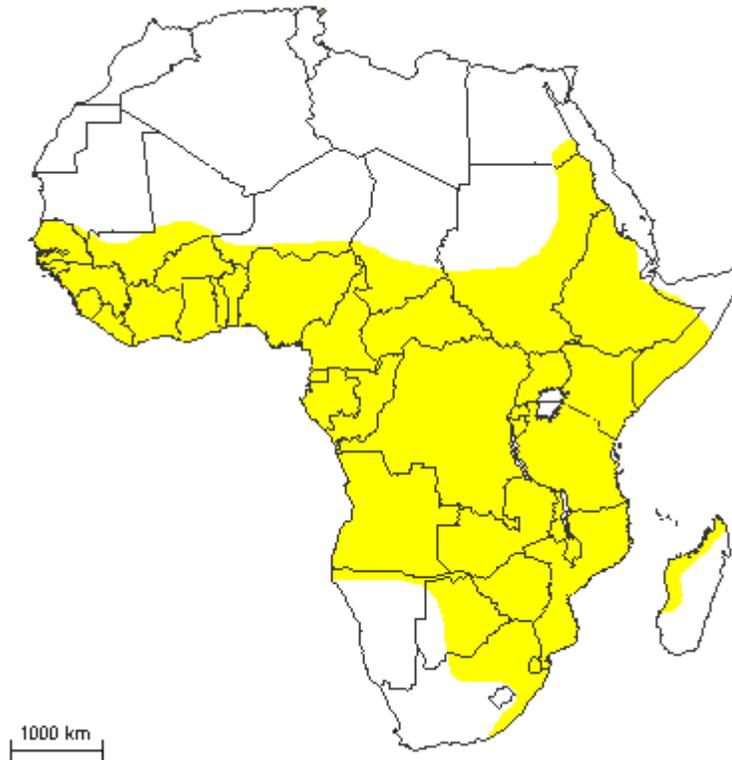


Figure 1. The distribution of Nile Crocodiles (*Crocodylus niloticus*) in Africa. Areas where *C. niloticus* occur are shaded and include Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Congo, Egypt, Ethiopia, Equatorial Guinea, Gabon, Gambia, Ghana, Guinea, Guinea Bissau, Ivory Coast, Kenya, Liberia, Madagascar, Malawi, Mali, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo, Uganda, Zaire, Zambia, Zimbabwe (the distribution map was taken from the website www.flmnh.ufl.edu/cnhc/cst_cnil_dh_map.htm on 10/01/2011 and modified in Microsoft[®] Paint).

ANNEX I. Etymology of the Nile Crocodile from the website

http://en.wikipedia.org/wiki/Nile_crocodile#Taxonomy_and_etymology on 14/08/2013.

Etymology

Binomial name: *Crocodylus niloticus*. Derived from the Greek words *kroko* ("pebble") and *deilos* ("worm", or "man"), referring to the rough skin of crocodilians *niloticus*, meaning "from the Nile River".

Taxonomy

Class: Reptilia

Order: Crocodylia

Family: Crocodylidae

Genus: *Crocodylus*

Species: *niloticus* Laurenti 1768

CHAPTER 2

Habitat Use by Nile Crocodiles in Ndumo Game Reserve, South Africa: a Naturally Patchy Environment

P. M. Calverley and C. T. Downs

School of Life Sciences, University of KwaZulu-Natal.

Private Bag X01, Scottsville, Pietermaritzburg, 3209 South Africa. Email:

calverleypeter@gmail.com.

Formatted for *Copeia*

2.1 ABSTRACT

*Distribution patterns reflect the interactions of organisms with their environment. We discuss the distribution patterns of Nile Crocodiles (*Crocodylus niloticus*) in a naturally patchy floodplain environment using aerial survey data collected over the last 40 years. Although only 10,000 ha in size Ndumo Game Reserve (NGR) supports one of the largest wild crocodile populations in South Africa, largely due to landscape complementation with neighbouring Mozambique. Distributions within the reserve were found to be influenced by landscape physiognomy and composition as well as connectivity and corridor quality. To quantify the effects of environmental conditions on crocodile distribution we conducted 40 diurnal counts at Lake Nyamithi in NGR between 2009 and 2012. Average monthly maximum temperature had a significant 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 programme be initiated in order to conserve the current population of Nile Crocodiles in the greater NGR area.*

2.2 INTRODUCTION

2.2.1 Spatial distribution patterns and the question of scale

Organisms are not randomly or evenly distributed within a given habitat but are aggregated in patches or form some other pattern of spatial distribution (Legendre and Fortin, 1989). These patterns reflect the interactions of a species with its environment (Brown et al., 1995). Generally, animals are positioned within their habitat according to spatial and temporal variations in environmental conditions and resources (Townsend, 2003) as well as complex social interactions (Lang, 1987). Patterns of distribution thus indicate factors influencing habitat use and have spatial (local, regional, continental, global), temporal (day, season, year) and demographic (individual, community, population) components that need to be considered. Different patterns emerge at different resolutions and studying distribution patterns becomes a question of scale (Turner, 1989). For example, examining distribution patterns of a population of animals can help identify underlying ecological processes that determine the location of individuals within a habitat while examining spatial distribution of individuals within a population may explicate social interactions (Perry, 2002). While there is no single correct scale at which to describe populations it is also impossible to sample at every resolution in the continuum of time and space (Levin, 1992). The “scale of scrutiny” or “scale of interest” is determined by the questions being asked (i.e. processes under study), technological or logistical constraints as well as the study organism itself (Wiens, 1989; Levin, 1992).

2.2.2 Landscape as a unit of spatial scale

Landscape as a unit of spatial scale is organism specific, generally incorporating an area between that of its home range and its regional distribution (Dunning et al., 1992). Dunning et al.

(1992) go on to describe a landscape as “the mosaic of habitat patches in which a particular patch (focal patch) is embedded”. The choice of landscape as the scale of scrutiny is appropriate for this study site for a number of reasons. Firstly, on a strictly spatial basis, at 42 km² the physical area under study falls between the traditional demarcation of local (1 km²) and regional (100 km²) spatial scales and into the landscape scale as described by Dunning et al. (1992). Secondly, the focal area has been a Game Reserve for nearly 100 years and as a protected area forms a natural patch distinct from the surrounding area even if the distinction lies solely in the protection it offers. The study organism, the Nile Crocodile (*Crocodylus niloticus*), is free to move in and out of Ndumo Game Reserve (NGR, Fig. 1) and does so on a seasonal basis (Pooley, 1982). NGR is therefore one of at least two distinct patches used by the study organism. Thirdly, the study area itself is inherently patchy and is characterized by a mosaic of permanent and ephemeral pans, streams and rivers with various degrees of connectivity that fluctuate on a seasonal basis (Fig. 2). Previous studies here suggest that Nile Crocodiles display differential habitat use within these patches on both a spatial and temporal scale (e.g Ward, 1989). And finally, within the study area, the pan with the highest crocodile density, Lake Nyamithi (Fig. 2), forms the focal point of study. Pooley (1982) recorded large seasonal fluctuations in the number of Nile Crocodiles residing in the Lake Nyamithi and a primary aim of this study was to examine the temporal changes in population density and relate this to environmental resources and conditions as well as possible social interactions. Examining distribution patterns from the landscape level allows for the scrutiny of processes and patterns at the local micro-scale within NGR (Lake Nyamithi) through to the macro-scale extending outside of the reserve (Rio Maputo floodplain) (Dunning et al., 1992). This is particularly suitable for the study of the spatial ecology of Nile Crocodiles in NGR as they move freely between the reserve and the Rio Maputo

floodplain in Mozambique on a seasonal basis (Pooley, 1969). The scale of scrutiny is therefore also dependent on the study organism, information on which is supplied below.

2.2.3 Habitat use of Nile Crocodiles

Nile Crocodiles are semi-aquatic predatory reptiles and their distribution in South Africa includes lakes, artificial impoundments, rivers, fresh water swamps and brackish/saline estuarine systems from the Tugela River in the south to the Limpopo River in the north (Jacobsen, 1984; Branch, 1998; Combrink, 2004; Botha, 2005; Champion, 2011; Van Vuuren, 2011; Combrink et al. 2011; 2013; Bourquin and Leslie, 2012; Combrink, 2013). Previous studies of Nile Crocodiles suggest that within these systems different habitats are used on a seasonal basis (Leslie, 1997; Swanepoel, 1999; Botha, 2005). Generally, as water levels and temperatures drop during winter, thermoregulatory needs become paramount and individuals congregate around suitable basking sites defined by deep pools (to avoid threats and for thermoregulatory requirements) with gently sloping banks or sandbanks exposed to direct sunlight (Pooley, 1969; Kofron, 1993; Swanepoel et al., 2000). With the onset of spring focus shifts to reproduction and adults congregate at the most favourable basking sites close to deep water where courtship displays and mating take place (Botha, 2005; Champion, 2011). As spring moves into summer ambient temperatures rise resulting in an increased metabolic rate and habitat use is influenced by prey concentrations (Leslie, 1997; Wallace and Leslie, 2008). During this period reproductively active females go in search of suitable nesting sites and often do so before the arrival of summer rainfall and rising water levels (Kofron, 1993; Champion, 2011). Breeding females guard their nesting sites during the incubation period and are therefore confined to

nesting habitat over the summer, only returning to winter basking sites as water levels start to drop after hatching in late summer (Pooley, 1969).

However, while these generalizations on seasonal habitat use may for the most part be true, Nile Crocodiles also display differential habitat use according to size (Cott, 1961; Hutton, 1989; Botha, 2005; Radloff et al., 2012b). An ontogenetic shift in diet results in different dietary requirements that are fulfilled in different habitats (Hutton, 1987a; Wallace and Leslie, 2008; Radloff et al., 2012b). Hatchling and juvenile Nile Crocodiles [up to 600 mm snout vent length (SVL) or 1.2 m total length (TL)] feed mainly on insects, crustaceans and small amphibians and occupy shallow marshy habitat and along vegetated fringes of water bodies close to nesting sites (Pooley, 1982; Hutton, 1987a; Wallace and Leslie, 2008). Predation threats from birds, fish, terrapins and intermediate-sized crocodiles further restrict hatchlings and juveniles to these ‘nursery’ areas where they can avoid or evade predation until they are large enough to disperse to new habitat (Pooley, 1982; Hutton, 1987a). Hutton (1987a) found a marked shift in diet after the dispersal of crocodiles of 1.2 m in size and attributes this change to the availability of prey items in habitats occupied before and after dispersion. Intermediate sized crocodiles (1.2 - 2.2 m) that fall within Hutton’s dispersal size class are not tolerated in nesting areas possibly because of their predatory attitude towards hatchlings and are expelled by breeding females as well as by large males during the breeding season (Kofron, 1993). Intermediate sized crocodiles are also preyed upon by larger individuals and are often ‘problem animals’ (animals that may prey on livestock and in some instances attack humans) that move out of protected areas in search of new, unoccupied habitat (Pooley, 1982; Hutton, 1987a). In protected areas such as NGR individuals that leave such areas in search of new habitat during periods of high water levels generally return as water levels drop and anthropogenic activities and disturbances become

concentrated around remaining water sources outside of the protected areas (Pooley, 1969; Kofron, 1993).

Distribution patterns are also likely to vary between the sexes since females often attend to their nests during the 3 month incubation period over summer. In some cases females establish and defend a nursery area in close proximity to the nest site where they will protect their hatchlings for several months after hatching (Modha, 1967). For males and non-breeding females the increase in water levels during summer makes more habitat available, and warmer temperatures associated with the onset of summer results in dispersal away from winter basking sites in search of good foraging sites (Pooley, 1969; Kofron, 1993; Botha, 2005).

2.2.4 Distribution records of Nile Crocodiles in Ndumo Game Reserve – the temporal scale

Effective conservation and management of a population of animals starts with an accurate description of their distribution and abundance (Bayliss, 1987). More often than not, abundance is estimated from sample counts through a study area and any data regarding distribution patterns is overlooked or considered subjectively (Pople, 2007). However, effective management of crocodile habitat requires in depth knowledge as to where and when crocodiles use various habitats (Botha, 2005). Distribution patterns can provide valuable information on habitat use of Nile Crocodiles in relation to season (Pooley, 1982) and life history parameters (Hutton, 1989). At NGR population estimates of Nile Crocodiles have been carried out over the last 40 years with the objective of obtaining estimates of numbers and distribution of animals within the reserve, and for monitoring programmes (Mathews, 1994). There have been no analyses of the distribution data of Nile Crocodiles within the reserve and one of the primary objectives of this study was to examine changes in temporal and spatial distribution patterns of Nile Crocodiles in

the reserve over the past 40 years. At the landscape level the aim of the current study was to identify the role that NGR plays as a protected area in the habitat use of Nile Crocodiles in the greater Phongola/Usuthu/ Rio Maputo floodplain areas. At the local scale we aimed to determine how the size, distribution and connectivity of habitat patches within the floodplain mosaic influenced patterns of crocodile distribution over time. On a finer scale, by focusing on a single pan within the reserve, we aimed to determine which environmental and social factors influenced habitat selection by Nile Crocodiles. We predicted that Nile Crocodiles would not be evenly distributed within NGR on either a spatial or temporal scale and that habitat use was influenced by changes in water level and temperature.

2.3 METHODS

2.3.1 Study site

Proclaimed in 1924 as a sanctuary for Hippopotamus (*Hippopotamus amphibius*) NGR (Fig. 1) supports South Africa's third largest Nile Crocodile population (Combrink, 2004; Pooley, 1982). The 10 000 ha reserve is situated in the Mozambique Coastal Plain between the latitude 26° 50' to 26° 54' South and longitude 32° 09' to 32° 21' East (Figs. 1 and 2). NGR is an elongated trapezoid in shape with the longest axis lying east to west. 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 north east 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).

2.3.1.1 Usuthu River

The Usuthu exits Swaziland through a gorge in the Ubombo mountain range and soon encounters the flat Mozambique coastal plain which creates a reduced flow rate depositing sediments in a floodplain composed mostly of sandy alluvium (Wadeson, 2006). The Usuthu River demarcates the 20 km northern border of NGR and feeds two pans; Banzi and Shokwe (Fig. 2). However, due to extensive flooding in 2000 the main course of the Usuthu has altered its course and now flows southward into the reserve and through Banzi Pan (Wadeson, 2006). The new course of the Usuthu meets the old course of the Phongola in the region of Bakabaka Pan and the main course of the Phongola in the north eastern corner of the reserve. Banzi Pan is the largest pan in NGR at 270 ha.

2.3.1.2 Phongola River and floodplain

Exiting the Lebombo Mountain range in KwaZulu-Natal at Jozini the river meets the flat Maputoland coastal plain depositing finely sorted sediment in a 100km x 3km strip forming the Phongola floodplain, of which 8 km of river frontage is conserved in NGR (Fig. 2). Upon entering the reserve, the main course of the 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 (Fig. 2) 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. The major pans in the Phongola floodplain include Lake Nyamithi and Polwe Pan (Fig. 2).

2.3.1.3 Lake Nyamithi

The largest permanent pan in the Phongola floodplain is Lake Nyamithi (157 ha, Fig. 2) which also has the highest density of Nile Crocodiles in NGR (Chapter 3) and forms the focal point of study where seasonal variation in abundance was recorded. Nyamithi is irregularly oval in shape with the 4.2 km longest axis running east to west and a peak width of 700 m on a north-south axis in the centre. During high water levels the pan may reach depths of 5 m while the average depth during winter is less than 1 m (Pooley, 1982; Forbes and Demetriades, 2006). 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 Phongolo river channels, particularly during the winter months (Pooley, 1969). The northern shore is characterized by a fringe forest of Fever Trees (*Acacia xanthophloea*) with gently sloping *Cynodon dactylon* grazing lawns (Pooley, 1982). The southern shore is somewhat more rocky and steeper in slope. Nyamithi is fed by the seasonal Balamhlanga stream in the west which creates a narrow channel which cuts through the shallower mud flats and *Cynodon* grazing 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 the Phongola or Usuthu floodwaters via the outlet in the eastern periphery of the pan. Similarly, there is a channel that is maintained by hippopotami which serves as a water course and is somewhat deeper than the surrounding mudflats. The difference between the east and west shores is that in the east the mudflats are more extensive and have also been colonized by a large stand of *Phragmites* sp.(pers obs.).

2.3.1.3 The Maputo River (Rio Maputo) and floodplain

The confluence of the Usuthu and Pongola Rivers in the north eastern corner of NGR marks the start of the Maputo River (Rio Maputo) and floodplain. The river is eponymous to the outlet in Maputo Bay 135 km to the north east. The river channel is characterized by a low gradient, so much so that the tidal water amplitude is the same in the Maputo Bay (1.5 m) as it is at Salamanga 40 km inland and tidal fluctuations in water level are noticeable 70km upstream from the mouth (Kramer, 2003). As such salt intrusion is fairly extensive as high up the river as Salamanga (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 10km downstream of NGR.

The Rio Maputo flows through the Matutuíne District, Maputo Province, and is one of the poorest regions in Mozambique. Human populations are low and rely mostly on subsistence agriculture in the fertile soils of the floodplain. Water extraction for agriculture is achieved by hand and most fields are in close proximity to the main channel. Fishing practices such as netting are limited in the main river channel but are extensive in Lake Pandejene.

2.3.2 Methods

The study ran for a period of 3.5 years from March 2009 to November 2012 and took place at two spatial and temporal scales. 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 making use of aerial survey data initiated in 1971 through to 2012.

2.3.2.1 Diurnal counts

Diurnal counts allow for an estimation of the size of crocodiles but not of numbers (Montague, 1983). However, Pooley (1969) conducted successful day count surveys of Nile Crocodile numbers at Lake Nyamithi from 1962 to 1968, concluding that knowledge of the habitat, good visibility, accessibility and in depth knowledge of the species made diurnal counts a useful survey tool (Combrink, 2004). Lake Nyamithi is circumnavigated by a road which is on average 30 m from the shoreline offering a clear field of view across the lake which (Pooley, 1969). These specific conditions at Lake Nyamithi make diurnal surveys a useful monitoring tool here.

Between March 2009 and November 2012 a total of 40 diurnal counts were carried out at Lake Nyamithi. 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 was observed using binoculars and recorded using Microsoft Excel spreadsheets on a Hewlett-Packard (HP) personal digital assistant (PDA) (USA) and later transferred to a spreadsheet for computer analyses. The date, time and duration of each survey as well as weather conditions were recorded. Minimum and maximum temperature ($^{\circ}\text{C}$), humidity (%) and rainfall data (mm) were collected at NGR Head Office 5 km SE 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>). The identity and location of tagged crocodiles (Chapter 3) were recorded using a Garmin eTrex[®] Vista Cx global positioning system (GPS) (Kansas, USA).

2.3.2.2 Stratification of the study site

A study site (in this case NGR) may be separated into contiguous areas according to a qualitative factor such as habitat type with no inherent loss of information (Perry, 2002). Consequently NGR was divided into three major regions/systems consisting of five sub-regions for the aerial surveys and in accordance with previous crocodile survey methodology employed in the reserve. The reason for this was to demarcate NGR according to different sub-habitats with reference to a water source (either river or pan). It would then be possible to determine if distribution patterns and abundance were different between these sub-habitats to test the hypothesis of uneven distribution of Nile Crocodiles within the reserve. As such (during aerial surveys) crocodile numbers were recorded in the following regions and sub-regions: **Region 1.** The Phongola River system consisting of the following sub-regions: Nyamithi Pan and the Phongola floodplain. **Region 2.** The Usuthu River system consisting of the following sub-regions: Shokwe Pan, Banzi Pan and Usuthu River. **Region 3.** The Rio Maputo system consisting of the Maputo River and Lake Pandejene.

2.3.2.2 Aerial Surveys

Data obtained from 13 Ezemvelo KZN Wildlife (EKZNW) Nile Crocodile aerial counts from 1971 - 2009 was used to examine the spatial distribution of abundance of Nile Crocodiles in NGR. These data were obtained from the EKZNW database at Tembe Elephant Reserve for the period 1971 – 1994 and by assisting in the 2009 EKZNW surveys. The Bateleurs (non-profit organization who make pilots and aircraft available for conservation projects) kindly assisted with a further 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. Added to this were data on an aerial survey of the Rio Maputo conducted in 2010 and kindly supplied by the Mozambique Provincial Directorate of Environmental Affairs.

The methods employed in the 1971-1994 surveys as well as the 2009 - 2012 survey are detailed and discussed in Chapter 5 (Population Dynamics) and appear in this chapter in Annex 2.

2.3.3 Statistical analyses

2.3.3.1 Between systems and within systems

One way Analysis of variance (ANOVA) was run in STATISTICA 7.0 (Statsoft, Tulsa, Oklahoma) to determine any significant differences in the number of Nile Crocodiles recorded between the Usuthu and Phongola systems from 1971 to 2009. One-way ANOVA's were suitable for determining the effect of a single categorical independent variable (Location i.e. either Phongola or Usuthu) on the number of Nile Crocodiles between the two systems. Similarly, one-way ANOVA's were used to determine any significant differences in crocodile density (number of crocodile per hectare of water) in the different sub-regions found within the Phongola and Usuthu systems.

In order to analyze any differences/changes in the proportion of crocodiles found in each system, as well as the sub-regions within each system over the last 40 years, the data were transformed using the arcsine square root transformation (SQASIN). This transformation is commonly used for proportions as values range from 0 – 1 in size or in analyzing percentages. One-way ANOVA's were then run to determine any significant differences in the SQASIN transformed 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. This was done to determine any changes in habitat use by the NGR Nile Crocodile population over the last 40 years.

2.3.3.2 Lake Nyamithi

Due to the non-independence of variables we used regression analysis to check for significant influences of continuous environmental variables (water level, temperature, rainfall) on the density of Nile Crocodiles in Lake Nyamithi.

2.4 RESULTS

Results and analyses were generated based on estimates of population size from aerial surveys (relative abundance) rather than total number of Nile Crocodile present in NGR (absolute abundance).

2.4.1 Distribution of abundance of Nile Crocodiles between river systems

Nile Crocodiles were unevenly distributed between the two major river systems in NGR with significantly more occupying the Phongola system than the Usuthu system during the respective winter seasons from 1971-2009 (ANOVA $F_{(1, 22)} = 49.06$, $p = 0.00$, Fig. 3). There was no correlation between the area of habitat available in each system and total number of crocodile counted (GLIM ANOVA $F_{(1,4)} = 0.64$, $p = 0.49$) suggesting different carrying capacities for the two systems. The Usuthu held a minimum of 6 crocodiles in 1971 and a maximum of 202 in 1994, while the minimum number of crocodile counted in the Phongola system was 258 in 1973 and a maximum of 693 in 1993. Interestingly, the proportion (SQASIN) of crocodile found in

each system remained relatively constant (but not significantly so) over consecutive count years (ANOVA $F_{(10, 12)} = 0.00$, $p = 1.00$) despite significant increases in population size in each system from 1971-2009 (Fig. 4).

The proportion of crocodiles counted within each system (Phongolo and Usuthu) remained (significantly) constant (ANOVA $F_{(1, 22)} = 160.28$, $p = 0.00$) from 1985 – 2009 and was unrelated to changes in total population size (ANOVA $F_{(11, 12)} = 0.00$, $p = 1.00$) during this period. That is to say, despite successive population increases in each system the proportion of crocodiles counted in each system remained much the same. The only changes in the proportion of crocodile counted in each system did occur at times of low crocodile density (1971-1973), and when one river system experienced flooding while the other did not (1989; DWAF station WH4009 11/08/1989, Fig. 4). This is thought to be due to a) NGR having a low density of crocodiles in the early 1970's and one system (Phongola) being favored by crocodiles over the other (Usuthu) and b) due to the disparate water levels biasing the results of counts conducted in 1989.

Excluding the counts of the 1970's, 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).

2.4.2 Distribution of abundance of Nile Crocodiles within river systems

2.4.2.1 Usuthu River system

Historically Lake Banzi and Shokwe Pan (Fig. 5) accounted for the majority of the Usuthu crocodile population with less than 1% found in the Usuthu River over the last 25 years. The same pattern is visible currently with Banzi having around 75% of the population and the remaining 25% in Shokwe. This relationship has persisted since 1988 to the present with Banzi

having a significantly greater proportion of crocodile over the years (ANOVA $F_{(2, 33)} = 50.76$, $p = 0.00$). The Usuthu system is therefore made up of two primary components, Lake Banzi and Shokwe Pan. Significantly more Nile Crocodiles were counted in Lake Banzi than in Shokwe and the Usuthu River (ANOVA $F_{(2, 33)} = 15.14$, $p = 0.0002$). The Usuthu is a wide, shallow river with many sandbanks and is therefore not prone to survey bias. The low number of crocodiles counted here is most likely a function of habitat suitability. The northern bank of the river borders on Mozambique and is not protected, possibly elevating human disturbance to levels unsuitable for crocodiles. However, in order for crocodile to be present in Shokwe they almost certainly have to use the Usuthu River and thus it plays an important role in connecting the different habitats available to Nile Crocodiles in the Usuthu river system.

2.4.2.2 Phongola River System

Since 1971 the majority (61%) of Nile Crocodiles in the Phongola river system were found in the Phongola floodplain during the winter period when the surveys took place. There is a significant difference in the number of Nile Crocodiles counted in the Phongola floodplain compared with Lake Nyamithi from 1971-2009 (ANOVA $F_{(1, 22)} = 6.34$, $p = 0.02$). Despite successive, and often dramatic population increases, the proportion of crocodiles counted in the Phongola floodplain and Lake Nyamithi remained relatively constant and distinct from one another (ANOVA $F_{(1, 22)} = 17.30$, $p = 0.0004$, Fig. 6). Unusually, in 2009 the majority (69%) of crocodiles were counted in Lake Nyamithi.

2.4.2.3 Lake Nyamithi

Although the Phongola floodplain contained more crocodiles than Lake Nyamithi during the winter surveys, Lake Nyamithi held a greater density of Nile Crocodiles than the floodplain. Generally Nile Crocodiles moved from the floodplain and back into Lake Nyamithi as water levels in the floodplain dissipated and temperatures decreased with the onset of winter (Fig. 8.). Numbers of crocodiles at Lake Nyamithi climb steadily from an average of 61 (SE \pm 5.5) in March to a peak of 306 (SE \pm 13.5) in July. Numbers then oscillated around 273 (SE \pm 13.5) in August dropping to 192 (SE \pm 24.3) in September 2009 and to 61 (SE \pm 1.4) by December.

Total crocodile density in Lake Nyamithi was significantly and negatively related to average monthly ambient temperature (GLIM ANOVA $F_{4, 25} = 18.5$, $p = 0.006$) (Fig. 10). Rainfall and water level had strong negative effects on the total number of crocodiles in Lake Nyamithi but these effects were not significant. However, Nile Crocodiles show differential habitat use according to size (TL) (Cott and Pooley, 1971; Botha, 2005; Radloff et al., 2012a;b) and it is necessary to delineate the population into various size classes (Swanepoel, 1999) in order to identify environmental variables specific to each size class (Radloff et al., 2012a).

None of the environmental variables measured had a significant influence on the number of Nile Crocodiles counted in the < 1.5 m; 2.5 – 3.5 m; 3.5 – 4.5 m and 4.5 m+ size classes in Lake Nyamithi. Environmental variables had a significant effect on the number of crocodiles counted in the 1.5 - 2.5 m size class only. Minimum average monthly temperature and rainfall both had a significant and negative effect on the number of crocodile between 1.5 - 2.5 m TL counted over the 2 years. A summary of these results is presented in Table 1. Although not always significant, environmental variables had varying impacts on the number of Nile Crocodiles counted in each size class and are discussed below in greater detail.

2.5 DISCUSSION

2.5.1 Environmental conditions influencing habitat use

Variations in spatial abundance are a function of resource availability and conditions (Townsend, 2003). 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. In Lake St. Lucia Leslie (1997) attributed seasonal movement of Nile Crocodiles to food availability, water salinity, breeding status and human activity. In a seasonal river in Zimbabwe Kofron (1993) described seasonal habitat use as a function of anthropogenic disturbance, selection of suitable nesting habitat and changes in habitat availability associated with fluctuations in water level. In NGR Pooley (1982) suggested that Nile Crocodiles chose winter habitats according to food availability, anthropogenic disturbances and thermoregulatory requirements while habitat use during the summer months was influenced by reproductive status and an increase in habitat available due to the flooding of the Phongola and Rio Maputo floodplains. However, Nile Crocodiles feed less in winter due to lower body temperatures in the colder winter months (Hutton, 1987b) and food availability may not explain winter habitat choice of crocodiles in NGR. Studies conducted at Lake Nyamithi in NGR showed that maximum ambient temperature, rainfall and water levels had strong influences on crocodile density and would therefore appear to be key environmental variables determining habitat use in NGR.

2.5.1.1 Lake Nyamithi and the influence of temperature

Almost all behavioral aspects of ectotherms are influenced by body temperature including locomotion, immune function, foraging ability, sensory input as well as rates of

feeding and growth (Angilletta et al., 2002). The amount of solar radiation available for controlling body temperature varies on a spatial and temporal scale (Angilletta et al., 2002) necessitating adaptations in thermoregulatory behavior (Grigg et al., 1998). In crocodylians this is generally achieved behaviorally (Seebacher, 1997; Downs et al., 2008) and through habitat selection (Cott, 1975). In NGR Nile Crocodiles selected Lake Nyamithi as a winter habitat primarily because of the thermal benefits offered by the lake. These include basking sites that are protected from disturbance, sun exposed and with gently sloping banks in close proximity to deep water (Swanepoel et al., 2000). Observations by Pooley (1969) suggest that the seasonal influx of crocodiles into the lake over winter has been taking place for at least 50 years and Lake Nyamithi forms an important winter habitat for Nile Crocodiles in NGR and possibly the outlying Rio Maputo floodplain. This has important management implications for the outlying pans and floodplain in terms of protecting suitable crocodile habitat.

Reproductively active crocodiles in particular may benefit from maintaining high body temperatures during winter (Seebacher, and Grigg 1997). High temperatures facilitate testicular and ovarian development while also allowing higher levels of activity for intraspecific competition during the early breeding season (Seebacher, and Grigg 1997). Kofron (1989) found that ovarian follicle growth and vitellogenesis occurred from April to mid-August in Zimbabwe while courtship and breeding occurred from late June to mid-August. However, as NGR is further south than Zimbabwe it could be expected that vitellogenesis and mating would start somewhat later in the year. For example at NGR and Pongolapoort Dam, (100km south east of NGR) breeding activities commence in early August through to October and laying takes place in early November – late December (Pooley, 1969; Champion, 2011). Vitellogenesis and ovarian follicle growth might be expected to start in June in NGR. The selection of favorable

basking sites during winter may therefore facilitate the development of testes and ova in time for mating and may partially explain the influx of crocodiles into Lake Nyamithi in May and the sudden departure in October/November after courtship and mating has taken place. However, Nile Crocodiles are well known to form breeding aggregations during the breeding season (Swanepoel et al., 2000; Champion, 2011) and mating could take place in Lake Nyamithi simply due to the high density of crocodiles using the lake as a winter refuge. Nonetheless, the fact that so many Nile Crocodiles are in Lake Nyamithi over the breeding season earmarks the lake as an important breeding habitat for the NGR and possibly the Rio Maputo population.

The majority of Nile Crocodiles leave Lake Nyamithi before laying takes place (November - December) and Pooley (1982) suggested that they leave not only the lake but the reserve as well in search of more suitable nesting habitat in the Rio Maputo floodplain. However, since mating has already taken place this does not explain the movement of males out of the lake and possibly the reserve as well. For reptiles, an increase in ambient temperature results in an increased metabolic rate, placing more emphasis on finding food resources than suitable basking habitat. Crocodiles (males and females) thus move away from winter basking sites in search of foraging sites. At Lake St. Lucia Nile Crocodiles follow seasonal migrations of striped mullet (*Mugil cephalus*). In the Kruger National Park Swanepoel (1999) noted that crocodiles positioned themselves in the Olifants River Gorge where topography naturally funneled or concentrated prey items (fish). Botha (2005) suggested the same for crocodiles in the Loskop dam. In the Phongolo 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 floodplain fish species move between the main channel and the pans/lakes

during high water levels (Kramer, 2003). Crocodiles are highly adept at making use of ephemeral prey resources (Webb et al., 1982) and congregate at the outlets/inlets of the pans and feed on the numerous fish species that try to gain entrance or exit the pans (pers. obs.). Crocodiles could be positioning themselves in the Rio Maputo to take advantage of seasonal migrations of estuarine fish species such as striped mullet (e.g. Leslie, 1997) as well as the numerous freshwater fish species of the Phongola floodplain which move up from the Maputo estuary and have been found in pans as far inland as Lake Nyamithi in NGR (Kyle, 2002). By moving out of the extensive floodplain within NGR and into the comparatively narrow channel of the Rio Maputo crocodiles will be positioning themselves where prey densities are greater.

