Aspects of Nile crocodile (*Crocodylus niloticus*) population ecology and behaviour in Pongolapoort Dam, KwaZulu-Natal

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INYUVESI YAKWAZULU-NATALI

ABSTRACT

Pongolapoort Dam is one of the largest dams in South Africa by volume. It is also home to a breeding population of Nile crocodiles (*Crocodylus niloticus*). Crocodiles are keystone species which play an important ecological role in their aquatic habitats but are under threat globally. Consequently the aims of this project were to investigate the population number, nesting ecology, and behavioural aspects of gaping in Nile crocodiles at Pongolapoort Dam. Data were captured from July 2014 to August 2015, where there was a marked decrease in water levels in Pongolapoort Dam due to a drought occurring throughout KwaZulu-Natal. An estimated 549 Nile crocodiles occurred in Pongolapoort Dam in 2015, an increase in population from a conservative estimate of 273 individuals in 2010. The majority (80%) of the Nile crocodile population occurred in the inlet section of the dam, and with dropping water levels, the crocodiles congregated in large numbers in the Croc Bay region of the inlet. The population structure changed from 2010 when the majority occurred in the juvenile class to the majority of the crocodiles occurring in the sub-adult and adult size class in 2014/2015.

The reproductive output of a population can be an indicator of population health. Consequently nesting ecology of Nile crocodiles was investigated at Pongolapoort Dam for the 2014/2015 nesting season. A total of 38 Nile crocodile nests were found over four nesting sites in the river section of Pongolapoort Dam. Nest effort decreased from 73% in 2009/2010 to 43% in 2014/2015, with a density of 4.9 nests per kilometre in the river section. All nests were found in alluvial deposits where *Phragmites australis* was the dominant vegetation. Some nests were predated by water monitors (*Varanus niloticus*); however, two nurseries were found containing hatchlings, while many nests showed signs of being dug up by the nesting females. The N2 Bend and Buffalo Bend floodplain were the most important nesting grounds, and this was attributed to the presence of suitable nesting conditions.

Gaping behaviour in Nile crocodiles has received little attention as there are conflicting ideas as to why gaping occurs. The majority of literature suggests that gaping is a thermoregulatory response aimed at cooling the head of the crocodile. We aimed to identify other possible behaviours associated with gaping, at a basking bank in Pongolapoort Dam during winter. Preliminary results suggest that gaping may be a communicative or behavioural posture brought on by the following factors; position of the crocodile relative to the water, total length of the crocodile, time of gape, degree of gape, nearest neighbouring crocodile and number of neighbouring crocodiles. Further research is needed to help understand this behaviour of Nile crocodiles and its importance in their ecology and behaviour.

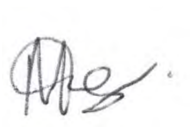
The study showed that the population of Nile crocodiles in Pongolapoort Dam is increasing and remains in a healthy state compared with other population in South Africa. Insights into their behaviour may be applicable to other crocodilian taxa.

Keywords: Nile crocodile, population estimate, nesting, gaping, Pongolapoort Dam.

PREFACE

The data described in this thesis were collected at Pongolapoort Dam, Republic of South Africa, from July 2014 to August 2015. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Science and Engineering, University of KwaZulu-Natal, Pietermaritzburg campus, represents original work by the author and 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.



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Mark K. Summers

December 2015

I certify that the above statement is correct and as the candidate's supervisor I have approved this thesis for submission.

………………………….

Professor Colleen T. Downs

Supervisor

December 2015

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DECLARATION 1 - PLAGIARISM

I, Mark Kai Summers, 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.

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DECLARATION 2 – PUBLICATIONS

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

Publication 1

M Summers & CT Downs

Population size, structure and habitat use of Nile crocodiles in Pongolapoort Dam, South Africa

Author contributions:

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

Publication 2

M Summers & CT Downs

Nest abundance, distribution and site selection of Nile crocodiles at Pongolapoort Dam, South Africa

Author contributions:

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

Publication 3

M Summers & CT Downs

A preliminary study of gaping in Nile crocodiles at Pongolapoort Dam, South Africa

Author contributions:

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

Signed: ………………………………………………

Mark Kai Summers

December 2015

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CHAPTER 1

Introduction

The distribution of ectotherms may be limited by the influence of the thermal environment on the species energy requirements (Bozinovic 1989), therefore their options for activity are far more limited than those of endothermic animals (Vitt 2009). As a result, their distribution may be limited to areas which suit their energy requirements, as their physiological functions such as growth, locomotion and reproduction are influenced by environmental temperature (Deutsch et al. 2008). Reptiles are considered ectothermic, and due to their environmental thermal limit, their distribution tends to be clumped between the tropics. Crocodilians are reptiles which belong to the great group called archosaurs (ruling reptiles), which also included extinct thecodonts (Bellairs 1987). Crocodilians of today all belong to the clade Eusuchia, which comprises of 27 species and sub-species, all belonging to a single family called the Crocodylidae. This family is sub-divided into three sub-families, the Alligatorninae (*Alligator, Caiman, Paleosuchus, Melanosuchus*), the Gavialinae (*Gavials, Tomistoma*) and Crocodylinae (*Crocodylus*, *Osteolaemus*,Taplin 1984, Bellairs 1987). Of the Crocodylidae sub-family, the genus *Crocodylus, Mecistops and Osteolaemus* are the only Crocodylidae found in Africa. Crocodiles were once widespread throughout Africa and this is due to their ability to adapt to their environment through their superior morphology, which allowed them to colonize many fresh water (and brackish water) habitats.

Crocodiles are widespread throughout Sub-Saharan Africa, but are absent from the southern and south-western parts of Africa (Leslie and Spotila 2001). There are four species of crocodiles in Africa, the African dwarf crocodile (*Osteolaemus tetraspis*), the African slender-snouted crocodile (*Mecistops cataphractus*), the West African crocodile (*Crocodylus suchus*) and the Nile crocodile (*Crocodylus niloticus*). The most common and widespread of the African crocodile species are the Nile crocodiles, which are found in forty two countries, including Madagascar (Ross 1998, Calverley 2013). Crocodiles are keystone species which play an important ecological role in their aquatic habitats (Ross 1998, Leslie and Spotila 2001, Champion 2011). Crocodiles are top of the food chain predators and they maintain ecosystem structure and function as they impact lower trophic levels and recycle nutrients (Ross 1998, Leslie and Spotila 2001, Champion 2011). Rivers, lakes, wetlands, estuaries, swamps and impoundment structures (such as dams) are inhabited by crocodiles.

Due to heavy exploitation throughout Africa in the 1950's and 1960's (Cott and Pooley 1971, Watson et al. 1971, Leslie and Spotila 2001), many populations of Nile crocodiles were reduced to low numbers. Of the 42 countries where Nile crocodiles occur, less than half have a defined population status; of these only 10% of countries have a population which is not depleted, 60% have a somewhat depleted population and 30% of these countries have a severely depleted population (Ross 1998, Botha 2005, Calverley 2013). Causes of the decline in Nile crocodile distribution include habitat degradation, desertification and anthropogenic persecution (Leslie 1997, Champion 2011, Combrink et al. 2011). Since the 1930s the main driving factors for the decline in Nile crocodile populations were the skin trade, "vermin control," development of agricultural land and human population increases throughout Africa (Cott and Pooley 1971, Gans and Pooley 1976, Pooley 1982, Jacobsen 1984, Blake and Jacobsen 1992, Leslie 1997, Combrink 2004, Botha 2005, Bourquin 2008, Champion 2011). Cott and Pooley (1971) reviewed the status of the Nile crocodiles in Africa, which resulted in the Nile crocodile being listed under Appendix I of CITES (Convention of International Trade in Endangered Species of wild fauna and flora) in 1973 (Leslie 1997). In 1996 in South Africa, the Nile crocodile transferred from Appendix I to Appendix II of Cites, pursuant of Resolution Conf. 3.15 (ranching criteria), which placed Nile crocodiles on the threatened list (Leslie and Spotila 2001). This allowed permits to be issued for commercial ranching and regulated trade in Nile crocodile products (Leslie 1997, Ross 1998, Champion 2011).

Nile crocodiles in South Africa

Nile crocodiles are limited to the northern and eastern parts of South Africa (Pooley 1982). Nile crocodiles were hunted to extinction by the early settlers in the Cape (Cott and Pooley 1971). Climatic conditions were considered unsuitable for Nile crocodiles in the Cape provinces and the species never occurred plentifully, the last known specimen was shot in 1903 in the Elliotdale District (Cott and Pooley 1971). However, in 1977 six juvenile crocodiles were introduced into the Kolobe River in the Dwesa-Cwebe Nature reserve (Feely 2010, Combrink et al. 2011), and are still present (Venter, pers. comm.).

In the region north of the Vaal river (formerly known as the Transvaal), the Nile crocodiles are protected in nature reserves and wildlife sanctuaries. Hunting occurred extensively along the major rivers in the Transvaal, and within Kruger National Park during the early days of its existence; crocodiles were shot at every opportunity as it was thought that "controlling" the crocodiles was good for predator-prey relationships. This demise of the population occurred particularly in the period from 1933 to 1960. However, many of the rivers flow into Mozambique, where they may not receive the same protection as in South Africa. Factors reducing Nile crocodile numbers north of the Vaal River through habitat destruction have been extensive irrigation schemes, industrial use of water and dams (Cott and Pooley 1971).

Formerly the Nile crocodile occurred along the length of the KwaZulu-Natal (KZN) coastline, from the Umtamvuna River to Kosi Bay (Cott and Pooley 1971). However due to extermination, the species is rarely found south of the Tugela River (Nile crocodiles exist in the Umngeni River due to escape from a local crocodile farmer (pers. obs.)). A variety of anthropogenic disturbances reduced the numbers of Nile crocodiles in KZN such as commercial and indiscriminate hunting on the borders of game reserves and unprotected areas; and, poaching by indigenous people for medicinal purposes and defence of livestock (Cott and Pooley 1971). In Cott and Pooley (1971) on the status of crocodiles in Africa, they noted that there were fewer than 800 individuals in the whole of KZN. In 2011 the crocodile population was numbered around 900 individuals in Lake St. Lucia alone (Van Vuuren 2011). Twenty three years ago the South African crocodile population was estimated at 9500 non-hatchling individuals (Blake and Jacobsen 1992). Although there are no recent population estimates of Nile crocodiles in the whole of South Africa, preliminary evidence suggests that the number of crocodiles and their populations are decreasing (Marais 1991, Combrink 2004, Myburg 2007, 2009, Ashton 2010, Botha et al. 2011, Calverley 2011, Combrink et al. 2011, Ferreira and Pienaar 2011).

South Africa is home to three secure large populations of Nile crocodile which are in Kruger National Park (seven major rivers are home to crocodiles), Ndumo Game Reserve and Lake St. Lucia. There are several smaller fragmented populations of wild crocodiles in South Africa which persist in the Black- and White Mfolozi Rivers, Pongolapoort Dam, Flag Boshielo Dam, Limpopo River, dams and rivers of Mpumalanga, Limpopo and KZN (Combrink et al. 2011). Kruger National Park has the largest population of Nile crocodiles in South Africa, however, an outbreak of pansteatitis resulted in 208 individuals dying in one and a half years (Osthoff et al. 2010, Calverley 2013, Lane et al. 2013). A combination of factors aligning at the same time seems to have caused the pansteatitis outbreak. The most likely cause of the pansteatitis was industrial and agricultural development and pollution of the Olifants River upstream of Kruger National Park (Ashton 2010, Ferreira and Pienaar 2011), and the completion of Massingir Dam, just outside Kruger National Park in Mozambique. Massingir

Dam formed a sediment trap in the Olifants Gorge, and seasonal upstream spawning of phytoplankton feeding silver carp (*Hypophthalmichthys molitrix*) into the Olifants Gorge provided food for sharptooth catfish (*Clarius gariepinus*) and Nile crocodiles, which are likely to have started the pansteatitis outbreak (Huchzermeyer et al. 2013). Pansteatitis also affected Loskop Dam (on the Olifants river), where the crocodile population declined from 25 individuals in 2007 to just 4 individuals in 2011 (Botha et al. 2011, Woodborne et al. 2012). Lake St. Lucia, which is home to the second largest population of crocodiles in South Africa, has faced ongoing changes in salinity levels due to drought, which has been exacerbated by the divergence of freshwater out of the system for agricultural purposes, resulting in a crocodile population decline (Pooley 1982, Leslie 1997, Whitfield and Taylor 2009). The Lake Sibaya Nile crocodile population has decreased from over 100 individuals in 1990 to seven in 2009 (Combrink et al. 2011). Flag Boshielo's Nile crocodile population has declined from 135 individuals in 2005 to just 98 in 2009 (Ashton 2010). All three of the main crocodile populations in South Africa are threatened (Combrink 2004, Steyn 2008, Champion 2011), and smaller populations are declining, which highlights the need for comprehensive surveys to update the status of Nile crocodiles and to create a conservation strategy for the species (Combrink et al. 2011).

Freshwater problem in South Africa

The quality of South Africa's river systems has progressively worsened due to increasing urbanisation, industrialisation and pollution (Ashton 2010). South Africa is a semi-arid, water poor country, so freshwater is a limited and is a sought after resource (Steyn 2008, Champion 2011). The expanding human population puts pressure on freshwater systems in a social, industrial and agricultural aspect which results in a decrease in the area of conserved freshwater systems, as well as a decline in the associated aquatic life (Steyn 2008, Ashton 2010, Champion 2011). The increase demand for water by humans has resulted in a reduction in the availability of water, and the water that is available to humans is becoming progressively degraded (Kingsford et al. 2011). Causes of freshwater habitat degradation is river altercation (through changing traditional river courses), regulation of water levels, water extraction, pollution, the introduction of alien plant species and untreated human effluent (Kingsford et al. 2011). The alterations of South Africa's river systems through the building of canals, dams and irrigation schemes has resulted in major changes in the hydrological systems, where the changes include the decrease in river flow rate and perennial rivers only flowing sporadically (Zhai 2010). The infiltration of pollutants into altered water ways puts further strain on the aquatic biota as the concentration of contaminants builds up (Nel 2009). The pansteatitis outbreak on the Olifants River is an example of how pollution can cause mass ecological die-offs. Pansteatitis is an inflammatory reaction that co-occurs with fat cell necrosis that can cause death in a wide range of species (Woodborne et al. 2012).