2.5.1.2 Water level and rainfall

Other environmental conditions that were related to crocodile density in Lake Nyamithi were water level and rainfall. The dry season in South Africa coincides with winter and the ensuing lowering of water levels in the floodplain places emphasis on habitats with permanent bodies of water (Swanepoel, 1999; Botha, 2005). The physical amount of habitat available to Nile Crocodiles decreases during drier winter months and as the floodplain dries up (Heeg and Breen, 1982). In NGR the surface area of the floodplain decreases from roughly 4,200 ha to 1,200 ha (Kyle and Marneweck, 1996) and this suggests that a significant seasonal change in the amount of habitat available to Nile Crocodiles. Seasonal changes in habitat availability may 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) is heavily used for fishing and disturbance levels for crocodiles are high here. As the

Rio Maputo floodplain dries up in winter crocodiles move into NGR where permanent pans, deep water channels and basking sites are abundant and protected.

2.5.2 Ontogenetic changes in environmental conditions influencing habitat use

Crocodiles utilize habitats differently according to size (TL) and such niche partitioning may help sustain large populations in confined areas through reducing intraspecific competition for essential resources (Radloff et al., 2012b). At Lake Nyamithi environmental conditions influenced the number of crocodiles in each size class differently (Table 1.). Nile Crocodiles < 1.5 m 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 km²) (Hutton, 1989) and Nyamithi (0.17 km²) 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.

Density of crocodiles in the dispersal size class (1.5 – 2.5 m TL) was most strongly influenced by minimum monthly temperatures and rainfall. Density of crocodiles larger than 1.5 m TL were most strongly influenced by rainfall as opposed to water levels. This suggests that while 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 NGR.

2.5.3 Distribution of abundance from a landscape perspective

Water level and temperature alone do not explain why Lake Nyamithi has such a high density of crocodiles compared to other pans within the reserve. Pooley (1982) attributes this to the composition of the Lake in terms of availability of suitable basking sites and abundance of prey items. However, adult Nile Crocodile radio tagged in Lake Nyamithi were found to move in and out of the lake numerous times during the winter season (Chapter 4) suggesting that they may be supplementing their resource intake by frequenting the Phongola floodplain. Where resource supplementation takes place the focal patch (Lake Nyamithi) may maintain a population far greater than in similar isolated patches (Dunning et al., 1992). Nyamithi is highly connected in terms of both physiognomy and the biophysical nature of the corridors which facilitates movement between the various patches (Henein and Merriam, 1990; Taylor, 1993) accessed by crocodile over wintering in the lake.

2.5.3.1 Landscape complementation

Significantly more Nile Crocodiles were counted in NGR during the dry season than during the wet season. Although it is well known that high water levels negatively influence crocodile surveys (Montague, 1983; Combrink, 2004; Malvasio, 2006; Simpson and Mediyansyah, 2009) correction factors applied to count data support the theory that Nile Crocodiles leave NGR over the wet season (see Chapter 3). NGR and the Rio Maputo floodplain form spatially discrete habitat patches that are used by Nile Crocodiles on a seasonal basis. NGR provides protection, permanent water and a favorable thermal environment during winter when these factors are limited in the Rio Maputo floodplain. The Rio Maputo more than likely provides good foraging and possibly nesting habitat (e.g. Swanepoel, 1999). Crocodiles access

these respective resources by moving between the two habitats. The close proximity and excellent connectivity (spatially contiguous) between these resource patches supports a larger population than if these patches were further apart or not as well connected through landscape complementation (Dunning et al., 1992).

2.5.3.2 Landscape composition and physiognomy

Aerial surveys from 1971 – 2009 showed that Nile Crocodiles were unevenly distributed within NGR. Landscape composition and landscape physiognomy help quantify the distributions of resource patches within a landscape and can therefore illuminate factors effecting habitat use (Dunning et al., 1992). For example, Pooley (1982) suggested that the Phongola system has a significantly greater Nile Crocodile population than the Usuthu system (e.g. Mathews, 1994) because of the differences in landscape composition between the two systems. The Usuthu River is plagued by anthropogenic disturbance and is too shallow with few deep pools to offer protection to crocodiles, while Lake Banzi has insufficient basking sites to support a large population of Nile Crocodiles (Pooley, 1982). The Phongola on the other hand has a far greater diversity and abundance of fish species which may support a larger Nile Crocodile population and Lake Nyamithi has numerous suitable basking sites (Pooley, 1982).

Although un-described until the present, the landscape physiognomy of the two systems may also play a part in crocodile distribution (e.g. Dunning et al., 1992). 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 (Fig 2.). However, movement between habitat patches is also determined by the landscape through which an animal must travel (Tischendorf and Fahrig, 2000) and the extent to which a landscape

promotes or inhibits movement between resource patches is known as landscape connectivity (Taylor, 1993). From a physiognomy perspective the Usuthu system has poorer connectivity due to the greater distances between the habitat patches held within its system which may result in under utilization of suitable habitat and lower population densities in outlying patches due to “neighborhood effects” (Dunning et al., 1992). On a biophysical level the Usuthu River has poorer connectivity due to anthropogenic disturbances along its northern bank and extremely low water levels during winter reducing its quality as a corridor (e.g. Henein and Merriam, 1990). The Phongola River on the other hand is deeper with numerous pools and has a mandatory winter flow rate controlled by the Pongolapoort/ Jozini Dam (Heath and Plater, 2010) and up until recently was protected from anthropogenic disturbances along both banks.

Consequently landscape connectivity (Taylor, 1993) influences the movement of crocodile between and within the two systems. Ward (1989) suggested that the Nile Crocodile population in Phongola floodplain tends to fluctuate with the Nyamithi population while the Usuthu-Lake Banzi-Shokwe populations tend to interchange. Certainly each of these systems is fed by its own river and would be expected to maintain a greater degree of connectivity within itself than with the neighboring system. Poor mixing between systems could be a product of poor connectivity and neighborhood effects where resources are more accessible in contiguous patches than those that are further away (Dunning et al., 1992) and crocodiles remain mostly within each system rather than moving between the two. Our data showed that the ratio of crocodiles between the Usuthu and Phongola systems has stayed the same over the last 50 years despite the distribution of crocodiles within each system changing, suggesting that Ward may well be correct.

However, the recent divergence of the main course of the Usuthu River through Lake Banzi (Wadeson, 2006) may serve to increase connectivity not only within the Usuthu system but between the two systems as well. From a physiognomic point of view the Usuthu River and Lake Banzi now share a higher degree of connectivity while from a biophysical point of view Shokwe and Lake Banzi are better connected. Similarly, the erosion of Lake Banzi's headwaters around the fish ladder and the main course of the Usuthu now flowing through the pan provide a better biophysical connection between Banzi and the Phongola floodplain including Lake Nyamithi because the confluence with the Phongola has shifted upstream reducing the distance between these habitat patches (Wadeson, 2006). However, the new course of the Usuthu is characterized by a faster flow rate and numerous vegetative obstructions in the main channel (Wadeson, 2006) and an improvement in biophysical connectivity that can be navigated on a large scale by Nile Crocodiles may only be achieved in years to come as the channel stabilizes. As such it could be expected that a greater proportion of crocodiles will be found in the Usuthu system as time progresses.

The unusually high density of crocodile counted in Lake Nyamithi during 2009 in particular may be attributed to inaccuracy associated with fixed wing surveys in NGR where the winding nature of the Phongola River makes fixed wing aircraft unsuitable for aerial surveys (Pooley, 1982). This factor along with the fact that crocodiles were more visible and therefore easier to count on the open banks of Lake Nyamithi may 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 floodplain within NGR (Calverley, 2009). 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 explaining the results of the 2009 survey.

2.5.4 The Rio Maputo floodplain

Significantly more Nile Crocodiles were counted in NGR during the dry season than during the wet season. Although it is well known that high water levels negatively influence crocodile surveys (Montague, 1983; Combrink, 2004; Malvasio, 2006; Simpson and Mediyansyah, 2009) the movement of crocodiles out of NGR and into the Rio Maputo floodplain in Mozambique often begins before water levels start to rise (Pooley, 1982) (see Chapter 3). Aerial surveys conducted in the Rio Maputo floodplain suggest that movement out of the reserve starts in November. Diurnal counts at Lake Nyamithi and telemetry studies (Chapter 3) validate this and suggest movement back into the reserve takes place during April/May. Large scale seasonal movements of Nile Crocodiles have been attributed to seasonal changes, foraging, breeding, nesting or thermal requirements of Nile Crocodiles (e.g. Swanepoel, 1999).

The majority of crocodiles in the Rio Maputo floodplain are concentrated between the outlet of Lake Pandejene and Salamanga 90km downstream of the outlet. Lake Pandejene in particular is known as a fish rich lake (Kramer, 2003). Crocodile numbers gradually diminish downstream of Pandejene petering out completely in the region between Salamanga and Bela Vista (Fergusson, 2010). This is probably due to increased salinity levels in the river the closer one gets to the Rio Maputo mouth and because salt water intrusion normally occurs up to Bela Vista and in dry years/seasons intrusion may 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 would provide good nesting habitat for

crocodiles during the summer as nest sites could be located above the high water mark. This goes some way to validate Pooley's (1969) theory that crocodiles leave the reserve in search of suitable nesting habitat. More than likely it is an interplay between high concentrations of prey resources in the Rio Maputo in close proximity to suitable nesting habitat that sees the majority of crocodiles leaving the reserve over the summer months. The extensive movement of crocodiles from NGR as far down the Rio Maputo as Salamanga and back into the reserve could be facilitated by seasonal changes in water levels and the gradient of the Rio Maputo. Certainly, flood waters in summer would facilitate the downstream movements from NGR into the Rio Maputo. However, during winter tidal influence in the Rio Maputo extends 70 km upstream from Maputo Bay and could facilitate upstream movements of crocodiles (Campbell et al., 2010).

2.6 CONCLUSION

High costs of aerial surveys did not allow for sufficient repetition to determine which environmental factors associated with season had a significant effect on the distribution of Nile Crocodiles in NGR over the last 40 years. This was examined at a finer spatial and temporal scale at Lake Nyamithi. Temperature, water level and rainfall influenced the habitat selection of Nile Crocodiles within the reserve. However, environmental conditions had different influences on different size class of Nile Crocodiles suggesting that the manner in which individuals react to environmental conditions and resources is determined by size (TL).

The high number of Nile Crocodiles in NGR during winter months followed by a decline in numbers during summer is a product of landscape complementation with both NGR and Mozambique providing essential seasonal resources. When water levels in the Rio Maputo floodplain contract in winter, anthropogenic activities are concentrated around remaining water

bodies and Nile Crocodiles move into and use NGR as a winter refuge. With the onset of the rainy season in October/November Nile Crocodiles make their way out of the lakes and pans and enter the floodplain within NGR, ultimately making their way into the Rio Maputo floodplain where they position themselves according to prey densities and the availability of suitable nesting habitat. Nile Crocodiles leaving NGR and venturing into the Phongolo or Usuthu River systems in South Africa are not tolerated by the human populace and no viable populations exist outside of the reserve in these areas. These areas are therefore considered sink habitats as crocodiles entering them are forced back into the reserve due to anthropogenic disturbances (sometimes caught and released into other reserves), or are extirpated due to the threat they pose to local communities and their livestock. The viability and conservation of Nile Crocodiles in NGR may thus ultimately depend on events that take place in the Rio Maputo floodplain (Mozambique), which is considered a priority for future research.

Within NGR water levels dropped during winter and crocodile aggregated around suitable basking sites defined by deep pools with gently sloping banks exposed to direct sunlight. Pans that hold water throughout winter, such as Lake Nyamithi and Banzi Pan, had the highest density of crocodile within their respective systems and density increased as water levels and temperatures dropped from April through October. Areas that are exposed to disturbance such as the Usuthu River and the new course of the Phongola River were generally avoided. During September/October the majority of crocodile left the winter basking sites before water levels rose in late October, only returning as water levels started to drop in April.

2.7 ACKNOWLEDGEMENTS

Ezemvelo KZN Wildlife is thanked for permission to work in NGR and particularly Ferdi Myburgh for his assistance. Xander Combrink, Garreth Champion and Jon Warner are thanked for their assistance in the field. We are most grateful to Paul Dutton, Donovan Barton-Hobbs and Chris van den Berg as well as the Bateleurs for aerial survey assistance. We thank Mazda Wildlife for vehicle support. Taryn Bigwood of Ezemvelo KZN Wildlife kindly assisted with mapping. The University of KwaZulu-Natal, Hans Hoheisen Trust and the Water Research Commission are thanked for funding.

2.8 REFERENCES

- ANGILLETTA, M. J., NIEWIAROWSKIB, P. H. AND C. A. NAVAS. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27:249–268.
- BAYLISS, P. 1987. Survey methods and monitoring within crocodylian management programmes. In: *Wildlife Management: Crocodiles and Alligators* p. 157-175. Surrey Beatty and Sons, Sydney. pp 157-175.
- BOURQUIN, S. L. AND A. J. LESLIE.2012. Estimating demographics of the Nile crocodile (*Crocodylus niloticus* Laurenti) in the panhandle region of the Okavango Delta, Botswana. *African Journal of Ecology* 50: 1-8.
- BOTHA, P. J. 2005. The ecology and population dynamics of the Nile crocodile *Crocodylus niloticus* in the Flag Boshielo Dam, Mpumalanga Province, South Africa. MSc thesis. University of Pretoria, Pretoria.
- BRANCH, W. R. 1998. Status of the Nile Crocodile in Natal, South Africa. Unpublished report.

- BROWN, J. H., MEHLMAN, D. W. AND G. C. STEVENS. 1995. Spatial variation in abundance. *Ecology* 76:2028-2043.
- CALVERLEY, P. 2009. Ndumo Game Reserve aerial and ground survey report October 2009. Unpublished report.
- CAMPBELL, H. A., WATTS, M. E., SULLIVAN, S., READ, M. A., CHOUKROUN, S., IRWIN, S. R., and FRANKLIN, C. E. 2010. Estuarine crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology* 79:955-964.
- CHAMPION, G. 2011. The Ecology of Nile Crocodile (*Crocodylus niloticus*) in Pongolapoort Dam, Northern KwaZulu-Natal, South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, A. S. 2004. Population status of *Crocodylus niloticus* (Nile Crocodile) at Lake Sibaya, Republic of South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X. 2013. Spatial and reproductive ecology and population dynamics of the Nile Crocodile (*Crocodylus niloticus*) in the St Lucia Estuarine system, South Africa. PhD thesis in prep., University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X., J. L. KORRÛBEL, KYLE, R., TAYLOR, R. AND R.PERRAN.2011. Evidence of a declining Nile Crocodile (*Crocodylus niloticus*) population at Lake Sibaya, South Africa. *South African Journal of Wildlife Research* 41: 145-157.
- COMBRINK, X., WARNER, J. AND DOWNS, C. T. 2013. Crocodiles, p. 332 - 253. *In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. D. D. S. a. R. H. T. Renzo Perissinotto (ed.). Cambridge University Press, Cambridge.

- COTT, H. B. 1961. Scientific results of an enquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. Transactions of the Zoological Society of London 29:211-356.
- COTT, H. B. 1975. The Nile Crocodile. In: Looking at Animals: a Zoologist in Africa. Charles Scribner's Sons, New York. pp.135-153.
- COTT, H. B., and A. C. POOLEY. 1971. Crocodiles: The status of crocodiles in Africa. In: IUCN Conference Paper No. 33. Vol. 2, Gland, Switzerland.
- DOWNES, C. T., GREAVES, C., AND R. TAYLOR. 2008. Body temperature and basking behaviour of Nile Crocodiles (*Crocodylus niloticus*) during winter. Journal of Thermal Biology 33:185–192.
- DUNNING, J. B., DANIELSON, BRENT J., PULLIAM, AND H. RONALD. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.
- FORBES, A. T., AND N. T. DEMETRIADES. 2006. The benthos of Nyamithi Pan, Ndumo Game Reserve, KwaZulu-Natal. Unpublished report prepared for Ezemvelo KZN Wildlife by: Marine and Estuarine Research.
- GRIGG, G. C., SEEBACHER, F., BEARD, L. A. AND D. MORRIS. 1998. Thermal relations of large crocodiles, *Crocodylus porosus*, free-ranging in a naturalistic situation. Proceedings: Biological Sciences 265:1793-1799.
- HEATH, S. K., AND A. J. PLATER. 2010. Records of pan (floodplain wetland) sedimentation as an approach for post-hoc investigation of the hydrological impacts of dam impoundment: The Pongolo river, KwaZulu-Natal. Water Research 44:4226-4240.
- HEEG, J., AND C. M. BREEN. 1982. Man and the Pongolo floodplain. National Scientific Programmes Unit: CSIR, SANSP Report 56, 1982, pp 129

- HENEIN, K., AND G. MERRIAM. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecology* 4:157-170.
- HUTTON, J. M. 1987a. Growth and feeding ecology of the Nile Crocodile (*Crocodylus niloticus*) at Ngezi, Zimbabwe. *Journal of Animal Ecology* 56:25-38.
- HUTTON, J. M.. 1987b. Incubation temperatures, sex ratios, and sex determination in a population of Nile Crocodiles (*Crocodylus niloticus*). *Journal of Zoology (London)* 211:143-155.
- HUTTON, J. M. 1989. Movements, home range, dispersal and the separation of size classes in Nile Crocodiles. *American Journal of Zoology* 29:1033-1050.
- JACOBSEN, N. H. G. 1984. Distribution and status of crocodile populations in the Transvaal outside the Kruger National Park. *Biological Conservation* 29:191-200.
- KOFRON, C. P. 1993. Behavior of Nile Crocodiles in a Seasonal River in Zimbabwe. *Copeia* 2:463-469.
- KRAMER, A. 2003. Managing Freshwater Ecosystems of International Water Resources – The Case of the Maputo River in Mozambique. Working Paper On Management in Environmental Planning 07/2003.
- KYLE, R. 2002. More information from the mark and recapture of fish at Kosi Bay, South Africa. *Koedoe* 45:121-122.
- KYLE, R., and G. MARNEWECK. 1996. Ndumo Game Reserve, South Africa: Information Sheet for the site designated to the List of Wetlands of International Importance. Department of Environmental Affairs and Tourism, Pretoria.
- LANG, J. W. 1987. Crocodylian behaviour implications for management. *In: Wildlife management; Crocodiles and alligators*. G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.). Beatty and Sons, Sydney. Pp. 273-294.

- LEGENBRE, P., AND M.-J. FORTIN. 1989. Spatial pattern and ecological analysis. *Vegetation* 80:107-138.
- LESLIE, A. J. 1997. The ecology and physiology of the Nile Crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. PhD thesis. Drexel University, Philadelphia.
- LEVIN, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73:1943-1967.
- Malvasio, A. 2006. Studies of *Melanosuchus niger* and *Caiman crocodilus* populations in the Javaes River, Araguaia National Park, Tocantins, Brazil. *Crocodile Specialist Group Newsletter* 25:11-12.
- MATHEWS, W. S. 1994. Hippo and crocodile counts in the northern KwaZulu-Natal region. Unpublished report, Natal Parks Board, Pietermaritzburg.
- MODHA, M. L. 1967. The ecology of the Nile Crocodile, *Crocodylus niloticus* Laurenti. 1786, on Central island, Lake Rudolph. *East African Wildlife Journal* 5:74-95.
- MONTAGUE, J. 1983. Influence of water level, hunting pressure and habitat type on crocodile abundance in the Fly River Drainage, Papua New Guinea. *Biological Conservation* 26:309-339.
- PERRY, J. N., LIEBHOLD, A. M., ROSENBERG, M. S., DUNGAN, J., MIRITI, M., JAKOMULSKA, A., AND S. CITRON-POUSTY. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25:578-600.
- POOLEY, A. C. 1969. Preliminary studies on the breeding of the Nile Crocodile, *Crocodylus niloticus*, in Zululand. *Lammergeyer* 10:22-24.

- POOLEY, A. C. 1982. The ecology of the Nile Crocodile, *Crocodylus niloticus*, in Zululand, South Africa. MSc thesis. University of Natal, Pietermaritzburg.
- POPLE, A. R., PHINN, S.R., MENKE, N., GRIGG, G. C., POSSINGHAM, H. P. AND C.MCALPINE. 2007. Spatial patterns of kangaroo density across the South Australian pastoral zone over 26 years: aggregation during drought and suggestions of long distance movement. *Journal of Applied Ecology* 44:1069-1079.
- RADLOFF, F. G. T., HOBSON, K. A. AND A. J. LESLIE. 2012. Characterising ontogenetic niche shifts in Nile crocodile using stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses of scute keratin. *Isotopes in Environmental and Health Studies* 48:439-456.
- SEEBACHER, F. AND G. C. Grigg. 1997. Patterns of body temperature in wild Freshwater Crocodiles, *Crocodylus johnstoni*: Thermoregulation versus thermoconformity, seasonal acclimatization, and the effect of social interactions. *Copeia* 3:549-557.
- SIMPSON, B. K., AND H. MEDIYANSYAH. 2009. A preliminary wet season assessment of the tomistoma (*Tomistoma schlegelii*) in the Lake Siawan-Belida area, upper Kapuas River, West Kalimantan, Indonesia. *Fauna & Flora International*: Jakarta.
- SWANEPOEL, D. J. G. 1999. Movements, nesting and the effects of pollution on the Nile Crocodile *Crocodylus niloticus* in the Olifants River, Kruger National Park. MSc thesis. University Natal, Pietermaritzburg.
- TAYLOR, P. D., FAHRIG, L., HENEIN, K. AND G. MERRIAM. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571-573.
- TISCHENDORF, L., AND L. FAHRIG. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90:7-19.

- TOWNSEND, C. R., BEGON, M. AND J. L. HARPER. 2003. *Essentials of Ecology*. Blackwell Science Ltd.
- TURNER, M. G. 1989. Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-197.
- VAN VUUREN, L. 2011. KwaZulu-Natal : it's man versus croc : conservation. *Water wheel* 10:13-18.
- WADESON, R. 2006. Lower Usuthu River-diversion channel. Unpublished scoping report. Department of Water Affairs and Forestry, Pretoria.
- WALLACE, K. M., AND A. J. LESLIE. 2008. Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42:361–368.
- WARD, M. C. 1989. Aerial survey of Ndumo Game Reserve. Unpublished report. Natal Parks Board, Pietermaritzburg.
- WEBB, G. J. W., MANOLIS, S. C., and BUCKWORTH, R. 1982. *Crocodylus johnstoni* in the McKinlay River Area, N.T.I. Variation in the diet, and a new method of assessing the relative importance of prey. *Australian Journal of Zoology* 30:877-99.
- WIENS, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.

LIST OF FIGURES

Figure 1. The location of Ndumo Game Reserve in KwaZulu-Natal, South Africa, indicating the major pans and rivers in the reserve.

Figure 2. Ndumo Game Reserve, KwaZulu-Natal, highlighting the Usuthu and Phongola floodplains and their various pans and channels.

Figure 3. The proportion (SQASIN transformed) of Nile Crocodiles (Mean \pm SD) in the respective Phongola and Usuthu River systems from aerial surveys (n = 12) 1971 to 2010.

Figure 4. The proportion (SQASIN transformed) of Nile Crocodiles counted in the Usuthu and Phongola river systems from 1971-2010 in Ndumo Game Reserve.

Figure 5. Average distribution of abundance (mean \pm SD) of Nile Crocodiles within the Usuthu River System, Ndumo Game Reserve, from 1971- 2009.

Figure 6. The average proportion (SQASIN transformed; mean \pm SD) of Nile Crocodiles in Lake Nyamithi and the Phongola floodplain from 1971- 2009.

Figure 7. The average distribution of Nile Crocodiles (mean \pm SD) within the Phongola River system from 1971- 2009.

Figure 8. The monthly change in abundance of Nile Crocodiles at Lake Nyamithi in Ndumo Game Reserve from 03/2009 – 08/2012.

Figure 9. The relative monthly abundance of Nile Crocodiles counted in Lake Nyamithi according to size class (TL) from 03/2009 – 10/2010.

Figure 10. The negative relationship between maximum monthly temperature ($^{\circ}$ C) and Nile Crocodile density in Lake Nyamithi, Ndumo Game Reserve, over the period 2009 – 2012.

Table 1. The influence of environmental variables on the number of Nile Crocodiles counted within different size classes (< 1.5 m; 1.5 - 2.5 m; 2.5 - 3.5 m; 3.5 - 4.5 m and 4.5 m +) at Lake Nyamithi from 03/2009 – 11/2012.

p values				
Size class	Water level	Min temp	Max temp	Rainfall
< 1.5 m	0.88	0.49	0.22	0.91
1.5 - 2.5 m	0.26	0.02	0.98	0.02
2.5 - 3.5 m	0.33	0.49	0.58	0.17
3.5 - 4.5 m	0.52	0.16	0.86	0.18
4.5 m +	0.50	0.89	0.73	0.07

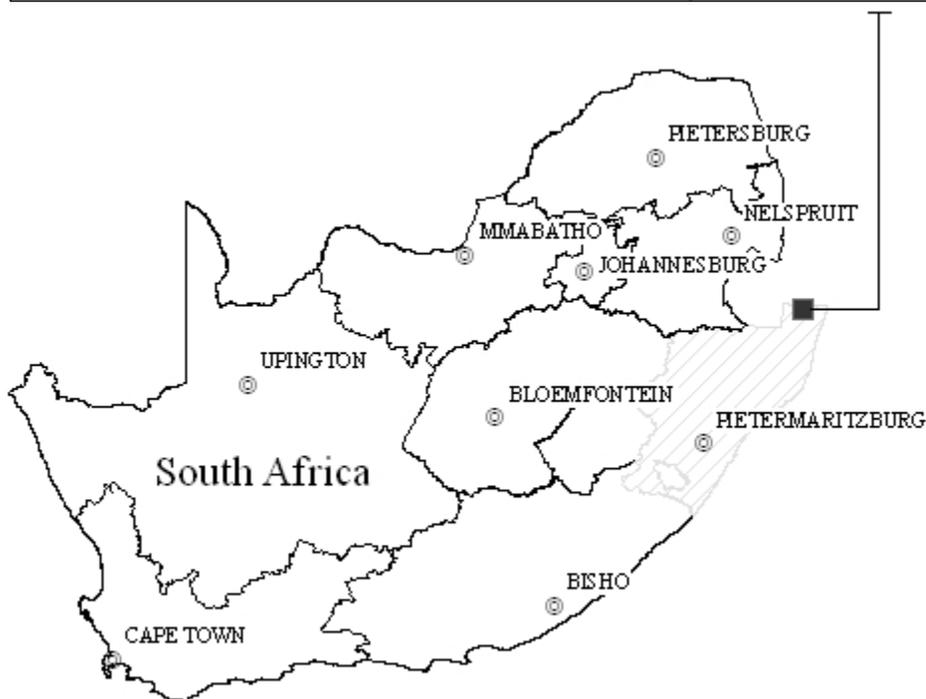
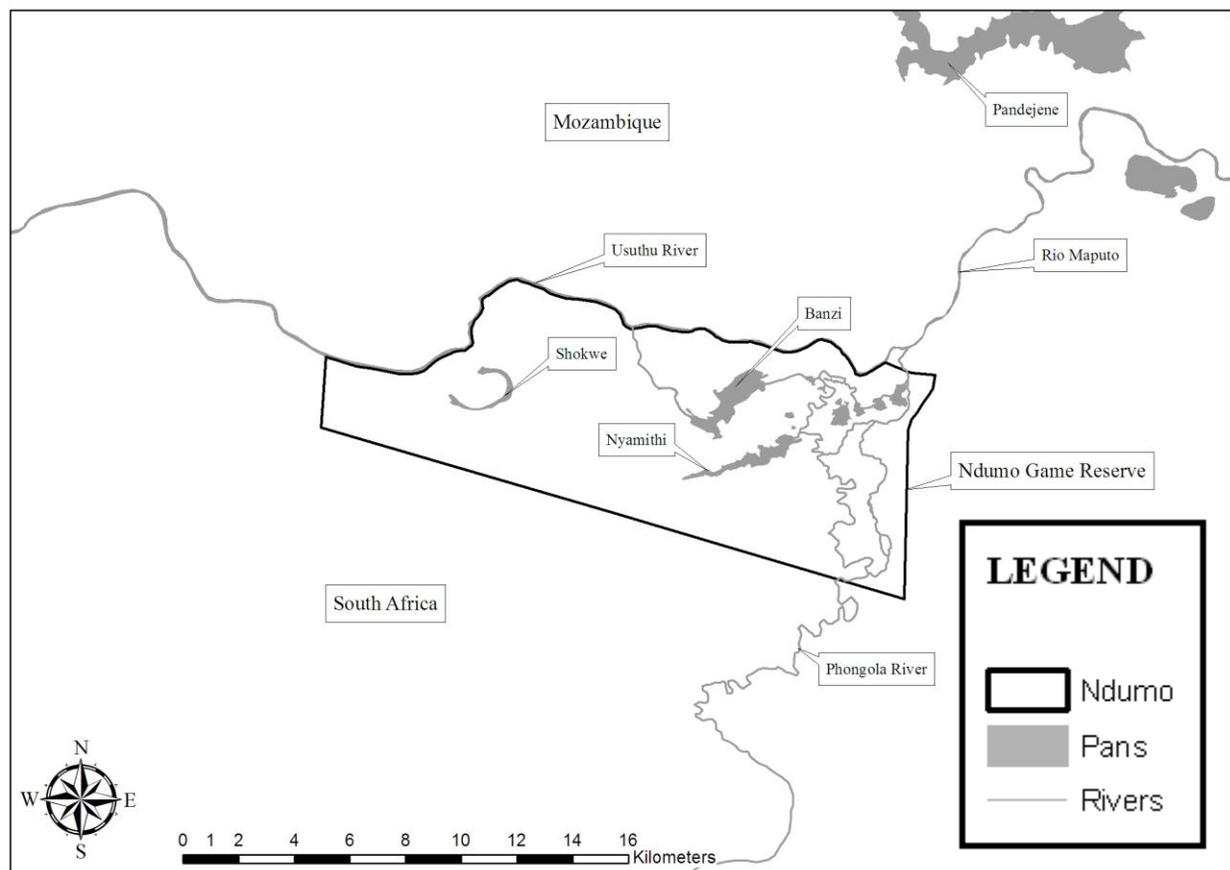


Figure 1. The location of Ndumo Game Reserve in KwaZulu-Natal, South Africa, indicating the major pans and rivers in the reserve.