As previously mentioned, pansteatitis has caused the Loskop Dam population of Nile crocodiles to decline to only a few individuals (Ashton 2010, Botha et al. 2011, Woodborne et al. 2012), but mass mortalities of crocodiles due to pansteatitis has also occurred downstream of Loskop Dam, in the Olifants River Gorge in Kruger National Park, and Lake Massingir, Mozambique (Osthoff et al. 2010, Ferreira and Pienaar 2011). Pansteatitis affects fat depots and renders the animal stiff and lethargic and unable to hunt. The crocodile then dies through starvation or drowning (Woodborne et al. 2012). In the Olifants River system, pansteatitis has also been identified in sharptooth catfish and Mozambique tilapia (*Oreochromis mossambicus,* Woodborne et al. 2012). The cause of pansteatitis in the Olifants River Gorge was because of the back-flooding of Lake Massingir, which caused a shift of the Olifants River from a rock and sand substrate river to a clay substrate lake. Woodborne et al. (2012) discovered that isotopic analysis of sharptooth catfish caused the species to shift from a vegetarian diet to that of a piscivorous diet, which was highly correlated with pansteatitis prevalence, which coincidently caused crocodiles and tiger fish (*Hydrocynus vittanus*) to increase in the trophic level. The ecosystem change caused a shift in the structure of the food web and an exotic or pioneer fish species was the vector of pansteatitis, which invaded the confluence of the river. They concluded that the damming of the river caused an unintentional ecological consequence of the pansteatitis epidemic (Woodborne et al. 2012).

Another example of how a natural waterway has been negatively altered by humans is that of the St. Lucia Estuary. The diversion of the Mfolozi River as well as the abstraction of water from the Mkuze and Hluhluwe rivers for agricultural purposes, resulted in a change in the hydrological processes within the Lake (Whitfield and Taylor 2009, Champion 2011, Combrink et al. 2013). The changes in the hydrological processes caused a local extinction of the African skimmer (*Rynchops flavirostris*) and has had many negative effects on the local biota (Whitfield and Taylor 2009). Lake St. Lucia has the second largest population of Nile crocodiles in South Africa, which seems to be suffering from the high salinity levels accentuated by years of drought. Freshwater should reduce salinity of the system, but the reduced inflow of freshwater has caused high salinity levels in the estuary. The absence of the historical mullet run has put further stress on the crocodiles in the lake, one of the reasons why crocodiles have apparently declined in population numbers and have reduced nesting effort (Champion 2011, Combrink et al. 2013). The reduced nesting effort may be due to reduced health of the crocodiles and favourable nesting areas becoming distant from water due to low water levels of the lake (Champion 2011, Combrink et al. 2013).

Alien invasive plants also play a role in threatening our water ways and its associated biota. Invasive species are thought to be one of the major causes of biodiversity loss worldwide (Czech and Krausman 1997). Invasive plants tend to choke waterways and reduce sunlight at a ground level. Crocodiles have temperature-dependant sex-determination (Hutton 1987, Leslie 1997), and in St. Lucia, crocodiles tend to choose open, sunny and sandy nesting sites to deposit their eggs (Leslie 1997, Leslie and Spotila 2001). The alien plant *Chromolaena odorata* is a major problem in KwaZulu-Natal and blocks many waterways, plantations and natural vegetation, and has also affected the banks of Lake St. Lucia. Leslie and Spotila (2001) found that soil temperatures of nesting sites covered with *C. odorata* were 5 – 6°C cooler (25 cm depth) than sunny nesting sites at the same depth. The nests under *C. odorata* thickets were well below the pivotal temperature (where a 1:1 sex ratio is achieved), which most likely produced a female biased sex ratio, or may have prevented embryo development altogether (Leslie and Spotila 2001).

All the above mentioned issues and facts show that Nile crocodiles are under threat, and with their population decreasing all over South Africa, quick management and conservation needs to be done to address the issues. Studying smaller populations of Nile crocodiles allows us to find out whether these populations are viable, so that conservationists do not need to rely solely on a few large populations as a buffer for the species. Also, gaining an understanding of their physiological functioning and basking behaviour may limit the chances of human-crocodile conflicts.

Basking behaviour and mouth-gaping

The distribution of ectotherms may be limited by the influence of the thermal environment on the species energy requirements (Bozinovic 1989), therefore their options for activity are far more limited than those of endothermic animals (Vitt 2009). As a result, their distribution may be limited to areas which suit their energy requirements, as their physiological functions such as growth, locomotion and reproduction are influenced by environmental temperature (Deutsch et al. 2008). Ectotherm physiology is largely controlled by the thermal environment. A better understanding of the effect of temperature on physiology can improve our knowledge of ectotherm metabolic and physical function. Most ectotherms rely on environmental heat sources in the form of direct solar radiation, reflection, conduction, convection and thermal radiation to control body temperature (Gvoždík 2001). These affect ectotherm performance, metabolic expenses and fitness (Gvoždík 2001). The influence of temperature on metabolism is variable among different ectotherm species, and this variation in metabolism may be attributed to the level of activity of the individual (Wilder 1937, Vernberg 1952). Conversely, an ectotherm's level of activity (and behaviour) may be influenced by their metabolism, which may be affected by temperature, gender and inert seasonal variations. Physiology and behaviour work hand in hand to maintain body temperature (T_b), which has a profound effect on the ecology of ectotherms (Huey and Stevenson 1979); and in crocodilians, thermoregulation is affected by habitat selection and behavioural adaptations (Cott 1975, Downs et al. 2008).

To maintain a stable T_b, semi-aquatic ectotherms such as crocodiles thermoregulate by basking in the sun and shuttling between land and water (Seebacher et al. 1999, Downs et al. 2008). Other behavioural mechanisms used to modifying body temperature include postural changes and eye bulging (Bogert 1959, Heath 1970). The frequency and occurrence of basking behaviour seem to change with latitude and environmental temperature (Downs et al. 2008). Mass also affects basking frequency. Grigg et al. (1998) showed empirically that smaller massed crocodiles (*Crocodylus porosus*) would need to thermoregulate at a higher frequency than larger massed individuals, as increasing body mass would increase the stability of T_b, and larger massed individuals would have a warmer T_b than smaller massed individuals. This phenomenon was later confirmed mechanistically by Seebacher et al. (1999).

Gaping is present in most reptilian orders (there is no data on Sphenodonta); however, only in Lacertilia (Squamata) and Crocodilia is there a thermoregulatory function related to gaping (Crawford and Kampe 1971, Jacobson and Whitford 1971, Moll and Legler 1971b, Heatwole et al. 1973, Firth and Heatwole 1976, Crawford et al. 1977, Spotila et al. 1977, Tattersall et al. 2006). The function of gaping is to increase evaporative cooling of the head, which is a behavioural response to a physiological problem. This works by increasing the surface area for evaporation by cooling the buccal cavity and upper airways during respiration (Tattersall et al. 2006). Spotila et al. (1977), showed that gaping was a useful mechanism for cooling the head region of *Alligator mississipiensis*; however, in Johnson et al. (1978) study on *A. mississipiensis,* gaping had little effect on reducing head temperature. There are also conflicting views regarding Nile crocodiles where some studies have shown that gaping is effective in cooling Nile crocodiles down (Cott 1961, Cloudsley-Thompson 1969, Loveridge 1984), while other studies show that gaping is ineffective in cooling individuals (Diefenbach 1975). There may be other behavioural functions as to why Nile crocodiles gape. For example, in winter, basking Nile crocodiles in Zimbabwe showed gaping behaviour as a threat display towards other animals such as hippopotamus and crocodiles (Kofron 1993), and nesting females have also been shown to gape as a threat display towards water monitors (Combrink 2015). However, none of these behaviours can explain why crocodiles gape at night or in early morning (Cott 1961, Loveridge 1984, Kofron 1993).

The problem

Considered as keystone species in aquatic environments, the Nile crocodile population in southern Africa has seen a marked rise in numbers since their near demise in the 1960's due to over-exploitation and uncontrolled hunting (Cott and Pooley 1971, Gans and Pooley 1976, Gans 1989, Blake and Jacobson 1992, Combrink 2004), yet they are still classified as threatened according to the International Union for the Conservation of Nature (IUCN) Red list (IUCN 2009). The population of Nile crocodiles in South Africa now faces new threats that could once again lead to a drastic decrease in their numbers, such as pollution and habitat degradation (Bourquin 2008, Combrink et al. 2011). Generally, Nile crocodile populations are found, but not exclusively, in large bodies of water (Bishop et al. 2008). Classified as a as semi-arid, water poor country, South Africa has seen an increase in the number of impoundment structures (Roux et al. 2008), created to meet the demands of the ever increasing anthropogenic requirements for fresh water (Jacobson and Klenhans 1993). Impoundment structures have associated negative effects such as influencing water flow downstream, disruption of hydrological processes, effect water quality, river geomorphology and ecology, as well as ecosystem services (Heath and Plater 2010b). However, despite this loss of riverine habitat through higher dam levels and invasive alien vegetation growth, there is a necessity to correctly manage the existing impoundments to conserve the freshwater species now threatened as a result of degradation of this habitat. An example of the potential negative and positive effects of an impoundment on a riverine system in terms of conservation is Pongolapoort Dam, KZN, South Africa.

The construction of Pongolapoort Dam has disturbed the natural function of the lower Phongola River flood plain, threatening a number of aquatic species found there (Mwaka et al. 2003). It has however, also created a new stable fresh water habitat and sanctuary for a number of species, including common hippopotamus (*Hippopotamus amphibious*), Nile crocodile and tiger fish, all of which are listed on the IUCN red list of threatened species (Combrink et al. 2010). Although these species do occur downstream of the Dam, those populations are currently at great risk as a result of over exploitation, poaching and habitat destruction (Champion 2011, Calverley 2013), especially Nile crocodiles. Hence, it is necessary to continue to monitor and study the population demographics of the Nile crocodile in the Pongolapoort Dam ecosystem.

There is much uncertainty as to why Nile crocodiles actually gape. Work has been done on the effect of temperature and thermoregulation on gaping (Cott 1961, Cloudsley-Thompson 1969, Diefenbach 1975, Loveridge 1984, Kofron 1993); however, conflicting results cause uncertainty around thermoregulation as an indicator of gaping behaviour. It is necessary to confirm why Nile crocodiles gape as we will then know if it is a threat display, whether they are sensing their environment through chemoreception or whether it is a behavioural response involved with thermoregulation.

The aims of this study were to:

1) determine total population size and structure of the Nile crocodiles in Pongolapoort Dam and compare these findings with the previous population estimates of 1981, 1989 and 2011
2) determine the number and distribution of nesting sites and reproductive potential of female Nile crocodiles in Pongolapoort Dam.
3) determine, through a preliminary study, if there are behavioural or communicative factors associated with gaping in Nile crocodiles at Pongolapoort Dam.

To achieve these aims, the study was separated into three research chapters. Chapter 2 focused on population estimates, size classes and distribution of Nile crocodile in Pongolapoort Dam in 2014-2015. Chapter 3 focused on the nesting ecology and abundance of Nile crocodile nest sites in Pongolapoort Dam. Chapter 4 is a preliminary study into behaviour associated with gaping in Nile crocodiles in Pongolapoort Dam. Chapter 1 and Chapter 5 are the introduction and conclusion chapters respectively. Repetition is unavoidable because of each chapter being prepared as a stand-alone manuscript.

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CHAPTER 2

Population size, structure and habitat use of Nile crocodiles in Pongolapoort Dam, South Africa

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2.1. ABSTRACT

Nile crocodile (*Crocodylus niloticus*) populations in South Africa are in decline because of increased pressure from a combination of anthropogenic sources. Surveying Nile crocodile populations and their size structures allows estimates of how populations are changing over time and is important for managing these populations. The population of Nile crocodiles in Pongolapoort Dam, KwaZulu-Natal was estimated using aerial, spotlight and diurnal surveys. It was predicted that the population of Nile crocodiles has increased in size from 2010, when a previous survey was undertaken, and the population structure had remained the same. The number of Nile crocodiles had increased by 101.1% to 549 crocodiles, with 80.7 % of them being found in the inlet section of Pongolapoort Dam. Most were sub-adults and adults, which suggests that the high juvenile ratio found in 2010 has grown into the sub-adult size class. A total corrected estimate was seen as a better estimate of population size than a density estimate, as the non-linear nature of the dam formed basking aggregations. The only environmental factor that negatively affected the number of crocodiles seen was cloud cover. Aerial surveys were the most effective surveying method with spotlight surveys being the least effective surveying method. The high numbers of crocodiles seen in the inlet could be attributed to low water conditions in a drought period while the lack of crocodiles seen in the main dam is as a result of a combination of factors. This Nile crocodile population continues to increase in size and should be considered a conservation priority.

Keywords: Survey, aerial, spotlight, diurnal, population, size class, Pongolapoort Dam, Nile crocodile

2.2. INTRODUCTION

Crocodilians are seen as indicators of ecosystem health (Mazzotti et al. 2009, Lane et al. 2013, Combrink 2015), but as a result of their longevity and apex predator status, they are susceptible to accumulation of anthropogenic contaminants (Rainwater et al. 2007, Guillette and Edwards 2008, Combrink 2015). Nile crocodiles (*Crocodylus niloticus*) are considered a keystone species as they maintain the structure and function of an ecosystem through predation of species and nutrient recycling (Craighead 1969, King and Burke 1989, Botha 2005). Widespread eradication of Nile crocodiles occurred from the 1930s and continued into the 1960s throughout Africa, as they were considered vermin due to the threat they posed on humans and livestock (Cott 1961, Pooley 1982, Bourquin and Leslie 2012). The trade for crocodile skins, meat "vermin" control, habitat loss and pollution have all contributed to the decline of Nile crocodiles in Africa (Cott 1961, Thorbjarnarson et al. 1992, Bourquin and Leslie 2012).

Nile crocodiles were widespread throughout the waterbodies of northern and eastern South Africa, as far south as the Eastern Cape (Pooley 1982), but are now restricted to Limpopo, Mpumalanga and KwaZulu-Natal (KZN, Combrink 2015). Major populations occur in Kruger National Park, on the Olifants and Letaba Rivers (Ferreira and Pienaar 2011), Lake St. Lucia (Combrink 2015) and Ndumo Game Reserve (Calverley and Downs 2014). Pongolapoort Dam was recently considered to have a growing viable population of Nile crocodiles (Champion 2011), while Flag Boshielo Dam had a relatively low, but stable population (Botha 2005), whereas Loskop Dam had a very low population that was in decline (Botha et al. 2011).

The construction of Pongolapoort Dam, KZN, has disturbed the natural function of the lower Phongola River flood plain, threatening a number of aquatic species found there (Mwaka 2003). It has however, also created a new stable habitat for a number for a number of aquatic species, including hippopotamus (*Hippopotamus amphibious*) and Nile crocodile (Champion 2011). In order to successfully manage a population, the size and structure should be monitored regularly (Chabreck 1966, Games et al. 1992, Champion 2011). Population trends can then be used to make timeous management decisions (Stirrat et al. 2001, Calverley 2013). There is limited population data for Nile crocodiles in Pongolapoort Dam, where counts were conducted in 1981, 1989 (Jacobsen 1991) and 2009/2010 (Champion 2011). Considering that most populations of Nile crocodiles are under threat in South Africa, it is necessary to continue to monitor and study the Pongolapoort Dam population.

Consequently the aim of this study was to determine the population number and structure of Nile crocodiles, and to find out which habitat areas they utilize in Pongolapoort Dam. Our objectives were to use aerial surveys and diurnal and nocturnal boat surveys to estimate the population number, and determine the population structure in Pongolapoort Dam. We predicted that the population had increased in size and that the population structure would be similar to that presented in Champion (2011). Most of the crocodiles were expected to be concentrated in the inlet section of Pongolapoort Dam as previously documented by Champion (2011).

2.3. METHODS

2.3.1. Study area

Pongolapoort Dam is situated in northern KZN and on the southern border of Swaziland (Fig. 1). The Phongolo River; the only perennial river to enter Pongolapoort Dam enters in the west and exits in the east in the Lebombo Mountains. The sub-tropical climate has a mean annual rainfall of 600 mm, with a mean temperature range of 24.5°C in summer and 15.8°C in winter (Mucina and Rutherford 2006, Champion 2011). The maximum capacity of Pongolapoort Dam is 2 500 million m^3 with a maximum surface area of 12 470 ha. The surrounding vegetation is classified into three veld types; Zululand Thornveld, Lowveld and Arid Lowveld (Acocks 1953, Shannon et al. 2006). The western section of Pongolapoort Dam consists of the river section and inlet, which opens into the main section of Pongolapoort Dam. The Lebombo Mountains form a barrier on the eastern section where the Pongolapoort Dam enters the gorge section. Pongolapoort Dam was split up into three main sections for the purpose of this study; the inlet section which contained the river and inlet section (area a, Fig. 1), the main dam (area b, Fig. 1), and the gorge (area c, Fig.1). Logistical costs limited surveying the entire dam by boat every month for the duration of the study period, instead the majority of the surveys focused on the inlet section, which was estimated to contain approximately 80 % of the Nile crocodile population in Pongolapoort Dam (Champion 2011).

Pongolapoort Dam was perceived as a closed system and as such a total population estimate was chosen (Champion 2011). Nile crocodiles were allocated into size classes based on total length estimates, which were categorised as <1.5m (juveniles), 1.6-2.5m (sub-adults),

>2.6m (adults). Population increase over time was calculated using the maximum estimated rate of increase of a typical Nile crocodile population of 13% per year (Graig et al. 1992). A correlation analysis was performed on total crocodiles seen in all surveys and the variables effecting total crocodiles seen, using STATISTICA 7.0 (Statsoft, Tulsa, Oklahoma). Density was calculated in number of crocodiles per km using the perimeter of Pongolapoort Dam.

2.3.2. Aerial surveys

Aerial surveys are the most effective way to sample Nile crocodile populations as large areas which may be inaccessible by boat or foot are covered, in a short space of time, and are also the most cost effective for large areas such as dams (Jacobsen 1984, Brown et al. 2004, Cherkiss et al. 2004, Botha 2005, Calverley 2013). However, aerial surveys are also susceptible to many forms of bias which may affect the accuracy of the survey (Games 1994, Combrink 2004, Ferreira and Pienaar 2011, Calverley 2013). Observer bias and visibility bias were considered when correcting for the population count. Observer bias occurs when the number of visible crocodiles are not seen in a survey (Combrink 2004) and visibility bias occurs when the crocodile is not visible by the observer (Bayliss 1987, Calverley 2013). Both observer and visibility bias are likely to change with changes in habitat, location, aircraft and observer (Combrink 2004, Calverley 2013). We reduced observer bias by using the same observer (M. Summers) in each of the surveys while flying in a similar aircraft to the previous survey (Combrink 2004). Visibility bias was reduced by conducting surveys during winter, when the majority of crocodiles are basking out of water, which increased the number of observable crocodiles (Bayliss 1987). Correction factors are used to account for various forms of observer and visibility bias, and literature was consulted for a suitable correction factor to apply to surveys (Baylis et al. 1987, Calverley 2013). A correction factor of 1.28 was used for aerial surveys. This correction factor was calculated by Bourquin (2008), which was used in low water conditions and it was assumed that crocodiles would be clearly visible while basking; as such, was applied to both aerial surveys at Pongolapoort Dam. Weather can play a critical role in the success of an aerial survey, where overcast rainy conditions with wind will increase the period in which Nile crocodiles will stay in the water for (Pooley 1982, Downs et al. 2008).

Pongolapoort Dam was split up into three main transects during the aerial surveys. The first transect started at the southern tip and included the western portion of Pongolapoort Dam, until the inlet section (Pongolwane North). The second section included the inlet and river sections up to the N2 Bridge, and along the shoreline to the Swaziland border. The third transect included the eastern section and gorge section of Pongolapoort Dam, until the southernmost point of Pongolapoort Dam.

We conducted the first aerial survey on the 29th October 2014. The Pongolapoort Dam had its annual flood water release between15 October 2014 and 07 November 2014, with the majority of the release occurring on 28 and 29 October 2014. The discharge over 24 h from 09:00 on the 28th to 09:00 on the 29th was 800m^3/s, which resulted in the dam dropping from 70.2% to 65.2%. The annual flood release is supposed to simulate the natural flooding of the Phongola floodplain (Heath and Plater 2010). It was thought that conducting an aerial survey when water levels dropped caused crocodile movements to slow down due to the muddy banks on the shore. This would make it difficult for the crocodiles to escape into the water when hearing an aircraft overhead; additionally, the sudden drop in water level would opened up large basking areas for the crocodiles. The survey started at 07:25, earlier than desired, as high winds were expected later on that morning. A Cessna C150 two seater aircraft was used in this survey which started from the southern tip of Pongolapoort Dam in a clockwise direction, keeping the bank of the observer's right hand side. The entire shoreline of Pongolapoort Dam, including the river section up to the N2 Bridge, but excluding the Swaziland section, was surveyed. Due to the safety risk and wind, the gorge section was flown above the height of the Lebombo Mountains instead of in the gorge. This made it extremely difficult to view any possible Nile crocodiles which may have been there. The wind blew from the North East at approximately 10.8 km. h^{-1} with no cloud cover (0/8). The temperature was 23 °C and the average height above water was 213 m (altitude increased to 610m in the gorge), and the aircraft travelled at 112 kph. Each time a crocodile was seen, its coordinates were captured using a handheld Global Positioning System (GPS, Garmin eTrex, Kansas, USA), and its total length (TL) estimated (TL was later allocated into size classes). In areas of high crocodile densities, aerial photographs were taken and the timestamp of that photo was correlated with the time stamp of the on board GPS system of the aircraft. This allowed for the coordinates of the corresponding crocodiles to be established (Calverley 2013).

We conducted the second aerial survey on the 10th July 2015, starting at 10:10 in a two seater Fixed-wing Bushcat aircraft, under favourable conditions. The shoreline was followed in a clockwise direction, keeping the bank on the observer's right hand side. The wind blew in a southerly direction at approximately 3.6 kph, with no cloud cover (0/8) and a temperature of approximately 23°C. The average flying height was 40 m above water with an average speed of 80km. h^{-1}. The same survey route as the previous aerial survey was followed, however, the gorge section was flown at a much lower altitude due to low wind conditions. The same process was used as the previous survey, when a crocodile was seen, the GPS coordinate and TL was recorded. Areas of high crocodile densities were photographed and using the images timestamp and correlating that with the timestamp of the on-board GPS system, the GPS coordinates could be captured.

2.3.3. Diurnal and nocturnal surveys

Boat surveys performed under favourable conditions can result in the highest number of counts in a river based population (Brown et al. 2004). Monthly boat surveys were conducted from September 2014 to July 2015. A total of 16 daytime surveys and six spotlight surveys were completed during the study period to investigate changes in Nile crocodile density in the inlet section of Pongolapoort Dam (Fig. 2). A correction factor of 1.28 was applied to boat surveys. The changes in water levels made some areas impossible to survey over the study period. A survey on the second and third of June 2015 included the whole dam, excluding the inlet section. A 4.5 m single-hull aluminium boat with an Evinrude VRO 40 hp motor was used for boat surveys. At the start of every survey, temperature (°C), wind speed (kph), wind direction, cloud cover, start time and end time were taken. When a crocodile was seen, its GPS coordinate was recorded as close to the crocodile as the water level would allow, and without frightening the crocodile off. Additionally the TL of the crocodile was estimated and a size class was allocated. Shallow areas and areas of high hippopotamus density were surveyed using binoculars and a spotting scope, however, there were areas such as Croc Bay, which were cut off due to low water and could not be accessed by boat.

When conducting spotlight surveys, a spotlight (Lightforce 140, Australia) was connected to a 12V battery and used to identify eye shine. During spotlight surveys, if the crocodile could not be allocated a TL due to it diving or the water being too shallow, it was allocated as eyes only (EO). An area was avoided if hippopotamus posed danger to the survey crew or boat.

The number of observers varied from one to three observers per survey. One person would scribe while the skipper and other observer would search for Nile crocodiles.

Occasionally the skipper had to observe, scribe and take the crocodiles GPS position at the same time. This was done by stopping the boat and taking the necessary readings down. The shoreline was followed as closely as the water depth allowed and the average speed travelled was 11 kph.

2.4. RESULTS

2.4.1. Aerial surveys

On the first aerial survey (Table 1) October 2014 we recorded a total of 90 Nile crocodiles greater than 1.5 m (Fig. 3). The shoreline of the first transect (transect B) was extremely muddy due to the NE wind picking up waves and mud, which reduced visibility and yielded observations of only 14 crocodiles (15.5% of total crocodiles seen). The second transect (transect A) was more sheltered than the first, possibly accounting for the greater number of crocodiles observed (75 crocodiles; 83.3% of total crocodiles seen). The eastern section of the dam (third transect, transect C), which included the gorge section, yielded only one crocodile (1.1% of crocodiles seen). This crocodile was seen in the gorge itself, which is highly unusual due to limited basking sites. When the population was corrected for observer and visibility bias, a population estimate of 114 Nile crocodiles was estimated for Pongolapoort Dam in October 2014. The density of Nile crocodiles was calculated to be 1.02 Nile crocodiles per km in this survey. However, this is biased as only the perimeter of the dam was searched, and density does not account for aggregations of crocodiles (Fig. 4).

The second aerial survey (Table 1, Fig. 3) flown in July 2015 recorded a total of 432 crocodiles greater than 1.5 m. Transect B (western shoreline up to the inlet, Pongolwane North and main section of the Dam) had 86 crocodiles (19.9%), while transect A (inlet and river section) had 346 crocodiles (80.1%). Zero crocodiles were seen in transect C (eastern shoreline), which included the gorge section of the dam. There were also areas which we found in this aerial survey that we could not access during our boat surveys. After applying a correction factor to the total count, an estimated 549 Nile crocodiles was present in Pongolapoort Dam in July 2015 with a density of 4.9 Nile crocodiles per km.

2.4.2. Diurnal and nocturnal boat surveys

Dropping water levels caused the water level in Pongolapoort Dam to decrease and change the length of surveys. In September 2014, the water level allowed for surveys to go as far up as the Railway Bridge and into Croc Bay. By the final boat survey in July 2015, both these areas were completely inaccessible by boat due to shallow water.

A diurnal survey on the second and third of June 2015 yielded six Nile crocodiles in total. These crocodiles were all found on the western edge of the main dam (transect A), comprising of four sub-adults and two adults. No crocodiles were seen in the gorge section (transect C). The rest of the diurnal surveys (n = 16) were completed in the inlet section of Pongolapoort Dam, where the number of Nile crocodiles seen varied from two to 251 individuals, with a mean of 96 ± 21 individuals (Fig. 5). The only environmental variable that significantly affected the number of Nile crocodiles seen was cloud cover, where increased cloud cover decreased the number of crocodiles seen (Pearson Correlation r = -0.489, p = 0.027).

A total of six spotlight surveys were completed in the inlet section of Pongolapoort Dam. The number of crocodiles seen ranged from 21 to 113 individuals, with a mean of 56 ± 13 Nile crocodiles seen over all spotlight surveys. The majority of Nile crocodiles seen during spotlight surveys were classified into the eyes only category (88%) as they would dive before being categorized. The presence of hippopotamus and shallow water prevented surveying areas of known high densities of Nile crocodiles.

2.4.3. Population structure

The male: female sex ratio of Nile crocodiles in Pongolapoort Dam was assumed to be 1:1 to calculate the number of each sex per size class; and, a correction factor was applied to the aerial survey in July 2015, and combined boat surveys on the inlet of Pongolapoort Dam. Size structure of both the aerial survey and combined boat surveys showed that the sub-adult (1.6-2.5 m) size class has the highest number of individuals, while the juvenile (<1.5 m) size class had the lowest number of individuals in the Pongolapoort Dam population (Fig. 3). While the size class structure remained the same between the combined boat surveys and the aerial survey in July 2015, the percentage of individuals in size classes was different between the two surveys (Fig. 3). The highest percentage of Nile crocodiles in each size class was recorded using different survey methods. Diurnal boat surveys were best for counting the <1.5 m, 3.6-4.5 m and >4.5 m; while, aerial surveys were best for counting the 1.6-2.5 m and 2.6-3.5 m size class. Although a variety of survey methods was used to estimate population size, the aerial survey in July 2015 was considered as the most reliable count, and therefore the population estimate of Nile crocodiles in Pongolapoort Dam is considered to be 549 individuals.

Using Champion (2011) estimate of population size (273 individuals), the population was projected (at 13% annual increase, Graig et al. 1992) to have a total estimate of 503 individual Nile crocodiles by 2015 (Table 2). With the same correction factor added to this population projection, a corrected population of 639 individuals would exist in Pongolapoort Dam in 2015. The total value and corrected estimate of the current study fall below the 13% maximum estimated rate of increase of a typical Nile crocodile population.

2.4.4. Temporal changes and spatial use in the inlet

Monthly changes in population number occurred in the inlet section of Pongolapoort Dam. The lowest mean count per month occurred in September 2014 with 11 individuals, while the highest mean count was in July 2015 with 239 individuals. Between October 2014 and April 2015 the number remained fairly stable with the mean range of 70-35 individuals. The population increased sharply from 47 individuals in April 2015 to 156 individuals in May 2015. A further mean increase in individuals occurred between June 2015 (223 Nile crocodiles) and July 2015 (239 Nile crocodiles, Fig. 5).