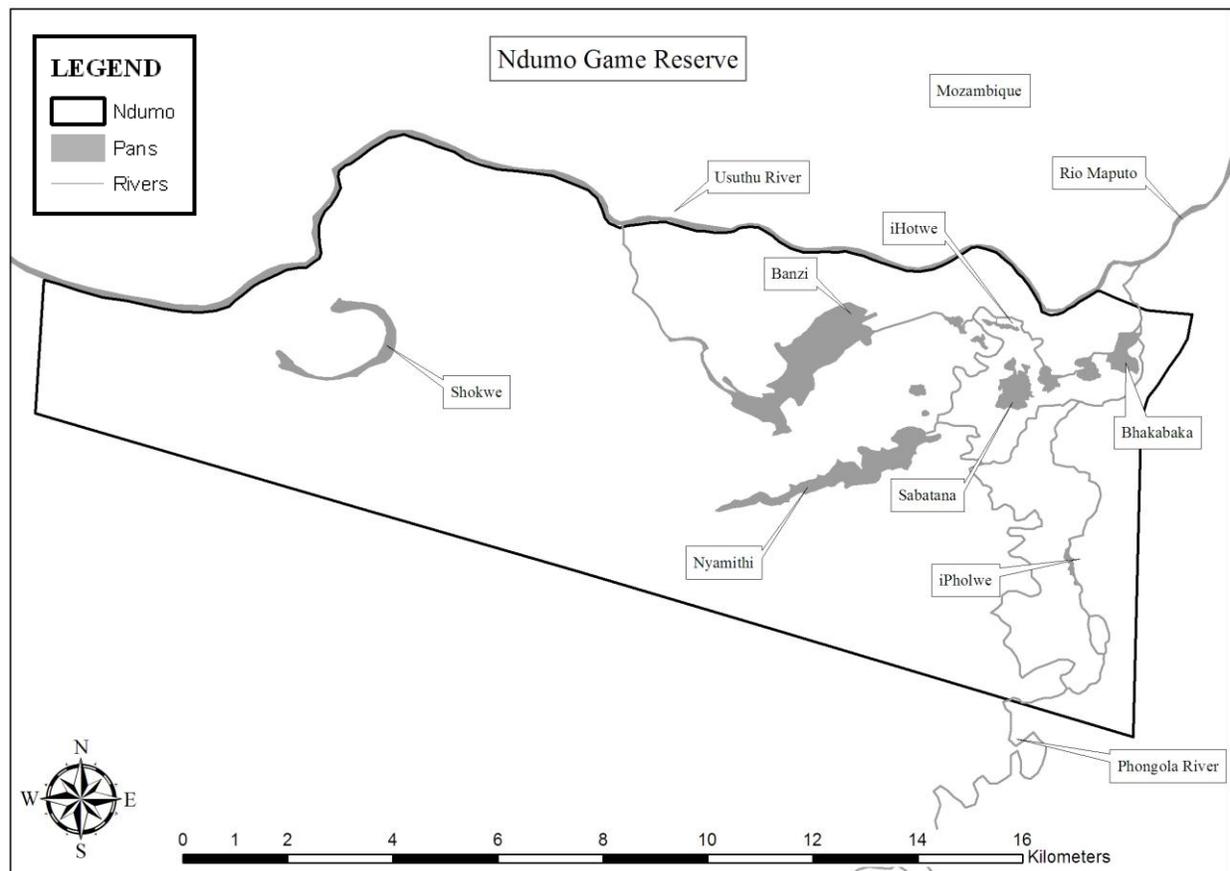


Figure 2. Ndumo Game Reserve, KwaZulu-Natal, highlighting the Usuthu and Phongola floodplains and their various pans and channels.

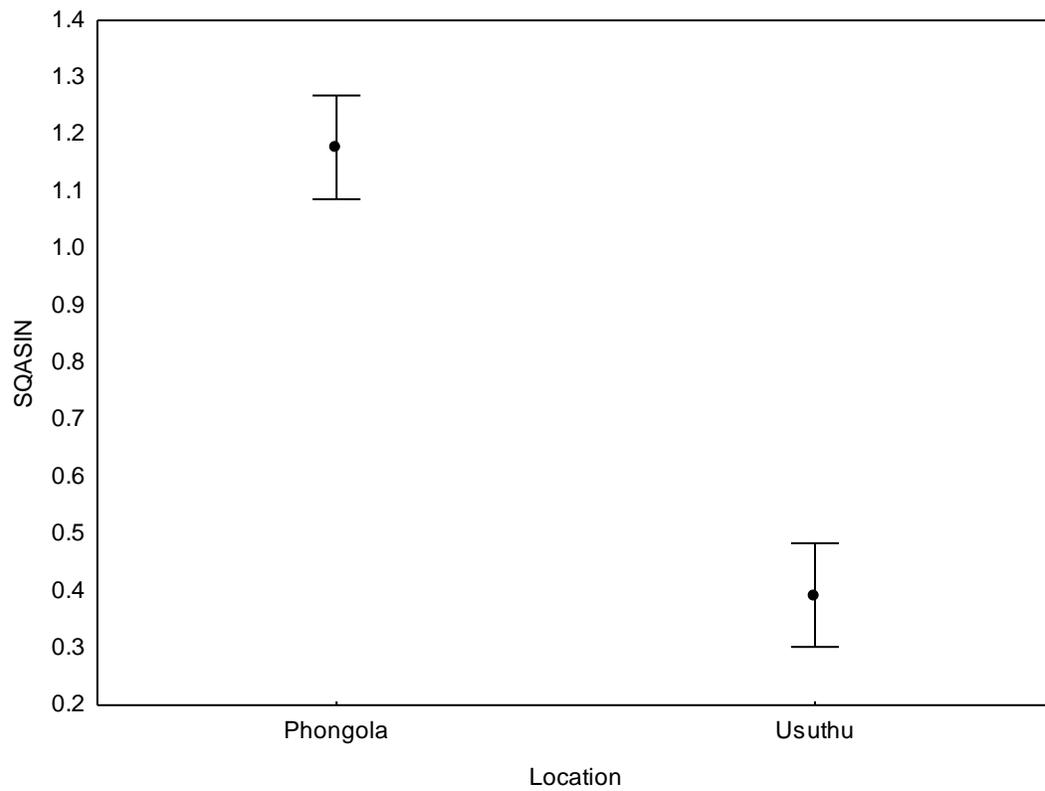


Figure 3. The proportion (SQASIN transformed) of Nile Crocodiles (Mean \pm SD) in the respective Phongola and Usuthu River systems from aerial surveys (n = 12) 1971 to 2010.

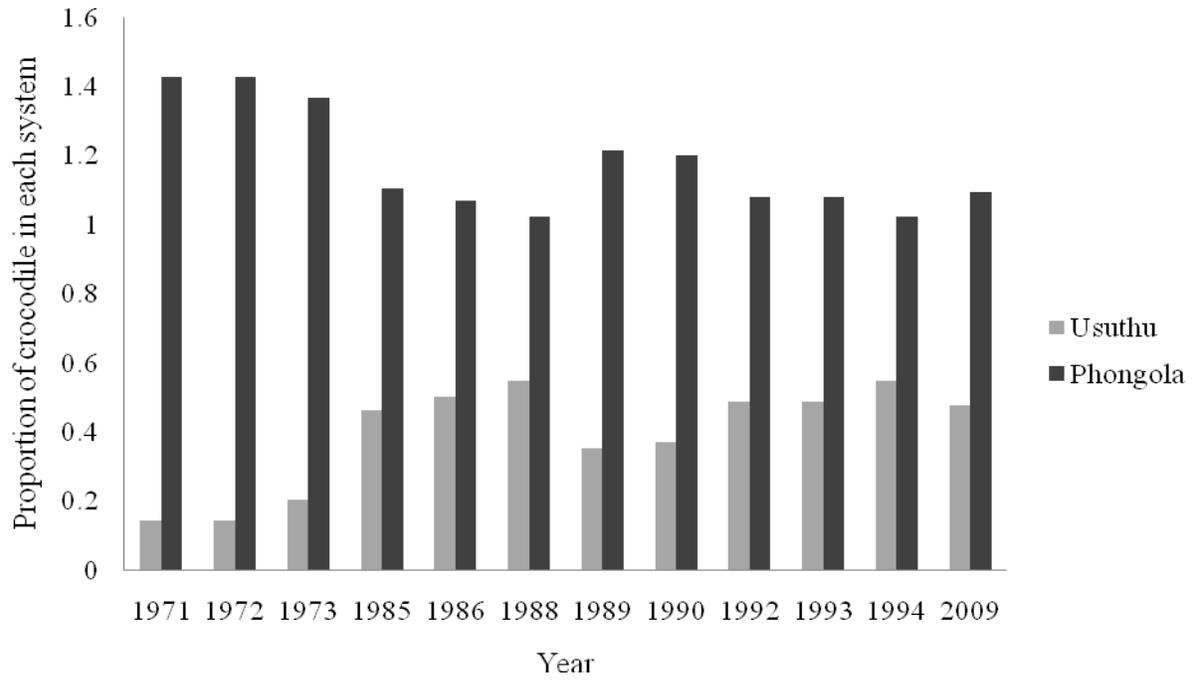


Figure 4. The proportion (SQASIN transformed) of Nile Crocodiles counted in the Usuthu and Phongola river systems from 1971-2010 in Ndumo Game Reserve.

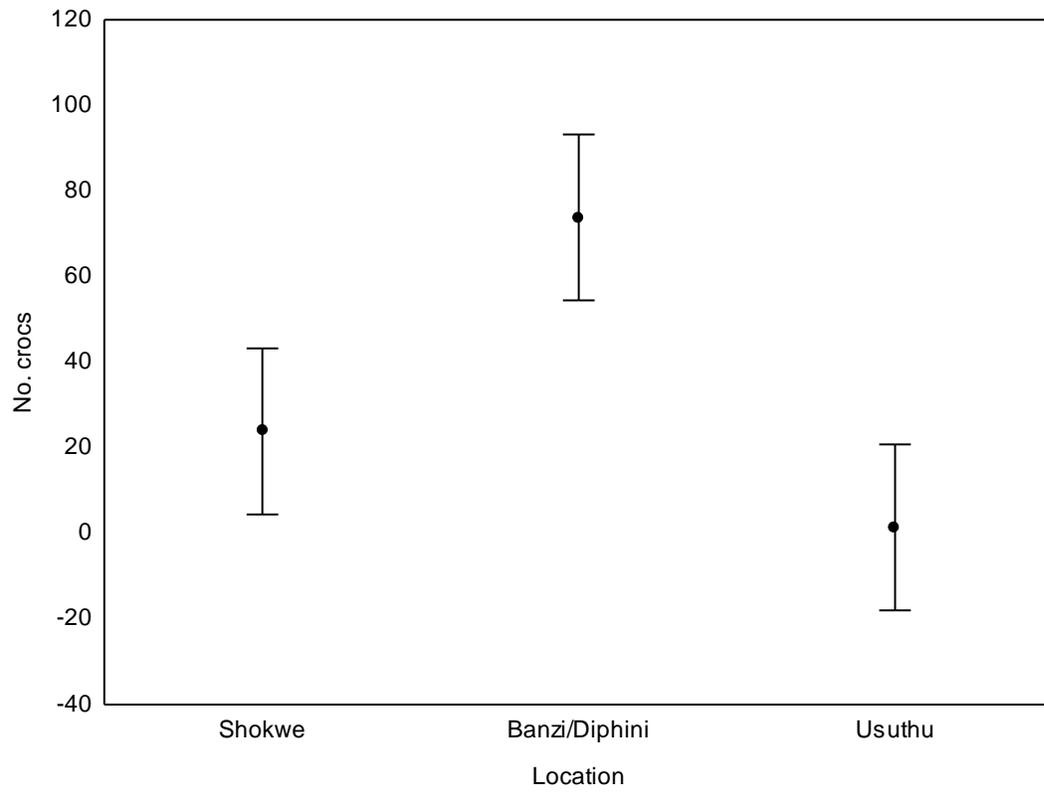


Figure 5. Average distribution of abundance (mean \pm SD) of Nile Crocodiles within the Usuthu River System from 1971- 2009.

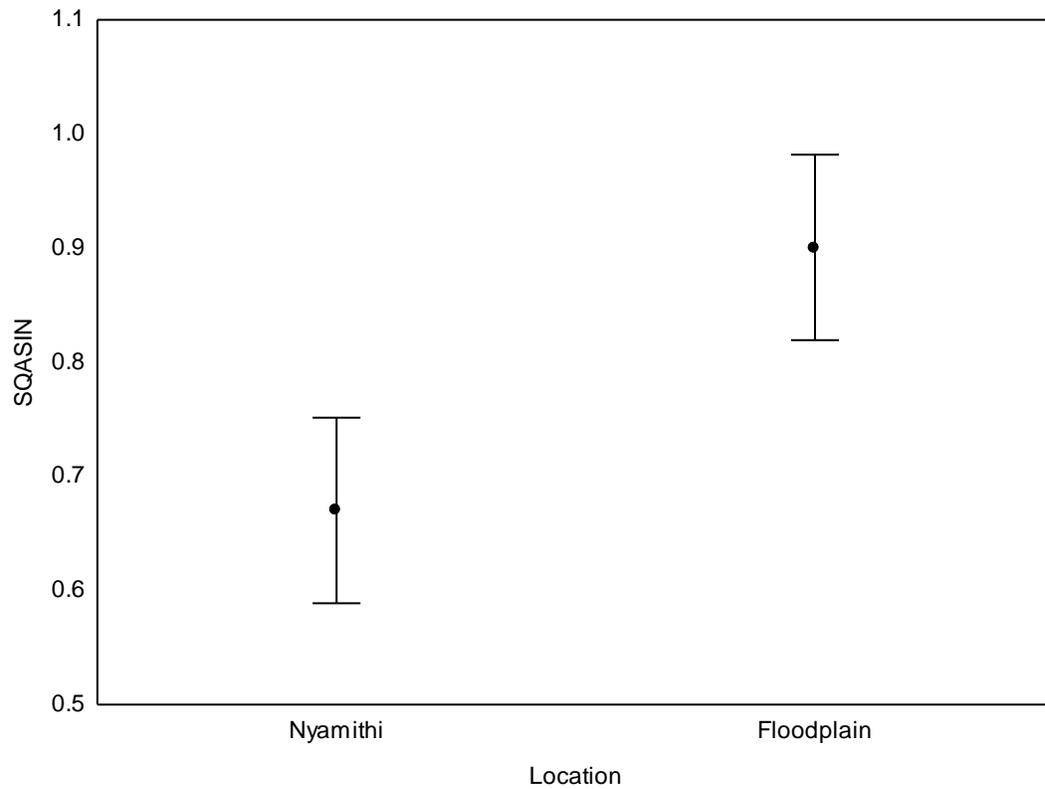


Figure 6. The average proportion (SQASIN transformed; mean \pm SD) of Nile Crocodiles in Lake Nyamithi and the Phongola floodplain from 1971- 2009.

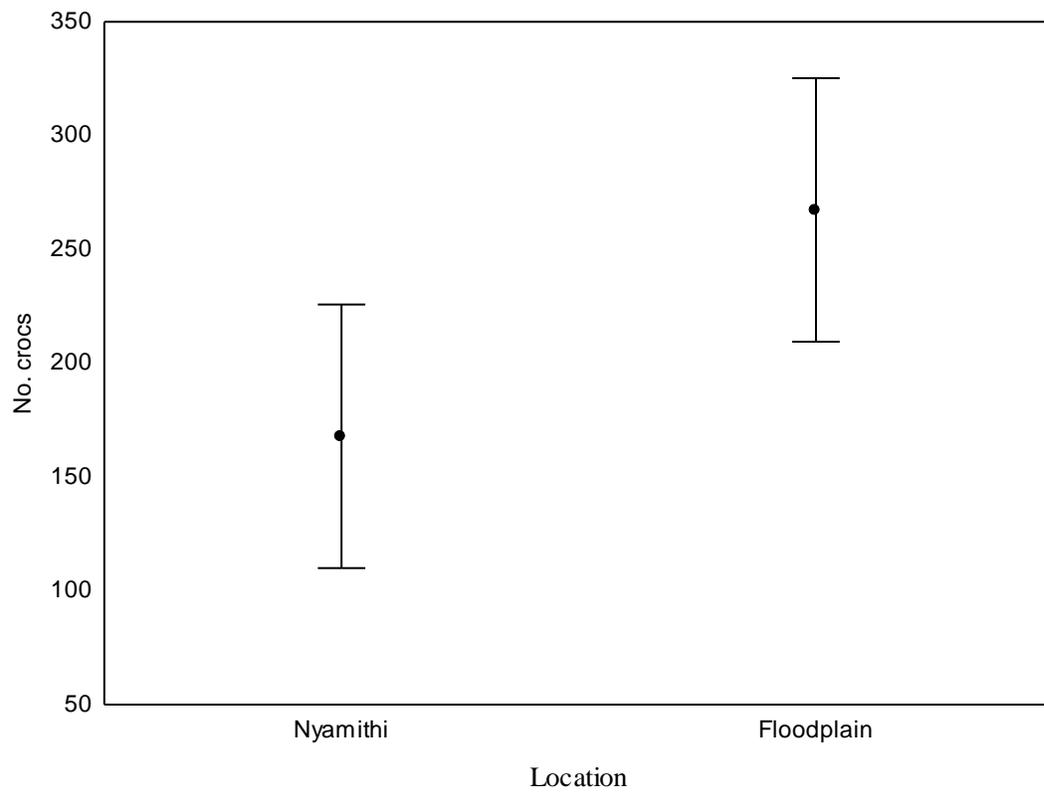


Figure 7. The average distribution of Nile Crocodiles (mean \pm SD) within the Phongola River system from 1971- 2009.

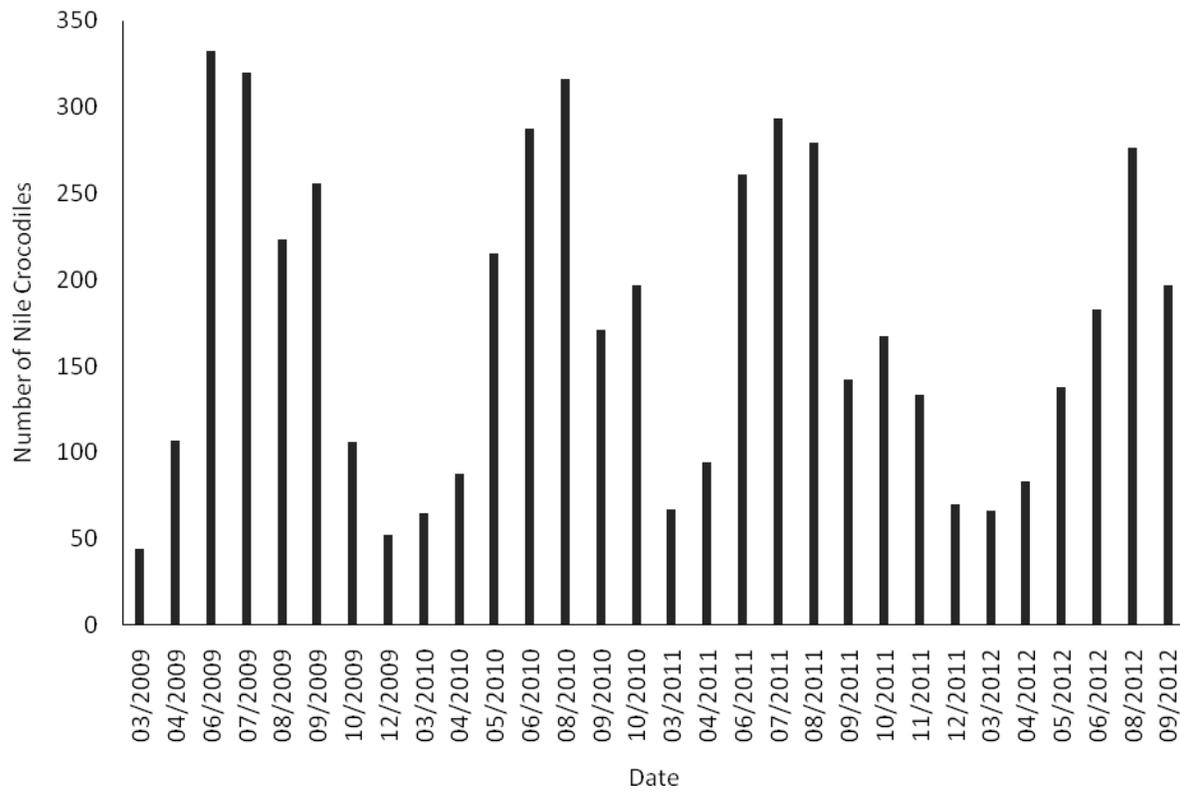


Figure 8. The monthly change in abundance of Nile Crocodiles at Lake Nyamithi in Ndumo Game Reserve from 03/2009 – 08/2012.

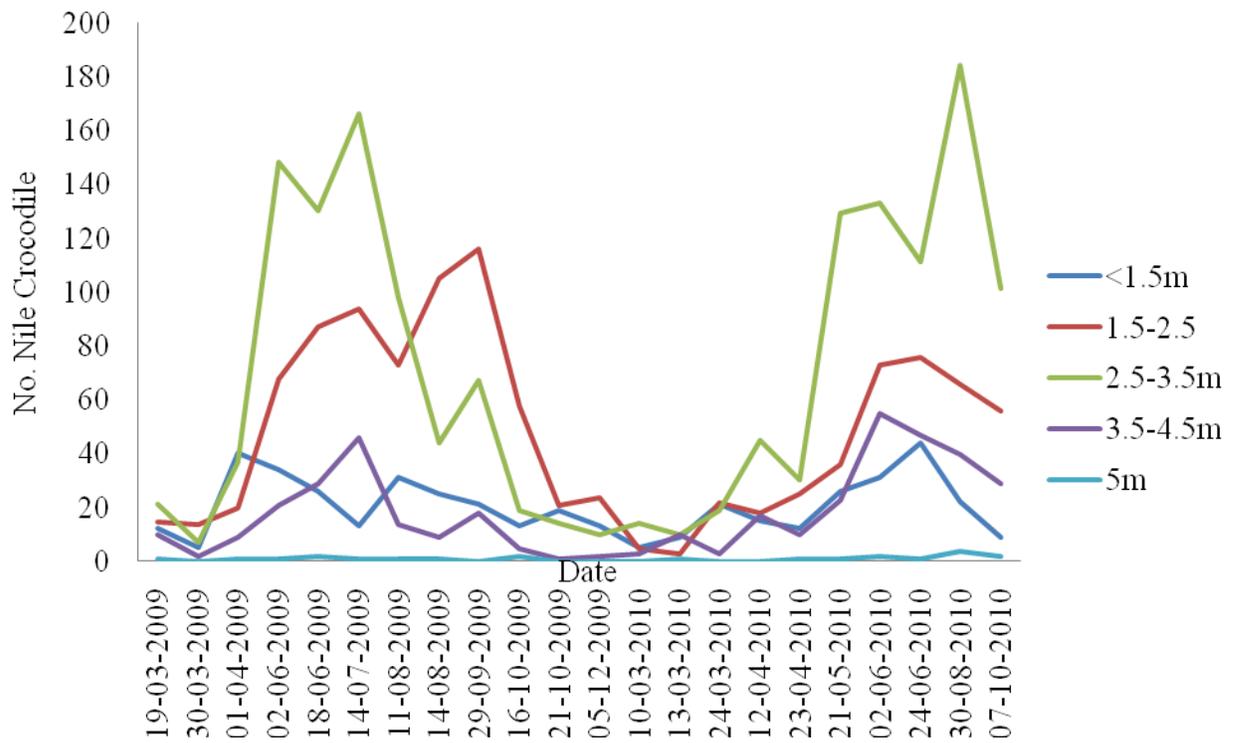


Figure 9. The relative monthly abundance of Nile Crocodiles counted in Lake Nyamithi according to size class (TL) from 03/2009 – 10/2010.

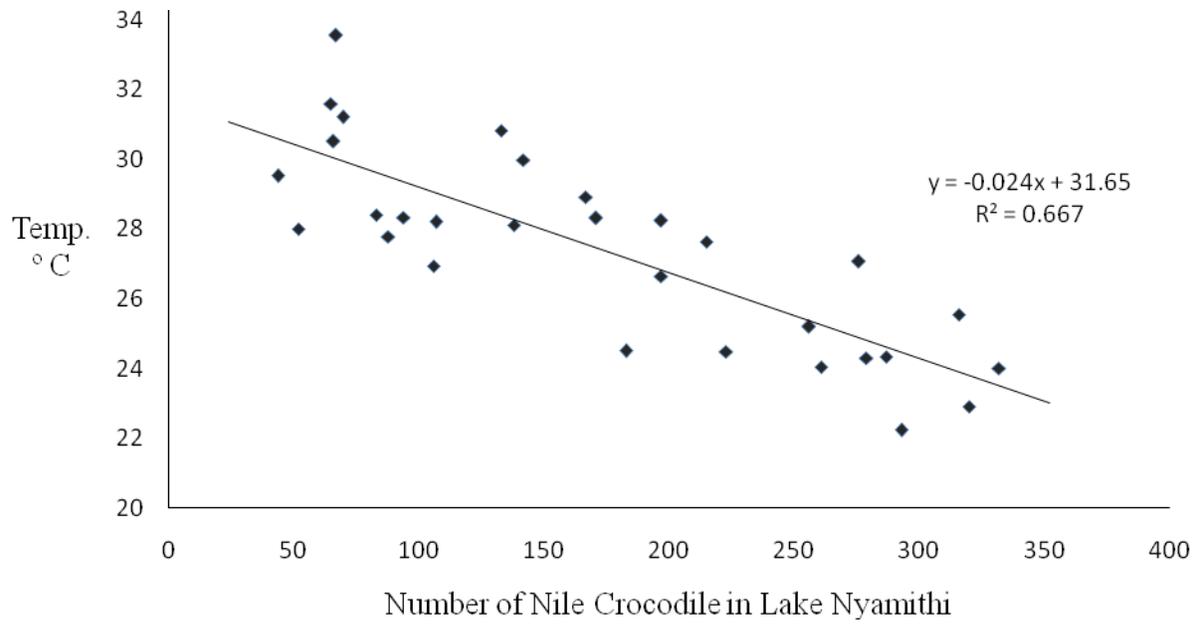


Figure 10. The negative relationship between maximum monthly temperature (°C) and Nile Crocodile density in Lake Nyamithi, Ndumo Game Reserve, over the period 2009 – 2012.

ANNEX 2

During 2009 two aerial surveys were undertaken to estimate the relative abundance of Nile Crocodile in Ndumo Game Reserve. The first survey was conducted with the help of KZN Wildlife and follows the methods used in aerial surveys for Nile Crocodiles in NGR from 1971 – 1994. The second survey was assisted by The Bateleurs (Flying for Conservation) and necessitated adopting a new technique. Both methods are described below.

Following historical method employed in all the surveys at NGR a helicopter, in this case aAS350 Ecureuil helicopter (Eurocopter), was used with four observers including the pilot. Flight speed and altitude was low (flight speed of 75 km/h; average altitude of 25 m). Each crocodile observed was recorded per sub-region and totals recorded on a 1:50 000 map of the reserve. Counting areas were divided amongst observers with observers on the left of the helicopter searching only the left bank and the observers on the right searching only the right bank. Weather conditions were good, the survey lasted 1 h but water levels were high due to high rainfall in the Usuthu catchment area.

A Piper Supercub aircraft was used for further aerial surveys with two observers seated longitudinally. The pilot had been a ranger at NGR and was familiar with the area. 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 Vista[®] Cx Global Positioning System (GPS) was synchronised with a dictaphone (HP PDA) and a running commentary of the flight recorded while the GPS simultaneously recorded the route flown by creating waypoints at 50 m intervals. Data captured at these waypoints included time and location. The time at which sightings were recorded on the dictaphone could thus be related to a GPS waypoint and the co-ordinates for sightings established. A Canon EOS 400D digital camera was used to record areas of high crocodile density when counting from the air proved inaccurate. The number of crocodiles captured in these photographs were counted after the survey and added to the tally. The time the photograph was taken was related to a GPS waypoint for the co-ordinates of the sighting to be established. Weather conditions were favourable to start with but became gusty towards mid-morning. Temperature ranged between 18°C and 20°C. The count took place between 08:42 and 10:22 including take-off and landing from the nearby Tembe Elephant Park with an average flying speed of 139 km/h at an average altitude of 173 m a.m.s.

CHAPTER 3

Movement and Home Range of Nile Crocodiles in Ndumo Game Reserve, South Africa

P. M. Calverley and C. T. Downs

School of Life Sciences, University of KwaZulu-Natal.

Private Bag X01, Scottsville, Pietermaritzburg, 3209 South Africa. Email:

calverleypeter@gmail.com.

Formatted for *Copeia*

3.1 ABSTRACT

*The study of movement patterns and home range is fundamental in understanding the spatial requirements of individuals and is one of the first steps in generating information for the conservation and management of threatened species. Movement patterns of 50 Nile Crocodiles (*Crocodylus niloticus*) between 202 – 472 cm total length (TL) were followed over 18 months using mark-resight ($n = 36$), radio ($n = 10$) and satellite ($n = 3$) telemetry at Ndumo Game Reserve (NGR) in north eastern KwaZulu-Natal, South Africa. The duration of radio transmitter attachment (131 days, $SE \pm 11.35$) was significantly and negatively related to TL and reproductive status. Satellite transmitters suffered electronic failure after an average of 15 days ($SE \pm 12.53$). 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 TL with sub-adults (1.5 - 2.5 m TL) occupying smaller, more localized home ranges than adults (> 2.5 m TL). The largest home ranges were for adults (> 2.5 m). Home ranges overlapped extensively suggesting that territoriality, if it does indeed take place, 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. 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. 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. Movement out of the reserve and into the Rio Maputo is thought to be in response to seasonal concentrations/migrations of prey species and starts in November. Crocodiles then move back into NGR as water levels in the floodplain recede in May.

3.2 INTRODUCTION

Studying movement patterns and the distribution of animals is fundamental in understanding basic population processes (Nathan et al., 2008) and is often a prerequisite for effective conservation and management (Rubenstein and Hobson, 2004). Movement studies normally consist of four key components namely; dispersal, migration, territoriality and home range (Swanepoel, 1999). Dispersal can be defined as the unidirectional movement of individuals out of the area occupied during the early part of their lives (Hutton, 1989a). Nile Crocodiles generally go through two dispersal events in a lifetime. The first occurs roughly 6-8 weeks after hatching whereby hatchlings leave the crèche area (Pooley, 1969; Leslie, 1997). Tucker *et al.* (1997) found that crèche dispersal of freshwater crocodiles (*Crocodylus johnstoni*) was related to a threshold in mass/length ratios. The second dispersal event is related to body size and takes place between 1.2 – 1.5m total length (TL) and is related to an ontogenetic shift in diet and habitat requirements (Hutton, 1989a; Wallace and Leslie, 2008; Radloff et al., 2012b). However, Tucker *et al* (1998) identified a third possible dispersal event where male *C. johnstoni* dispersed

further than females after sexual maturity had been reached. From an evolutionary perspective, inclusive fitness is maximized when daughters remain in close proximity to favorable nesting habitat and sons disperse out of territories defended by dominant males (Tucker et al., 1998) and sex biased dispersal could occur in other crocodylian species such as the Nile Crocodile. Dispersal may therefore be innate or due to changes in environmental conditions and resources (Howard, 1960).

While dispersal involves the unidirectional movement of individuals away from a particular area, migrations are defined by the sequential abandonment and return to an area by a population of animals in response to seasonal changes in resource availability (Swanepoel, 1999). Generally crocodylians do not display migratory behavior although the Nile Crocodile may be the exception (Russell et al., 2005) with recent studies showing that both *C. niloticus* and *C. porosus* have homing capabilities (Combrink, 2013). Swanepoel (1999) found that Nile Crocodiles in Kruger National Park move up to 36 km between South Africa and Mozambique on a seasonal basis. Pooley (1982) noted similar movement patterns in Ndumo Game Reserve (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, 2013). There is also evidence that Nile Crocodiles undertake large scale seasonal movements in response to spatial and temporal changes in prey abundance (Leslie, 1997). Habitat requirements of Nile Crocodiles therefore change on a seasonal basis which often result in seasonal changes in distribution patterns of a particular population (Botha, 2005; Champion, 2011). Where critical resources in one habitat patch, such as nesting sites, are

far apart from critical resources in another accessible habitat patch, such as basking or foraging sites, large scale seasonal movement between the habitat patches may be expected.

Factors driving seasonal movement may help define home range – “the area an animal may traverse in search of food, shelter or a mate” (Burt, 1943). For crocodilians, shelters may need to fulfill thermal or protective needs, while searching for a mate can be extrapolated more broadly to include mating and nesting sites. Ontogenetic changes in feeding, breeding, shelter requirements and social interactions result in the formation of activity centers within the home range that may change on a daily or seasonal basis (Hocutt et al., 1992). Generally home ranges contract around suitable basking sites in winter and expand to include favorable breeding (mating and nesting) and foraging sites in summer (Hutton, 1989a). Adult male Nile Crocodiles have the largest home ranges followed by intermediate males and females (Hutton, 1989b). The home ranges of reproductive females contract around nesting sites during the summer and together with pre-dispersal juveniles (<1.2 m TL) form the smallest home ranges (Hutton, 1989a). Home ranges of Nile Crocodiles are therefore influenced by size/age, sex, season, reproductive status and habitat (Hocutt et al., 1992; Swanepoel, 1999).

The “exclusion of a conspecific from a particular part or all of the home range” is known as territoriality (Henschel and Skinner 1991) and has been reported in Nile Crocodiles (Modha, 1967; Gans and Pooley, 1976). Territoriality is displayed most often by reproductively active crocodilians around mating sites (Cott, 1961; Rootes and Chabreck, 1993) and during the breeding season. However, some studies suggest that if territorial behavior 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). The effects of territoriality on

migration, dispersal and home ranges of Nile Crocodiles may therefore be profound and vary on a seasonal basis and between ecosystems.

Arguably, movement, migration and territoriality all take place within the conventional home range paradigm. However, defining a single home range may become problematic for migratory species that occupy several discrete habitats for shelter, feeding or breeding purposes throughout the year. In order to understand the spatial requirements and hierarchical status of individual animals, territoriality and movement must therefore be studied (Brien et al., 2008). To achieve this different techniques are used depending on the objectives of the study and the processes under investigation. In crocodylians the study of movement patterns is normally achieved through the use of capture-mark resight/recapture activities as well as satellite, radio and more recently acoustic telemetry (Hutton, 1989b; Franklin et al., 2009; Campbell et al., 2010). Capture-mark recapture/resight techniques provide good base line data on crocodylian movement but often lack the resolution necessary for evaluating finer scale movement patterns (Kay, 2004a) and radio telemetry is used most often to investigate movement, dispersal patterns, habitat use and home range (Strauss et al, 2008; 61; Brien, 2008). However, Hutton (1989) found that home range determined through capture-mark resight techniques compared favorably with that determined by radio telemetry, although mark resight based home ranges were consistently smaller due to fewer sightings obtained using this method. Whether this is a reflection on the merits of capture-mark resight or the inadequacy of VHF telemetry remains unsure. Nonetheless, satellite tracking systems are considered the most accurate, affordable and efficient method of tracking crocodylians in remote areas and would be the ultimate way of following crocodile movement (Kay, 2004a; Thomas et al., 2011).

However, crocodiles are notoriously hard to study with one of the biggest challenges being transmitter attachment (Botha, 2005; Strauss et al, 2008; Franklin et al., 2009; Champion, 2011; Combrink, 2013). Hutton (1989) remains one of the few studies in which home range of Nile Crocodiles has been successfully quantified. The initial outlay for satellite telemetry can be prohibitively expensive (Richter and Cumming, 2008; Rosenblatt and Heithaus, 2011) particularly if transmitter attachment/longevity is uncertain and it is prudent to conduct *a priori* investigations into attachment and longevity of transmitters (Strauss et al, 2008).

In the current study radio telemetry and capture mark recapture/ resight techniques were used to investigate the movement ecology of Nile Crocodiles in Ndumo Game Reserve (NGR) KwaZulu-Natal, South Africa and as an antecedent to satellite telemetry. The aim of the study was to quantify home range, migration and territoriality of Nile Crocodiles in NGR. In particular we wanted to compare seasonal changes in habitat use and movement, and to determine whether crocodiles move out of the reserve and into unprotected areas. We predicted that home ranges were influenced by season, size and sex of crocodiles and that a seasonal migration from NGR into the Rio Maputo floodplain took place over the wet season.

3.3 METHODS

3.3.1 Study site

Ndumo Game Reserve (NGR) is a relatively small (10 000 ha) Ezemvelo KZN Wildlife Game Reserve (EKZNW) in north eastern KwaZulu-Natal and is home to South Africa's third largest Nile Crocodile population, at perhaps the highest density in the country. NGR conserves two major river systems; 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 (Fig. 1). The confluence of these two river systems in the north east corner of the reserve and the flat nature of the floodplain combine to inundate large tracts of the reserve during times of high rainfall. During the average dry season roughly 12% of the surface area of the reserve is covered by water in the form of permanent pans and river courses. During the wet season over 40% of the reserve becomes inundated. There is a large degree of seasonal movement of Nile Crocodiles in the floodplain as habitat availability fluctuates on a seasonal basis (Pooley, 1969).

The Usuthu system consists primarily of the Usuthu River, the Dipini-Banzi Pan area and Shokwe Pan (Fig. 1). The Phongola system consists of the Phongola floodplain and Lake Nyamithi (Fig. 1). Ward (1989) suggested that the Phongola and Usuthu systems are home to two sub-populations of Nile Crocodiles that remain for the most part discrete. Ward (1989) therefore hypothesised that the density of crocodiles at a particular site (e.g. Lake Nyamithi) within a particular system (e.g. Phongola system) is a function of the total number of crocodiles at the other sites within that system (e.g. Phongolo floodplain) and unrelated to the number of crocodile in the neighbouring system (Usuthu system). The largest permanent pan in the Phongola floodplain is Lake Nyamithi (157 ha) which also has the highest density of Nile Crocodiles in NGR (Fig. 1) and forms the focal point of study where seasonal variation in abundance was recorded. Further details and description of the study area are presented in Chapter 2.

3.3.2 Capture techniques

All Nile Crocodile capture in NGR in the present study took place in Lake Nyamithi (Fig 1). At its most populous the 1.7 km² lake holds 400 Nile Crocodiles at a density of 235

crocodiles km^{-2} and is thus the most practical place to carry out capture exercises (pers. obs., Chapter 4). During winter the deepest part of the lake or lake basin 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 favor noosing as a capture technique described in (Hutton and Woolhouse, 1989). Crocodiles were approached at night from a 3.5 m aluminum mono hull “tinny” 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.

Crocodiles that submerged upon approach of the boat were often spotted under the clear water and were harpooned as described in Webb and Messel (1977). 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 animal uses its feet to dig itself 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 animal decided to ‘dig in’, the boat was pulled towards

the crocodile by reeling in. Once positioned above the crocodile the animal was either noosed if the head or tail broke the surface or was harpooned. As mentioned, fishing necessitated the use of heavy angling equipment so a Penn Power Stick rod (Philadelphia, USA) was used as it was sturdy and has a flexible head to achieve accurate and long distance casting. Because the capture process necessitated casting, a large coffee grinder reel was used (Finn Norr Offshore, USA) with 400 m 80 lb braided fishing line which was attached to 200lb Marlin monofilament nylon.

Regardless of capture technique all captured crocodiles were taken ashore for morphometric measurements, scute notching and color tagging before being released. A unique color 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. All crocodiles captured were between 92.6 cm and 472 cm total length (TL) with a mean TL of 216.7 cm. Seventy one crocodiles were marked with unique identification color tags for mark-resight activities and 10 were fitted with radio transmitters and 3 were fitted with satellite transmitters.

3.3.3 Transmitter attachment

VHF transmitters (150 MHz) were fitted to 11 Nile Crocodiles of varying size and sex. When fitting transmitters to crocodiles it is important to place the transmitter in a position that is out of the water for the maximum amount of time so as to improve signal quality and trackability (Botha, 2005). Transmitters were thus attached between the four nuchal scutes on the nuchal

plate as described by Kay (2004b); 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. Radio-tagged individuals were uniquely scute notched for permanent long-term identification and fitted with a unique sequence of colored tags for short-term visual identification in the advent of transmitter failure or dislodgement.

Three satellite transmitters supplied by African Wildlife Tracking (Pretoria, South Africa) were fitted to Nile Crocodiles; two in 2011 and one in 2012. Following mixed success with the method described by Kay (2004b) with radio transmitters, satellite transmitters were attached using the method described by Brien and Webb (2010) for satellite transmitters. This method had been used on Nile Crocodiles in St. Lucia by Combrink (2013) with much success. 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 (Vortex) 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 (Kay, 2004b).

3.3.4 Radio and satellite tracking activities to estimate home range

Thirty one tracking excursions were undertaken from March to November 2009. After November 2009 radio transmitters could 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 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.

3.3.5 Mark-resight

Between March 2009 and November 2010 diurnal counts were carried out at Lake Nyamithi for mark-resight studies. A vehicle was driven around the 9.5 km periphery of the lake with an average search time of 2 h 53 min. The 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 crocodiles were recorded using a Garmin Vista GX GPS. By 2011 some or all of the colored tags fitted to crocodiles had either been dislodged or were indiscernible due to a covering of mud or algae bringing an end to re-sighting activities. Permission was not granted to attach further tags to new animals by Ezemvelo KwaZulu-Natal Wildlife (EKZNW) as it was felt that a representative amount of the population had been tagged.

3.4 STATISTICAL ANALYSES

3.4.1 Home Range

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 (KDE's) provide the most accurate fit (Worton, 1989), minimum convex polygons (MCP's) most closely follow Burt's (1943) definition of home range. Furthermore, MCP's 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; Kay, 2004b). Since some of the data were significantly autocorrelated (Schoener Index $< 1.6 > 2.4$; Swihart and Slade Index > 0.6) MCP's as well as KDE's were determined for all samples.

The majority of locations achieved through VHF tracking and all of the mark-resight locations were obtained on the water margin. This can be problematic in sinuous water ways or lakes with large bays or outcrops and where few geographic fixes/locations are available as MCP's and KDE's 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 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 RCA's and MSLD's 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 MCP's 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 KDE's were used to calculate 95, 90 and 50% polygons using LSCV as the smoothing factor. Similarly, fixed mean MCP's were constructed for 95, 90 and 50% contours. One way ANOVA's 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 ANOVA's were suitable in determining the effect of a single categorical independent variable (sex or reproductive status) on the home range of Nile Crocodiles.

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. GLIM ANOVA's were run to test for differences in home range estimates produced by the KDE's, MCP's and manually drawn polygons.

3.4.2 Transmitter attachment longevity

Calculating the time period that a transmitter remains attached to a crocodile is problematic because monitoring attachment once the transmitter fails to transmit is difficult, and the transmitter may remain attached after signal/battery failure (Brien and Webb, 2010). However, transmission life can be used as an index of a minimum attachment life (Brien and Webb, 2010). 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 ANOVA's 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.

3.4.3 Statistical analysis

All mean values were presented as mean \pm standard error. Significance was assessed at a p value of 0.05.

3.5 RESULTS

3.5.1 Catching and transmitter fitting

The majority of Nile Crocodiles (82 % of total captured) were caught using the noosing technique. Twelve crocodiles (9 % of total captured) were caught using the harpoon method and six crocodiles were caught using angling equipment (4 % of total captured). 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.

3.5.2 Morphometrics

Between March and May 2009, 10 Nile Crocodiles were caught and fitted with radio transmitters at Lake Nyamithi. This consisted of seven males between 234 cm – 358 cm TL and three females between 202 cm – 281 cm TL (see Table 1.).

Between March 2009 and November 2010 a further 88 crocodiles were caught and fitted with colored tags for mark resight studies, of these 45 were females between 100 cm and 319.4 cm and 43 were males between 84.3 cm and 472 cm.

3.5.3 Radio tracking to show movements

Between March 2009 and November 2009 thirty one radio tracking excursions were undertaken. 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 \pm 1.27). From December onwards no signal could be obtained for the radio tagged crocodiles.

The smallest Nile Crocodile radio tagged (frequency 150.237) was a 202 cm female. She remained in the capture area in the shallow north eastern corner of Lake Nyamithi for the majority of the study, seldom moving from her chosen basking site.

The next largest Nile Crocodile fitted with a transmitter was a 232 cm female (frequency 150.455). She was also caught in the north eastern corner of Lake Nyamithi, however one month later she left Nyamithi and entered the Phongolo Floodplain in the vicinity of iHotwe Pan and did not return to Lake Nyamithi. On the 3rd of September, 5 months after fitting the transmitter she was located in the new course of the Usuthu River below Banzi Pan (Fig. 1).

The smallest male fitted with a transmitter was 234 cm TL (frequency 150.196) on the mid southern shore of Lake Nyamithi on the 24th March 2009. The following night the same individual was spotted within 100 m of the capture site and was not startled by the approaching boat. The night after that (26th March) this same individual was nearly noosed again by mistake and was on the northern bank opposite the capture site. Tracking surveys over the next 5 months would show this to be a regular occurrence with the male regularly moving from basking sights on the northern shore to basking sites on the southern shore. The maximum distance across the lake is 320 m at this point and the male stayed within a 500 m stretch of shoreline on the northern and southern banks (Fig. 1, Appendix 1).

The next largest male was 254 cm TL (frequency 150.215) and was caught in the western inlet of Lake Nyamithi on the 27 March 2009. This part of the lake is only inundated during the wet season. The following day he was spotted 550 m from the capture sight on the northern shore of the lake where he remained for 2 days. Following this he remained in the western half of the lake until June where he moved to the old course of the Phongola River in close proximity to the outlet of Lake Nyamithi and progressed to Bhakabakha Pan over 5.5 km from the capture site. In July he was back in the western half of the lake where he remained until 6 September when signal was lost (Fig. 1, Appendix 2).

A 281 cm male was captured on the 1st of May 2009 in the north western part of Lake Nyamithi. At 19:31 he was released with a radio transmitter attached (frequency 150.276). At 12:00 the following day he was successfully radio tracked and spotted basking on the north eastern portion of the lake, over 1.5 km from the capture sight. He remained in this area until the 29th of May when he was tracked to the central part of Lake Nyamithi where he remained for the duration of June and July. In August a location was obtained at Mavilo Hill – a historical nesting ground in the eastern periphery of the floodplain 5km's from the previous location. Two days after this a location was obtained 6.4 km to the north-west at a concrete bridge across the new course of the Usuthu river below Banzi Pan. On the 12th of November he was back in Lake Nyamithi 6.5 km from the previous radio location. By the 19th November he was located on the causeway at the outlet to Lake Nyamithi and 2 days later was back at Mavilo Hill (Fig. 1, Appendix 4). After this, signal was lost.

Crocodile 295 was a 315 cm male (frequency 151.295) and was captured on the 2nd of May 2009 in the north eastern part of Lake Nyamithi. Five days later he had left Lake Nyamithi and was located at Bakhabakha Pan 3.8 km north east in the Phongolo Floodplain. By the 29th May he was at the entrance to Lake Nyamithi at the causeway and on the 4th of June was back in the western part of Nyamithi where he remained until the 26th of June when he was located in the old course of the Phongola River north of the outlet of Lake Nyamithi. He was not located again until August when he was once again found in Bakhabakha Pan where he remained until signal was lost on the 30th August 2009 (Fig. 1, Appendix 5). This crocodile was never found in the central or western parts of Lake Nyamithi.

The next largest crocodile was a 3.39 m male (frequency 150.316) caught on the 26th of March 2009 in the western inlet of Lake Nyamithi. The following day he was located 1 km to the

east but still in the western part of the lake. On the 29th of March he was located 3.3 km away at the outlet of Lake Nyamithi. The following day he was located in the old course of the Phongola River 200 m south of the causeway. Signal was lost for one month and the next fix was back in Lake Nyamithi at Ndlozi point 1.9 km to the west. Five days later on the 4th June he was spotted back at the outlet of Lake Nyamithi. After this the transmitter was lost and he was identified by the unique color coded tags on nine further occasions throughout Lake Nyamithi until the end of September. It must be noted that re-sighting activities are only practical in open bodies of water or where a clear line of sight of basking individuals is possible. No re-sightings were obtained in the Phongolo Floodplain (Fig. 1, Appendix 6).

The largest crocodile fitted with a transmitter was a 358 cm male (frequency 150.396) caught on the 2nd of May 2009 in the western part of Lake Nyamithi. Three days later he was located at a known basking site (Deception Point - DP) on the southern shore of the lake 1.2 km to the east and in the centre of the lake. For the next 24 days no locations were achieved, however on the 29th May he was again located at DP. By the 18th August he was in Bhakhabhaka Pan and remained until the 30th August. On the 31st August he was back at DP. In September he was located at Mavilo Hill 5 km to the north east in the Phongolo Floodplain where he remained until signal was lost (Fig. 1, Appendix 7).

3.5.4 Mark-resight

Between March 2009 and October 2010, 27 mark-resight exercises were carried out at Lake Nyamithi. 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 activities 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 (Chapter 2, pers. obs.).

3.5.5 Home range

Only home range estimated using KDE's showed significant relationships between home range size and TL of Nile Crocodiles. Core home range (GLIM ANOVA $F_{(1, 5)} = 10.09$, $p = 0.024$), 90 % (GLIM ANOVA $F_{(1, 5)} = 7.07$, $p = 0.045$) and 95% (GLIM ANOVA $F_{(1, 5)} = 6.81$, $p = 0.048$) home range estimates were significantly related to TL (Fig. 2b). Adult Nile Crocodiles occupied larger home ranges (2200.7 ± 373.45 ha) than sub-adults (419.4 ± 466.77 ha) for the 95 % polygons (ANOVA $F_{(1, 7)} = 21.51$, $p = 0.035$) (Fig. 2c). Core area (50 % polygon) used by adults was also larger (510.4 ± 98.90 ha) than sub-adults (2.4 ± 3.26 ha) (ANOVA $F_{(1, 6)} = 13.43$, $p = 0.011$) (Fig. 2d).

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, 1987a) while those of adult Nile Crocodiles ($n = 4$) formed 24 % of the 95 % kernel estimation. 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.

3.5.6 Transmitter attachment longevity

Radio transmitters ($n = 10$) lasted on average 131 ($SE \pm 11.35$) days on Nile Crocodiles in NGR before becoming dislodged or failing to transmit. Duration of transmitter attachment/life was significantly related to size (TL) (GLIM ANOVA $F_{(1, 9)} = 8.54$, $p = 0.02$). Nine of the ten transmitters were dislodged between August and November which coincided with the onset of the breeding season in NGR. Four transmitters were recovered, two of which had visible bite marks. The transmitters were found still embedded in the dental acrylic and with the cable ties still attached. The 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. Crocodile 150.196 gave ample opportunities for observation and we noted each cable tie 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 and possibly increased drag and the likelihood of the transmitter becoming entangled in vegetation, thus increasing the likelihood and speed of detachment.

Satellite transmitters lasted on average 15 days ($SE \pm 12.53$, $n = 3$) on Nile Crocodiles in NGR. No transmitters were recovered.

3.6 DISCUSSION

Improvement in tracking technologies are allowing for more accurate studies on movement and home range, however in many instances attachment and reliability remain a problem (Strauss et al, 2008; Thomas et al., 2011). General findings indicate that crocodilians are capable of travelling further than previously thought (Swanepoel, 1999; Campos et al., 2006; Read et al., 2007; Combrink et al. 2013; Combrink, 2013) while home range size is strongly

influenced by topography, reproductive status, season and size of individuals (Brien et al., 2008). It is necessary to discuss the movement ecology of Nile Crocodiles within this context and in comparison with movement studies conducted on other crocodylian species.

3.6.1 Telemetry

High rates of transmitter loss and detachment in crocodylians 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; pers. obs.; Chapter 5). During this period the majority of transmitters on Nile Crocodiles in NGR were dislodged suggesting that courtship and possible mate competition behavior 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. Once again this could be due to mating behavior as sexual maturity is 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, 2004b; Franklin et al., 2009).

In the current study VHF transmitters were more robust and reliable than GPS transmitters (Thomas et al., 2011). Brien et al. (2010) found that 10% of satellite transmitters fitted to *C. porosus* failed within 16 days of attachment. A further 10% failed within 76 days of attachment bringing the total failure rate for the study to 20% (Brien et al. 2010). Of this 6.7% of failure was definitely due to electronic failure and the remaining 13.3% either due to electronic

failure, attachment failure or transmission failure due to interference from vegetation. However, Combrink (2013) fitted 20 satellite transmitters to Nile Crocodiles in Lake St. Lucia, of which only one failed outright and another was dislodged 535 days after attachment. In both the current study at NGR and Combrink's (2013) study at St Lucia satellite transmitters were attached using subcutaneous stainless steel wires as described by Brien et al. (2010). Furthermore, at NGR Combrink assisted with transmitter attachment and the same materials and methods were used. However, at NGR all 3 satellite transmitters failed within 28 days. All three units recorded locations in the open lacustrine environment of Lake Nyamithi only. No locations were obtained from the Phongola floodplain where vegetative cover is considerably thicker and river channels are narrow with steep banks (Pooley, 1982). Attachment failure is unlikely as the method worked well for Brien et al. (2010) on *C. porosus* with a minimum average attachment period of 463 ± 69 days and for Combrink (2013) with a minimum average attachment period of 339 ± 49.67 days. We concluded that the units either failed electronically or due to an inability to transmit in heavily vegetated areas.

3.6.2 Movement patterns – within seasons

Movement patterns of crocodylians generally constrict during the dry season (Hocutt et al., 1992; Campos et al., 2006; Thomas et al., 2010). Radio transmitters fitted to Nile Crocodiles in NGR show 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 numerous and extensive forays into the Phongolo floodplain and to the new course of the Usuthu River below Banzi Pan, returning to Lake Nyamithi thereafter. Extensive movements during winter is unusual in crocodiles (Hutton, 1989a; Hocutt et al., 1992) and warrants discussion.

Lake Nyamithi is well stocked with fish (pers. obs.) 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 behavior. Furthermore the lake provides excellent basking habitat (Pooley, 1982) with aggregations of up to and exceeding 100 animals in a single locality observed (pers. obs.). 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 behavioral 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 behaviorally through selection of fresh water habitats (Leslie and Spotila, 2000). Movement out of Lake Nyamithi and into the fresh water of the Phongola and Usuthu River channels could be a behavioral osmoregulatory strategy (Kirschner 1970).

3.6.3 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, 1989a; Leslie, 1997;

Swanepoel, 1999; Botha, 2005; Champion, 2011). In winter or during the dry season movements are mostly nocturnal and are focused around basking sites (Hutton, 1989a). 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 has 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 (pers. obs., Chapter 2). 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 (pers. obs., Chapter 2) 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 an absolute abundance of 242 (Fergusson, 2010) while a survey conducted by us 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 90km 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 proof 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.

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). The movement of 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 favorable nesting habitat is triggering movement into the Rio Maputo floodplain. Furthermore, nesting surveys carried out in NGR (Chapter 5) 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.

Crocodiles are highly adept at exploiting ephemeral prey resources such as concentrations of fish (Webb et al., 1982; pers obs) 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. Leslie (1997) suggested that Nile Crocodile movement patterns in Lake St Lucia follow the migration patterns of striped mullet (*Mugil cephalus*) 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.

Crocodiles need to bask for longer durations in winter than in summer (Kofron, 1993). 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.

3.6.4 Home range

This is only the second study to calculate the home range of Nile Crocodiles and comparative data are therefore lacking. However, similar to Hutton's study on Nile Crocodile (Hutton, 1989b) and other studies on saltwater crocodiles (Kay, 2004a; Brien et al., 2008) we found no difference in home range between male and females during the dry season. 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, 1989b; Kay, 2004a; Brien et al., 2008). However, home ranges for *C. niloticus* in NGR during the dry season were 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 (Chapter 2) allowing crocodiles to move freely throughout the reserve and the fact that Lake Ngezi is a closed system.

In contrast to Hutton (1989) we found that home range increased with size (TL) and that adult crocodiles (> 2.5 m TL) occupied larger total home ranges than sub adult crocodiles (< 2.5

m TL). 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.

Only one of the telemetered crocodiles captured in the Phongola system ventured into the Usuthu River system or Banzi Pan. 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 Pongola River populations in the future due to the recent divergence of the Usuthu.

3.6.5 Territoriality

Territorial behavior has been observed by Nile Crocodile in numerous studies (Modha, 1967; Pooley and Gans, 1976; Garrick and Lang, 1977; Swanepoel, 1999; Champion, 2011). However, territoriality as a component of crocodylian movement ecology is becoming increasingly questionable (e.g. Kay, 2004a; Brien et al., 2008; Combrink, 2013). By comparing the degree of home range overlap territoriality can be investigated. For example Kay (2004a) 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.

Kaufmann (1983) defines a territory as “a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others who have priority elsewhere or at another time.... priority of access must be achieved through social interactions”. It is these social interaction that numerous crocodile researches have observed and documented as territorial behavior (Garrick and Lang, 1977). Territorial interactions are aimed at securing resources advantageous to genetic success as displays/conflicts normally take place at breeding sites and for the right to reproduce with females (Cott, 1961; Rootes and Chabreck, 1993). However, Kaufmann (1983) emphasizes that territoriality may take place only at specific sites (breeding sites) during specific times of the year (breeding season). Along similar lines Swanepoel (1999) suggested that Nile Crocodiles suspended territorial behavior in the non-breeding season, so facilitating large scale movement or migrations at certain times of the year as well as aggregations around basking sites (Lang, 1987). 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). Thus, for territoriality to take place there must be a degree of home range overlap at some point in time. Remote monitoring is not sensitive enough to document these brief periods of social intolerance. If territoriality in crocodiles does only take place at particular sites, such as breeding sites and during a particular period of the year, such as during the breeding season even satellite telemetry may not be sensitive enough to document territorial behavior as encounters are likely to be of too short a

duration to be discernible through examining home range overlap. Using the extent of which home ranges overlap as an indication of territoriality may therefore not be a suitable method and we may have to rely on observations.

3.7 CONCLUSION

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. 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. Crocodiles then move back into NGR as water levels in the floodplain contract in May.

3.8 ACKNOWLEDGEMENTS

We are most grateful to the following people for their help in capturing and marking Nile Crocodiles at NGR: Ferdi Myburgh, Clint Halkett-Siddal, Gareth Champion, Jon Warner, Bongani Gumede and Xander Combrink. The Mazda Wildlife Fund are thanked for providing a vehicle. The Hans Hoheisen Charitable Trust and Water Research Council are thanked for financial assistance. Cliff Dearden is thanked for radio transmitter assembly and guidance. Ezemvelo KZN Wildlife kindly gave permission for the study. We had ethical clearance from the University of KwaZulu-Natal Ethics Committee.

3.9 REFERENCES

- BOTHA, P. J. 2005. The ecology and population dynamics of the Nile Crocodile *Crocodylus niloticus* in the Flag Boshielo Dam, Mpumalanga province, South Africa. MSc thesis. University of Pretoria, Pretoria.
- BRIEN, M. L., READ, M. A., MCCALLUM, H. I., and GRIGG, G. C. 2008. Home range and movements of radio-tracked estuarine crocodiles (*Crocodylus porosus*) within a non-tidal waterhole. *Wildlife Research* 35:140-149.
- BRIEN, M. L., and WEBB, G. J. W. 2010. A Method for attaching tracking devices to crocodilians. *Herpetological review* 41.3:305-308.
- BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.
- CAMPBELL, H. A., WATTS, M. E., SULLIVAN, S., READ, M. A., CHOUKROUN, S., IRWIN, S. R., and FRANKLIN, C. E. 2010. Estuarine crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology* 79:955-964.
- CAMPOS, Z., COUTINHO, M., MOUR, O, G., BAYLISS, P., and MAGNUSSON, W. E. 2006. Long distance movements by *Caiman crocodilus yacare*: implications for management of the species in the Brazilian Pantanal. *The Herpetological Journal* 16:123-132.
- CHAMPION, G. 2011. The Ecology of Nile Crocodile (*Crocodylus niloticus*) in Pongolapoort Dam, Northern KwaZulu-Natal, South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.

- COMBRINK, X. 2013. Spatial and reproductive ecology and population dynamics of the Nile Crocodile (*Crocodylus niloticus*) in the St Lucia Estuarine system, South Africa. PhD thesis in prep., University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X., WARNER, J. AND DOWNS, C. T. 2013. Crocodiles, p. 332 - 253. *In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. D. D. S. a. R. H. T. Renzo Perissinotto (ed.). Cambridge University Press, Cambridge.
- COTT, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society of London* 29:211-356.
- DOWNS, C. T., GREAVER, C., and TAYLOR, R. 2008. Body temperature and basking behaviour of Nile Crocodiles (*Crocodylus niloticus*) during winter. *Journal of Thermal Biology* 33:185–192.
- DUTTON, P. 1971. Some factors affecting the fluctuations of waterfowl populations on Lake Nyamithi. Unpublished report.
- FERGUSON, R. 2010. Wildlife survey phase 2 and management of human-wildlife conflicts in Mozambique. *In: Survey of Crocodile Populations in Mozambique*. Vol. Part 5. AGRECO G.E.I.E., Brussels, Belgium.
- FORBES, A. T., and DEMETRIADES, N. T. 2006. The benthos of Nyamithi Pan, Ndumo Game Reserve, KwaZulu-Natal. Unpublished report prepared for Ezemvelo KwaZulu-Natal Wildlife by: Marine and Estuarine Research.
- FRANKLIN, C. E., READ, M. A., KRAFT, P. G., LIEBSCH, N., IRWIN, S. R., and CAMPBELL, H. A. 2009. Remote monitoring of crocodylians: implantation, attachment and release methods for transmitters and data-loggers. *Marine and Freshwater Research* 60:284-292.

- GAMES, I. 1990. The feeding ecology of two Nile Crocodile populations in the Zambezi Valley. PhD thesis. University of Zimbabwe, Harare.
- GANS, C., and POOLEY, A. C. 1976. Research on crocodiles? Ecology 57:839-840.
- GARRICK, L. D., and LANG, J. W. 1977. Social Signals and behaviors of adult alligators and crocodiles. American Zoologist 17:225-239.
- HEEG, J., AND C. M. BREEN. 1982. Man and the Pongolo floodplain. National Scientific Programmes Unit: CSIR, SANSP Report 56, 1982, pp 129.
- HENSCHEL, J. R. AND J. D.SKINNER.1991. Territorial Behaviour by a clan of spotted hyaenas *Crocuta crocuta*. Ethology 88:223-235.
- HOCUTT, C. H., LOVERIDGE, J. P., and HUTTON, J. M. 1992. Biotelemetry monitoring of translocated *Crocodylus niloticus* in Lake Ngezi, Zimbabwe. Journal of Zoology 226:231-242.
- HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63:152-161.
- HUTTON, J. M. 1987. Growth and feeding ecology of the Nile Crocodile (*Crocodylus niloticus*) at Ngezi, Zimbabwe. Journal of Animal Ecology 56:25-38.
- HUTTON, J. 1989a. Movements, Home range, dispersal and the separation of size classes in Nile Crocodiles. American Zoologist 29:1033-1049.
- HUTTON, J. M. 1989b. Movements, home range, dispersal and the separation of size classes in Nile Crocodiles. American Journal of Zoology 29:1033-1050.
- HUTTON, J. M., and WOOLHOUSE, M. E. J. 1989. Mark-recapture to assess factors affecting the proportion of a Nile Crocodile population seen during spotlight counts at Ngezi,

- Zimbabwe, and the use of spotlight counts to monitor crocodile abundance. *Journal of Applied Ecology* 26:381-395.
- KAUFMANN, J. H. 1983. On the definitions and functions of dominance and territoriality. *Biological Reviews* 58:1-20.
- KAY, W. R. 2004a. Movements and home range of radio tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. *Journal of Wildlife Research* 31:495-508.
- KAY, W. R. 2004b. A new method for attaching electronic devices to crocodilians. *Herpetological review* 35:354-357.
- KOFRON, C. P. 1993. Behavior of Nile Crocodiles in a seasonal river in Zimbabwe. *Copeia* 2:463-469.
- KYLE, R. 2002. Interesting new record and further notes on the occurrence of marine fish in Nyamithi Pan, Ndumo Game Reserve, South Africa. *Koedoe* 45:123-125.
- LANG, J. W. 1987. Crocodilian behaviour: implications for management. *In: Wildlife management; Crocodiles and alligators*. G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.). Surrey Beatty and Sons.
- LESLIE, A. J. 1997. The ecology and physiology of the Nile Crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. PhD thesis. Drexel University, Philadelphia.
- LESLIE, A. J., and SPOTILA, J. R. 2000. Osmoregulation of the Nile Crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. *Comparative Biochemistry and Physiology* 126:351-365.
- MADSEN, T. AND R. SHINE. 1996. Determinants of reproductive output in female water pythons (*Liasis fuscus*: Pythonidae). *Herpetologica* 52:146-159.