Utilisation of basking areas in the inlet remained largely unchanged, although the number of crocodiles increased with the onset of winter (May, June, and July 2015). Preferential basking sites occurred between White Elephant Jetty and the Railway Bridge, with the majority (55% of all individuals of the highest boat survey count, 9th July 2015) of crocodiles occurring in the Croc Bay area (Fig. 6 and 7). A large island formed close to croc bay which became an ideal basking site (Fig. 6), which had 88 crocodiles basking (aerial survey 2015). With the decrease in water level from drought conditions in 2014 - 2015, the entrance of Croc Bay became inaccessible by boat. The aerial survey in July 2015 showed that the inaccessible Croc Bay had 72 crocodiles in it, which would have been missed by boat surveys. Croc Bay had a narrow shallow channel which was used to access the main river (Fig. 7).

2.5. DISCUSSION

2.5.1. Aerial surveys

As mentioned, aerial surveys are considered to be the most efficient means of surveying crocodilian populations due to reduced costs per km, time efficiency, the ability to cover large areas, and gives a reliable population estimate (Bayliss 1987). An aerial survey of the whole of Pongolapoort Dam completed by Champion (2011), recorded a total of 134 Nile crocodiles, with the majority of the crocodiles being found in the Northern half of the dam. A second aerial survey focusing on the Northern section of Pongolapoort Dam recorded a total of 126 Nile crocodiles. Helicopter surveys flown in 1979-1981 and 1988-1989 from Commondale to, but not including Pongolapoort Dam (along the Phongolo River), found 11 (1979-1981) and 16 (1988-1989) Nile crocodiles (Jacobsen 1991). However, it was noted that Pongolapoort Dam was disappointing in the number of Nile crocodiles present, although some large crocodiles were spotted (Jacobsen 1991).

Accuracy and precision of aerial counts allow for population trends to be more comparable between years (Downs et al. 2008). The aerial surveys in this study highlighted a couple of important factors that may have affected aerial survey efficiency. Time of year should be considered when conducting aerial surveys. Winter is the best time to do population counts with Nile crocodiles as this is when water temperatures are at a minimum and crocodiles are most visible due to them basking on banks (Combrink 2015). Surveys should start after 10:00 as this is when the majority of Nile crocodiles would leave the water to bask (Downs et al. 2008). In a dam scenario, windy conditions cause waves to increase in size, and when combined with a rapid drop in water levels from the Pongolapoort annual flood release, water becomes dirty, and exposed vegetation as well as the reflection of the sun off the water decreased the chances to spot crocodiles. This was evident in the first aerial survey in the current study, and combined with flying early in the morning in spring, the low count was due to a combination of these factors. The second aerial survey was flown in winter, at the ideal time of day (after 10:00) and when weather conditions were perfect for basking (Downs et al. 2008). As such, the second aerial survey should be considered a precise count of the population of Nile crocodiles in Pongolapoort Dam. The second aerial survey also supported Champion (2011) in that the inlet section of Pongolapoort Dam was used by 80% of the population during certain times of the year.

A total corrected count was preferred to a density estimate of the population of Nile crocodiles in Pongolapoort Dam. When a population is distributed continuously over a wide area, a density estimate is preferred (Begon et al. 1996); however the Nile crocodile population was not distributed continuously throughout Pongolapoort Dam, so a total corrected estimate was seen as a better indicator of population size.

2.5.2. Diurnal and nocturnal boat surveys

Diurnal boat surveys yielded greater counts of Nile crocodiles in the inlet of Pongolapoort Dam compared to nocturnal surveys. Provided the diurnal survey starts around 10:00 in winter (Downs et al. 2008), and 09:00 in summer (pers. obs., 2015), a large percentage of the population of Nile crocodiles would be basking on various banks in the inlet, depending on the time of the year. Although there may be large differences in the number of individuals per size class when comparing aerial surveys with boat surveys, the structure of the size classes remains the same.

Spotlight surveys have been used in estimating population trends for Nile crocodiles for many years (Hutton 1984, Combrink 2004, Botha 2005, Bourquin 2008, Calverley 2013, Combrink 2015). Crocodilians have a reflective layer in the eye known as the tapetum lucidum (Grenard 1991) which allows them to be spotted over 100 m away (Bourquin 2008). Classifying Nile crocodiles into a size class at this distance is highly unlikely, and approaching them by boat in Pongolapoort Dam would cause them to dive under water. As a result, the majority of crocodiles seen in spotlight counts were classified as "eyes only." Pongolapoort dam had the highest percentage of "eyes only" crocodiles compared with other populations, where the narrows in St. Lucia ranged from 33.3-74.3 % (Combrink 2015), Flag Boshielo Dam was 3.3 % (Botha 2005), Lake Sibaya was 28.0 % (Combrink et al. 2011), and the Okavango Delta was 17.0 % (Bourquin 2008). Up to 38% of crocodiles may be underwater at any time (Bayliss et al. 1986, Hutton 1989, Bourquin 2008), so, a large number of animals were missed in spotlight surveys. Bayliss (1987) noted that large areas in the Northern Territory of Australia could not be sampled by spotlight boat surveys due to poor or impossible boat access. A combination of low water conditions from Mpalane Jetty to the Railway Bridge, hippopotami, and crocodile wariness limited the success of spotlight surveys in the inlet, and were not the preferred Nile crocodile survey technique at Pongolapoort Dam.

2.5.3. Population structure

The population structure of Nile crocodiles at Pongolapoort Dam changed from 2010 to 2015. Champion (2011) found a higher number of juveniles in the system compared with sub-adults and adults. The population structure for 2014/2015 showed an increased number of sub-adults and adults than in 2010, suggesting that juveniles had grown into the sub-adult size class, and that fewer juveniles were entering the system. There are a number of nesting sites in Pongolapoort Dam (Chapter 3), and with high numbers of individuals in each size class, this suggests that the population is on the increase, and may continue to increase for many years. Champion (2011), mentioned that the Pongolapoort Dam population is a viable population that is able to sustain itself, which appears so.

Other impoundments in South Africa that are home to viable Nile crocodiles are Flag Boshielo Dam, where they had an estimated total population of around 210 individuals (Botha 2005), with a population structure similar to that of Pongolapoort Dam in 2010 (Champion 2011). Loskop Dam, on the Olifants River has had a very low number of Nile crocodiles, where numbers have remained fewer than 10 individuals over the past 34 years (Botha et al. 2011). The last survey completed at Loskop Dam (August 2010) showed a total of four crocodiles with no Nile crocodiles greater than 2.1m total length, showing that there are few sexually mature Nile crocodiles in the Loskop Dam population (Botha et al. 2011).

The current study showed that the Pongolapoort Dam Nile crocodile population fell within the maximum estimated rate of increase of a typical Nile crocodile population (Graig et al. 1992, Combrink 2015), suggesting that their carrying capacity in Pongolapoort Dam had not been reached yet.

2.5.4. Temporal changes and spatial use in the inlet

Changes in the number of Nile crocodiles in the inlet section of Pongolapoort Dam over the study period were likely a result of dropping water levels in the river section and aggregations of mating crocodiles in winter. In July 2014, 86 crocodiles were seen in the river section at a view point by Buffalo Bend floodplain, and in July 2015, two crocodiles were seen on the aerial survey in that same area (unpublished data, pers. obs., 2015). The low river conditions are thought to have caused a shift in the population of Nile crocodiles to the dam over a year at Pongolapoort Dam. At Chipinda Pools, Zimbabwe, Nile crocodiles congregated in the pools during drought years (1983-1985) and dispersed upstream when the river flowed (Kofron 1993). Champion (2011) witnessed the commencement of the mating season at Buffalo Bend floodplain, with the increase from 12 (July 2009) to 75 (August 2009) Nile crocodiles. However, the dam was at a higher level (between 61 and 80 %, Champion 2011), and crocodiles could move upstream at night, as had been described by Blake and Loveridge (1987). The high densities of Nile crocodiles in the Croc Bay area could be as a result of mating activity for July 2015, where previously mating may have occurred in the river section.

The lack of Nile crocodiles in the main section of Pongolapoort Dam suggests a few things regarding their distributions. Firstly, the main section of the dam may not have as many food resources and therefore would not support as many crocodiles as the inlet section. Nile crocodiles in Ndumo Game Reserve and Lake St. Lucia have been known to choose areas according to food availability (Pooley 1982, Leslie 1997). Secondly, the main section of the dam may not have ideal basking sites, and Pooley (1982) suggested that thermoregulatory requirements may influence distribution of Nile crocodiles at Ndumo Game Reserve. Thirdly, breeding behaviour could cause Nile crocodiles to congregate at the start of the breeding season, and this was seen in Lake St. Lucia, where breeding status (among other factors) contributed to seasonal movement (Leslie 1997). Fourthly, dropping water levels may affect seasonal use of areas (Kofron 1993), as dropping water levels may expose preferential basking sites. Lastly, Pongolapoort Dam may not have reached its carrying capacity and therefore Nile crocodiles can chose preferential habitats instead of being forced into areas which are not preferential.

2.6. CONCLUSIONS

Pongolapoort Dam may be one of a very few sites in South Africa where the population of Nile crocodiles is increasing. A total corrected count showed that the population of Nile crocodiles has doubled since 2010 with a high sub-adult and adult component. Nile crocodiles were distributed unevenly with 80% of the population utilising the inlet section of Pongolapoort Dam, while the inlet section had an increase in population number during winter. The formation of Pongolapoort Dam has positively affected the population of Nile crocodiles in the Phongola River system.

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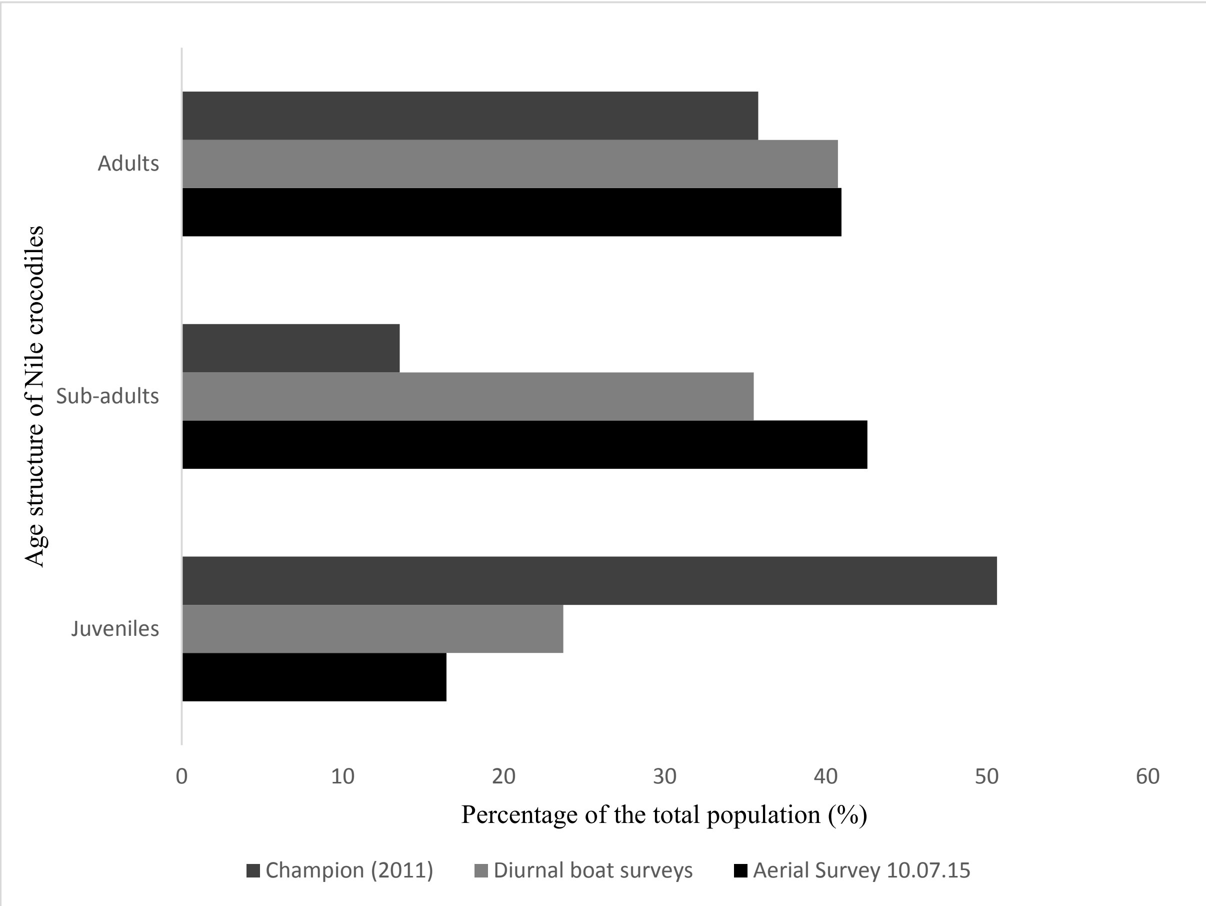