- MODHA, M. L. 1967. The ecology of the Nile Crocodile, *Crocodylus niloticus* Laurenti. 1786, on Central island, Lake Rudolph. East African Wildlife Journal 5:74-95.
- NATHAN, R., W.M. GETZ, E. REVILLA, M. HOLYOAK, R. KADMONA, D. SALTZE, AND P.E. SMOUSE. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105:19052-19059.
- POOLEY, A. C. 1969. Preliminary studies on the breeding of the Nile Crocodile, *Crocodylus niloticus*, in Zululand. Lammergeyer 10:22-24.
- POOLEY, A. C. 1982. The ecology of the Nile Crocodile, *Crocodylus niloticus*, in Zululand, South Africa. MSc thesis. University of Natal, Pietermaritzburg.
- POOLEY, A. C., and GANS, C. 1976. The Nile crocodile. Scientific American 234:114- 124.
- RADLOFF, F. G. T., HOBSON, K. A., and LESLIE, A. J. 2012. Characterising ontogenetic niche shifts in Nile crocodile using stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analyses of scute keratin. Isotopes in Environmental and Health Studies 48:439-456.
- READ, M. A., GRIGG, G. C., IRWIN, S. R., SHANAHAN, D., and FRANKLIN, C. E. 2007. Satellite tracking reveals long distance coastal travel and homing by translocated estuarine crocodiles, *Crocodylus porosus*. PloS ONE 2:e949.
- RICHTER, H. V., and CUMMING, G. S. 2008. First application of satellite telemetry to track African straw-coloured fruit bat migration. Journal of Zoology 275:172-176.
- ROGERS, A. R. AND A. P. CARR 1998. HRE: The home range extension for ArcView. C. f. N. F. E. R. Ontario Ministry of Natural Resources, Canada.
- ROOTES, W. L., and CHABRECK, R. H. 1993. Cannibalism in the American Alligator. Herpetologica 49:99-107.

- ROSENBLATT, A. E., and HEITHAUS, M. R. 2011. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *Journal of Animal Ecology* 80: 786-798.
- RUBENSTEIN, D.R. AND K.A. HOBSON. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *TRENDS in Ecology and Evolution* 19:256-263.
- RUSSELL, A. P., BAUER, A. M., and JOHNSON, M. K. 2005. Migration in amphibians and reptiles: An overview of patterns and orientation mechanisms in relation to life history strategies, p. 151 - 203. *In: Migration of Organisms: Climate, Geography, Ecology*. Vol. 12. A. M. T. Elewa (ed.). Springer London, Limited.
- SEAMAN, D. E., and POWELL, R. A. 1996. An evaluation of the accuracy of Kernel Density Estimators for home range analysis. *Ecology* 77:2075-2085.
- SEAMAN, E. D., MILLSPAUGH, J. J., KERNOHAN, B. J., BRUNDIGE, G. C., RAEDEKE, K. J., and GITZEN, R. A. 1999. Effects of sample size on Kernel home range estimates. *The Journal of Wildlife Management* 63:739-747.
- STRAUSS, M., BOTHA, H. AND W. VAN HOVEN. 2008. Nile Crocodile *Crocodylus niloticus* telemetry: observations on transmitter attachment and longevity. *South African Journal of Wildlife Research* 38:189-192.
- SWANEPOEL, D. J. G. 1999. Movements, nesting and the effects of pollution on the Nile Crocodile *Crocodylus niloticus* in the Olifants River, Kruger National Park. MSc thesis. University Natal, Pietermaritzburg.
- THOMAS, B., HOLLAND, J. D., and MINOT, E. O. 2010. Home range and movement patterns of an estuarine crocodile *Crocodylus porosus*: A satellite tracking pilot study. *Northern Territory Naturalist* 22:60-74.

- THOMAS, B., HOLLAND, J. D., and MINOT, E. O. 2011. Wildlife tracking technology options and cost considerations. *Wildlife Research* 38:653-663.
- TUCKER, A. D., LIMPUS, C. J., MCCALLUM, H. I., and MCDONALD, K. R. 1997. Movements and home ranges of *Crocodylus johnstoni* in the Lynd River, Queensland. *Wildlife Research* 24:379-396.
- TUCKER, A. D., MCCALLUM, H. I., LIMPUS, C. J., and MCDONALD, K. R. 1998. Sex-biased dispersal in a long-lived polygynous reptile (*Crocodylus johnstoni*). *Behavioral Ecology and Sociobiology* 44:85-90.
- WALLACE, K. M., and LESLIE, A. J. 2008. Diet of the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42:361–368.
- WARD, M. C. 1989. Aerial survey of Ndumo Game Reserve. Unpublished report.
- WEBB, G. J. W., MANOLIS, S. C., and BUCKWORTH, R. 1982. *Crocodylus johnstoni* in the McKinlay River Area, N.T.I. Variation in the diet, and a new method of assessing the relative importance of prey. *Australian Journal of Zoology* 30:877-99.
- WEBB, G. J. W., and MESSEL, H. 1977. Crocodile capture techniques. *The Journal of Wildlife Management* 41:572-575.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.

LIST OF FIGURES AND TABLES

Figure 1. Ndumo Game Reserve, KwaZulu-Natal, South Africa, showing the main pans and rivers.

Figure 2. Scatter plot showing the relationship between transmitter attachment longevity and total length (TL) of Nile Crocodiles at Ndumo Game Reserve.

Figure 3. Home range of Nile Crocodiles at Ndumo Game Reserve where a. is Mean (\pm SE) home range (95% KDE) of sub-adults ($n = 3$) and adults ($n = 5$); and b. is Mean (\pm SE) core home range for adults ($n = 5$) and sub-adults ($n = 3$) with \pm 95% confidence intervals

Table 1. Radio and mark re-sight occurrences of ten Nile Crocodiles 202-358 cm Total length (TL) over a 7 month period (March-November 2009) in Ndumo Game Reserve.

Table 2. Home range estimates for 8 Nile Crocodiles (202 – 358m TL) in Ndumo Game Reserve.

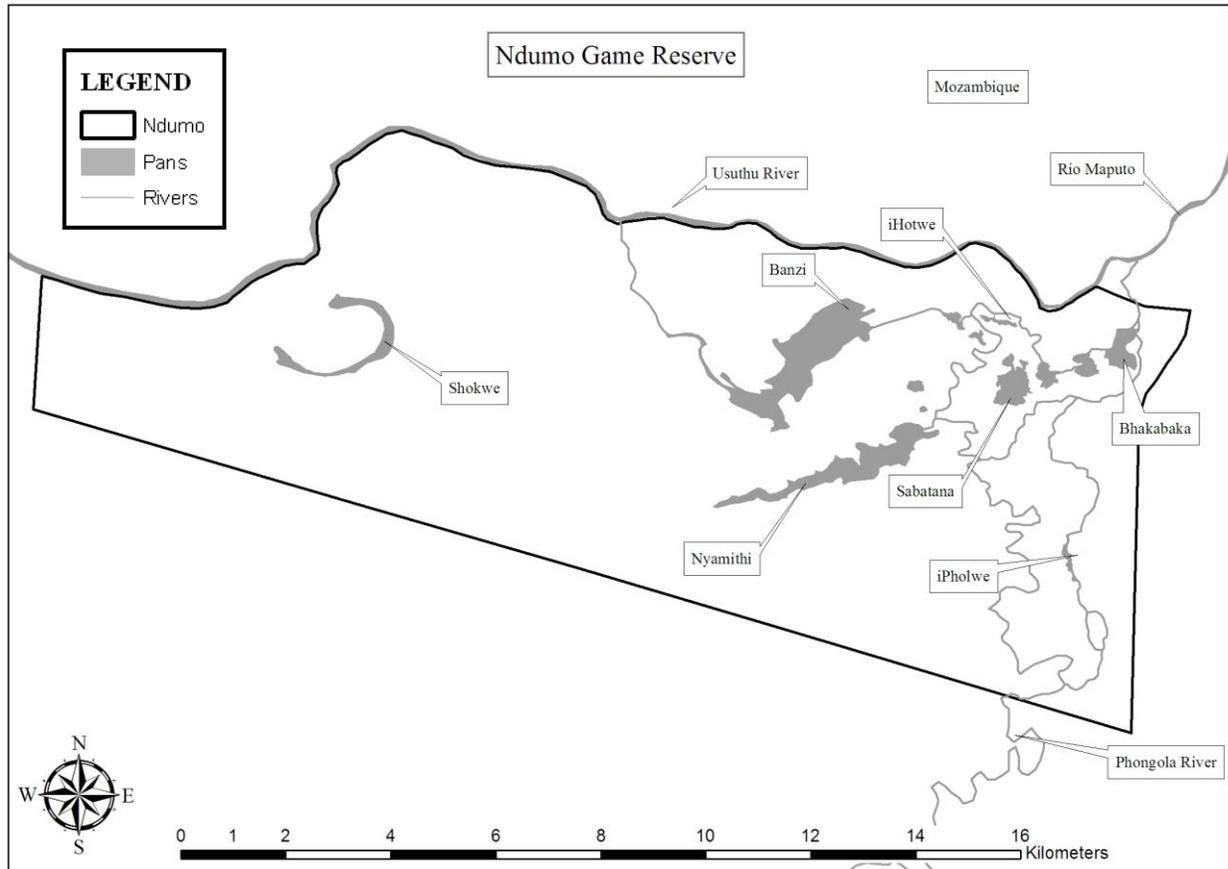


Figure 1. The Ndumo Game Reserve, KwaZulu-Natal, South Africa, showing the major pans and rivers that make up the hydrology of the reserve.

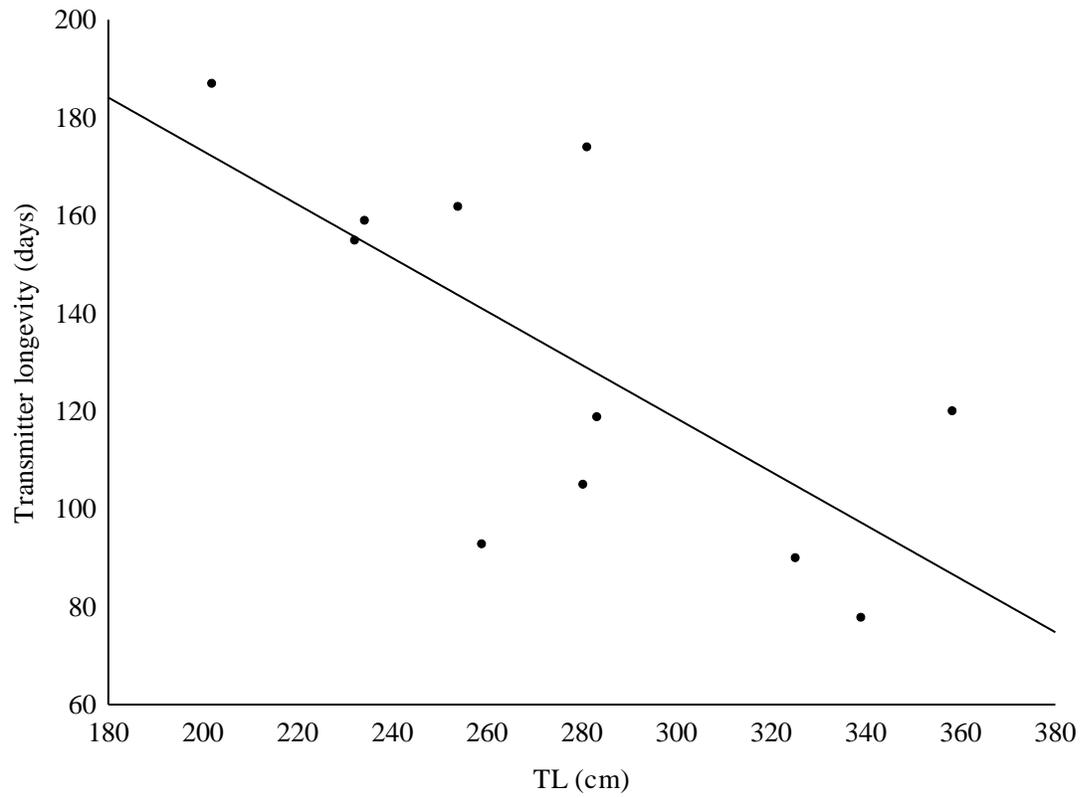


Figure 2. Scatter plot showing the relationship between transmitter attachment longevity and total length (TL) of Nile Crocodiles at Ndumo Game Reserve.

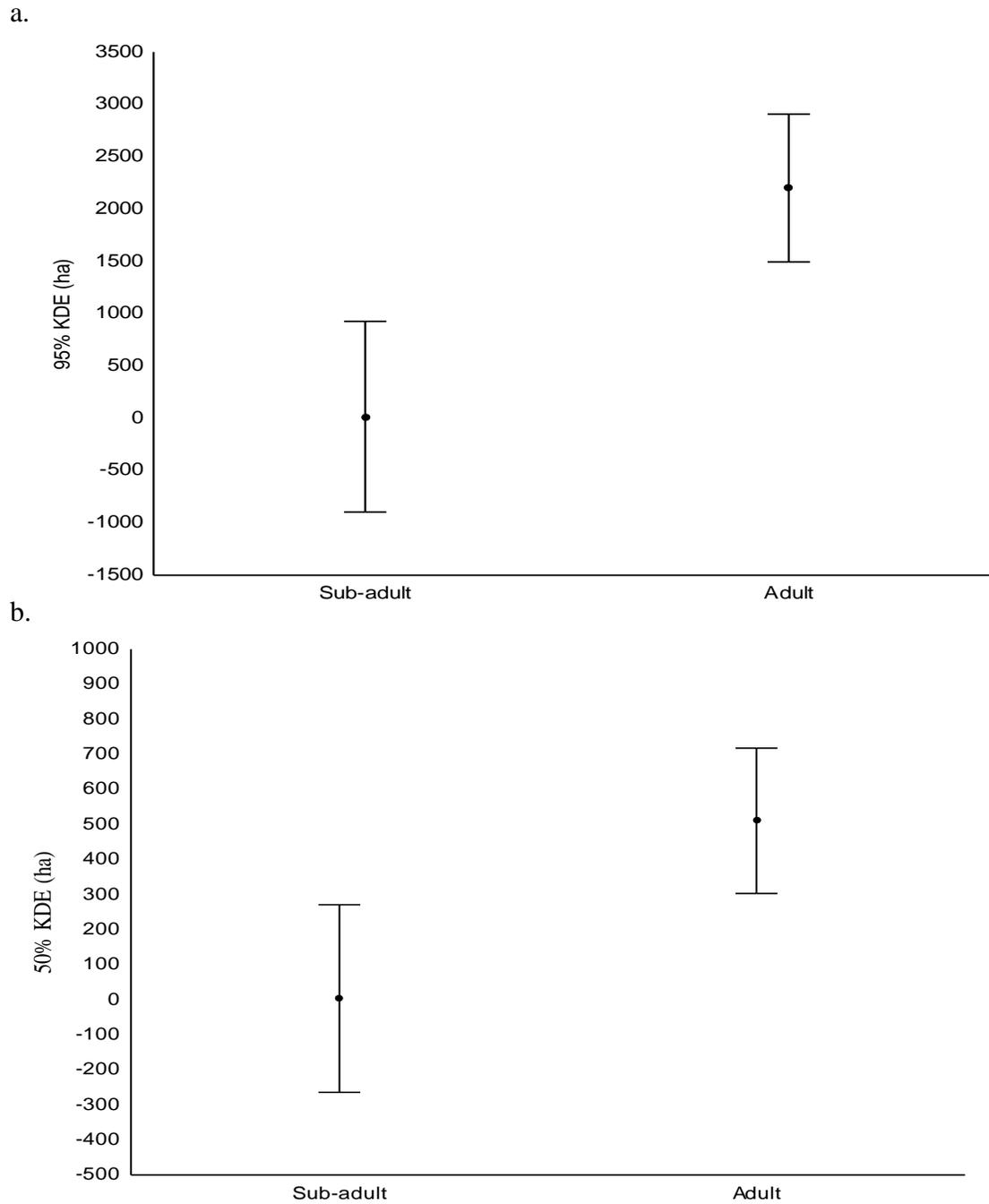


Figure 3. Home range of Nile Crocodiles at Ndumo Game Reserve where a. is Mean (\pm SE) home range (95% KDE) of sub-adults ($n = 3$) and adults ($n = 5$); and b. is Mean (\pm SE) core home range for adults ($n = 5$) and sub-adults ($n = 3$) with \pm 95% confidence intervals.

Table 1. Radio and mark re-sight occurrences of ten Nile Crocodiles 202-358 cm Total length (TL) over a 7 month period (March-November 2009) in Ndumo Game Reserve.

No. Crocodile	Sex	Capture Date	TL (cm)	No. Fixes	Resight	Transmitter Loss
26	Female	03-05-2009	283	7	0	09-2009
10	Female	28-03-2009	232	12	0	03-09-2009
25	Male	02-05-2009	358	16	0	09-2009
8	Male	27-03-2009	280	7	0	11-07-2009
24	Male	02-05-2009	325	10	4	08-2009
3	Female	26-03-2009	202	27	1	11-2009
11	Male	29-05-2009	259	15	0	09-2009
23	Male	01-05-2009	281	16	6	22-10-2009
1	Male	24-03-2009	234	18	0	09-2009
6	Male	26-03-2009	339	6	10	12-06-2009
7	Male	27-03-2009	254	17	0	06-09-2009

Table 2. Home range estimates for 8 Nile Crocodiles (202 – 358m TL) in Ndumo Game Reserve.

Size (cm)	Sex	Frequency	95% kernel (ha)	90% kernel (ha)	50% kernel (ha)
202	F	237	3.2	2.4	0.6
232	F	455	36.7	27.6	8.0
234	M	196	5.7	4.5	1.2
254	M	215	1631.9	1266.1	288.1
281	M	276	2750.7	2145.2	555.6
315	M	295	2244.6	1787.9	595.0
339	M	316	1221.6	961.4	280.6
358	M	396	3154.6	2521.6	832.8

Appendix 1. Home range of crocodile 196 in Lake Nyamithi, Ndumo Game Reserve.



Appendix 2. Home range of crocodile 215 in Ndumo Game Reserve.



Appendix 3. Home range of crocodile 237 in Lake Nyamithi Ndumo Game Reserve.



Appendix 4. Home range of crocodile 276 in Ndumo Game Reserve.



Appendix 5. Home range of crocodile 295 in Ndumo Game Reserve.



Appendix 6. Home range of crocodile 316 in Lake Nyamithi, Ndumo Game Reserve.



Appendix 7. Home range of crocodile 396 in Ndumo Game Reserve.



CHAPTER 4

Population status of Nile Crocodiles in Ndumo Game Reserve, KwaZulu-Natal, South Africa (1971 - 2012).

P. M. Calverley and C. T. Downs

School of Life Sciences, University of KwaZulu-Natal.

*Private Bag X01, Scottsville, Pietermaritzburg, 3209 South Africa. Email:
calverleypeter@gmail.com.*

Formatted for *Copeia*

4.1 ABSTRACT

*Establishing and monitoring population trends is essential for implementing informed and timely management decisions and in the conservation of threatened species. We examined changes in the Ndumo Game Reserve (NGR) Nile Crocodile (*Crocodylus niloticus*) population size and changes in the size-class distribution within the population using aerial and ground survey data from 1971 – 2009. In addition crocodiles were caught opportunistically for aging, sexing and tagging. The precision and accuracy of population estimates was affected by water level, season and the use of different observers. In future all surveys should take place during winter months and at low water levels to provide the most accurate results and by the same observers where possible to improve precision and accuracy. The NGR population increased from an absolute abundance of 348 (± 3.39) in the early 1970's to maximum absolute abundance of 992 (± 58.70) in 1994 as a result of a restocking program initiated in the late 1960's and early 1970's. The population structure of Nile Crocodiles in NGR is currently skewed towards sub-adults and adults suggesting that the current population decline is a result of low recruitment levels in NGR*

that are unable to sustain the artificially high population size created by the restocking program. Contributing to this decline is the poaching of Nile Crocodiles in NGR, destruction of suitable and historical nest sites due to land invasions and possible harvesting of eggs and carcasses in adjacent Mozambique where the crocodiles move for periods of the year. In particular, current destruction of suitable nesting sites within NGR is predicted to have further negative impacts on the already declining population. Sex ratios were skewed towards females in the juvenile and sub-adult size classes and towards males in the adult size class while the overall sex ratio was even between males and females. The current NGR Nile Crocodile population is estimated at an absolute abundance of 846 (SE \pm 263). It is predicted that the NGR Nile Crocodile population will decline in the future and is a natural process, but will be accelerated at unnatural speeds and to an unnatural extent due to poaching, uncontrolled harvesting and destruction of nesting habitat.

4.2 INTRODUCTION

Ndumo Game Reserve (NGR) in North East KwaZulu-Natal is one of the oldest game reserves in South Africa. Proclaimed in 1924 as a sanctuary for Hippopotamus (*Hippopotamus amphibius*), the reserve coincidentally protects habitat equally suitable for Nile Crocodiles (*Crocodylus niloticus*). 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 1960's and over 1200 yearling crocodiles were released into the reserve from the late 1960's to the early 1970's (Pooley, 1982). A monitoring program was initiated in 1971 by

Pooley and conducted sporadically thereafter as successive counts showed a general trend in population increase and the NGR Nile Crocodile population was thought to be at an acceptable level to consider implementing a harvesting program as early as the 1990's (Mathews, 1994).

NGR thus has one of the longest, if incomplete, Nile Crocodile monitoring programs in South Africa spanning some 40 years and pre-dating official protection afforded to Nile Crocodiles in South Africa in 1976 (Pooley, 1982). In the past aerial surveys were conducted with the objective of obtaining estimates of numbers and distribution of Nile Crocodiles within the reserve (not of size/age structure) (Mathews, 1994). These figures were used in the development of management plans for the reserve and to act as a record for monitoring programs at regional level (Mathews, 1994). Data from this monitoring program offers an excellent opportunity to follow trends in population change over the years and to examine the efficacy of restocking programs as a management tool in population recovery of wild crocodiles. This is particularly pertinent in the current climate of severe population reductions within protected areas in southern Africa (Botha et al., 2011; Combrink et al., 2011; Ferreira and Pienaar, 2011; Bourquin and Leslie, 2012; Wallace et al., 2011, 2013) and globally (Ballouard et al., 2010; Wang et al., 2011). Furthermore, the determination of population trends is essential in managing threatened species (Joseph et al., 2006) and monitoring changes in population size is necessary to collect objective information upon which timely management actions can be based (Stirrat et al., 2001). From such studies a basis of knowledge for the purpose of conservation and management of the NGR population can be generated (Bayliss, 1987). We aimed to use relative indices of abundance (counts) to follow trends in population change over the last 40 years and to calculate absolute abundance in order to obtain a more accurate estimate of current population size.

By examining population age structure it is possible to predict future changes in

population size (Townsend, 2003). For example, population structures skewed towards juveniles and sub-adults are indicative of an increasing population while an age structure skewed towards adults could be a sign of a population on the decline (Townsend, 2003). By collecting data on the distribution of different size classes within the NGR Nile Crocodile population we aimed to determine whether the population structure was stable or still changing. It was hypothesised that Nile Crocodile numbers in NGR were increasing and that the different age-classes were well represented and the population was stable.

4.3 METHODS

4.3.1 Study site

Ndumo Game Reserve (NGR) is a relatively small (10 000 ha) reserve in North Eastern KwaZulu-Natal, home to South Africa's third largest Nile Crocodile population. NGR is situated in the Mozambique Coastal Plain between the latitude 26E 50' to 26E 54' South and longitude 32E 09' to 32E 21' East. The reserve is an elongated trapezoid shape with the longitudinal axis lying East to West (Chapter 2). 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 major river systems in the north east corner of the reserve and the flat nature of the Mozambique Plain combine to inundate over 40% of the reserve during times of high rainfall (Pooley, 1982). Further details of the study site are presented in Chapters 1 and 2.

4.3.2 Historical data

Historical records of Nile Crocodile aerial surveys were obtained from the Ezemvelo KZN Wildlife (EKZNW) data base at Tembe National Elephant Park. This allowed for the comparison of population estimates obtained in surveys as well as the method employed in attaining these estimates. Pooley's (1982) doctorate thesis "The Ecology of the Nile Crocodile *Crocodylus niloticus* in Zululand" was searched for data relevant to the study of population trends.

4.3.3 Aerial surveys

Aerial surveys are the most effective way to census crocodile populations over extensive or remote areas where rough terrain and the shyness of the animal make other forms of survey unfeasible (Jacobsen, 1984; Botha, 2005). Furthermore, aerial surveys are the most cost-effective way of surveying large stretches of crocodile habitat (Games, 1994; Brown et al., 2004; Cherkiss et al., 2004). Despite these advantages aerial surveys are inherently prone to various forms of bias that may influence the accuracy and/or the precision of the survey (Games, 1994; Combrink, 2004, 2013; Ferreira and Pienaar, 2011). These primarily include visibility and observer bias. Visibility bias occurs when the subject or any sign of the subject being counted is not visible to the observer (Bayliss, 1987) and observer bias is the amount of visible subjects that are not observed in a survey (Combrink, 2004). Visibility bias may change from location to location or within different habitat types within a location while observer bias is observer specific and may change with aircraft type (Combrink, 2004).

In an effort to reduce visibility bias and improve accuracy, surveys normally take place during winter when populations are aggregated around permanent water sources spending more time out of the water for basking purposes and are therefore more visible and easier to count

(Bayliss, 1987). To reduce observer bias the same observers should be used in successive surveys and a similar type of aircraft should be used (Combrink, 2004). Nevertheless, aerial surveys give an indication of the relative abundance of crocodiles and correction factors that negate the various forms of bias need to be calculated to obtain an indication of the absolute abundance of a population (Combrink, 2004).

Aerial surveys at NGR carried out before the onset of this project in 2009 give distribution patterns for the dry season only. In 2009 a helicopter was only available for Nile Crocodile counts in the wet season. An aeroplane was used during the dry season in an effort to achieve a count comparable to previous surveys. This also allowed for the investigation of seasonal changes in abundance as three surveys were carried out in 2009 during high, medium and low water levels incorporating the summer and winter seasons.

Following historical methods employed in all the surveys at NGR a helicopter, in this case a AS350 Ecureuil helicopter (Eurocopter), was used with four observers including the pilot. Flight speed and altitude was low (flight speed 75 km/h; average altitude 25 m agl). Each crocodile observed was recorded per sub-region and totals recorded on a 1:50 000 map of the reserve. Counting areas were divided amongst observers with observers on the left of the helicopter searching only the left bank and the observers on the right searching only the right bank. Weather conditions were favorable, the survey lasted 1 h but water levels were high due to high rainfall in the Usuthu catchment area.

A Piper Supercub aircraft was used for further aerial surveys with two observers seated longitudinally. The pilot had been a ranger at NGR and was familiar with the area. The right window was opened to facilitate counting and the aircraft flown in such a manner that all counting was done on this side. On larger waterbodies, where both banks could not be observed

from the right hand window, transects were flown to cover both shorelines. A Garmin Vista[®] Cx Global Positioning System (GPS, Kansas, USA) was synchronised with a dictaphone (HP PDA, California, USA) and a running commentary of the flight recorded while the GPS simultaneously recorded the route flown by creating waypoints at 50 m intervals. Data captured at these waypoints included time and location. The time at which sightings were recorded on the dictaphone could thus be related to a GPS waypoint and the co-ordinates for sightings established. A Canon EOS 400D digital camera (Tokyo, Japan) was used to record areas of high crocodile density when counting from the air proved inaccurate. The number of crocodiles captured in these photographs were counted after the survey and added to the total amount counted during the survey. The time the photograph was taken was related to a GPS waypoint for the co-ordinates of the sighting to be established. Weather conditions were favourable to start with but became gusty towards mid-morning. Temperature ranged between 18 - 20^o C. The count took place between 08:42 and 10:22 including take-off and landing from the nearby Tembe National Elephant Park with an average flying speed of 139 km/h at an average altitude of 173 m agl.

4.3.4 Correction factors

Generally, where different aircraft types are used for surveys (helicopter and aeroplane) 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). A correction factor needs to be calculated to allow comparison of the results of the two different survey techniques (Combrink, 2004). Correction factors for aerial surveys are normally calculated by conducting follow up spotlight surveys (Bayliss et al., 1986).

However, in areas such as the Phongola and Usuthu floodplains spot light surveys are 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).

At Lake Nyamithi land based diurnal and boat based spotlight counts were conducted to calculate a correction factor for fixed wing aerial surveys of lacustrine habitat in NGR. However, a fixed wing survey yielded 21% more crocodiles at Lake Nyamithi than a diurnal survey conducted one hour later and 34% more than a spotlight survey conducted the previous night (Calverley, 2009). Correction factors for aerial surveys could therefore not be calculated and relevant literature was consulted in order to identify a suitable correction factor.

For fixed wing surveys Botha calculated a correction factor of 1.54 for Loskop Dam and used this on a survey of the Olifants River as well (Botha, 2005; Botha, 2010). Fergusson (2010) used a correction factor of 2.0 for the fix winged surveys of the Rio Maputo just outside of NGR. Combrink (2004) calculated a factor of 1.72 for fixed wing surveys of Lake Sibaya. Bourquin (2009) calculated a correction factor of 1.28 for low water levels and 1.78 for high water levels in the Okavango delta.

Ferreira and Pienaar (2011) calculated a correction factor of 1.28 for helicopter surveys in the Olifants River Gorge in Kruger National Park.

It was decided to apply a correction factor of 1.28 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 survey we calculated a minimum and maximum absolute population estimate and used the mean of these two values to estimate absolute abundance.

4.3.5 Stratification

NGR was divided into the same strata as earlier surveys. 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, Bakabaka/Shabatana. **Region 2.** The Usuthu River system consisting of the following sub-regions: Shokwe, Banzi/Diphini, Usuthu River. During aerial counts the number of crocodiles were recorded per sub-region. Analysis tested for 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.

4.3.6 Capture techniques

Capture was necessary to gather morphological data pertinent to an investigation into the population structure of Nile Crocodiles in NGR. All Nile Crocodile capture in NGR in the present study took place in Lake Nyamithi. The shallow nature of the lake and high density of crocodiles favoured noosing as a capture technique (Hutton et al., 1987). Nile Crocodiles were caught using this technique between March 2009 and June 2010. Crocodiles were then taken ashore for morphometric data measurements, unique scute notching and colour tagging before being released. Animals took on average 20 min to process. Details are presented in Chapter 3. Capture exercises carried out from 2011 - 2012 were focused on catching individuals large enough for transmitter attachment and were therefore not indicative of population structure and were not used in this analysis.

4.4 RESULTS AND DISCUSSION

4.4.1 Aerial surveys

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). Precision can be measured by the standard error surrounding an estimate with low standard errors indicating high levels of precision (Graham, 1987). Accuracy on the other hand is a measure of how close an estimate is to the actual population size (Combrink, 2004). Aerial surveys carried out in the 1970's and 1980's using the same observers, aircraft and pilot provided the estimates with the least standard error while surveys in the 1990's with different observers provided larger standard error. Surveys carried out in 2009 where water level, season, observers and aircraft varied provided the highest standard error (Table 1). It is therefore suggested that future Nile Crocodile surveys in NGR take place during winter when individuals are more likely to be out of the water basking and would therefore be more visible from the air and during periods of low water levels where poor visibility is less likely to bias results (Combrink, 2004; Downs et al., 2008). Furthermore, wherever possible it is suggested that helicopters be used due to their ability to operate safely at lower and slower count speeds thus facilitating more accurate counts (Combrink, 2004).

4.4.2 Population growth

Relative abundance of Nile Crocodiles in NGR increased significantly from the 1970's (1971-1973; mean = 272, SE \pm 1.53) to the 1980's (1985-1988; mean = 507.67, SE \pm 3.71) and then again in the 1990's (1990-1994; mean = 774.75, SE \pm 22.93) (Table 1). This rapid increase in population size is due to the restocking program initiated in NGR. From January 1967 to

November 1974, 1257 Nile Crocodile hatchlings were reared and released as part of a restocking program in NGR (Pooley, 1982). The first phase of the restocking program saw hatchlings (1967/1968 season) reared for two to three years, thereafter 700-800 individuals were released. The second phase saw roughly 500 hand reared crocodiles (1969/1970 season) released into the reserve between 1972 and 1974. The crocodiles released in the restocking program would not have been noticed in the first series of aerial counts from 1971-1973 due to their small size as only individuals over 2 m in length are easily noticeable from the air (Games, 1994). According to literature it takes about 14 years for males to reach 2 m in length and about 17 years for females (Hutton, 1987a). However, individual growth rates are determined by temperature, resource availability and genetics and it becomes impossible to accurately age crocodiles according to body length after three years of age (Hutton, 1987a; Kofron, 1990). Hutton collected his data in Zimbabwe and it is likely that the Nile Crocodiles in NGR will show different growth rates because of these factors. Nonetheless, Hutton's study provides a good guideline in estimating an upper limit for when the released crocodiles would be visible in aerial surveys and we assume that after 20 years all released hatchlings that survived and are residing in NGR would be visible in aerial surveys.

The second series of aerial counts were initiated in 1985 (Ward, 1989). The first crocodiles released in the restocking program would have been 17 years old and would have been visible from the air explaining the sharp increase in crocodile numbers recorded between 1973 and 1985. The second batch of crocodiles released would have been between 12 and 14 years old during the 1985 survey and would only reach a size of 2 m between 1988 and 1990. This may explain the second drastic increase in the population between 1989 and 1990. Ward (1990) who conducted the aerial surveys over this time suggests that an improvement in survey

method could have resulted in the increase in yield. However, it is unlikely that observer bias alone accounted for such a large change in survey yield.

The NGR Nile Crocodile population assumes a sequential, stepwise growth form in the 1990's. After the initial large increase of 1990, the population within the reserve increased evenly year by year, until 1994 when the population decreased. However, Mathews (1994) attributes the drop in crocodile numbers in 1994 to count technique. However, the pattern of population growth in the 1990's may be explained by the differential and/or sexually dimorphic growth rates of Nile Crocodiles (Hutton, 1987a). The faster growing individuals, in this case most likely the males would be the first to be noticed in aerial surveys, after this the females and slower growing individuals explaining the smaller, sequential steps of population growth.

4.4.3 Population stabilization

The earlier restocking program in NGR explains the pattern of population increase depicted by the aerial surveys but fails to explain the extended periods of zero population growth between the population increases (Table 1). While crocodilians are capable of displaying density dependent methods of population regulation such as cannibalism (Cott, 1961; Pooley, 1982) and exclusion (Hutton, 1989b; Richardson et al., 2002) this is unlikely the case in NGR because periods of population stability in the 1970's and 1980's are followed by dramatic increases in population size. Historical data show that nesting effort has declined as the NGR population has increased (Chapter 5). That is to say that the increase in population size has not translated into more nesting taking place within the reserve and recruitment is unable to sustain the artificially high population size brought about by the restocking program. Nesting effort is low at 21%

(Chapter 5) and Pooley (1982) estimated only a 1 – 2% survival rate of Nile Crocodiles past the first year at NGR.

All crocodiles captured ($n = 103$) were between 92.6 cm and 472 cm total length (TL) with a mean TL of 230.5 ± 71.0 (SD). When compared with other demographic studies on Nile Crocodiles in Africa, NGR has a lower proportion of juveniles (13%) compared to sub-adults (39%) and adults (48%) (Table 2). We therefore suggest that the restocking program initiated in the late 1960's and early 1970's elevated the NGR Nile Crocodile population to an artificially high density and that cannot be sustained by recruitment within the reserve. The population has therefore stabilized and is not increasing but will in time decrease as the cohort released in the re-stocking programs age and die.

However, the future population decline in NGR may not only be attributed to natural causes. During this study we observed 15 Nile Crocodiles in Lake Nyamithi with snares around their necks (Fig. 1). These individuals were all large (> 2.8 m) and possibly represent a small proportion of snared individuals that manage to break free from traps by snapping the cable used to snare them. It is likely that many smaller individuals were caught and a percentage of larger animals were not able to escape the snares. Furthermore viable and historic crocodile nesting habitat within NGR is currently being destroyed and unavailable to crocodiles as illegal resource use and agriculture is taking place within the reserve (Calverley, 2009).

4.4.4 Sex ratios and population structure

Hutton (1987c) found that Nile Crocodiles in Zimbabwe had a significantly female biased sex ratio across all size classes. This was attributed to temperature-dependent sex determination in crocodylians and low nest temperatures (Hutton, 1987c). 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 the Okavango Delta in Botswana (61.8% and 61.2% respectively) followed by a slight bias towards females in the adult and sub adult size classes (54.8% and 55.3% females respectively). Bourquin attributes the slight prevalence of females to a higher mortality rate in males due to aggressive male-male competition for reproductive rights. At NGR sex ratios were biased toward females in the juvenile (80.0%) and the sub-adult age group (63.0%) (Table 3). Adult sex ratios however were biased towards males (64.7%). Average sex ratio across all size classes was even (50.6% female and 49.4% male). The intercept of equal sex ratios fell in the 2.5 – 3.5 m size class at ± 3.1 m (Fig. 3). The female biased sex ratio in NGR may be a consequence of sex biased dispersal in juvenile crocodilians causing male juvenile males to disperse further away from nesting sites which are located at Lake Nyamithi (Tucker et al., 1998). This could explain why adult sex ratios are biased towards males as males would be more likely to disperse into NGR and Lake Nyamithi than females who stay in closer proximity to nesting sites (Tucker et al., 1998).

The interplay between sex biased dispersal and temperature determined sex (TDS) / environmental sex determination (ESD) could have interesting evolutionary implications when discussed in light of the selfish gene theory. In favorable nesting habitat more females should be produced so that philopatry would result in daughters being in close proximity to good nesting habitat. Comparatively fewer sons would then disperse to colonize new habitats and to spread genetic material. Un-favorable nesting conditions should produce more sons to disperse in search of better habitat. If (nesting) conditions are favorable in the new habitat benefits would be almost

substantial as the first generation of offspring would for the most part be female and would then remain closer to the new favorable nesting site.

The even sex ratio at the 3.1 m age class could also be a product of incubation temperatures selected for during the restocking program favoring neither sex over the other. If this is the case we would expect the development of a female biased sex ratio seen in the juvenile and sub-adult size classes to filter through to the adult size class in the future. Other causes of biased sex ratios throughout size classes may be due to differential mortality and habitat selection between the different sexes (Thorbjarnarson, 1997) and because only one habitat type was sampled in NGR (i.e. Lake Nyamithi). Nonetheless, the 1:1 sex ratio at the reproductive size class in 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.

4.5 CONCLUSION

The current NGR Nile Crocodile population has stabilized since the last survey in 1994. Demographic information collected through capture exercises 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 NGR which is discussed in Chapter 5. As the population of artificially introduced individuals ages, population decline in NGR can be expected to decline because recruitment levels within the reserve are low.

The current nesting effort in NGR is relatively poor but suggests a self-sustaining population size of 230 Nile Crocodiles in NGR. A much larger population size may be maintained or achieved by securing breeding grounds within the reserve and in adjacent wetlands in neighboring Mozambique, and by preventing illegal harvesting of Nile Crocodiles both inside and outside of the NGR.

Time of year and water level had a significant influence on the number of Nile Crocodiles counted at NGR and in order to accurately follow population changes all surveys in the future should be conducted at low water levels in winter in order to collect comparable results. Management of water releases from the upstream impoundment are important as they affect numbers and distribution of crocodiles in NGR.

The restocking of Nile Crocodiles at NGR has been a success, however, long term monitoring programs are necessary to follow population trends as crocodiles are long lived animals. For restocking programs to be truly successful and sustainable sufficient protected nesting habitat needs to be available (Combrink, 2004).

4.6 ACKNOWLEDGEMENTS

The following people are thanked for assistance with capture activities: Ferdi Myburgh, Clint Halkett-Siddal, Gareth Champion, Jon Warner and Xander Combrink. We are most grateful to Paul Dutton and Donovan Barton-Hobbs as well as the Bateleurs for aerial survey assistance. We thank Mazda Wildlife for vehicle support. Ezemvelo KZN Wildlife kindly gave permission for the study. We had ethical clearance from the University of KwaZulu-Natal Ethics Committee. The University of KwaZulu-Natal and the Water Research Commission are thanked for funding.

4.7 REFERENCES

- BAYLISS, P. 1987. Survey methods and monitoring within crocodilian management programmes. In: *Wildlife Management: Crocodiles and Alligators* p. 157-175. Surrey Beatty and Sons, Sydney. pp 157-175.
- BAYLISS, P., G. J. W. WEBB, P. J., WHITEHEAD, K. DEMPSEY, AND A. SMITH. 1986. Estimating the abundance of saltwater crocodiles, *Crocodylus porosus* Schneider, in tidal wetlands of the Northern Territory - a Mark-Recapture Experiment to correct spotlight counts to absolute numbers, and the calibration of helicopter and spotlight counts. *Australian Wildlife Research* 13:309–320.
- BOTHA, P. J. 2005. The ecology and population dynamics of the Nile Crocodile *Crocodylus niloticus* in the Flag Boshielo Dam, Mpumalanga Province, South Africa. MSc thesis. University of Pretoria, Pretoria.
- BOTHA, P.J. 2010, The distribution, conservation status and blood biochemistry of Nile crocodiles in the Olifants river system, Mpumalanga, South Africa, PhD thesis, University of Pretoria, Pretoria.
- BOTHA, H., VAN HOVEN, W. AND L.J. JR GUILLETTE. 2011. The decline of the Nile crocodile population in Loskop Dam, Olifants River, South Africa. *Water SA* 37:103–108.
- BOURQUIN, S. V. 2008. The population ecology of the Nile Crocodile (*Crocodylus niloticus*) in the Panhandle Region of the Okavango Delta, Botswana. PhD thesis. University of Stellenbosch, Stellenbosch.
- BOURQUIN, S. L. AND A. J. LESLIE. 2012. Estimating demographics of the Nile crocodile (*Crocodylus niloticus* Laurenti) in the panhandle region of the Okavango Delta, Botswana. *African Journal of Ecology* 50: 1-8.

- BROWN, C. J., P. STANDER, R. MEYER-RUST, AND S. MAYES. 2004. Results of a Crocodile *Crocodylus niloticus* survey in the river systems of north-east Namibia during August 2004. Namibia Nature Foundation, Wildlife Science and Lianshulu Lodge.
- CALVERLEY, P. 2009. Ndumo Game Reserve aerial and ground survey report October 2009. Unpublished report.
- CHERKISS, M. S., FLING, H. E., MAZZOTTI, F. J. AND K. G. RICE 2004. Counting and capturing crocodilians. *In*: Wildlife Ecology and Conservation Department, Florida Cooperative Extension Service. Institute of Food and Agricultural Sciences. University of Florida, Gainesville.
- COMBRINK, A. S. 2004. Population status of *Crocodylus niloticus* (Nile Crocodile) at Lake Sibaya, Republic of South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X. 2013. Spatial and reproductive ecology and population dynamics of the Nile Crocodile (*Crocodylus niloticus*) in the St Lucia Estuarine system, South Africa. PhD thesis in prep., University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X., J. L. KORRÛBEL, KYLE, R., TAYLOR, R. AND R.PERRAN.2011. Evidence of a declining Nile Crocodile (*Crocodylus niloticus*) population at Lake Sibaya, South Africa. South African Journal of Wildlife Research 41:145-157.
- COTT, H. B. 1961. Scientific results of an enquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. Transactions of the Zoological Society of London 29:211-279.

- DOWNES, C. T., GREAVES, C., AND R. TAYLOR. 2008. Body temperature and basking behaviour of Nile crocodiles (*Crocodylus niloticus*) during winter. *Journal of Thermal Biology* 33:185–192.
- FERREIRA, S. M. AND D. PIENAAR. 2011. Degradation of the crocodile population in the Olifants River Gorge of Kruger National Park, South Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21: 155-164.
- FERGUSON, R. 2010. Wildlife survey phase 2 and management of human-wildlife conflicts in Mozambique. *In: Survey of Crocodile Populations in Mozambique. Vol. Part 5. AGRECO G.E.I.E., Brussels, Belgium.*
- GAMES, I. 1994. Aerial surveys for monitoring trends and estimating population size of *Crocodylus niloticus* or the theory and practice of aerial survey in Africa. CSG Proceedings, Pattaya, Thailand, 2-6 May, 1994. *Crocodile Specialist Group. 1: 245-255.*
- GRAHAM, A. D. 1968. The Lake Rudolph crocodile (*Crocodylus niloticus*) population. Report to the Kenya Game Department
- GRAHAM, A. D. 1987. Methods of surveying and monitoring crocodiles. *In: Proceedings of the SADCC Workshop on Crocodile Management and Utilization, Kariba; Zimbabwe.*
- HUTTON, J. M. 1987a. Growth and feeding ecology of the Nile Crocodile (*Crocodylus niloticus*) at Ngezi, Zimbabwe. *Journal of Animal Ecology* 56:25-38.
- HUTTON, J. M. 1987b. Incubation temperatures, sex ratios, and sex determination in a population of Nile Crocodiles (*Crocodylus niloticus*). *Journal of Zoology (London)* 211:143-155.
- HUTTON, J. M. 1989. Movements, home range, dispersal and the separation of size classes in Nile Crocodiles. *American Journal of Zoology* 29:1033-1050.

- HUTTON, J. M., LOVERIDGE, J. P. AND D. K. BLAKE. 1987. Capture methods for the Nile Crocodile in Zimbabwe. *Wildlife Management: Crocodiles and Aligators* Surrey Beatty and Sons, Sydney. Pp 243-247.
- JACOBSEN, N. H. G. 1984. Distribution and status of crocodile populations in the Transvaal outside the Kruger National Park. *Biological Conservation* 29:191-200.
- JOSEPH, L. N., FIELD, S. A., WILCOX, C., AND H. P. POSSINGHAM. 2006. Presence–absence versus abundance data for monitoring threatened species. *Conservation Biology* 20:1679–1687.
- KOFRON, C. 1990. The reproductive cycle of the Nile Crocodile (*Crocodylus niloticus*). *Journal of Zoology* 211:477-488.
- LESLIE, A. J. 1997. The ecology and physiology of the Nile Crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. PhD thesis. Drexel University, Philadelphia.
- MATHEWS, W. S. 1994. Hippo and crocodile counts in the northern Kwa-Zulu region. Unpublished report. Natal Parks Board, Pietermaritzburg.
- POOLEY, A. C. 1982. The ecology of the Nile Crocodile, *Crocodylus niloticus*, in Zululand, South Africa. MSc thesis. University of Natal, Pietermaritzburg.
- RICHARDSON, K. C., G. J. W. WEBB, AND S. C. MANOLIS. 2002. Crocodiles inside: out a guide to the crocodylians and their functional morphology. Surrey Beatty & Sons, Sydney, p:59.
- STIRRAT, S. C., D. LAWSON, W. J. FREELAND, AND R. MORTON. 2001. Monitoring *Crocodylus porosus* populations in the Northern Territory of Australia: a retrospective power analysis. *Wildlife Research* 28:547-555.
- THORBJARNARSON, J. 1997. Are crocodylian sex ratios female biased? The data are equivocal. *Copeia* 1997:451-455.

- TOWNSEND, C. R., BEGON, M. AND J. L. HARPER. 2003. *Essentials of Ecology*. Blackwell Science, London.
- TUCKER, A. D., MCCALLUM, H. I. LIMPUS, C. J., AND McDONALD, K. R. 1998. Sex-biased dispersal in a long-lived polygynous reptile (*Crocodylus johnstoni*). *Behavioral Ecology and Sociobiology* 44:85-90.
- WANG, D., M. HEJAZI, X. CAI, AND A. J. VALOCCHI. 2011. Climate change impact on meteorological, agricultural, and hydrological drought in central Illinois. *Water Resources Research* 47:DOI: 10.1029/2010WR009845.
- WALLACE, K. M., LESLIE, A. J. AND T. COULSON. 2011. Living with predators: a focus on the issues of human–crocodile conflict within the lower Zambezi valley. *Wildlife Research* 38:747-755.
- WALLACE, K., LESLIE, A. J. AND T. COULSON. 2013. Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model. *Journal of Animal Ecology* 82:155-165.
- WARD, M. C. 1989. Aerial survey of Ndumo Game Reserve. Unpublished report. Natal Parks Board, Pietermaritzburg.
- WARD, M. C. 1990. Crocodile Nest Survey-KwaZulu Ubombo/Ingwavuma District. Unpublished Report. Natal Parks Board.

LIST OF FIGURES

Figure 1. Example of a Nile Crocodiles snared in Ndumo Game Reserve during 2009 – 2010 showing damage to the animal.

Figure 2. Anthropogenic disturbances in Ndumo Game Reserve during 2009 – 2010 affecting habitat used by Nile Crocodiles.

Figure 3. The intercept of equal sex ratios of Nile Crocodiles in Ndumo Game Reserve between 2.5 and 3.5 m.

Table 1. Changes in relative abundance of Nile Crocodiles in Ndumo Game Reserve from 1971-2009 with standard error (SE) as a measure of precision.

Year	Aircraft type		Water level		Time of year	Total	Precision (SE)
	Helicopter	Aeroplane	High	Low			
1971	X			X	September	273	1.53
1972	X			X	July	274	1.53
1973	X			X	July	269	1.53
1985	X					515	3.71
1986	X					503	3.71
1988	X			X	July	505	3.71
1989	X		X		August	420	*
1990	X			X	July	732	22.93
1992	X			X	August	789	22.93
1993	X			X	August/September	833	22.93
1994	X			X	August	745	22.93
2009	X		X		March	100	122.87
2009		X		X	October	516	122.87
2009	X		X		November	230	122.87

*1989 was not included in the calculation of SE due to high water levels during this survey biasing the survey yield.

Table 2. The proportion of juvenile, sub-adult and adult Nile Crocodiles in 6 African countries (adapted from Bourquin 2008).

Location	Juveniles	Sub-adults	Adults	Study
Okavango	55.4	19.2	25.4	Bourquin (2008)
Kenya	50	31	19	Graham (1968)
Uganda	54	25	21	Parker and Watson (1970)
Zimbabwe	44	33	23	Hutton and Woolhouse (1989)
Mozambique	48	34	18	Games (2004)
Ndumo Game Reserve	13	39	48	Current study

Table 3. Sex and sizes of Nile Crocodiles (n = 89) in Ndumo Game Reserve in 2009-2010.

Size class (m)	>2.5m	>2.6m	Total
No.	51	38	89
Male	18	26	44
Female	33	12	45
% Male	35	68	49
% Female	65	32	51

Table 4. Nile Crocodile aerial surveys at Ndumo Game Reserve (1971 - 2009) with a correction factor applied.

Year	Aircraft type		Water level		Month	Abundance Relative	Correction	Abundance Absolute
	Helicopter	Aeroplane	High	Low				
1971	X			X	Sep	273	1.28	349
1972	X			X	Jul	274	1.28	351
1973	X			X	Jul	269	1.28	344
1985	X					515	1.28	659
1986	X					503	1.28	644
1988	X			X	July	505	1.28	646
1989	X		X		Aug	420	1.28	538
1990	X			X	July	732	1.28	937
1992	X			X	Aug	789	1.28	1010
1993	X			X	Aug/Sep	833	1.28	1066
1994	X			X	Aug	745	1.28	954
2009	X		X		Mar	100	1.28	128
2009		X		X	Oct	516	1.64	846
2009	X		X		Nov	230	1.28	294

a.



b.



Figure 1. Example of a Nile Crocodiles snared in Ndumo Game Reserve during 2009 – 2010 showing injury to the animal.

a.



b.



Figure 2. Anthropogenic disturbances in Ndumo Game Reserve during 2009 – 2010 affecting habitat used by Nile Crocodiles.

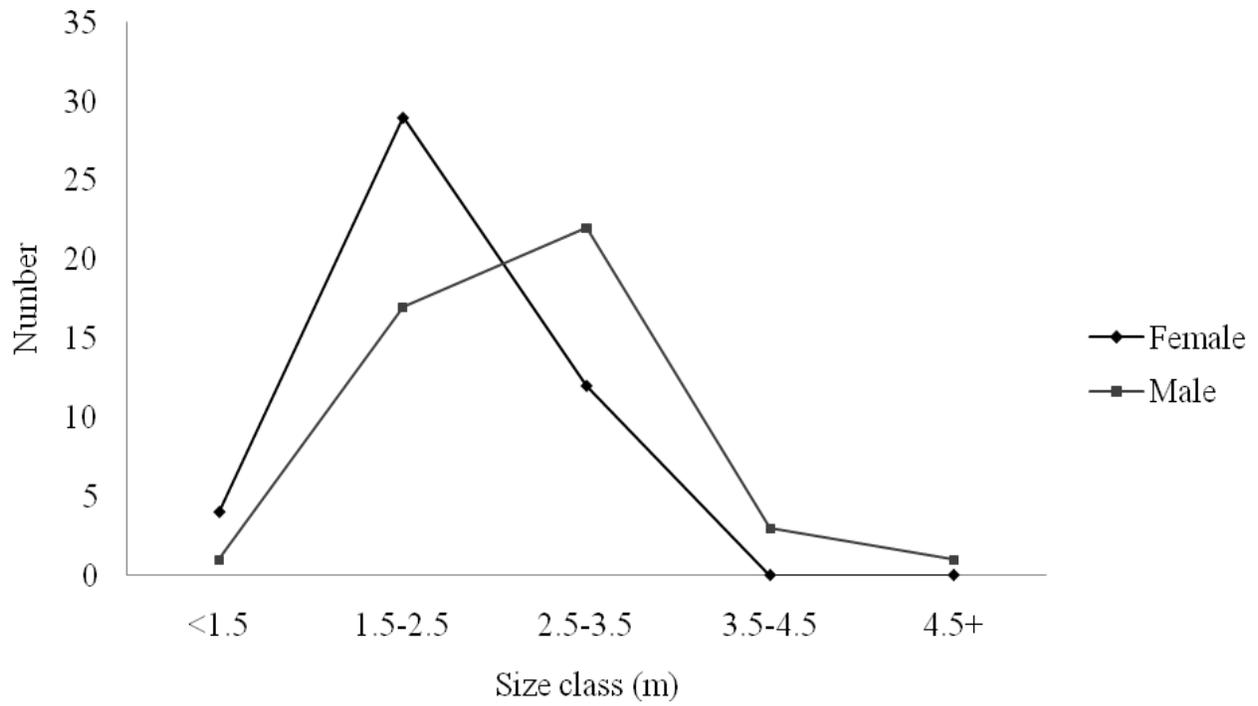


Figure 3. The intercept of equal sex ratios of Nile Crocodiles in Ndumo Game Reserve between 2.5 and 3.5 m.

CHAPTER 5

The Past and Present Nesting Ecology of Nile Crocodiles in Ndumo Game Reserve, South Africa: Reason for concern?

P. M. Calverley and C. T. Downs

School of Life Sciences, University of KwaZulu-Natal.

Private Bag X01, Scottsville, Pietermaritzburg, 3209 South Africa. Email:

calverleypeter@gmail.com.

Formatted for *Copeia*

5.1 ABSTRACT

*Knowledge of the distribution and abundance of crocodile nests and the threats facing them is essential in calculating recruitment and determining population trends. The nesting ecology of Nile Crocodiles (*Crocodylus niloticus*) was studied at Ndumo Game Reserve (NGR) in north eastern KwaZulu-Natal, South Africa from 2009 to 2012. Nesting effort in NGR was comparable to other *C. niloticus* 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 Water Monitor Lizards (*Varanus niloticus*). The number of nests located in NGR remained the same from 1964 - 2012 despite large population increases. Stocking programs have increased the number of Nile Crocodile in the greater Rio Maputo/Phongola floodplain areas but these numbers may not be sustainable as the majority of Nile Crocodile nest outside of the reserve in unprotected areas.*

5.2 INTRODUCTION

Nile Crocodiles (*Crocodylus niloticus*) are oviparous and nest terrestrially in a variety of habitats from swamps and marshes to lakes, artificial impoundments, strong flowing rivers and small streams (Shacks, 2006; Borquin, 2008; Champion, 2011; Combrink et al., 2011). Generally nest sites are selected according to favorable incubation conditions for offspring as well as risks or costs to the reproductive adult (Somaweera and Shine, 2012b). Nile Crocodiles are particular in their choice of nesting habitat with distance to water, elevation above water, substrate, slope, vegetative cover, amount of sunlight received and aspect all playing a role in nest site selection (Modha, 1967; Pooley, 1969; Hartley, 1990; Leslie, 1997; Swanepoel, et al., 2000; Combrink, 2004, 2013). As such, established nesting sites are often used repeatedly over successive seasons and are 'biologically sensitive' sites that need to be conserved to ensure successful recruitment (Hartley, 1990). In South Africa, and particularly in KwaZulu-Natal, suitable nesting habitat for Nile Crocodiles outside of protected areas is severely limited and it is important that adequate protection be given to breeding grounds within reserves (Pooley, 1969; Hartley, 1990).

Nesting surveys are necessary not only to record the location of nesting sites to ensure future protection but to identify the physical characteristics that define suitable nesting habitat and to estimate the breeding percentage of a population (Taylor and Blake, 1986; Villamarín et al., 2011). Data obtained from nesting surveys can be used to calculate changes in nesting effort and to predict changes in population growth patterns over time. However, undue anthropogenic disturbance at nest sites can have a negative impact on the success and use of available nesting sites (Pooley, 1969; Hartley, 1990; Platt and Thorbjarnarson, 2000; Shacks, 2006; Champion, 2011) and nesting surveys should be designed to minimize disturbance at nesting sites. The nesting ecology of Nile Crocodiles in north eastern KwaZulu-Natal has been well documented

(Pooley, 1969; Taylor and Blake, 1986; Hartley, 1990; Leslie, 1997; Combrink, 2004; Champion, 2011), particularly in Ndumo Game Reserve (NGR) (Pooley, 1969; Pooley, 1977) which is one of only three secure breeding populations of Nile Crocodile in South Africa (Combrink, 2004; Combrink, 2013). Consequently, a large amount of nesting data are available for Nile Crocodiles in Zululand, such as average clutch size, extent of the breeding season, duration of incubation, nest depth and temperature, predation pressure and the percentage of eggs likely to hatch (Pooley, 1969; Hartley, 1990) eliminating the need for unnecessary disturbance at the nest site through excavation or ongoing observation.

However, physical alterations to the environment wrought through natural processes such as floods or anthropogenic interference alter the quality and quantity of habitat available for nesting purposes and need to be quantified (Pooley, 1969; Hartley, 1990; Swanepoel et al., 2000; Combrink, 2004; Champion, 2011; Sigler, 2011). A number of significant large scale changes have occurred in the habitat available to Nile Crocodiles in NGR since nesting surveys were initiated in the 1960's. In 1972 the Pongolapoort Dam was completed and the flow rates and flooding of the Phongola River and Floodplain are now artificially controlled (Heeg and Breen, 1982). As a result of floods in 2000 the main course of the Phongola River has shifted further east, away from historical nesting grounds described by Pooley (1969) and Ward (1990). Similarly, floods in 2002 diverted the main course of the Usuthu River from a easterly to a south-easterly course that now flows through Banzi Pan, shifting the confluence with the Phongola River further south (Wadeson, 2006). In May 2008 the eastern boundary fence of the reserve was forcibly removed by the neighbouring Mbangweni community allowing unprecedented access to the Phongola River and floodplain (Meer, 2010). Since then agricultural activities and resource use in the form of fishing, reed and wood harvesting take place within the reserve throughout the

eastern floodplain from the Phongola River to the old fence line (Meer, 2010). Poaching activities in the form of snaring and gill netting also take place in this part of the reserve (Calverley, 2009). These activities impact on Nile Crocodiles with changes in habitat availability and quality. In particular, the impacts of these changes on the nesting ecology of Nile Crocodiles within the reserve need to be quantified as it affects the long-term viability of the population.

Pooley (1969) initiated the first investigation into the nesting ecology of Nile Crocodile in South Africa. Pooley's studies took place primarily in NGR and provide valuable information on the location of nest sites dating back to as early as 1967. This provides an excellent opportunity to examine any changes in the use of nesting habitat and to relate these changes to large scale changes in the hydrological and terrestrial landscape. Furthermore, NGR was involved in a restocking program whereby 1257 crocodile were released into the reserve (Pooley, 1982). Evaluating any changes in nest numbers and locations due to these releases could provide valuable information for management of recovering crocodile populations and the efficacy of restocking programs.

The aim of this study was to describe the nesting ecology of Nile Crocodiles in NGR currently and compare that with past trends. The objectives of the study were firstly to define the physical characteristics of nesting sites in NGR, and then to estimate the nesting effort of the NGR population. It was hypothesized that nesting effort was affected by the availability of suitable nesting sites. It was predicted that despite a relatively high population of Nile Crocodiles at NGR, nesting effort was relatively low and clumped in distribution because of the shortage of suitable nesting habitat due to anthropogenic disturbances within the reserve and at historical nesting sites.

5.3 METHODS

5.3.1 Study area

NGR is unique in that the 10 000 ha reserve conserves between 2000 – 4000 ha of floodplain depending on season and water levels. This is largely due to the confluence of two major river systems in the north east corner the reserve: The Usuthu River forms the northern boundary of NGR and the southern boundary of Mozambique while the Phongola River and floodplain run along the eastern boundary (Chapter 2, Fig. 1). Water levels in the Phongola River are controlled by the Pongolapoort dam 100km north west of the reserve while the water level of the Usuthu River is not influenced by any impoundments and fluctuates according to rainfall. Due to the flat nature of the floodplain either of these rivers can, and do, flood the entire reserve due to backfilling from the confluence in the north east corner of the reserve (Pooley, 1982).

5.3.2 Sub-division of the study area

NGR was divided 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 (Fig. 1). The reason for this was to demarcate NGR according to different sub-habitats 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 (Fig. 1).

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 (Fig. 1).

5.3.3 Nest surveys

Methods for conducting Nile Crocodile nest surveys include aerial surveys, ground surveys and surveys from the water all of which are effective methods of locating nesting sites (Magnusson et al., 1978; Combrink, 2004). All three of these methods were used in this study and are described in greater detail later in the chapter. Generally, extensive aerial surveys are undertaken before ground surveys and all observed potential nest site recorded (Swanepoel et al., 2000; Combrink, 2004; Botha, 2005). Follow up surveys on foot then closely examine nesting sites identified from

aerial surveys, accurately recording the geographical position and searching for any undiscovered nests within the area (Swanepoel et al., 2000; Combrink, 2004). Visibility and observer bias from aerial surveys can thus be negated and a correction factor to estimate the nesting population from aerial surveys calculated (Graham, 1987). Permission from the park authority (EKZNW) to search for nests by probing potential nesting sites with rods was not granted and could have resulted in nests not being discovered.

At NGR egg laying normally occurs from the 5th of November to the 6th of December followed by hatching between the 27th January and the 26th of March (Pooley, 1969). Nile Crocodile nest surveys in NGR were initiated in mid-December assuming that all nests would have already been laid at the onset of the survey. Local knowledge of the EKZNW game rangers and historical records of nesting sites were used to investigate historical nesting sites and the possibility of consecutive seasonal use, a phenomenon which has been widely reported (Pooley, 1969; Taylor and Blake, 1986; Hartley, 1990; Combrink, 2004; Shacks, 2006) but poorly validated. According to Pooley (1982) nests can be located in the following ways: From a boat – crocodiles are disturbed from their nesting sites by the sound of the outboard motor or the proximity of the boat and were spotted plunging into the river initiating an investigation into possible nesting in the immediate area; any Hippopotamus (*Hippopotamus amphibius*) pathways and small tracks leading away from the water's edge used by crocodiles as access routes from nests to a particular water source were followed and the area inland of these searched for nests; actual claw, scrape and slide marks on the river banks give away the presence of crocodiles, warranting further inspection; and while conducting foot patrols crocodiles are sometimes disturbed and seen or heard walking/running to water. This is a strong indication that there are nests in the area.

These factors were taken into account when searching for nests. Once nests and nest sites were found a geographical location was recorded using a hand held Garmin eTrex[®] Vista Cx global positioning system (GPS) (Kansas, USA) and allocated to a sub-region (1-8). Nest sites were revisited on three separate occasions spanning 6 weeks to determine successful hatching, record predation and other reasons for recruitment failure such as flooding, trampling by large herbivores or nest abandonment. Factors important to nesting ecology were recorded such as substrate, distance to water and height above water (Pooley, 1969), slope (Swanepoel et al., 2000), exposure to sunlight (Hartley, 1990), distance to nearest nest (Swanepoel et al., 2000) and vegetation cover (Taylor and Blake, 1986). No nests were opened to check for eggs as the smell may attract nest predators such as Water Monitor Lizards (*Varanus niloticus*). We relied on egg shells from hatching or predation to verify suspected nests. In the event that these were not visible well after the hatching season it was decided to dig up suspected nest sites to check for eggs.