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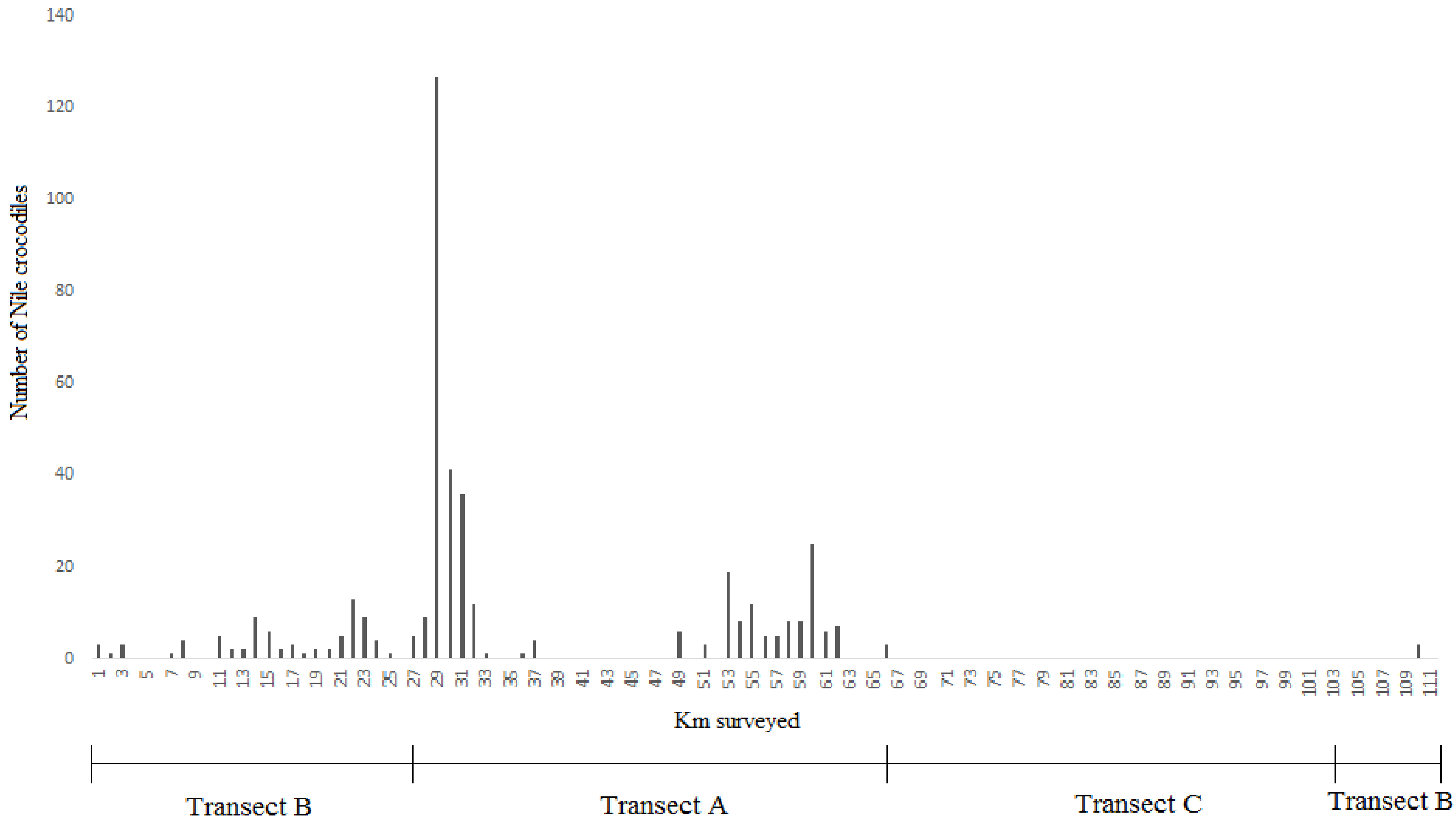

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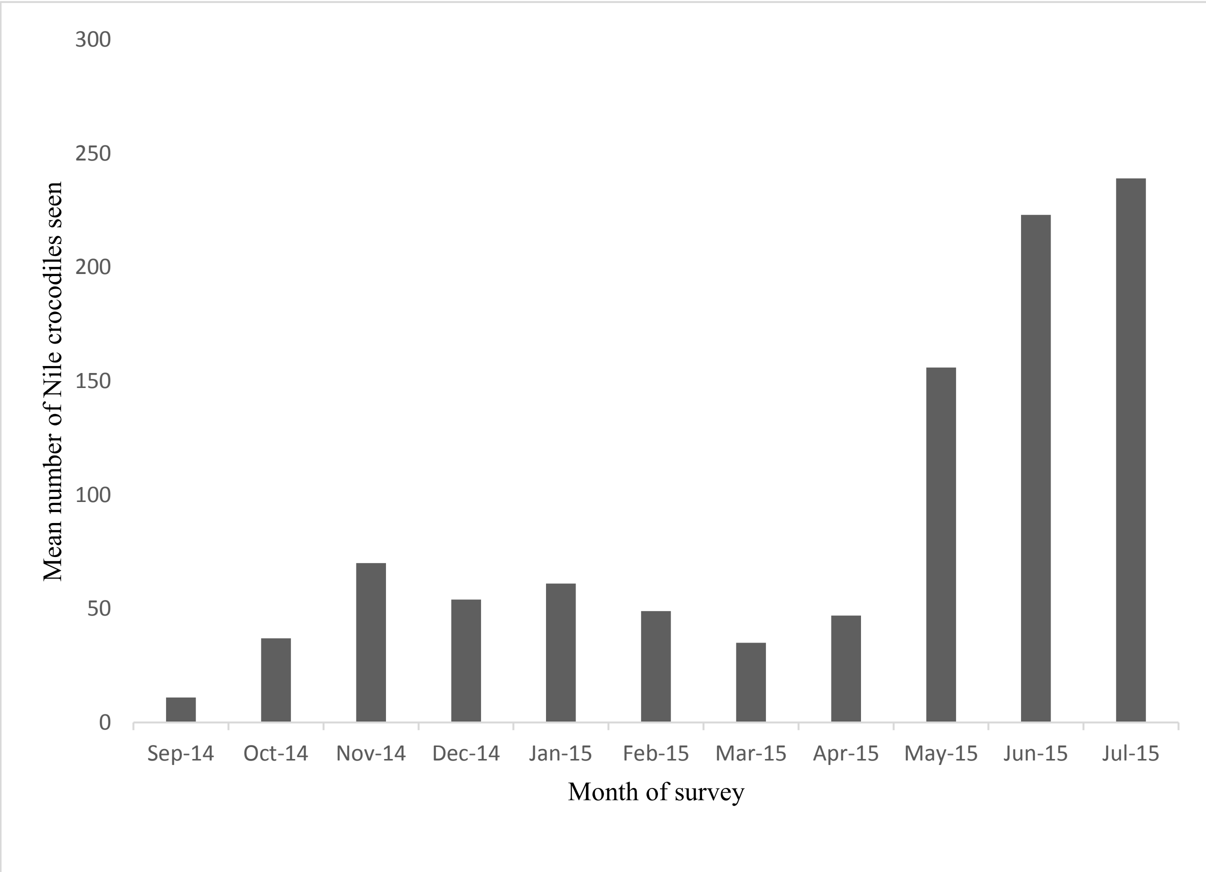

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Table 1: A comparison of the two aerial surveys flown at Pongolapoort Dam in 2014/2015 along with descriptive statistics.

		Juveniles	**Sub-adults**	**Adults**	**Total**
29.10.14	Total	5	42	43	90
	Females	2.5	21	21.5	45
	Males	2.5	21	21.5	45
	Percentage	5.56	46.67	47.78	100
	Std Err	0.06	0.05	0.07	
	Corrected total	6.35	53.34	54.61	114.3
10.07.15	Total	71	184	177	432
	Females	35.5	92	88.5	216
	Males	35.5	92	88.5	216
	Percentage	16.44	42.59	40.97	100
	Std Err	0.03	0.02	0.03	
	Corrected total	90.17	233.68	224.79	548.64

Table 2: The population projection of the maximum estimated rate of increase (13%) of a normal Nile crocodile population from Champion (2011) data (Graig et al. 1992).

Year	Total (Champion 2011)	Correction factor (Champion 2011)	Total (current study)	Correction factor (current study)
2010	273	347	-	-
2011	308	392	-	-
2012	349	443	-	-
2013	394	500	-	-
2014	445	565	-	-
2015	**503**	**639**	**429**	**549**

2.10. APPENDIX 1

Management recommendations and future research

- Considering the majority of the Nile crocodile population occurs in the inlet section of Pongolapoort Dam, this area should be considered a high conservation priority. Populations are under threat around South Africa, and Pongolapoort Dam may be one of the few places where the population of Nile crocodiles is increasing. Future research on why this population is thriving while others are declining is of utmost importance.
- A mark-recapture analysis should be done as a measure of the population size, where sex ratios can be calculated along with the mark-recapture program. Where possible, GPS/VHF transmitters should be attached as this will give us a better understanding of habitat use and spatial and temporal patterns of Nile crocodiles in Pongolapoort Dam.
- Aerial surveys of the Nile crocodile population in Pongolapoort Dam should occur annually so that population trends over time can track the health of the population. If possible, a simultaneous double-count would be advisable as observer bias could be reduced and a more accurate estimate would be made.
- The effect of changing water levels, water quality and nutritional ecology could be studied to further answer questions on the ecology of Nile crocodiles in Pongolapoort Dam.

CHAPTER 3

Nest abundance, distribution and site selection of Nile crocodiles (*Crocodylus niloticus*) in Pongolapoort Dam, South Africa

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3.1. ABSTRACT

Nest abundance, distribution, recruitment, site selection and nest effort are important in understanding the population ecology of Nile crocodiles (*Crocodylus niloticus*), especially when populations are increasingly under threat from anthropogenic disturbances. Consequently, the nesting ecology of Nile crocodiles was studied at Pongolapoort Dam, KwaZulu-Natal, in the 2014/2015 nesting season. The number of nesting sites increased from the 2009/2010 nesting season from 30 nests to 38 nests, and there was a shift in nest site distribution, where all nests were found in the river section of Pongolapoort Dam. Nest effort decreased from 73% in 2009/2010 to 43% in 2014/2015, however this was higher than any other nest effort in KwaZulu-Natal and possibly South Africa. All nests were located in alluvial deposits with *Phragmites australis* reeds as cover. The river section of Pongolapoort Dam generally escapes human disturbance and this has made it an important nesting area for female Nile crocodiles, with a density of 4.9 nests per kilometre.

Keywords: Nest effort, abundance, density, distribution, Pongolapoort Dam, Nile crocodile

3.2. INTRODUCTION

Nile crocodiles (*Crocodylus niloticus*) were once widespread throughout eastern South Africa, but as a result of varied anthropogenic disturbances, their distribution has been greatly reduced (Cott and Pooley 1971, Blake and Jacobsen 1992, Ross 1998, Ashton 2010, Champion 2011). Factors such as pollution, habitat alteration and poaching are seen as the main causes of a declining Nile crocodile population (Leslie 1997, Ashton 2010, Champion 2011, Combrink 2015). These anthropogenic factors are evident in the three main populations of Nile crocodiles in South Africa, Kruger National Park, Lake St. Lucia and Ndumo Game Reserve (Ferreira and Pienaar 2011, Calverley 2013, Combrink 2015). This underlines the importance of understanding the state of other populations of Nile crocodiles in South Africa. Monitoring assists in conserving a population as declines in population numbers (in this case nest effort of Nile crocodiles) can be addressed early enough (Combrink 2015).

Smaller populations of Nile crocodiles exist at Flag Boshielo Dam (Botha 2005), Loskop Dam (Botha et al. 2011) and Pongolapoort Dam (Champion 2011). Dams are known to usually lower the ecosystem integrity of the impounded river (Zhai 2010), and Loskop Dam is an example of this. Conversely, impoundments have had a positive effect on some ecosystems through creating permanent refugia for Nile crocodiles and other species in the population (Jacobsen 1993, Champion 2011).

Nesting is an important factor that contributes to population persistence. Understanding crocodilians biological aspects such as reproduction (Webb 1977), gives us insight into their population dynamics, ecological functioning and nest site selection.

Nile crocodiles are oviparous and nest at the end of the dry season (onset of summer), when sandbanks are exposed (Cott 1961, Blomberg 1976, Pooley 1982, Bourquin 2008). Females will reproduce every two to three years (Graham 1968, Kofron 1989, Bourquin 2008), at nesting sites which are often used repeatedly over successive seasons (Hartley 1990, Calverley 2013). In KZN, suitable nesting habitat for Nile crocodiles outside of protected areas is limited, therefore nesting habitats within reserves should be conserved (Pooley 1969, Hartley 1990, Calverley 2013).

Reproductive output is key in maintaining population sizes, it is imperative to study nesting ecology of Nile crocodiles, especially in a population where there is minimal data available. Champion (2011), was the first to study nesting ecology of Nile crocodiles in Pongolapoort Dam, and although he did find active nesting sites and brooding females, a flash flood washed all the nests away (Champion 2011). Therefore there has been no completed study on the reproductive output, nesting success rate and number of females nesting in Pongolapoort Dam. The aim of this study was to quantify the number of nest sites and nesting females, to map nest distributions, and to investigate nest site selection of Nile crocodiles in Pongolapoort Dam. The objectives of this study were to identify and record nesting areas and nest site choice for the 2014/2015 nesting season and compare nesting data and site selection with that previously described by Champion (2011).

3.3. METHODS

3.3.1. Study area

Pongolapoort Dam is situated in northern KZN and on the southern border of Swaziland (Fig.1). The Phongola River; the only perennial river to enter Pongolapoort Dam, enters in the west and exits in the east in the Lebombo Mountains. The sub-tropical climate has a mean annual rainfall of 600 mm, with a mean temperature range of 24.5°C in summer and 15.8°C in winter (Mucina and Rutherford 2006, Champion 2011). The maximum capacity of Pongolapoort Dam is 2 500 million m^3 with a maximum surface area of 12 470 ha. The surrounding vegetation is classified into three veld types; Zululand Thornveld, Lowveld and Arid Lowveld (Acocks 1953, Mucina and Rutherford 2006, Shannon et al. 2006). The majority of the nesting data were collected between the N2 Bridge (27.394313 S; 31.826631 E) and the railway bridge (27.369604 S; 31.856118 E) from October 2014 to March 2015.

3.3.2 Nest surveys

A combination of survey methods are effective in identifying nesting areas of crocodiles such as aerial surveys, boat surveys and ground surveys (Magnusson et al. 1978, Combrink 2004, Calverley 2013). In the case of this study, aerial and foot surveys were used. An aerial survey flown on the 29th October 2014, in combination with a crocodile population count of the dam, was ineffective at identifying nesting sites as the aircraft height above water was too high and no nesting sites were identified. In addition to the logistical costs of aerial surveys, it was decided to use foot surveys as the main survey method.

To minimize disturbance at the nesting sites, foot surveys were done once monthly from November 2014 to March 2015. The surveys were done by walking along the Phongola River bank close to the water line and searching for any signs of crocodile activity by looking for tracks, slide marks or egg shell fragments. The presence of a crocodile fleeing to the water often gave away nest site locality (Pooley 1982, Champion 2011, Calverley 2013, Combrink 2015). Using the knowledge of the game guards, historical and current nesting sites were examined intensively and were often identified by diggings or nest depressions. The sites described by Champion (2011) were also surveyed. Coordinates for the nest sites were recorded using a global positioning system (GPS, Etrex, Kansas, USA). If the female was present on the nest site, a size estimate was taken. Nest opening was not done as nest predators such as water monitors (*Varanus niloticus*) could be attracted to freshly disturbed nests (Calverley 2013).