Substrate was divided 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). Distance to water was measured by taking a GPS waypoint at the nest and another at the water's edge and measuring the distance between the two. Height above water was estimated using man height units as an estimation as constantly fluctuating of water levels rendered more accurate methods superfluous (Hartley, 1990). Slope was then calculated using the Cotan of the distance to water over height above water and converted into degrees (Swanepoel et al., 2000). Distance to nearest nest was

measured with a 30 m tape measure where possible or by measuring distance between waypoints created at each nest where dense vegetation or long distances rendered the tape measure ineffectual. The amount of vegetative cover was measured by estimating the percentage of open sky visible from the nest in degrees/180⁰ along an east/west axis with an accompanying estimation of hours of direct sunlight received per day.

Four camera traps were set up at nesting sites in an effort to record nest site attendance by the female and to identify possible nest predators. Two camera traps were Bushnell (Overland Park, Kansas, USA) and 2 were Cuddeback (Green Bay, Wisconsin, USA). 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 were hammered into the soil.

5.3.4 Historical nesting data

Initial ground based Nile Crocodile nest surveys were conducted annually in NGR by Pooley from 1967-1974 (EKZNW records). 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 out by Ward from 1988-1990 (EKZNW records). 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.

5.3.5 Aerial survey for nests

An aerial nesting survey was conducted on the 31st of January 2010. 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 (Olathe, Kansas, USA) 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. With an ambient temperature of 28° C 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 minutes.

5.3.6 Ground surveys

Terrestrial Nile Crocodile nest surveys took place from mid-December through to March in the 2009/2010 and 2011/2012 nesting seasons at NGR. Historical nesting sites were investigated and new sites searched for. Foot surveys were carried out 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 EKZMW 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 all water bodies within NGR and searching for signs characteristic of nesting behavior 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).

5.3.7 Boat survey

During the 2009/2010 nesting season at NGR a once off boat survey was used to search for nests in otherwise inaccessible parts of the Phongola River. River surveys covered 6.5 km over 2h using a 3.5 m aluminum "tinny" boat with a 40 hp Yamaha motor (Hamamatsu, Japan). 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.

5.3.8 Estimates of Nile Crocodile nesting effort

Following Leslie (1997) and Combrink (2004) an equation first described by Chabreck (1966) was used to calculate nesting effort of Nile Crocodiles in NGR. Where historical data allowed, calculation of nesting effort was carried out in order to identify any trends in nesting effort over the years. The equation was as follows:

$$N = \frac{X}{A * F * E} \text{ (Chabreck, 1966)}$$

N = population size

X = number of nests

E = nest effort (proportion of mature females nesting)

A = fraction of mature animals in the population (number of mature crocodiles / sample size)

F = fraction of females in the mature population (number of mature females / number of mature crocodiles)

N was calculated through total population counts (Chapter 3), X through nesting surveys while A and F were calculated through capture activities (Chapter 4). The equation was then solved for E . Calculations are shown in Table 2.

5.3.9 Statistics

The various descriptive statistics and a correlation matrix were run in STATISTICA 7.0 (Statsoft Inc, Tulsa, USA).

5.4 RESULTS

5.4.1 Nest surveys

Nile crocodile nesting surveys in NGR during the late 1960's and late 1980's showed that the majority of nesting sites occurred along the old Phongola River course (sub-region 6). The river has subsequently diverged and now runs along the eastern boundary of the reserve (sub-region 8) (Fig. 1). During the course of the current study no nests were found along the old or

new river courses. The eastern boundary fence of the reserve has recently been forcibly removed by the local inhabitants offering unprecedented access to the Phongola floodplain and subsequent disturbance to nest sites. In 2009-2010 at least two historical nesting sites along the new course of the Phongola River were abandoned due to increased anthropogenic disturbance. These sites were not used in the 2011/2012 nesting season. Furthermore, no nests were located along the eastern periphery of the Phongola floodplain where the majority of anthropogenic disturbance was taking place, including Mavilo Hill, a historical nest site. In 2009/2010 prime historical nesting sites along the old course of the Phongola River were not used and it was unlikely that this was because of disturbance as this part of the reserve remains relatively isolated. However, in 2011 the swing bridge which grants field rangers access to this part of the reserve and allows for foot patrols was destroyed. In the past field guides excavated eggs from these areas to show guests which could negatively impact nesting here (pers. comm. G.Bloy). Anthropogenic disturbance in this part of the reserve is therefore higher than previously thought. The lack of crocodiles nesting here could also be attributed to the change in the Phongola River's main course altering the nesting landscape (pers.obs).

In January 2010, four nests were found along the western periphery of the Phongola floodplain in Sub-region 6. Although these nests were in historical nest sites, they were significantly further inland (west) due to high water levels. No nests were found in Sub-region 6 in 2011/1012. Two nests were found at historical nesting sites on the south eastern shore of Lake Nyamithi (Sub-region 5) in both 2009/2010 and 2011/2012 surveys. One nest was found 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 and could be in response to disturbance in more favorable parts of the reserve or a change in the nesting landscape due to the change in the

course of the Usuthu River. Three new nesting sites were found 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.

A new nesting site was found on the banks of the Balamhlanga stream in 2010 as it enters Lake Nyamithi. The nest site contained 4 active nests and 1 active burrow which was used by at least one female and numerous hatchlings. The stream is narrow and shallow and the burrow provided shelter for the female during the incubation period and shelter for hatchlings.

5.4.2 Nest success

In 1964 Pooley documented the abandonment of 5 Nile Crocodile nesting sites at Lake Nyamithi due to disturbance associated with increased motor vehicle activity (Pooley, 1969). Pooley listed the Water Monitor Lizard as the primary predator of crocodile eggs during his 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 Lizards. 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 once again found in this area, however only one was predated. The un-predated nest was closely guarded by a female who refused to move from the nest site, emitting a warning hiss to researchers who approached too closely.

Three of the 4 nests attended by female Nile Crocodiles 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. 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 (100 %). Consequently, there was zero recruitment from the 7 Nile Crocodile nests located in NGR over the 2009/2010 breeding season.

Conversely, none of the 9 nests located in 2011/2012 were flooded and 66 % were predated. 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.

Camera traps located at 4 nest sites during the 2011/2012 season failed to capture images of females attending their nests. Images of potential nest predators captured at the nesting site included the Cape Porcupine (*Hystrix africaeaustralis*) and the Vervet Monkey (*Chlorocebus ethiops*).

5.4.3 Characteristics of nesting sites

Nile Crocodile nests were found in lacustrine and riverine habitats in NGR and in a variety of substrates. Nests located on the south eastern bank of Nyamithi Pan were elevated 2-3 m above water level and 1 - 4 m from water and were laid in hard, red rocky soils in a boulder bed outcrop. Nesting sites located on the banks of the western inlet of Nyamithi in an area known

as the Balamhlanga stream were 1 m above water level and 1–2 m from the water and in white sandy soil. Nesting sites on the western periphery of the floodplain were found in fine white sand and were 5 – 25 m away from water. These nests were attended by females but were abandoned later in the season possibly due to predation or flooding owing to their low elevation above water (< 2 m). Nests in the same area, but closer to the water, were deposited in a substrate of white sand and alluvial silt/clay.

Considering the fluctuations in water levels throughout the rainy season, measuring height above and distance to water provided incidental data dependent on the date of inquiry, and was of little comparative use. Perhaps the only standardized method of collecting such data would be to accurately record the altitude of nests and calibrate this to water level data for the particular river/lake being investigated.

5.4.4 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. When nesting effort (E) was calculated using winter estimations of total population size (N), a significant decrease ($p = 0.001$) in the nesting effort of Nile Crocodiles in NGR from over 20 % in the 1960's to just over 5 % in 2010 and 6 % in 2012 (Fig. 2) was found. This was a function of an increasing Nile Crocodile population size with time, while the number of nests remained constant ($p = 0.285$). The number of nests found within NGR has stayed relatively constant over the years, while the population has increased threefold (Fig. 3) resulting in a much lower nesting effort with time (Fig. 4). When E was calculated using N during summer E was calculated at 18 – 22 % and no significant difference in E was found from the 1960's to the present.

5.5 DISCUSSION

5.5.1 Location of nesting sites

In the past the majority of nesting sites were found on the banks of the main course of the Phongola River (Pooley, 1982). 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 Pongola River and historical nesting sites in this area have been abandoned due to increased anthropogenic disturbance and habitat transformation (Calverley, 2009). 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.

5.5.2 Nesting effort

Historical records suggest that the nesting effort of Nile Crocodiles in NGR is 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. 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 Crocodiles (Modha, 1967; Pooley, 1969). Low nesting effort in areas of relatively high crocodile density could be an indication of unfavorable nesting habitat (Swanepoel et al., 2000) or excessive disturbance within suitable nesting habitats (Pooley, 1982).

However, in the past population estimates have been carried out in winter/low water months when crocodiles are most visible and nesting surveys take place in summer months when water levels are higher. As such nesting effort (E) has been calculated using winter population sizes (N) and the number of nests (X) found in summer (Chabreck, 1966). While Swanepoel et al. (2000) found no difference in the nesting ecology of Nile Crocodile between open and closed systems, crocodile in open systems are free to move out of the study area and often do so on a seasonal basis (Pooley, 1982). In open systems N may vary, particularly between seasons and E can only be accurately calculated using N during summer. In NGR, E calculated using summer N was significantly higher (18 – 22 %) than E calculated using winter N (5 – 6 %). 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 Crocodiles (Bourquin, 2008).

Anthropogenic disturbance resulted in the abandonment of at least 2 historical 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 crocodiles to ‘make the best of a bad situation’ and nest elsewhere in the reserve in the future (Somaweera and Shine, 2012b).

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

When examining the amount of suitable habitat available for crocodiles to nest in, it is important to differentiate between that which constitutes a nest site and that which constitutes a nest (Shacks, 2006). Nest sites may contain more than one nest and are often used repeatedly over many seasons/years and by different females (Combrink, 2013). The substrate, slope and vegetation communities are generally the same within a particular nesting site but can vary

between different nesting sites. The nests themselves are cavities excavated for the deposition of eggs, are located within the nesting site, are not re-used and new cavities are dug each year. While nests within a nest site may be less than 1m or more than 100m 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 than nest sites are to one another. This clumping of nests is often attributed to a scarcity of suitable nesting habitat forcing crocodiles to nest in what suitable nest habitat there is (Pooley, 1982; Blake and Loveridge, 1987; Somaweera et al., 2011a).

In the past the evaluation of nesting habitat used by crocodiles has been rather stringently interpreted in terms of the physical characteristics of the nest itself. These include the distance of the nest to water, the elevation above water, the presence of shade for the female, the type of substrate in which the nest is chamber is excavated, the hours of direct sunlight the nest receives, the type of vegetative cover and the angle of the slope between the nest and the water (Pooley, 1969; Kofron, 1989; Hartley, 1990; Leslie, 1997; Swanepoel et al., 2000; Combrink, 2004; Botha, 2005; Shacks, 2006; Champion, 2011). The inclusion of all of these variables is an indication of the uncertainty associated with exactly why crocodiles choose to nest where they do and why crocodile nests are often clumped in distribution. One possible explanation which has not been explored is that suitable nesting habitats or nesting sites are identified first and the location of nests within the nesting site are then positioned according to shade, substrate, distance to water etc. Interplay between these variables would then determine the exact location of nests within the nesting site and their proximity to one another. A different set of variables (apart from substrate, shade and slope) would influence the choice of nest site or nesting habitat. These variables would include the following:

5.5.4 The availability of fresh water and burrows

In the Okavango Delta the nesting season coincides with periods of low water levels and nesting sites are strongly associated with permanent channels of deep water (Bourquin, 2008). In Kruger National Park Swanepoel et al.(2000) found that nests were clumped around deep pools as did Kofron (1989) in Zimbabwe. In Lake Sibaya and Lake St. Lucia Nile Crocodile nests were found in closer proximity to fresh water nursery habitats (seepages, marshes, streams and pans) than to the saline water of the main lake (Leslie, 1997; Combrink et al., 2011). Where there is insufficient water for the female to escape into or to thermoregulate, burrows are excavated from the stream bank to create a cool microhabitat to see out the summer (Combrink, 2013, Combrink, et al. 2013). While burrows could be seen as an adaptation of the nesting site due to low water or drought conditions by both male and female Nile Crocodiles, Combrink (2013) found that nesting females return to the same burrow during the nesting period and that burrows were in close proximity to the nest. In Niger, Nathalie (2011) found that habitat use of Nile Crocodile was influenced by suitable substrate for burrow excavation. Nathalie (2011) also found hatchlings clustered around a burrow site in what appeared to be crèche formation. Pooley (1969) found that hatchlings in captivity in NGR constructed communal burrows in order to escape predation and for thermoregulatory reasons.

While suitable nesting habitat does not hinge on the availability of suitable substrate for burrow excavation, the presence of burrows enables the females to remain undetected and in close proximity to the nest until hatching occurs. Burrows also allow females to nest in areas where small, secluded and shallow water bodies provide good nursery habitat for hatchlings but

would otherwise be too small to hold the female. The assistance of females in releasing hatchlings both from the nest and the egg is well documented and is considered essential in the hatching process (Charruau and Hénaut, 2012; Somaweera and Shine, 2012a). The presence of burrows may therefore have significant implications for hatchling survival and since burrows are used repeatedly by the same female may influence nest site selection.

5.5.5 Availability of prey items

Nile Crocodiles in St Lucia follow seasonal migrations of striped mullet (*Mugil cephalus*) (Leslie, 1997) and Pooley (1982) suggested that the location of nest sites could be related to areas of high density of mullet. Botha (2005) found that crocodile nest sites were concentrated in the narrow upper reaches of the Flag Bosheilo Dam, and where rivers and inlets entered the dam. Nile Crocodile nests at Pongolapoort Dam are similarly found on the banks of the Pongola River upstream from the tail waters of the dam (Champion, 2011). The majority of nesting sites in KNP are located in the Olifants River Gorge which forms the entrance to the Massinger Dam in Mozambique (Swanepoel et al., 2000). Hocutt et al.(1992) used radio telemetry to follow the movement patterns of a female Nile Crocodile in Lake Ngezi, Zimbabwe. The female moved 12km from the point of release in the main body of the Lake and nested along the banks of the Ngezi River at the inlet to the dam.

Both Botha (2005) and Champion (2011) noted a change in seasonal habitat use by Nile Crocodile whereby inlet sections of impoundments were selected for during summer months by both males and females. Summer months are associated with warmer temperatures, increased metabolism and an increased intake of food compared with winter months (Wallace and Leslie, 2008). Changes in habitat use from winter basking sites to summer habitat could quite

reasonably be assumed to be influenced by prey availability and concentrations. In Lake Nyamithi Nile Crocodiles move away from winter basking sites and concentrate around the inlet/outlet of the pan where fish densities are the highest (pers. obs.). Numerous fish species show potodendric movement patterns and by moving to narrower inlets crocodiles concentrate their food source. The location of nesting sites could therefore be influenced by prey density. Reliable seasonal aggregations of prey items at specific locations could result in the establishment and use of nesting sites over many years. Two historical nesting sites were found in close proximity to the outlet of Lake Nyamithi. The mass seasonal movement of Nile Crocodile out of NGR during the summer months and over the nesting season is most likely in response to prey densities in the Rio Maputo Floodplain (pers. obs.; Chapter 3). Females are then more likely to nest in close proximity to these food resources which happen to be outside of the reserve (pers. obs.). Gravid females have a narrower window of opportunity in which to accumulate enough reserves to see out the 3 month vigil of the nest as they rarely feed while in attendance of the nest. It may be energetically worth while to travel extensive distances from winter basking sites to areas of high food concentrations and then to find suitable nesting habitat in this area.

5.5.6. Nursery habitat

On a finer scale, few (if any) crocodile nesting surveys take into account the role that the aquatic habitat in the immediate vicinity of the nest site plays in the selection of nest sites and in doing have inadvertently assumed that it has no bearing on nest site selection. There is strong evidence suggesting the opposite may be true. Crocodile hatchlings are at the greatest risk to predators in the first week after hatching (Magnusson, 1980) and predation rates are generally

lower where suitable nursery habitat is available (Kushlan and Mazzotti, 1989). Mothers that select nesting sites in close proximity to favorable nursery habitat increase the chances of offspring survival. Nursery habitats provide hatchlings with suitable cover from predators, sustenance and a viable thermal environment such as warm, shallow, well vegetated water margins with abundant food sources well away from open bodies of water and large aquatic predators (Pooley, 1982; Hutton, 1984; Somaweera and Shine, 2012b). Furthermore, crocodilians establish and defend specific nursery areas in the immediate vicinity of the nest and hatchlings remain in the nursery area for a period ranging from days, weeks, months and even years (Pooley, 1969; Platt and Thorbjarnarson, 2000). Dispersal in hatchlings is related to a threshold in mass/length ratios and habitats that are rich in prey items and provide a suitable thermal environment allowing hatchlings to disperse sooner and disperse further (Tucker et al., 1997). Nursery habitats therefore provide a number of critical resources at a vital life history stage where mortality rates are extremely high (Somaweera et al., 2011b) and should be in close proximity to increase hatchling survival rates (Platt and Thorbjarnarson, 2000).

Platt and Thorbjarnarson (2000) found 30 % of *C. acutus* nests adjacent to fresh water lagoon nursery areas and concluded that successful nesting relied on these nursery habitats. In Lake Sibaya and Lake St. Lucia Nile Crocodile nests were found in closer proximity to fresh water nursery habitats (seepages, marshes, streams and pans) than to the saline water of the main lake (Leslie, 1997; Combrink et al., 2011).

Nesting sites at NGR were clumped in distribution, however, the availability of suitable nesting habitat in the classical sense was not a limiting factor which forced us to explore other possibilities that could better explain distribution patterns of nests. We suggest that the exact location of nests within a nesting site may well be influenced by substrate, shade and distance to

water but that the selection of nesting sites or nesting habitat is influenced by suitable nursery habitat. If this is true then nesting surveys should take into account the presence or absence of nursery habitat and include a description of said habitat. Shacks (2006) used a Geographic Information System (GIS) to overlay suitable nesting habitat in the Okovango Delta (Botswana) with areas of human disturbance to indicate the amount of available suitable nesting habitat vulnerable to anthropogenic disturbances. By overlaying maps of suitable nursery habitat with those of existing nesting sites in NGR a clearer picture of how Nile Crocodiles select nest sites may be attained.

1. The quality of nursery habitat could be evaluated in terms of: Primary habitat – the area in the immediate vicinity of the nest where crèche formation and parental care would be expected to take place; and secondary habitat – the habitat available to hatchlings once they disperse out of the primary habitat.

When the requirements of the aquatic habitat are taken into account as well as the terrestrial habitat we may gain a better insight into the nesting requirements of Nile Crocodiles and which factors may be considered limiting.

5.5.7 Communal nesting – limited habitat hypothesis

Nile Crocodile nests found in NGR were clumped in distribution and nesting sites were used repeatedly during the course of the study. The spatial clumping of nests has been recorded in numerous crocodylian species and is a far more common occurrence in reptiles (and amphibians) than previously thought (Doody et al., 2009). In crocodiles the spatial clumping of nests is most often attributed to a paucity of suitable nesting habitat (Pooley, 1982; Ward, 1990;

Swanepoel et al., 2000; Somaweera et al., 2011a). Where nests are particularly clumped speculation has arisen around the occurrence of communal nesting as a strategy to reduce predation rates (Pooley, 1969; Swanepoel et al., 2000; Botha, 2005). However, there is no clear definition as to what comprises communal nesting in crocodiles, or more specifically what distance nests must be from one another and in what density to be termed “communal” (Swanepoel et al., 2000; Botha, 2005). Nonetheless, both the spatial clumping of nests and communal nesting in crocodiles has only been discussed with reference to limited terrestrial nesting habitat as a causal factor and has not taken into account the role that nursery areas may play in the spatial clumping of nest sites. For example, should a particular aquatic habitat be selected for due to the advantages it offers hatchlings, depending on the size of the aquatic habitat, females may be forced to nest in close proximity to one another in order for their hatchlings to access this habitat. It is further likely that a combination of terrestrial factors such as the distribution of suitable substrate, shade (i.e. tree-line), elevation, distance to water and access to the ad hoc nest site via Hippopotamus pathways or gulleys would further confine the choice of nest location and increase the probability of clumping. Indeed, for a gravid female an investigation into the suitability of the aquatic environment would precede an investigation into that of the terrestrial nest site and may have important implications for nest site selection and the spatial distribution of nests.

5.5.8 Communal nesting – reduced predation hypothesis

Communal nesting in crocodiles is also believed to be a strategy adopted to reduce predation rates (Blake and Loveridge, 1987). However, a recent study on freshwater crocodiles (*Crocodylus johnstoni*) found that spatial clumping of nests did not influence rates of egg

predation (Somaweera et al., 2011a). When examining the role that predation pressure plays in the occurrence of communal nesting it may be important to consider the predation of the eggs as well as of hatchlings in the nursery habitat. Communal nesting implies some form of parental care of young that is not specific to one's own offspring (Swanepoel et al., 2000). However, maternal care of nests is generally poor and decreases over time with over 50 % of nests being abandoned within 2.5 months, 80% of which were predated (Kofron, 1989). Furthermore Nile Crocodile have never been reported to protect neighboring nests from predators and in some cases do not even protect their own nests from predators. However, once the eggs are ready to hatch maternal care seems increase with most crocodile species aiding in freeing hatchlings from the nest cavity (Charruau and Naut, 2012; Somaweera and Shine, 2012a). Hatchlings vocalize from within the egg and nesting cavity prompting the female to excavate the nest, free hatchlings from eggs where necessary and transport them safely to the nursery habitat (Vergne and Mathevon, 2008). Hatchling vocalization is not parent-hatchling specific and females respond to hatchling calls from neighboring nests, freeing hatchlings and transporting them to the nursery habitat and protecting them for several months until dispersal took place (Pooley, 1969; Vergne et al., 2007). Communal nesting may in this way improve hatchling survival rates (particularly when one considers the high rate of nest abandonment in Nile Crocodile) but unless communal nesters are related, may be viewed as a form of brood parasitism as energy and time expended in freeing, carrying and protecting others offspring is at the cost of one's own offspring. A method to test this would be to test the relatedness between mothers or offspring within a particular nest site and compare this to the relatedness with those from other nest sites.

Nest site fidelity or philopatry has been used to explain theories on the evolution of EDS (Reinhold, 1998) and female biased sex ratios (Freedberg and Wade, 2001). In both instances

philopatry results in nesting aggregations of related females and could have important implications for the occurrence of communal nesting.

5.5.9 Historical nesting – cultural and genetic inheritance hypothesis

In NGR the majority of nesting sites found in 2009 - 2012 were previously recorded as nesting sites as early as 1964. Nile Crocodile are known to re-use historical nesting sites (Graham, 1968; Pooley, 1969; Kofron, 1989; Leslie, 1997; Combrink, 2004, 2013; Combrink et al., 2011) 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 to still be breeding or may have died in the interim. It is further unlikely that terrestrial nesting parameters are so strict, static, limiting and perceivable to crocodiles 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).

The strongest influence causing a change in the nesting ecology of Nile Crocodiles at NGR therefore seems to be anthropogenic disturbances in the eastern portion of the Phongola Floodplain. Anthropogenic disturbance at crocodile nest site has been shown to have a deleterious effect on recruitment (Hartley, 1990; Combrink, 2004). Female Nile Crocodiles flee

their nests when approached by humans (Pooley, 1969; Taylor and Blake, 1986; Hartley, 1990) creating opportunities for egg predators to raid the undefended nest. An increase in disturbance can therefore result in a decrease in recruitment indirectly by increasing predation, and directly through the destruction of suitable nesting habitat (Hartley, 1990) which is currently taking place along the eastern periphery of the Phongola floodplain in NGR (Calverley, 2009). These disturbances have influenced the distribution and abundance of nests within the reserve as historical nesting sites in these areas have been abandoned.

5.5.10 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; pers. obs.). According to Pooley (1969) no Nile Crocodile nests were found nor could the local inhabitants remember nesting incidences along this stretch of the river. Disturbance and agricultural activities within this area are more intense today than they were 50 years ago in Pooley's time (pers. comm. P. Dutton). Similarly no Nile Crocodile nests were found outside of the reserve 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 crocodiles nesting here from the 1960's to the present, presumably for similar reasons as those of the Phongola floodplain outside of the reserve.

The Rio Maputo 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. Previously with the onset of the laying period, the majority of

Nile Crocodiles of reproductive size leave NGR and enter Mozambique via the Rio Maputo (Pooley, 1969; pers. obs.). To conserve the current population of Nile Crocodiles in NGR, the nesting ecology of the Nile Crocodiles outside of the reserve needs to be investigated and the conservation status of adjacent wetlands in Mozambique highlighted.

5.6 CONCLUSION

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. 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 Crocodiles 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 Rio Maputo 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.

5.7 ACKNOWLEDGEMENTS

The following people are thanked for assistance with in nesting surveys: Ferdi Myburgh, Donovan Barton-Hobbs as well as the Bateleurs and Paul Dutton for aerial survey assistance. We thank Mazda Wildlife for vehicle support. Ezemvelo KZN Wildlife kindly gave permission for

the study and supplied field rangers who helped with nesting surveys. We are grateful to the University of KwaZulu-Natal and the Water Research Commission for financial support.

5.8 REFERENCES

- BLAKE, D. K., and LOVERIDGE, J. P. 1987. Observations on the behaviour of Nile Crocodiles *Crocodylus niloticus* in captivity. *In: Wildlife management: Crocodiles and Alligators*. G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.). Surrey Beatty and Sons, Sydney. Pp 295-300.
- BOTHA, P. J. 2005. The ecology and population dynamics of the Nile Crocodile *Crocodylus niloticus* in the Flag Boshielo Dam, Mpumalanga province, South Africa. MSc thesis. University of Pretoria, Pretoria.
- BOURQUIN, S. L. 2008. The population ecology of the Nile Crocodile (*Crocodylus niloticus*) in the Panhandle Region of the Okavango Delta, Botswana. PhD thesis. University of Stellenbosch, Stellenbosch.
- BROWN, G. P., and SHINE, R. 2007. Like mother, like daughter: inheritance of nest-site location in snakes. *Biological Letters* 22:131-133.
- CALVERLEY, P. 2009. Ndumo Game Reserve aerial and ground survey report October 2009. Unpublished report.
- CHABRECK, R. H. 1966. Methods of determining the size and composition of alligator populations in Louisiana, p. 102-112. *In: Proceedings of the Southeastern Association of Game Fish Commission*. Vol. 20.

- CHAMPION, G. 2011. The Ecology of Nile Crocodile (*Crocodylus niloticus*) in Pongolapoort Dam, Northern KwaZulu-Natal, South Africa. MSc thesis, University of KwaZulu-Natal, Pietermaritzburg.
- CHARRUAU, P., and HÉNAUT, Y. 2012. Nest attendance and hatchling care in wild American crocodiles (*Crocodylus acutus*) in Quintana Roo, Mexico. *Animal Biology* 62:29-51.
- COMBRINK, A. S. 2004. Population status of *Crocodylus niloticus* (Nile Crocodile) at Lake Sibaya, Republic of South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X. 2013. Spatial and reproductive ecology and population dynamics of the Nile Crocodile (*Crocodylus niloticus*) in the St Lucia Estuarine system, South Africa. PhD thesis in prep., University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X., J. L. KORRÛBEL, KYLE, R., TAYLOR, R. AND R.PERRAN.2011. Evidence of a declining Nile Crocodile (*Crocodylus niloticus*) population at Lake Sibaya, South Africa. *South African Journal of Wildlife Research* 41:145-157.
- COMBRINK, X., WARNER, J. AND DOWNS, C. T. 2013. Crocodiles. Pp. 332 - 253 in R. Perissinotto, D.D. Stretch, and R.H. Taylor (Eds), *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. Cambridge University Press, Cambridge.
- DOODY, S.J., S. FREEDBERG, and J. S. KEOGH. 2009. Communal egg-laying in reptiles and amphibians: Evolutionary patterns and hypotheses. *The Quarterly Review of Biology* 84:229-252.
- FREEDBERG, S., and WADE, M. J. 2001. Cultural inheritance as a mechanism for population sex-ratio bias in reptiles. *Evolution* 55:1049-1055.

- GRAHAM, A. D. 1968. The Lake Rudolph crocodile (*Crocodylus niloticus*) population. Report to the Kenya Game Department.
- GRAHAM, A. D. 1987. Methods of surveying and monitoring crocodiles. *In*: Proceedings of the SADCC Workshop on Crocodile Management and Utilization, Kariba; Zimbabwe.
- HARTLEY, D. D. R. 1990. A survey of crocodile nests in Umfolozi Game Reserve. *Lammergeyer* 41:3-12.
- HOCUTT, C. H., LOVERIDGE, J. P., and HUTTON, J. M. 1992. Biotelemetry monitoring of translocated *Crocodylus niloticus* in Lake Ngezi, Zimbabwe. *Journal of Zoology* 226:231-242.
- HEEG, J., AND C. M. BREEN. 1982. Man and the Pongolo floodplain. National Scientific Programmes Unit: CSIR, SANSP Report 56, 1982, pp 129
- HUTTON, J. M. 1984. The population ecology of the Nile crocodile, *Crocodylus niloticus* laurenti 1768, at Ngezi, Zimbabwe. PhD. University of Zimbabwe, Harare.
- HUTTON, J. M. 1987. Incubation temperatures, sex ratios and sex determination in a population of Nile crocodiles (*Crocodylus niloticus*). *Journal of Zoology* 211:143-155.
- KOFRON, C. 1989. Nesting ecology of the Nile Crocodile (*Crocodylus niloticus*). *African Journal of Ecology* 27:335-341.
- KUSHLAN, J. A., and MAZZOTTI, F. J. 1989. Population biology of the American Crocodile. *Journal of Herpetology* 23:7-21.
- LESLIE, A. J. 1997. The ecology and physiology of the Nile Crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. PhD thesis. Drexel University, Philadelphia.

- MAGNUSSON, W. E. 1980. Hatching and creche formation by *Crocodylus porosus*. *Copeia* 1980:359-362.
- MAGNUSSON, W.E., G. C. GRIGG, AND J. A. TAYLOR. (1978). An aerial survey of potential nesting areas of the saltwater crocodile, *Crocodylus porosus* Schneider, on the north coast of Arnhem Land, northern Australia. *Australian Wildlife Research* 5: 401-415.
- MEER, T. 2010. Finding the community in community-based natural resource management: The case of Ndumo Game Reserve, South Africa. Submitted in partial fulfilment of the requirements for the degree of Master of Arts. Dalhousie University, Halifax, Nova Scotia.
- MODHA, M. L. 1967. The ecology of the Nile Crocodile, *Crocodylus niloticus* Laurenti. 1786, on Central island, Lake Rudolph. *East African Wildlife Journal* 5:74-95.
- NATHALIE, N. 2011. Population of Nile crocodiles (*Crocodylus niloticus*) in the northern part of park w, Niger, p. 4-6. *in: crocodile specialist group newsletter*. Vol. 30.
- PLATT, S. G., and THORBJARNARSON, J. B. 2000. Nesting ecology of the American Crocodile in the coastal zone of Belize. *Copeia* 3:869-873.
- POOLEY, A. C. 1969. Preliminary studies on the breeding of the Nile crocodile, *Crocodylus niloticus*, in Zululand. *Lammergeyer* 10:22-24.
- POOLEY, A. C. 1982. The ecology of the Nile Crocodile, *Crocodylus niloticus*, in Zululand, South Africa. MSc thesis. University of Natal, Pietermaritzburg.
- POOLEY, A. C., and GANS, C. 1976. The Nile crocodile. *Scientific American* 234:114- 124.
- REINHOLD, K. 1998. Nest-site philopatry and selection for environmental sex determination. *Evolutionary Ecology* 12:245-250.