Environmental variables possibly affecting nest site choice were measured such as distance to water and height above water (Pooley 1969), distance to nearest neighbouring nest and slope (Swanepoel et al. 2000), vegetation cover (Taylor and Blake 1986), soil type (Kofron 1989), and exposure to sunlight (Hartley 1990). Exposure to sunlight was measured on an East-West plane, with 180° being a full day's worth of sunlight. Distance to water was measured by taking a waypoint at the nest site and at the water's edge and working out the difference (Calverley 2013), and any entrance and exit paths were noted and measured where available (Hartley 1990). Height above water was measured using man height unit estimates as constantly fluctuating water levels made it impossible to be one hundred percent accurate all the time (Hartley 1990, Calverley 2013). Predation was verified by looking at the placement and manner in which the egg shell was broken away from the opened nest (Pooley 1969), and the nest site at which predation may have occurred was noted. A disturbance factor was assigned to each nest site where 0 was very low, 1 was low, 2 was moderate and 3 was frequently disturbed (Champion 2011). Certain areas could not be surveyed due to the presence of Cape buffalo (*Syncerus caffer*) and African elephant (*Loxodonta africana*). Results are shown in means ± standard error. Regression analysis was used to test environmental variables using STATISTICA 7.0 (Statsoft, Tulsa, Oklahoma).

3.3.3 Nest effort

Nest effort for Nile crocodiles in Pongolapoort Dam were calculated by using an equation first described by Chabreck (1966), and was later used by Leslie (1997), Combrink (2004), Champion (2011), Calverley (2013) and Combrink (2015). Nest effort is an important parameter in estimating the proportion of mature females in the population that are nesting in that respective year (Combrink 2015).

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

N = Population estimate

X = Number of nests

E = Nest effort (proportion of mature females nesting)

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

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

The population estimate (N = 549) is the corrected estimate of the total population of Nile crocodiles in Pongolapoort Dam and this estimate was taken from an aerial survey flown in August 2015 (Chapter 2). X was calculated using the total number of nests found in the 2014/2015 nesting season (38 nests). The proportion of mature crocodiles in the population (A) was calculated by dividing the number of crocodiles greater than 2.5 m total length by the population estimate. The ratio of mature females in the mature population (F) was assumed to be 0.5, as found in several studies of the male to female sex ratio of Nile crocodiles (Cott 1961, Thorbjarnarson 1997, Calverley 2013, Combrink 2015).

3.4. RESULTS

3.4.1 Nest surveys

Although no mating was witnessed, large congregations of Nile crocodiles formed in the Phongola River section and Croc Bay (Fig. 1) from late July through to September in 2014 and 2015 respectively. An aerial survey conducted on the 29th October 2014 yielded no signs of nesting crocodiles, however, the first foot survey conducted on the 08th November 2014 found 14 nests in total, which would have put fertilization and mating around the end of July. For the duration of the nesting study, there was no flooding or heavy rain. Consequently no nest sites were lost in the 2014/2015 nesting season to flooding. The river water remained clear and shallow for the duration of the study period, with one deep channel where crocodiles escaped to.

Nile crocodile nest surveys conducted in the 2009/2010 breeding season indicated three main nesting areas in Pongolapoort Dam known as Croc Bay, Cliff Ledges and Causeway Bend as previously reported by Champion (2011). Cliff Ledges and Causeway Bend occur in the

Phongola River section flowing into Pongolapoort Dam, while Croc Bay is in the inlet section of Pongolapoort Dam. During the course of the current study, no nest sites were found at Causeway Bend and Croc Bay; however, nests were found at Cliff ledges (-27.387542 S, 31.855301 E), N2 Bend (-27.39575 S, 31.85272222 E), Buffalo Bend (-27.38058333 S, 31.84691667 E), and Dabula Floodplain (-27.38433333 S, 31.85052778 E).

A total of 38 Nile crocodile nests were found in Pongolapoort Dam in the 2014/2015 breeding season, with all of them situated in the river section, within a 7.76km stretch of river between the Railway Bridge and the N2 Bridge (density of 4.9 nests/km). All of the nest sites were similar in their attributes. The nests sites at Buffalo Bend could not be quantified for hatchling success at the end of the season due to the presence of African elephants and Cape buffalo. The total number of hatched eggs found was 107 eggs over 25 nests, with only 44 % of the nests producing hatchlings (these were the nests that could be quantified at the end of the nesting season). There were 99 eggs that were found to be predated, and when regressed against disturbance factor, there was a significant increase in eggs predated with an increase in disturbance (p <0.05; R^2 = 0.569). These eggs were found away from the nest and tended to be crushed by the predator (Fig. 2).

The Phongola River section of Pongolapoort Dam consists of a wide floodplain (300 m at its widest) has large deposits of alluvium which allow for easy excavation for Nile crocodile nesting sites. All nests found had alluvium deposits as the soil type and *Phragmites australis* as the closest vegetation type to the nest. Nile crocodiles used *P. australis* as shade and a cover from the heat with the mean distance to vegetation 1.53 ± 0.196 m (n = 38). The average exposure to sunlight was 127.5 ± 5.93°. When compared, exposure to sunlight was affected by the distance to vegetation (p = 0.002, R^2 = 0.232), and was explained by the shading effect of *P. australis* on the nest site itself. The nest sites were situated relatively close to water (13.5 ± 1.21 m; n = 38), with the greatest distance from nest to water being 32 m. The close proximity to water allowed females to escape from the heat during the day or disturbance. Most nest sites had an entrance and exit path to and from the water, with the entrance path (12.81 ±1.10 m; n = 38) being further away from the exit path (7.15 ± 1.180 m; n = 38), which allowed females to make a quick escape to the water when disturbed. Height above water was estimated to be 2.29 ± 0.094 m (n = 38), with the highest nest being 3.5 m above the level of the water. Slope did not play a role in nest site selection (p > 0.05; R^2 = 0.01). The average distance to the nearest neighbouring nest was 25.7 ± 10.30 m, with the longest distance between nests being 376 m.

3.4.2 Buffalo Bend Floodplain

The Buffalo Bend river section (Fig. 1) had a wide floodplain consisting of alluvial deposits, *P. australis* reed beds, grass plains and sand spits with basking sites often on these spits. The section of the river was shallow with one deep channel running down river left against a cliff ledge. Thick reed beds dominated this nesting site with patches of grass and *Parthenium hysterophorus* between reed bends. The floodplain is likely to be a result of alluvial deposits from years of flooding and the loss of gradient in this section of the river.

The Buffalo Bend nesting site had a total of 13 nests (34.2 % of the total number of nests) in the 2014/2015 nesting season. The nests were located on average 1.31 ± 0.374 m from the closest vegetation, which was *P. australis*. When the area was approached, the nest site was often given away by a female fleeing to the water. Female total length size estimates ranged from 2.7 m to 3.3 m in length. These nest sites were further away from the water (16.4 ± 1.57 m) than the average over all nest site locations (13.5 ± 1.21 m). Nests were on average 1.8 ± 0.09 m above water with the nearest neighbouring nest being on average 23.7 ± 10.94 m apart. Nests were in close proximity to one another (four nests were 3 m apart, and two nests were 2 m apart).

The nests at Buffalo Bend Floodplain were exposed to 126.5 ±11.40 ° of sunlight per day. Of interest was that two nests were exposed to 90 ° sunlight while one nest was exposed to 45 ° sunlight and they were no greater than 0.5m away from the closest *P. australis* stand.

Seven of the 13 nests (53.8 %) at the Buffalo Bend Floodplain had no disturbance. These nests were found in gaps in *P. australis* thickets. There were no elephant nor buffalo tracks and dung around these nests. These same nests had no eggs predated. Two nests had a disturbance factor of 1, as they were found to be close to an animal path and had no eggs predated. Four nests had a disturbance factor of 2 as these nests were in an area which was frequently visited by elephant and buffalo to forage and drink water. Due to this relatively high disturbance, these nests had many eggs predated, 42 in total (42.4 % of total predated eggs). There was a significant relationship between the number of eggs predated and the disturbance factor at the Buffalo Bend Floodplain ($p < 0.05$, $R^2 = 0.7944$). On the 2nd March 2015 at 11:56, a water monitor (*Varanus niloticus*) was seen searching for nests and would dig to test whether there were eggs available (Fig. 3). No eggs were seen to be predated at this time, although the likelihood of eggs being predated was good as eggs shell fragments were seen, but could not be verified.

3.4.3. Dabula Floodplain

Dabula Floodplain river bank was mainly covered in *P. australis* reed beds and alluvial deposits of river sand. The floodplain had a road running on the river side of it and the area just after the river bank to the high water mark was kept short by management mowing for game viewing.

Three nests were found in the Dabula Floodplain, two were 3 m apart from each other while the third nest was 33 m away from its nearest neighbouring nest. The average distance to water for these three nests was 7.7 ± 1.45m with the height above water being 2.2 ± 0.17 m. The distance to the nearest vegetation was 2.2 ± 0.44 m with the exposure to sunlight being 156.7 ± 3.3°. These nests were in an open area when compared with other nesting sites. One nest was situated on the sand road and animal path and was rated as 3/3 for disturbance. The other two nests sites were just off the main road but were in a relatively open area and they were each rated 1 for disturbance. We found 35 eggs that had been predated by the nest rated as 3/3 for disturbance, the highest number of predated eggs out of all surveyed nests. The other two nest sites had seven and 10 eggs predated respectively. Zero hatched eggs were found at these three nests suggesting that the females abandoned the nest site after heavy predation and high disturbance from animals and vehicles.

3.4.4. Cliff Ledges

Cliff Ledges were seen to be an important Nile crocodile nesting site in the 2009/2010 nesting season, with 19 nests being found here (Champion 2011). This bend of the river consisted of high cliffs with a narrow river bank, which meant it had to be surveyed using binoculars. Alluvial deposits and *P. australis* dominated the banks with very few clearings to view crocodiles through. No nests were seen here in an aerial survey completed on the 29th October 2014. While surveying the opposite bank, two females were seen laying on a nesting site (Fig 4). These females were estimated to be 2.7 m and 2.9 m in total length. The river channel flows on the Cliff Ledges side, which would provide an easy escape for the females if disturbed.

Although the Cliff Ledges nesting site only yielded two nests in the 2014/2015 season, this nesting site has the potential to have many more nests. The distance to vegetation was 1.5 m and 2 m respectively with both nests receiving 100° sunlight. The cliff ledges provided shade to these nests and the nesting females. Each nest was 2 m and 3 m away from the water, and 2.5 m and 3 m above the water, with 5 m between nests. One could see four eggs fragments on the bank below the nest site, but whether they were hatched or predated could not be identified. Due to the isolated nature of these nests, they were ranked 0 for disturbance.

3.4.5. N2 Bend

The N2 bend had the highest number of Nile crocodile nests (52.6 %) compared with other nesting sites in 2014/2015. This site comprised of a two high banks, one on the river bank itself and the other an island just off the main river bank, which would have been an isolated island if the river level was higher. The nesting site comprised of alluvial deposits (river sand) and *P. australis* reed beds. This made for ideal nesting conditions. Nest diggings were found on the river right, however these nests sites were abandoned by the female crocodiles. Therefore all the nests were found on river left. Only six females could be seen during surveys and they ranged in size from 2.7 m to 3.2 m. There was one deep channel running on river right, which made escaping to deep water difficult for female crocodiles, however there were isolated ponds partially covered by *P. australis* reeds. On the land side of the river bank there was an unused road with an excavation site which may have been used to mine river sand.

The mean distance from nest to vegetation was 1.6 ± 0.28 m, with the mean exposure to sunlight being 126.5 ± 8.12°. Exposure to sunlight at the nest was effected by distance to vegetation (p = 0.04, R^2 = 0.20), showing a shading effect of the vegetation on the nest site. Five nests were exposed to 90° sunlight while two nests were exposed to 70° sunlight. The *P. australis* reed beds were thick here with no game paths present. Interestingly no signs of elephant and buffalo were present here during the study period. Mean distance to water was 13.6 ± 1.78 m, with the height above water being 2.6 ± 0.12 m. Nests were well spaced from each other with nearest neighbour equalling 28.9 ± 18.44 m.

The N2 Bend nesting site had the highest hatchling success with 103 hatched eggs found, which was 96.3% of total eggs found. Interestingly only five eggs were found to be predated. This area had minimal disturbance with 11 of the 20 nests rated as 1 for disturbance. The rest of the nests were ranked 0 with no disturbance. This area did not have many signs of game but may have been used for sand mining at some stage.

Hatchlings were seen in ponds very close to the nests (Fig. 5a). These ponds formed ideal nurseries and a female crocodile was see at one of these nurseries with hatchlings present (Fig. 5b). This nursery was away from the main current of the river in an isolated channel partially covered by *P. australis* reeds. The number of hatchlings present could not be quantified due to some hatchlings hiding in the reeds and the female crocodile present. This nursery was 33.4 m away from the nearest nest site.

3.4.6. Nest Effort

Nest effort was calculated using winter estimations of population size (N = 549 crocodiles) and structure (see Chapter 2), with a 1:1 male to female sex ratio. Nest effort was calculated to be 0.43 in the 2014/2015 nesting season (this is lower than the 2009/2010 nesting season of 0.76 Champion 2011).

3.5. DISCUSSION

Determining the abundance and distribution of crocodilian nests is important when monitoring their populations as it directly effects the future of the population (Combrink 2015). There was no nesting in Pongolapoort Dam perimeter; but rather, in the inlet river section (above the railway bridge and before the N2 bridge), where there were 38 nests in 7.66 km (density of 4.96 nests per kilometre). Similarly this preference was evident in the 2009/2010 nesting season, except for one nest being found in Croc Bay (Champion 2011). The nesting ecology of Nile crocodiles in Pongolapoort Dam seems to follow that of Flag Boshielo Dam, particularly with regards to site selection and that most of the Flag Boshielo Dam's nests occurred in the "river like" area of the dam (Botha 2005). All of the nests in Pongolapoort Dam were found in the river section, where large deposits of river sand and available shade were present. The drought caused low river levels which may have assisted in historical nesting sites being exposed, however the river section seems to escape high dam water levels and there is minimal anthropogenic disturbance (Champion 2011). It may also be possible that changes in the Pongolapoort Dam nesting sites over the past five nesting seasons may be because of changes in alluvial deposits over years of flooding and receding waters.

3.5.1. Physical properties of nesting sites

Modha (1967), found that the most nesting sites were located in areas which had deep sandy soil, abundant shade with a gentle slope from the water's edge (Pooley 1982). The majority of the shoreline in Pongolapoort Dam is comprised of a shallow soil profile with a high gravel load and no nests were found here. Nest site selection conformed with conditions similar to that of river systems in that crocodiles preferred nesting in areas containing alluvial deposits (Pooley 1982, Leslie 1997, Swanepoel et al. 2000, Botha 2005, Bourquin 2008, Champion 2011). The river section had the only alluvial deposits in Pongolapoort Dam and considering this was the only area containing nests, one can conclude that soil substrate was the most important factor in nest site selection for Nile crocodiles. In Flag Boshielo Dam, 95.24 % of all nest sites were found in alluvial soil deposits, and the nesting occurred in an area of less than a quarter of the available shoreline (Botha 2005).

Vegetation is an important factor in Nile crocodile site selection as it provides shade for nesting females (Cott 1961, Hutton 1984, Leslie 1997, Botha 2005), and may affect the sex ratios of the clutch (Lang et al. 1989, Leslie 1997). All of the nest sites had *P. australis* as the main vegetation in the area. There was some *P. hysterophorus* in the Buffalo Bend floodplain, and this should be treated as it could alter nest sites negatively in the future. Leslie and Spotila (2001), found that crocodile nests shaded by *Chromolaena odorata* were on average 5.0 – 6.0°C cooler than nests in sunny sights, and *P. hysterophorus* grows in clumps similar to that of *C. odorata*. Additionally *P. australis* grows tall and in such close proximity to the nests in Pongolapoort Dam, that the shading affect could skew the sex ratio to a female biased sex ratio. In Lake St. Lucia, Nile crocodiles chose to avoid shaded or partly shaded nesting areas when given the choice (Leslie and Spotila 2001). However, there were nests which hatched successfully, which suggests that the amount of sunlight that nests received at the soil surface was not crucial for its survival; but rather, internal nest temperature was crucial for nest survival (Swanepoel et al. 2000). The presence of the *P. australis* may have reduced the effect of wind cooling the surface temperature of the nests (Swanepoel et al. 2000), and the ability of the soil type to retain heat may also have affected nest temperature (Leslie 1997). The majority of nests in Pongolapoort Dam received more than 8 h (120°) sun, even with the close proximity to *P. australis* reeds. In the panhandle region of the Okavango Delta, the majority of the nests received over 8 h of direct sunlight (Bourquin 2008), while in Flag Boshielo Dam 52.38% of nests received more than 6 h but less than 8 h of direct sunlight per day (Botha 2005).

The mean distance to water in Pongolapoort Dam (13.503 m) fell into the range of distances to water in other studies (Modha 1967, Pooley 1969, Blomberg 1976, Hutton 1984, Hartley 1990, Graham et al. 1992, Swanepoel et al. 2000, Botha 2005, Bourquin 2008). Distance to water may not be an important factor in site selection as each population of Nile crocodiles would experience different environmental and topographical differences.

Nests in Pongolapoort Dam were clumped in four main areas (Fig. 1), resembling communal nesting areas. Nests ranged between two and 145 m apart with 50 % of all nests being within 5 m of each other. Cott (1961); Pooley (1969); Hutton (1984) and Hartley (1990) all observed communal nesting in their respective study sites; however, a clear definition for a communal nesting site has not been defined yet (Swanepoel et al. 2000, Botha 2005, Calverley 2013), especially with regards to distance between nests. This close proximity to each other may suggest a form of communal nesting in which the female crocodiles benefit from each other for predator avoidance and protection of nests from predators. When we approached these nests, we noted more than one female fleeing at a time, while other females who did not flee immediately were in the alert pose, which suggests they take cues from each other. Graham (1968) had nests as close as 1 m apart in Lake Rudolf, yet no mention was made regarding whether this was due to communal nesting or whether it was due to limited nesting areas (Swanepoel et al. 2000, Botha 2005, Calverley 2013). There are two main reasons as to why crocodiles may nest communally; firstly, it is thought that communal nesting reduces predation rates (Blake and Loveridge 1987); secondly, it is thought that limited nesting habitat causes communal nesting (Pooley 1982, Ward 1990, Swanepoel et al. 2000, Somaweera et al. 2011). Due to limited available nesting sites in Pongolapoort Dam, communal nesting does occur. Females tolerated each other and even gained cues from each other; for example, when we approached a nest site in Buffalo Bend floodplain, two female crocodiles fled to water while other female crocodiles assumed the "alert" position.

3.5.2. Nest effort and abundance

Crocodiles are known to avoid nesting in areas with high human disturbance, where noise generated by boats, wave action and visitors cause females to avoid these areas (Botha 2005). This was reported in Flag Boshielo Dam, where a holiday resort was built in an area which was previously prime nesting habitat and subsequently, no nests were found along this bank (Botha 2005). Human disturbance on the eastern boundary of Ndumo Game Reserve, further downstream of Pongolapoort Dam, has resulted in no nests being found on the new course of the Phongolo River or at historical nesting sites in this area (Calverley 2013). The lack of nests in Croc Bay in this current study may be a result of the same anthropogenic disturbance as this bay is popular with fishermen. The nesting sites found in the 2014/2015 nesting season at Pongolapoort Dam are all situated in areas where they escape daily disturbance from humans. Occasional game drives on roads next to nesting sites occur, however this is not an option open to the public, hence minimal disturbance from humans. The two nest sites which had 3/3 for disturbance were on roads and these sites had total clutch failure. The majority of disturbance came from the presence of Cape buffalo and African elephant. Hartley (1990) mentioned in a survey of Nile crocodiles in Mfolozi game Reserve that high herbivore disturbance may affect nesting negatively. The *P. australis* reeds provided shade and food for these herbivores and the proximity to water meant that they utilised the river section where the crocodiles were nesting. Considering this is natural disturbance and the lack of human interference in the river section, this disturbance shouldn't be considered a major problem. The significant increase between number of eggs predated and increase in disturbance is a sign that nest predators are in the area. Water monitor was seen digging for nest eggs in the Buffalo Bend floodplain. No other nest predators were identified.

Nest effort in Pongolapoort Dam was high in the 2009/2010 nesting season with a nest effort of 76% (Champion 2011). Nest effort for the 2014/2015 nesting season was 43% of the total adult females in the Pongolapoort Dam population. In Lake Turkana the nest effort was reported to be 0.88 (Graham 1968), while in Lake Ngezi nest effort was found to be 0.63 (Hutton 1984). Nest effort in Pongolapoort Dam was higher compared to Lake St. Lucia (6.9%, Combrink 2015), and Ndumo Game Reserve (6%, Calverley 2013), and this could be attributed to the nesting areas being isolated from areas of high anthropogenic disturbance. The population of Nile crocodiles in Pongolapoort Dam may not have reached its ecological carrying capacity yet and this may mean that relatively high reproductive output (nest effort) may be a natural response to increasing the population. The decrease in Nest effort from 2009/2010 to 2014/2015 may be an indication that the population of Nile crocodiles is reaching its carrying capacity in Pongolapoort Dam, and after a few years would mirror the nest effort of Ndumo Game Reserve and Lake St. Lucia. With this in mind, nest effort may be a response to both anthropogenic disturbance and the need to reach the ecological carrying capacity.

When comparing Nile crocodile nest abundance in Pongolapoort Dam with other populations in South Africa, Pongolapoort Dam has the second highest number of nest sites in the past 15 years. Champion (2011) reported 30 nests in Pongolapoort Dam while the present study reports 38 nests. The Lake St. Lucia population of Nile crocodiles had 80 nests in the 2009/2010 nesting season and 60 nests in the 2011/2012 nesting season (Combrink 2015). In Ndumo Game reserve, Calverley (2013) reported eight nests in the 2009/2010 nesting season and nine nests in the 2011/2012 nesting season. In Lake Sibaya, three nests were identified in 2003 and zero nests were identified in 2004 (Combrink et al. 2011). From 2000 to 2004, five nests were found each season at Flag Boshielo Dam (Botha 2005), while in 1998, 42 nests were found in the Olifants River in Kruger National Park (Swanepoel et al. 2000). However, no recent data on the nesting ecology of the Olifants River has been published, and considering the recent die off of Nile crocodiles in the Olifants Gorge in Kruger National Park, one can suggest that the nesting population of Nile crocodiles in the Olifants Gorge is under threat.

Of interest is the identification of two nursey sites close to the N2 Bend nesting site. Female crocodiles have been known to establish and defend a nursery area for several months in close proximity to their nesting sites (Modha 1967, Calverley 2013). Nurseries generally consist of shallow, secluded and well protected areas where the hatchling can hide (Calverley 2013), with a deep channel close by to provide the female with sufficient cover. This was evident at the N2 Bend nursery, where a deep channel covered with *P. australis* reeds had a shallow edge where hatchlings were found (Fig. 5b). This channel was also completely isolated from the rest of the river, so no current could wash hatchlings downstream.

3.6. CONCLUSIONS

Nesting ecology of Nile crocodiles in Pongolapoort Dam generally escaped anthropogenic disturbance in the current study. Female Nile crocodiles selected nest sites on available alluvial deposits and with the presence of *P. australis* in the river inlet section. Nest effort and nest abundance was high compared with Ndumo Game Reserve, downstream of Pongolapoort Dam. However, river nest sites are vulnerable to flooding, as was seen in the 2009/2010 nesting season, where hatchling recruitment was assumed to be zero after a flash flood washed all nests sites away. A high density of nests in a small area make the Pongolapoort Dam nesting population of particular conservation concern, especially considering that this population has the second highest number of nesting sites and the highest nest effort in KZN based Nile crocodile populations.

3.7. ACKNOWLDGEMENTS

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3.9. LIST OF FIGURES

Figure 1: The Phongola River section of Pongolapoort Dam showing the clumping (in red) of Nile crocodile nesting sites (yellow place marks) in four major nesting areas for 2014/2015. From top to bottom: Buffalo Bend floodplain, Dabula Floodplain, Cliff Ledges and N2 Bend.

Figure 2: Nile crocodile predated eggs at the Dabula Floodplains nest site. Note how eggs have been taken into nearby vegetation to be fed on by the nest predator. The photo was taken on 11 November 2014.

Figure 3: *Varanus niloticus* searching for Nile crocodile eggs to feed at Buffalo Bend floodplain (encircled in black are egg fragments). This photo was taken on the 2 March 2015 just before midday when the female crocodiles would be resting in the shade or water.

Figure 4: These were the only two Nile crocodile nest sites at the Cliff Ledges nesting site in the 2014/2015 nesting season. The isolation of these nesting sites mean that no disturbance from large herbivores or humans is possible. Two female Nile crocodiles are circled in black.

Figure 5: Two separate Nile crocodile nurseries were present in the N2 nesting site area. No female was present at the first site (a) while a female was present at the second site (b). Hatchlings are encircled in white.

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a.

b.

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3.10. APPENDIX 2

Management recommendations and future research

- Annual nesting surveys which capture the above mentioned nest characteristics, as well attaching trail cameras for non-invasive study techniques will help us better understand trends and changes in nesting ecology over time.
- Capturing coordinates of all the nest sites over time will allow us to identify preferential nesting sites and to see how site selection changes with the changing environment. Coordinate capture also allows field rangers to include nesting sites in their patrols considering the importance of this nesting population in the overall context of South Africa's Nile crocodile population. Coordinates for new nest sites should be captured and added to the existing database which should be checked annually.
- Nesting females should be tagged for identification purposes and where possible, GPS/VHF transmitters should be attached before the nesting season to track activity during the mating and nesting season.
- Investigating clutch size, egg dimensions and nest temperatures have not been done at Pongolapoort Dam. Through the use of iButton®, one can track the changes in nest temperature over the duration of the nesting season, which helps us identify the sex ratios of hatchlings entering the system. These factors all influence recruitment rate of hatchlings entering the system.

CHAPTER 4

Gaping behaviour in Nile crocodiles at Pongolapoort Dam, South Africa

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4.1. ABSTRACT

Gaping behaviour associated with basking crocodilians has received conflicting views, where some literature suggests that gaping is a thermoregulatory response to overheating, while others believe this is not the case. Other factors may cause Nile crocodiles (*Crocodylus niloticus*) to gape. The aim of this study was to investigate gaping Nile crocodiles. Observations of basking Nile crocodiles were made at a viewpoint at Pongolapoort Dam in winter 2014. Preliminary results suggests that there may be behavioural factors driving gaping behaviour in Nile crocodiles such as nearest neighbouring crocodile, number of neighbouring crocodiles, total length of the gaping crocodile, position of the crocodile relative to the water, degree of gape of the gaping crocodile and the total time of the gaping event. It is suggested that these gaping events are a form of communication between crocodiles.

Key words: Nile crocodile, gaping, behaviour, communication.

4.2. INTRODUCTION

Thermoregulation in crocodiles (as with most ectotherms) is a behavioral (and physiological) mechanism aimed at maintaining a stable, optimal body temperature. This is achieved through shuttling between shade and sun, or land and water (Seebacher and Gordon 1997, Seebacher 1999, Downs et al. 2008). Another supposed mechanism crocodiles use to cool themselves is by lying with their mouths agape, thereby increasing surface area for evaporative cooling (Loveridge 1984, Branch 1998b, a, Downs et al. 2008).

In many Testudine studies, turtles were involuntarily exposed to high temperatures and it was assumed that gaping was a thermoregulatory response to lowering their body temperatures (Legler 1960, Boyer 1965, Hutchison et al. 1966, Pritchard and Greenhood 1968, Moll and Legler 1971, Lovich 1990), even though gaping is considered to be an inefficient cooling mechanism for turtles (Moll and Legler 1971, Bury and Wolfheim 1973, Lovich 1990). In *Alligator mississipiensis*, gaping was shown to be potentially useful in controlling head temperature heat gain, but not body temperature heat gain, in a controlled environment (Spotila et al. 1977). Gaping in Nile crocodiles (*Crocodylus niloticus*) has been insignificant in slowing down head temperature gain in some cases (Diefenbach 1975), and significant in others (Cloudsley-Thompson 1969).

There is uncertainty about whether mouth-gaping in Nile crocodiles has a physiological role (Downs et al. 2008), or whether it is behaviorally related. It is therefore important to find out whether mouth-gaping has any physiological or behavioral effect on Nile crocodiles. This may give us a better idea of physiological or behavioral effects on habitat choice or social structure.

Consequently the aims of this study were to investigate behavioural and positional factors of when a gaping event occurred in Nile crocodiles. The objectives were to identify factors causing possible threat displays or territorial behaviour of a gaping individual relative to other basking crocodiles. We conducted a preliminary study during winter when we expected gaping behaviour to be used less for thermoregulation and more for possible behavioural reasons.

4.3. METHODS

4.3.1. Study site

Pongolapoort Dam is situated in northern KwaZulu-Natal and on the southern border of Swaziland (Figure 1). The Phongola River; the only perennial river to enter Pongolapoort Dam enters in the west and exits in the east in the Lebombo Mountains. The sub-tropical climate has a mean annual rainfall of 600 mm, with a mean temperature range of 24.5°C in summer and 15.8°C in winter (Mucina and Rutherford 2006, Champion 2011). The maximum capacity of Pongolapoort Dam is 2 500 million m^3 with a maximum surface area of 12 470 ha. The surrounding vegetation is classified into three veld types; Zululand Thornveld, Lowveld and Arid Lowveld (Acocks 1953, Shannon et al. 2006). Observations of Nile crocodiles were conducted at a basking area known as Buffalo Bend (27.378318 S; 31.843993), with a viewpoint, which allowed for observations to be made without disturbing the Nile crocodiles.