- SHACKS, V. 2006. Habitat vulnerability for the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta. Botswana. Master of Arts. University of Stellenbosch, Stellenbosch
- SIGLER, L. 2011. American Crocodile recovery at Sumidero Canyon National park, Chiapas, Mexico, p. 7-9. *In: Crocodile Specialist Group newsletter*. Vol. 30.
- SOMAWEERA, R., and SHINE, R. 2012a. Australian freshwater crocodiles (*Crocodylus johnstoni*) transport their hatchlings to the water. *Journal of Herpetology* 46:407-411.
- SOMAWEERA, R., and SHINE, R. 2012b. Nest-site selection by crocodiles at a rocky site in the Australian tropics: Making the best of a bad lot. *Austral Ecology* 38:313-325.
- SOMAWEERA, R., WEBB, J., and SHINE, R. 2011a. It's a dog-eat-croc world: dingo predation on the nests of freshwater crocodiles in tropical Australia. *Ecological Research* 26:957-967.
- SOMAWEERA, R., WEBB, J. K., and SHINE, R. 2011b. Determinants of habitat selection by hatchling Australian freshwater crocodiles. *PloS ONE* 6:e28533.
- SWANEPOEL, D. G. J., FERGUSON, N. S AND M. R. PERRIN. 2000. Nesting ecology of Nile Crocodiles (*Crocodylus niloticus*) in the Olifants River, Kruger National Park. *Koedoe* 43:36-46.
- TAYLOR, R. H., and BLAKE, D. 1986. Crocodile nest survey Lake St. Lucia December 1985 - January 1986. Unpublished report. Natal Parks Board.
- TUCKER, A. D., LIMPUS, C. J., MCCALLUM, H. I., and MCDONALD, K. R. 1997. Movements and home ranges of *Crocodylus johnstoni* in the Lynd River, Queensland. *Wildlife Research* 24:379-396.
- VERGNE, A., AVRIL, A., MARTIN, S., and MATHEVON, N. 2007. Parent-offspring communication in the Nile crocodile *Crocodylus niloticus*: do newborns' calls show an individual signature? *Naturwissenschaften* 94:49-54.

- VERGNE, A. L., and MATHEVON, N. 2008. Crocodile egg sounds signal hatching time. *Current Biology* 18:R513-R514.
- VILLAMARÍN, F., MARIONI, B., THORBJARNARSON, J. B., NELSON, B. W., BOTERO-ARIAS, R., and MAGNUSSON, W. E. 2011. Conservation and management implications of nest-site selection of the sympatric crocodilians *Melanosuchus niger* and *Caiman crocodilus* in Central Amazonia, Brazil. *Biological Conservation* 144:913-919.
- WADESON, R. 2006. Lower Usuthu River-diversion channel. Unpublished scoping report. Department of Water Affairs and Forestry, Pretoria.
- WALLACE, K. M., and LESLIE, A. J. 2008. Diet of the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42:361–368.
- WARD, M. C. 1990. Crocodile Nest Survey-KwaZulu Ubombo/Ingwavuma District. Unpublished Report. Natal Parks Board.

LIST OF FIGURES

Figure 1. Ndumo Game Reserve showing the sub-habitats of the reserve to determine effect of subhabitat on Nile Crocodile nesting effort.

Figure 2. Localities of historical and current Nile Crocodile nests in Ndumo Game Reserve (1960-2010).

Figure 3. The number of Nile Crocodile nests in Ndumo Game Reserve and nesting effort from 1964-2012 (Data from Pooley 1969, EZKZNW records and current study).

Figure 4. Changes in Nile Crocodile population size at Ndumo Game Reserve from 1971-2009.

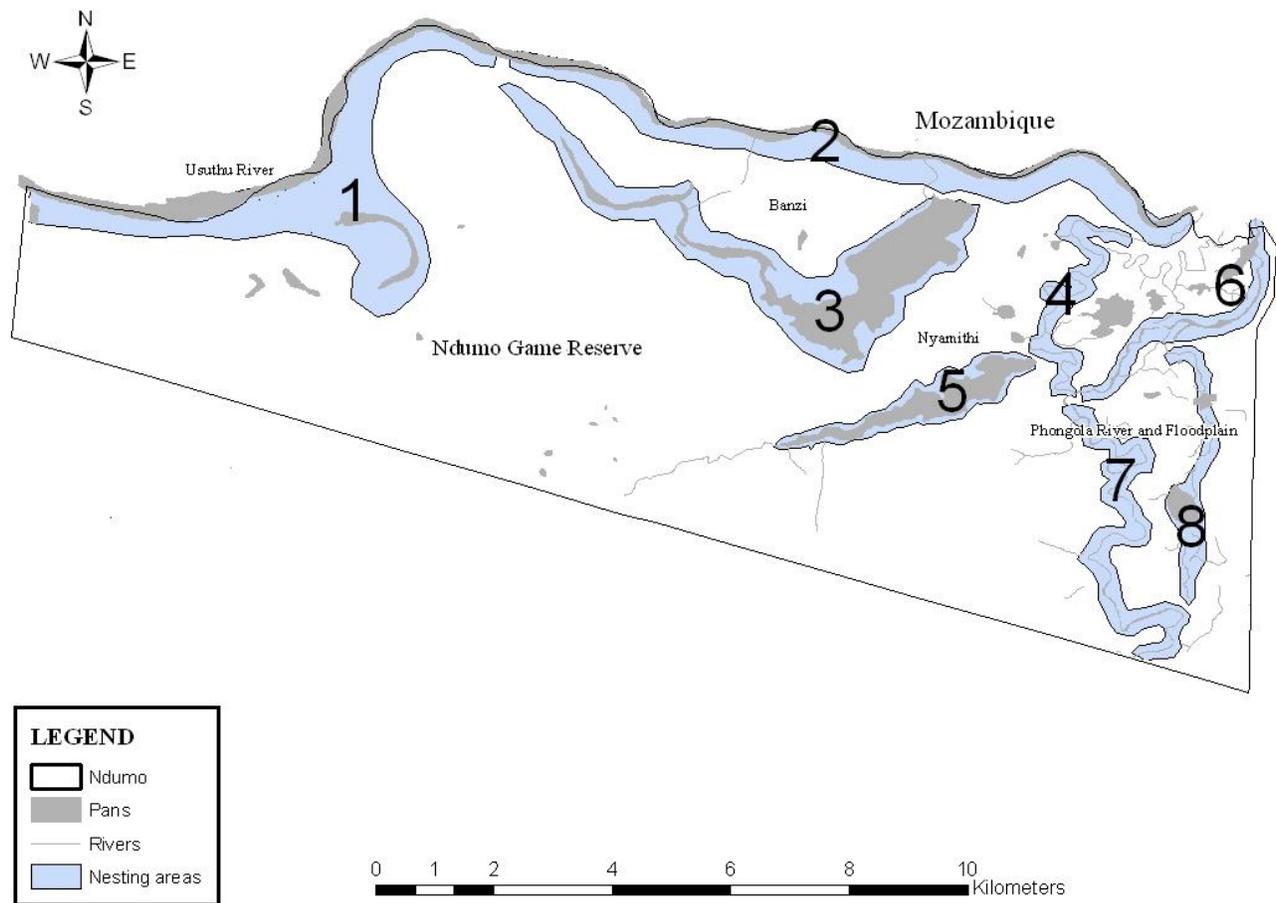


Figure 1. Ndumo Game Reserve showing the different sub-regions (1 - 8) demarcated for the nesting surveys.

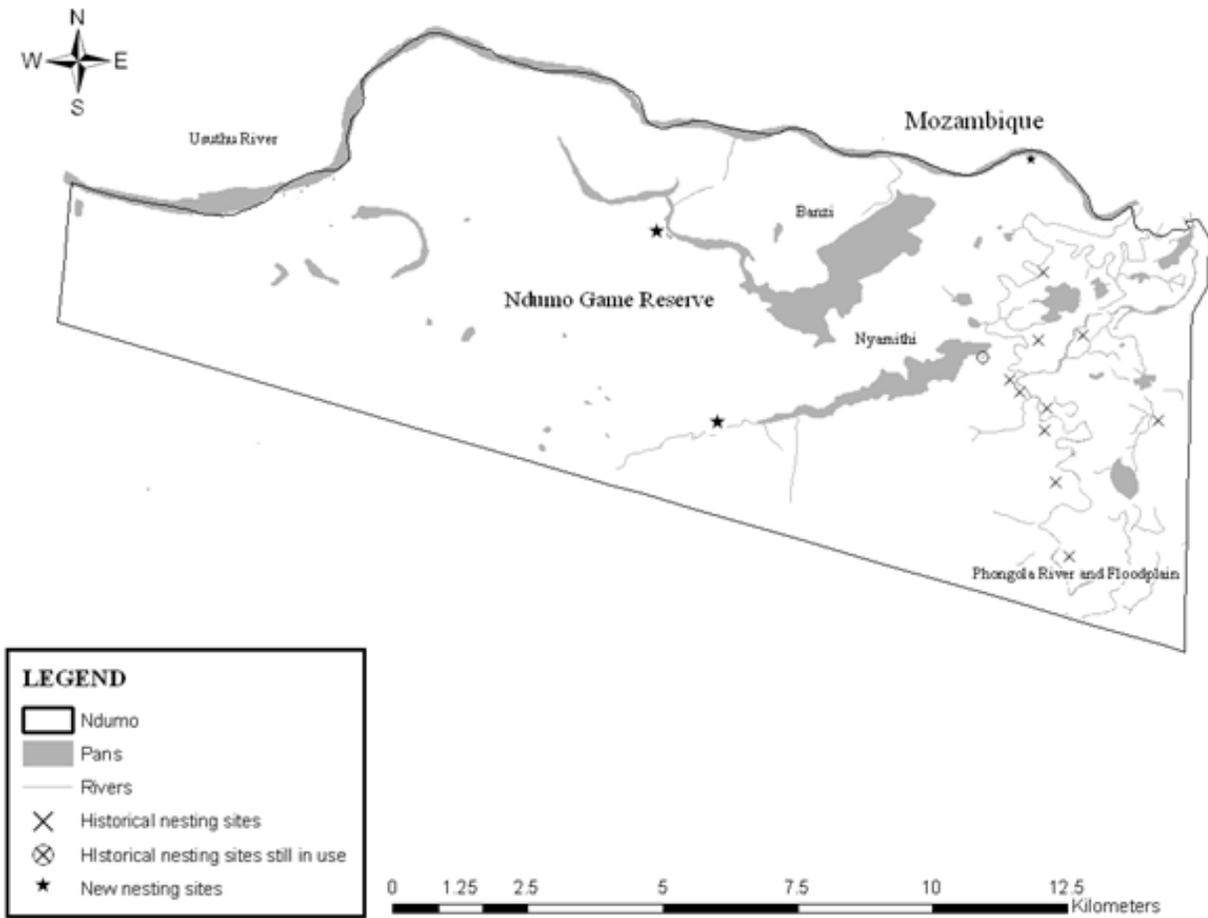


Figure 2. Localities of historical and current Nile Crocodile nests in Ndumo Game Reserve (1960-2012).

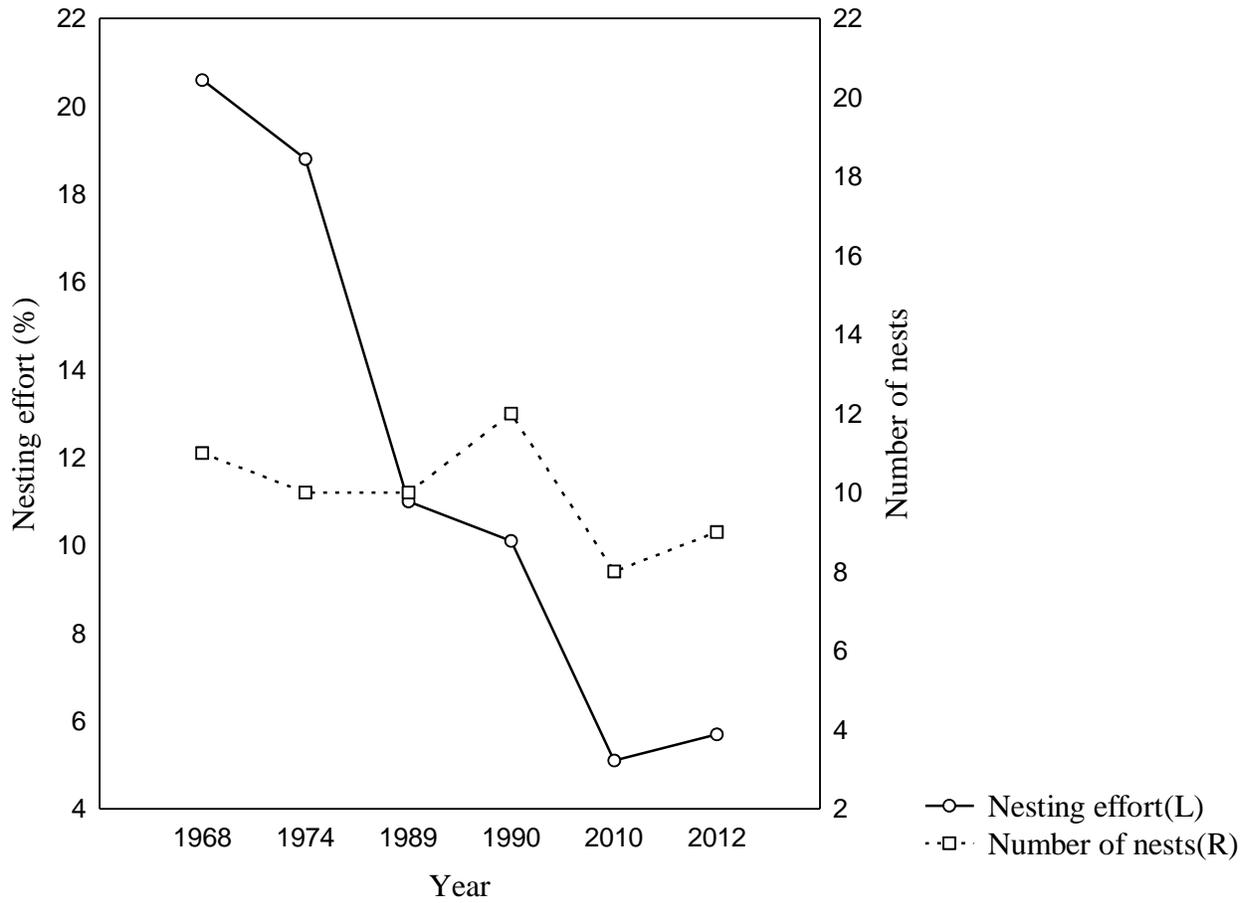


Figure 3. The relationship between the number of Nile Crocodile nests and the nesting effort in Ndumo Game Reserve from 1964-2012 (Data from Pooley 1969, EZKZNW records and current study).

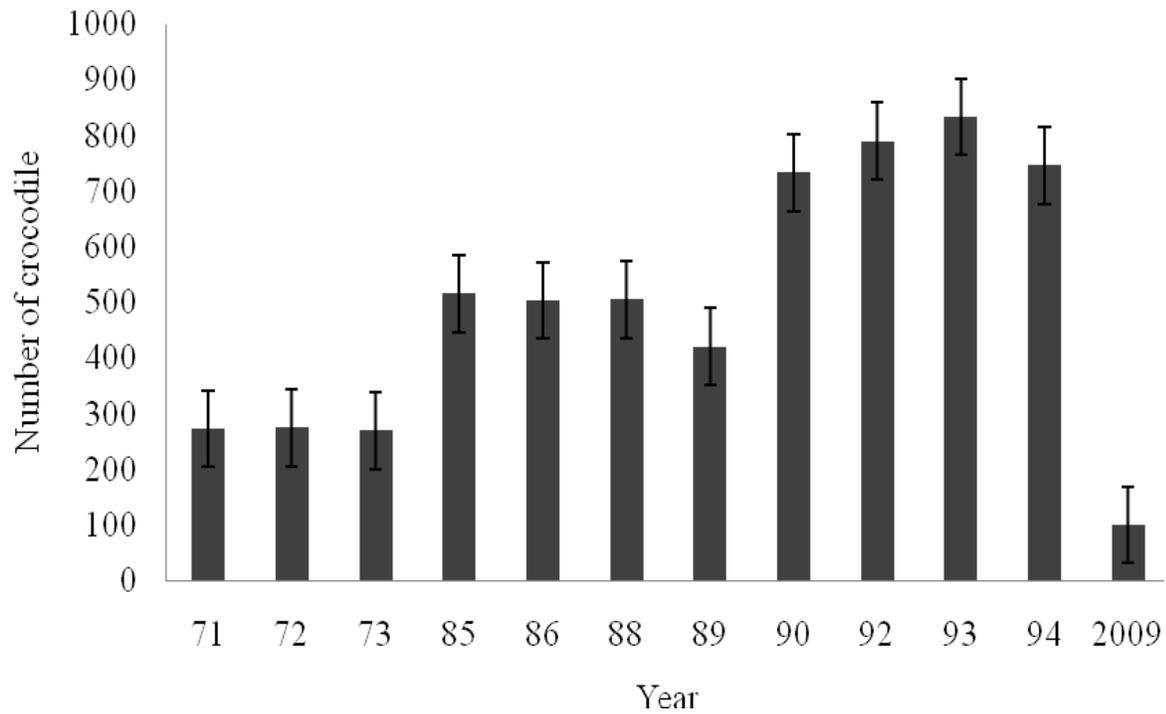


Figure 4. The changes in relative abundance of Nile Crocodiles at Ndumo Game Reserve from 1971-2009. The sudden increases and plateaus reached in the 1970's, 1980's and 1990's are attributed to the restocking program.

Table 1. The characteristics of active Nile Crocodile nesting sites found in Ndumo Game Reserve from 2009-2012.

Nest No.	Substrate	Distance to water (m)	Height above water (m)	Slope (Degrees)	Predated (Yes/No)	Flooded (Yes/No)
1	Finely sorted, silts, white sand	22	1.5	0.07	Y	Y
2	Finely sorted, silts, white sand	23	1.5	0.07	Y	Y
3	Finely sorted, silts, white sand	25	1.5	0.06	N	Y
4	Alluvial silt/clay, white sand	5.5	0.3	0.05	N	Y
5	Unknown	?	?	?	?	Y
6	Red granular sand, rocky soil	4	3	56	Y	N
7	Red granular sand, rocky soil	2.5	3	69	Y	N
8	Finely sorted, silts, white sand	4	1.5	0.38	Y	N
9	Finely sorted, silts, white sand	3.5	2	0.57	Y	N
10	Finely sorted, silts, white sand	5.5	1.2	0.22	N	N
11	Alluvial silt/clay, white sand	17	0.5	0.03	N	Y
12	Alluvial silt/clay, white sand	16.5	1	0.06	N	N
13	Alluvial silt/clay, white sand	11	1	0.09	Y	N

Table 2. The difference in nesting effort calculated for Nile Crocodiles using absolute abundance in summer compared to absolute abundance in winter.

Nesting season	2009/2010	2011/2012	2009/2010	2011/2012
	winter	winter	summer	summer
Population size (n)	846	846	211	211
Number of nests (x)	8	9	8	9
Fraction of mature crocodiles (a)	0.381	0.381	0.381	0.381
Fraction of mature females (f)	0.514	0.514	0.514	0.514
Nest effort (e)	0.047	0.0543	0.178	0.229

Chapter 6

Management Implications for the shared Ndumo Game Reserve and Rio Maputo Nile Crocodile Population

6.1 INTRODUCTION

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 (Chapter 1, Table 1.). 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, 2013; Combrink et al., 2013), Lake Sibaya (Combrink, 2004; Combrink et al. 2011); and Pongolapoort Dam in KwaZulu-Natal (Champion, 2011) as well as the current study in Ndumo Game Reserve (NGR). 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). The first step in achieving this is to conduct comprehensive population surveys and to estimate breeding and recruitment for the population in question (Combrink, 2004). In this chapter data collected from population surveys, capture activities, movement patterns, habitat use and nesting surveys are used to discuss the management requirements specific to the NGR Nile Crocodile population (Chapters 2-5).

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 NGR Nile Crocodile population drawn from the current study, existing literature, personal observations and the NGR Integrated Management Plan (IMP).

6.2 RECOMMENDATIONS

Recommendation # 1

Annual aerial surveys

It is suggested that annual aerial surveys be re-implemented. 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.

Recommendation # 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. Nesting surveys initiated in the 1960's 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 (Chapter 5). This will help predict future population changes of Nile Crocodiles within NGR.

Recommendation # 3

Protection of nesting sites

Nile Crocodile nesting sites located in annual nesting surveys in NGR need to be safeguarded from disturbances. 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 (Chapter 5). 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 (*Varanus niloticus*) to locate as the scent of the eggs permeates more easily in disturbed sites than if the eggs were left covered.

Recommendation # 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), 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).

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. Although proclaimed as a protected area in 1924, NGR continued to house members of the Mathenjwa and Tembe communities up until the early 1940's. These people were displaced under the pretence that they would be returned to the reserve once the Tsetse 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. These concerns are based on the following:

- NGR field rangers discovered three crocodile deaths due to snaring in 2009.
- 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.
- Cultivation of crops and harvesting of trees and reeds has been observed in the Phongola floodplain within Ndumo Game Reserve.

- Illegal and extensive fishing practices (gill netting) were observed in the Phongola floodplain within Ndumo Game Reserve.
- Snares have been frequently recovered from the Phongola floodplain within Ndumo Game Reserve.
- 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.
- 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.
- These factors together with the current political climate surrounding the reserve are reasons for concern for the reserve.

The implications of these anthropogenic effects for the NGR Nile Crocodile population are not good. 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

Recommendation # 5

Competition for food resources

Fish make up an estimated 98% of the diet of juvenile and sub-adult Nile Crocodiles (Games, 1990). 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 Pongola 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 Pongola 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.

Recommendation # 6

The illegal poaching of live animals

Snare 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. 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.

Recommendation # 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, 2009). 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 as 2008 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.

Recommendation # 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. Even at the comparably low density of approximately 270 Nile Crocodiles in the 1970's, 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 unsustainably low. The future of the NGR Nile Crocodile population therefore lies in Mozambique. 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:

- 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.

Recommendation # 9

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. 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.

6.4 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.

6.5 REFERENCES

- ASHTON, P. J. 2010. The demise of the Nile Crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in south africa: The case of the Olifants River. *Aquatic Conservation of Marine and Freshwater Ecosystems* 20:489–493.
- BOTHA, P. J. 2005. The ecology and population dynamics of the Nile Crocodile *Crocodylus niloticus* in the Flag Boshielo Dam, Mpumalanga Province, South Africa. MSc thesis. University of Pretoria, Pretoria.
- BOURQUIN, S. V. 2008. The population ecology of the Nile Crocodile (*Crocodylus niloticus*) in the panhandle region of the Okavango delta, Botswana. PhD thesis. University of Stellenbosch, Stellenbosch.
- CALVERLEY, P. 2009. Ndumo game reserve aerial and ground survey report october 2009. *In: Conservation Ecology of Nile Crocodiles (*Crocodylus niloticus*) in Ndumo Game Reserve*. P. C. T. Downs (ed.). School of Biological & Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg campus, Unpublished report.

- CHAMPION, G.2011. Conservation ecology of the Nile Crocodile (*Crocodylus niloticus*) in Pongolapoort Dam, north-eastern KwaZulu-Natal, South Africa. M.Sc. thesis, University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, A. S. 2004. Population status of *Crocodylus niloticus* (Nile Crocodile) at Lake Sibaya, Republic of South Africa. MSc thesis. University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X. 2013. Spatial and reproductive ecology and population dynamics of the Nile Crocodile (*Crocodylus niloticus*) in the St Lucia Estuarine system, South Africa. PhD thesis in prep., University of KwaZulu-Natal, Pietermaritzburg.
- COMBRINK, X., J. L. KORRÛBEL, KYLE, R., TAYLOR, R. AND R.PERRAN.2011. Evidence of a declining Nile Crocodile (*Crocodylus niloticus*) population at Lake Sibaya, South Africa. South African Journal of Wildlife Research 41:145-157.
- COMBRINK, X., AND R. TAYLOR. 2009. Nile Crocodile aerial survey at Lake Sibaya 26 July 2009. Ezemvelo KZN Wildlife. Unpublished Report.
- COMBRINK, X., WARNER, J. AND DOWNS, C. T. 2013. Crocodiles, p. 332 - 253. *In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. D. D. S. a. R. H. T. Renzo Perissinotto (ed.). Cambridge University Press, Cambridge.
- FERREIRA, S. M. AND D. PIENAAR. 2011. Degradation of the crocodile population in the Olifants River Gorge of Kruger National Park, South Africa. Aquatic Conservation: Marine and Freshwater Ecosystems 21:155-164.
- GAMES, I. 1990. The feeding ecology of two Nile crocodile populations in the Zambezi Valley. PhD thesis. University of Zimbabwe, Harare.

- LESLIE, A. J. 1997. The ecology and physiology of the Nile Crocodile, *Crocodylus niloticus*, in Lake St. Lucia, KwaZulu-Natal, South Africa. PhD thesis. Drexel University, Philadelphia.
- MATHEWS, W. S. 1994. Hippo and crocodile counts in the northern KwaZulu-Natal region. Unpublished report. Natal Parks Board, Pietermaritzburg.
- MCGREGOR, J. 2005. Crocodile crimes: People versus wildlife and the politics of postcolonial conservation on Lake Kariba, Zimbabwe. *Geoforum* 36:353–369.
- MEER, T. 2010. Finding the community in community-based natural resource management: The case of Ndumo Game Reserve, South Africa. Submitted in partial fulfilment of the requirements for the degree of Master of Arts. Dalhousie University, Halifax, Nova Scotia.
- OSTHOFF, G., A. HUGO, H. BOUWMAN, P. BUSS, D. GOVENDER, C. C. AND J. C. SWARTS. 2010. Comparison of the lipid properties of captive, healthy wild, and pancreatitis-affected wild Nile Crocodiles (*Crocodylus niloticus*). *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*. 155:64-69.
- POOLEY, A. C. 1969. Preliminary studies on the breeding of the Nile Crocodile, *Crocodylus niloticus*, in Zululand. *Lammergeyer* 10:22-24.
- POOLEY, A. C. 1982. The ecology of the Nile Crocodile, *Crocodylus niloticus*, in Zululand, South Africa. MSc thesis. University of Natal, Pietermaritzburg.
- ROSS, J. P. 1998. Crocodiles. Status survey and conservation action plan. 2nd Edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. 8:96.

- SWANEPOEL, D. J. G. 1999. Movements, nesting and the effects of pollution on the Nile Crocodile *Crocodylus niloticus* in the Olifants River, Kruger National Park. MSc thesis. University Natal, Pietermaritzburg.
- WALLACE, K. M., and LESLIE, A. J. 2008. Diet of the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42:361–368.
- WALLACE, K. M., LESLIE, A. J. AND T. COULSON. 2011. Living with predators: a focus on the issues of human–crocodile conflict within the lower Zambezi valley. *Wildlife Research* 38:747-755.
- WALLACE, K., LESLIE, A. J. AND T. COULSON. 2013. Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model. *Journal of Animal Ecology* 82:155-165.
- WARD, M. C. 1990. Crocodile Nest Survey-KwaZulu Ubombo/Ingwavuma District. Unpublished Report. Natal Parks Board.

CHAPTER 7

Conclusions

7.1 CONCLUSIONS

Ndumo Game Reserve (NGR) in north eastern KwaZulu-Natal (KZN) is home to the third largest Nile Crocodile (*Crocodylus niloticus*) population in South Africa (Mathews, 1994). This is largely due to a restocking program initiated in the late 1960's / early 1970's which saw the NGR population increase from 348 (± 3.39) in the 1970's to of 992 (± 58.70) in the 1990's and stabilise to 846 (± 263) in 2009. The relatively small (10 000 ha) reserve is able to support high densities of crocodiles due to habitat complementation with neighbouring Mozambique. The majority of the NGR population leave the reserve for Mozambique in early November and enter the Rio Maputo floodplain, only returning as water levels start to dissipate in early April. This movement is thought to be in response to high concentrations of fish species in the Rio Maputo during the summer. NGR provides protection from anthropogenic disturbances during periods of low water levels when accessibility to Nile Crocodile habitat increases outside of the reserve. The degree of connectivity and the quality of the Rio Maputo as a corridor connecting these two important habitat patches is vital in sustaining the current shared population. The obstruction of any one of these two services would have a negative impact on the Nile Crocodile population. The current unchecked anthropogenic disturbance taking place within NGR is therefore of grave concern (Chapters 2-6).

The large population increase brought about by the restocking program has not translated into an increase in the amount of nesting taking place in the reserve (Chapter 5) because the

majority of the NGR Nile Crocodile population move out of the reserve and into Mozambique over the nesting period. Nesting effort in NGR is low but comparable to other populations of Nile Crocodiles in southern Africa and would be able to sustain a population size of around 200 crocodiles. The future of the shared NGR – Rio Maputo crocodiles therefore lies chiefly on the nesting effort and recruitment in un-protected areas of the Rio Maputo floodplain and the destruction of riverine habitat in and around historical nesting sites within the reserve is of grave concern (Chapter 5) raising serious concerns as to the sustainability of the NGR Nile Crocodile population. These findings highlight the importance of an investigation into the nesting ecology of Nile Crocodiles in the Rio Maputo.

The distribution of Nile Crocodiles within NGR is influenced by landscape physiognomy and composition, as well as connectivity and corridor quality in relation to environmental resources and conditions (Chapters 2 - 6). Generally, pans that hold water throughout winter such as Lake Nyamithi and Banzi Pan have the highest density of crocodiles which increases as water levels and temperatures drop from April through October. Studies conducted at Lake Nyamithi suggest that NGR forms a valuable winter refuge for Nile Crocodiles due to the large permanent bodies of water held within the reserve as well as undisturbed basking habitat. However, larger Nile Crocodiles are not confined to areas such as Nyamithi during winter and range widely throughout the floodplain making use of riverine and lacustrine habitat. As such adult Nile Crocodiles had larger more expansive home ranges than sub-adults who remained within the pans/lakes throughout winter. Areas that were exposed to disturbance such as the Usuthu River and the new course of the Phongola River are generally avoided, even by adult Nile Crocodiles. Anthropogenic disturbances therefore influenced the functionality of the floodplain landscape negatively with impacts on habitat use and connectivity (Chapter 2).

Demographic information collected through capture exercises revealed that the NGR Nile Crocodile population structure is skewed with juveniles forming the lowest percentage at only 13 % while sub-adults and adults account for 39 % and 48 % of the population respectively. The age structure is indicative of a declining population and emphasizes the poor recruitment in NGR (Chapter 5). The current stable population of around 850 is expected to gradually decline as insufficient recruitment is occurring within the reserve to sustain the artificially high numbers. However, anthropogenic disturbance and habitat destruction taking place within NGR, particularly at historical nesting sites, along with snaring activities will accelerate the population decline at an unnatural speed and to an unnatural extent. In order to estimate the extent to which the NGR population will naturally decrease it will be necessary to conduct an investigation into the nesting activities taking place in Mozambique. To secure this population, NGR would need to protect riverine habitat within the reserve from anthropogenic disturbance, particularly at nesting sites. As mentioned earlier (Chapters 2 - 6), movement between habitat patches is also determined by the landscape through which an animal must travel (Tischendorf and Fahrig, 2000), and the extent to which a landscape promotes or encumbers movement between resource patches i.e. the landscape connectivity is also of importance (Taylor, 1993; Hodgson et al., 2011). In particular this is of importance to the Nile Crocodiles in NGR as although protected here they appear to move into neighboring Mozambique at certain periods of the year for nesting and so the population viability is vulnerable. Furthermore, Nile Crocodiles are important top predators and also indicators of ecosystem health within a variety of aquatic habitats and consequently regarded as a good flagship species (Ashton, 2010). With increased pressure on and pollution of South Africa's water systems (Ashton, 2010), continued monitoring of Nile Crocodiles in NGR is essential.

7.2 REFERENCES

- ASHTON, P. J. 2010. The demise of the Nile Crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in South Africa: The case of the Olifants River. *Aquatic Conservation of Marine and Freshwater Ecosystems* 20:489–493.
- HODGSON, J. A., A. MOILANEN, B. A. WINTLE, B.A. AND C. D. THOMAS 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology* 48:148-152.
- MATHEWS, W. S. 1994. Hippo and crocodile counts in the northern KwaZulu-Natal region. Unpublished report. Natal Parks Board, Pietermaritzburg.
- TAYLOR, P. D., FAHRIG, L., HENEIN, K. AND G. MERRIAM. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571-573.
- TISCHENDORF, L., and L. FAHRIG. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90:7-19.