4.3.2. Observations

Data were collected in July 2014 where the number of basking individuals ranged between 63 and 86 Nile crocodiles in approximately 600 m along the river bank. Nikon 10×42 mm binoculars and a Leupold 10-20×40 mm spotting scope were used to observe Nile crocodiles. At the start of every gaping event, the time of day was noted, along with the estimated total length of the crocodile, the nearest neighbour crocodile (meters away from visible crocodile), number of neighbouring crocodiles, degree of the gape (10; 15; 20; 25°) orientation of the crocodile relative to the sun (perpendicular or parallel), position of the crocodile relative to water (submerged, partially submerged or dry land) and the end time of the gaping incident. Chi-squared Likelihood ratio tests were used to evaluate count data, with Cramer's V Symmetric measure being used to evaluate the association of the factors, with tests being run on SPSS v 23. Descriptive statistics are reported as mean ± standard deviation. Only significant relationships are reported. These data form part of a preliminary study on why crocodiles gape.

4.4. RESULTS

A total of 232 gaping events occurred, with the highest frequency of gapes (43) occurring between 08:00 and 09:00 in the morning (Fig. 1). No gaping events occurred between 17:00 and 18:00 in the evening, while 1 and 2 gaping events occurred at 06:00 and 07:00 respectively. The mean duration of a gaping incident was 0:23 ± 0:45 h, with a mean Nile crocodile size of 2.6 ± 0.66 m.

There was a relationship between the degree of gape and whether the crocodile was on dry land or partially submerged ($X^2 = 10.84$; $df = 3$; $p = 0.013$). The association between degree of gape and the position of the crocodile on dry land or partially submerged was weak (0.236).

The total length of the crocodile significantly affected the position of the gaping crocodile on dry land or partially submerged ($X^2 = 52.192$; $df = 25$; $p = 0.001$), with a weak association of 0.455.

The total time in which the crocodile gaped was significantly related to the position of the gaping crocodile on the dry land or partially submerged ($X^2 = 92.327$; $df = 60$; $p = 0.005$) with a moderate association of 0.636.

The nearest neighbour from the gaping crocodile was significantly related to the number of neighbours (X^2 = 103.878; *df* = 65; *p* = 0.02), with a weak association (0.369) between nearest neighbour and number of neighbours.

4.5. DISCUSSION

Six factors were identified as possible causes or behaviours associated with gaping; degree of gape, total length of the crocodile, total time of gaping event, position of the crocodile on the basking bank, nearest neighbouring crocodile and number of neighbouring crocodiles.

The degree of gape changed when the crocodile was partially submerged or on dry land, and this may be attributed to a territorial response to entering the basking site. The total time of the gape may increase depending on the position of the crocodile on the basking banks. This may show preference for areas on the basking site itself, which could be explained by the size of the gaping crocodile relative to the position on the basking bank itself. Larger crocodiles may gape at smaller individuals or other crocodiles that may be close to their preferred position. The mean size of the gaping individuals may suggest that sub-adult Nile crocodiles are gaping in close vicinity of each other, possibly sizing each other up. The relationship between nearest neighbour and number of neighbours may suggest that the focal crocodile will gape as a threat based on the proximity and number of other crocodiles, or that it is a social display. This could be seen as a communicative behaviour.

Gaping as a communicative behaviour has occurred in the following studies. Simultaneous measurements of body temperatures of gaping water dragons (*Physignathus cocincinus*) and observations of their behaviour suggested that gaping was a communication tool (together with head bobbing and arm waving) between individuals, rather than a thermoregulation mechanism (Meek 1999). Gaping between Pacific pond turtles (*Clemmys marmorata*) occurred frequently during behavioural interactions (Bury and Wolfheim 1973). Gaping in eastern painted turtles (*Chrysemys picta picta*) was also rejected as a thermoregulatory response to increased temperatures (Lovich 1990). Diefenbach (1975) showed that gaping did not cool down overheated spectacled caiman (*Caiman crocodilus*) and Nile crocodiles; but, moving into water did reduce body temperatures. These studies suggest that gaping may form part of a communicative behaviour instead of just a thermoregulatory response to overheating.

Time of year may give a clue as to why the gaping occurred as frequently as it did. During July and August, Nile crocodiles congregate for mating at Buffalo Bend (Champion

2011), and the density of crocodiles and the high number of gaping incidences suggest that gaping at Pongolapoort Dam during July was a threat display. As it was winter and as the behaviour was exhibited throughout the day, it appears that gaping was not mainly for thermoregulatory purposes (Fig. 1). Kofron (1993) found that gaping occurred in winter when the crocodile was disturbed by another approaching crocodile, hippopotamus (*Hippopotamus amphibious*) or human, and after being alerted while sleeping or basking. Often, early in the morning when the first crocodiles came onto the basking bank, gaping behaviour was witnessed, and this could be threat display caused by daily habit of sharing the basking grounds (Kofron 1993). These results show that there may be a social aspect of gaping that occurs with crocodiles.

4.6. CONCLUSIONS

Although this is a preliminary study, results suggests that there is a possible behavioural function to gaping. Factors that influenced gaping were nearest neighbour crocodile, number of neighbouring crocodiles, the degree to which the crocodile gaped and the total length of the gaping crocodile.

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4.9. LIST OF FIGURES

Figure 1: Mean frequency of gaping events of Nile crocodiles per hour of the day at Pongolapoort Dam in winter 2014.

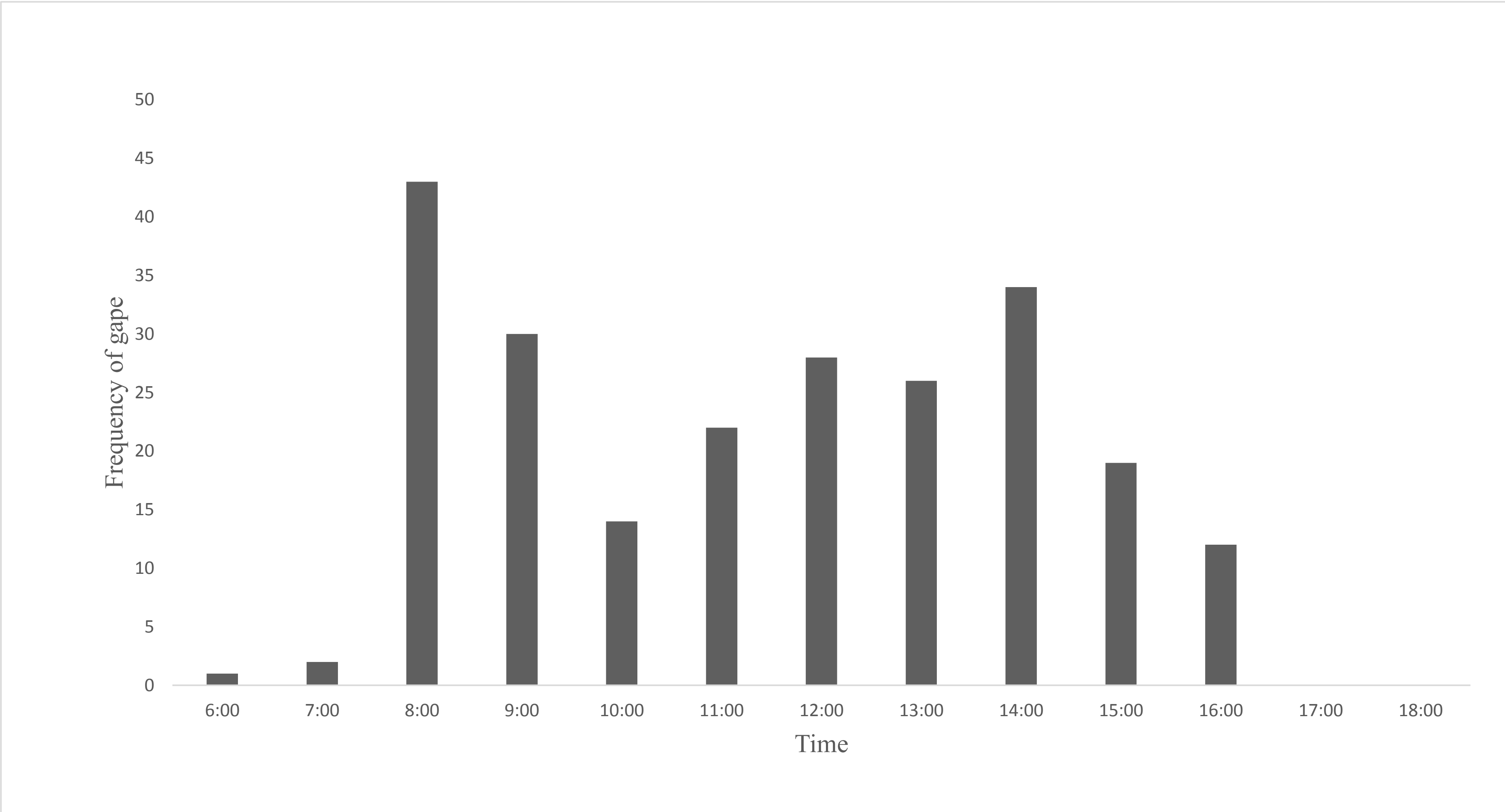

Figure 1: Mean frequency of gaping events of Nile crocodiles per hour of the day at Pongolapoort Dam in winter 2014.

4.10. APPENDIX 3: FUTURE RESEARCH

Further research should focus on three main aspects.

1. Laboratory experiments should be done on thermal effects on gaping with the use of Thermochron iButton® and infrared thermal photography. Thermal gradients could be used for this, and experiments should be run both day and night.
2. Olfactory cues could be used to identify whether crocodiles gape to better sense their environment through the use of scents and pheromones in a laboratory environment.
3. Further research should be done on the frequency of gaping with changes in the thermal environment, along with factors mentioned in the preliminary results.

CHAPTER 5

Conclusions

Numerous studies on the population ecology of the Nile crocodiles in South Africa have been done (Jacobsen 1984, Leslie 1997, Combrink 2004, Botha 2005, Champion 2011, Combrink et al. 2011, Calverley 2013, Calverley and Downs 2014, Combrink 2015); however some populations are under threat due to anthropogenic disturbances such as loss of habitat and pollution (Ashton 2010, Ferreira and Pienaar 2011, Calverley 2013). Impoundments influence the ecological functioning of rivers (Zhai 2010), and the Pongolapoort Dam, KwaZulu-Natal (KZN) is seen as a positive influence of the impoundment of the Phongola River. Consequently the aim of this thesis was to provide insight into the population and nesting ecology and thermal biology of wild Nile crocodiles at Pongolapoort Dam, in the hope of understanding more about a relatively new population.

Nile crocodiles in Pongolapoort Dam represent a growing population protected by game reserves. Population estimates of Nile crocodiles in Pongolapoort Dam have increased from 11 in 1981, 16 in 1989 (Jacobsen 1991), 273 in 2010 (Champion 2011), to 549 in 2015. Currently, Pongolapoort Dam has the fourth largest population of Nile crocodiles in South Africa, and the population continues to increase (Chapter 2). Furthermore, the population structure had a high sub-adult and adult component, suggesting that the high juvenile count of Nile crocodiles in 2010 had grown into the sub-adult and adult size class.

Habitat use of Nile crocodiles in Pongolapoort Dam was not linear, therefore a total count was used over a density estimate, with the majority (80.7%) of the population occurring in aggregations in the inlet section of the dam, while zero Nile crocodiles occurred in the gorge section (Chapter 2). Drought conditions and food resources were thought to be a major influence on the temporal and spatial distribution of Nile crocodiles in Pongolapoort Dam. Aerial and diurnal boat surveys were the preferred surveying method as Nile crocodiles had a high dive rate at night, and shallow inaccessible areas could not be accessed by boat. Our population counts will aid in future assessments of the Nile crocodile population in Pongolapoort Dam and in South Africa.

Reproductive output is a key aspect of population ecology as it directly contributes to population persistence and growth (Webb 1977). Nesting ecology of Nile crocodiles at Pongolapoort Dam was studied in the 2009/2010 nesting season, however a flash flood removed all nesting sites and a total recruitment failure was estimated for the 2009/2010 season

(Champion 2011). In the 2014/2015 nesting season, 38 Nile crocodile nests were found in the Phongola River section of Pongolapoort Dam (Chapter 3). No nests were located in the dam itself and this was attributed to the Phongola River section having ideal nesting habitat. Nests occurred in four areas, with only the Cliff Ledges nest site being used in the 2009/2010 nesting season. Nest effort (43%) was higher than other populations of Nile crocodiles in KZN, with a density of 4.9 nests per km. Every nest was dug into alluvial deposits with *Phragmites australis* reeds as the dominant vegetation in the nest sites. Signs of egg predation from water monitors was evident. Based on observations including two Nile crocodile nurseries, with an adult present at one nursery, and numerous egg shell fragments from hatched eggs, the 2014/2015 nesting season had a much higher recruitment rate compared to the 2009/2010 nesting season (Champion 2011).

Mouth gaping in crocodilians is thought to be a mechanism used in cooling themselves by increasing the area for evaporative cooling (Loveridge 1984, Branch 1998b, a, Downs et al. 2008). Some studies support gaping as a cooling mechanism in Nile crocodiles (Cloudsley-Thompson 1969), while others disagree (Diefenbach 1975). A preliminary study on field observations of gaping Nile crocodiles was conducted to see if any behavioural or communicative mechanisms may have influenced gaping (Chapter 4). We believe there may be a communicative reason for gaping in Nile crocodiles. Factors such as nearest neighbouring Nile crocodile, number of neighbouring Nile crocodiles, total length of the gaping Nile crocodile and position of the gaping Nile crocodile relative to the water were significant in a gaping event. If gaping is a communicative mechanism then there may be a social aspect to Nile crocodiles that we are not aware of. Gaping should be considered as an important aspect of crocodilian research.

In order to successfully conserve a species, an understanding of their behaviour and annual population trends is essential. Comparatively little ongoing research, monitoring or management has been allocated to the Nile crocodile population in Pongolapoort Dam, and considering this population is increasing in number with a high nest effort, it should be considered a conservation priority. Nile crocodiles are keystone species and with the increase in the Pongolapoort Dam population, it is suggested that the ecosystem is in good health. However, the Pongolapoort Dam population has not escaped effect of humans. Gill nets trapped a Nile crocodile in 2014 but the crocodile escaped (pers. obs.). A tagged Nile crocodile was poached in July 2015 for no apparent reason (pers. obs.). It is hoped that these two incidences were isolated and that the population continues to increase and remains healthy.

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