Spatial and reproductive ecology and population status of the Nile Crocodile (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

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ABSTRACT

The Lake St Lucia estuarine system, Africa’s largest and oldest protected estuary, also contains the largest Nile Crocodile (*Crocodylus niloticus*) population in a single waterbody in South Africa. We investigated the species’ spatial and reproductive ecology as well as population status in order to make management recommendations. During the first decade of the 21st century, the St Lucia estuarine lake experienced a prolonged drought, streams ceased flowing and in 2006 more than 90% of the total water area evaporated. We conducted 10 aerial surveys from 2009 - 2013 and recorded the majority of crocodiles in the Narrows, a ~27 km low salinity channel south of the lake. Above average rainfall at the end of 2010 resulted in the refilling of the lake, and most crocodiles moved north to the lake. We estimated the sub-adult and adult population at 1005 ± 137 individuals.

We investigated detailed movements and activity for 18 Nile Crocodiles using GPS-satellite transmitters. The overall activity level was 41.0 %, and it differed significantly throughout the day. There was a significant seasonal effect on activity, peaking during autumn (52.0 %), while crocodiles were most inactive in winter (30.5 %). Crocodile size and mobility were positively correlated with mean daily movement (1244 m). Adults moved more at night, but sub-adults were significantly more mobile during the day. There was a considerable seasonal variation in mobility, with the longest movements during autumn and the shortest in winter. About 60 % of total daily movements were < 1 km per day, but for sub-adults this calculation was 96 %.

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

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

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

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

We investigated homing behaviour and specific movements using a GPS-satellite transmitter by translocating an adult female (2.7 m), with a known home range, ~50 km north (straight line distance) to the False Bay area of Lake St Lucia. Following release, the individual moved a total distance of 178.3 km over 136 days (mean daily movement = 1311 ± 207 m), compared with 60.4 km (mean daily movement = 444 ± 32 m) for the identical time period the previous year. Homing movement was not continuous, but characterised by periods of extensive and directed mobility followed by prolonged periods of inactivity associated with freshwater or low salinity habitats. The translocated crocodile displayed remarkable navigational abilities, even though this required negotiating complex habitat challenges including extensive areas of the lake that were either hypersaline or completely dry, resulting in frequent and extensive overland movements. On 14 September 2012, the individual returned to the same freshwater pool where it was captured 136 days previous. This is the first study to confirm homing behaviour for Nile Crocodiles, and supports growing evidence that crocodilians and other ectothermic taxa possess complex navigational abilities.

Our study revealed numerous novel insights into the ecology and behaviour of Nile Crocodiles and some of the findings may be applicable to other crocodilian taxa. We hope the results will guide the management and conservation of this threatened species.

PREFACE

The data described in this thesis were collected at the Lake St Lucia estuarine system, Republic of South Africa, from February 2009 to May 2013. 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 Philosophiae Doctor 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.

Alexander S. Combrink
November 2014

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
November 2014

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DECLARATION 1 - PLAGIARISM

I, Alexander S. Combrink, declare that

The research reported in this thesis, except where otherwise indicated, is my original research. This thesis has not been submitted for any degree or examination at any other university. This thesis does not contain other persons’ data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

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November 2014

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DECLARATION 2 - PUBLICATIONS

Details of contributions to publications that form part and/or include research presented in this thesis.

Publication 1

Xander Combrink, J.K. Warner, R.H. Taylor and C.T. Downs

Population size and distribution of Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

Author contributions:

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

Publication 2

Xander Combrink, J.K. Warner, R.H. Taylor and C.T. Downs

Movements and activity of Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

Author contributions:

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Publication 3

Xander Combrink, J.K. Warner, R.H. Taylor and C.T. Downs

Home range and movements of Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

Author contributions:

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

Publication 4

Xander Combrink, J.K. Warner, R.H. Taylor and C.T. Downs

An overview of Nile Crocodile (*Crocodylus niloticus*) nest abundance and distribution in the Lake St Lucia estuarine system, South Africa

Author contributions:

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Publication 5

Xander Combrink, J.K. Warner, R.H. Taylor and C.T. Downs

Nesting behaviour of female Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

Author contributions:

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Publication 6

Xander Combrink, J.K. Warner, R.H. Taylor and C.T. Downs

Maternal care and predation of wild Nile Crocodile (*Crocodylus niloticus*) nests in the Lake St Lucia estuarine system, South Africa

Author contributions:

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Publication 7

Xander Combrink, J.K. Warner, R.H. Taylor and C.T. Downs

Homing behaviour and movements of a translocated Nile Crocodile (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

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This thesis is dedicated to Susan, Stanis, Anno & Bernard,

as well as my parents

"Can you catch a crocodile with a hook or put a noose around its jaw? Can you tie it with a rope through the nose or pierce its jaw with a spike? Will it beg you for mercy or implore you for pity? If you lay a hand on it, you will never forget the battle that follows, and you will never try it again! No, it is useless to try to capture it. The hunter who attempts it will be thrown down.

Who could pry open its jaws? For its teeth are terrible! The overlapping scales on its back make a shield. They are close together so no air can get between them. They lock together so nothing can penetrate them. When it sneezes, it flashes light! Its eyes are like the red of dawn. Fire and sparks leap from its mouth. Smoke streams from its nostrils like steam from a boiling pot on a fire of dry rushes. Yes, its breath would kindle coals, for flames shoot from its mouth. The tremendous strength in its neck strikes terror wherever it goes. When it rises, the mighty are afraid, gripped by terror. No sword can stop it, nor spear nor dart nor pointed shaft. To the crocodile, iron is nothing but straw, and bronze is rotten wood. Its belly is covered with scales as sharp as glass. They tear up the ground as it drags through the mud.

The crocodile makes the water boil with its commotion. It churns the depths. The water glistens in its wake. One would think the sea had turned white. There is nothing else so fearless anywhere on earth. Of all the creatures, it is the proudest. It is the king of beasts."

Job 40:20 - 41:25 - New Living Translation

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CHAPTER 1

General introduction

Why crocodiles?

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

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

Although aerial counts were used to monitor the Nile Crocodile population in the Lake St Lucia estuarine system since 1972 (Pooley 1969, 1974, 1982, Fawcett 1987, Leslie 1997), there is a paucity of information on ecological aspects such as crocodile movements and activity budgets, home range, nesting behaviour and population status, particularly within the context of the recent prolonged drought. The aim of this study was to address these issues and provide management recommendations. This study forms part of a larger bioregional research programme of the Nile Crocodile in Zululand, South Africa, including ecotoxicology and feeding ecology components.

Status and distribution of the Nile Crocodile in Africa

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

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

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

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

Status and distribution of the Nile crocodile in South Africa

Although South Africa probably never supported Nile Crocodile populations comparable in size with those of equatorial Africa, significant populations formerly existed in rivers of the

Limpopo and Mpumalanga Provinces, as well as wetlands, lakes, rivers and estuaries of coastal KwaZulu-Natal as far south as the Dwesa-Cwebe Nature Reserve in the Eastern Cape (Pooley 1976, Loveridge 1980, Blake and Jacobsen 1992, Feely 2010). Prehistoric museum specimens of teeth and skulls suggest a further range extension earlier than the 16th century southwest to the area between the Keurbooms and Keiskamma Rivers (Feely 2010). Nile Crocodile have been extirpated from the Eastern Cape since 1903 (Jacobsen 1988), but in 1977 six juveniles from Zululand were reintroduced into the Kobole River of the Dwesa-Cwebe Nature Reserve (Pooley 1980, Jacobsen 1988, Feely 2010).

The two largest and possibly secure Nile Crocodile populations remaining in South Africa today are KNP and the Lake St Lucia estuarine system. Ndumo Game Reserve, a very important and large population during the mid-1990’s (992 ± 59 individuals) is currently declining, and predictions are the decline will accelerate in future due to illegal killings and destruction of nest-sites (Calverley and Downs 2014b). The Pongolapoort Dam was until recently not considered a substantial population as very low densities were encountered (0.06 crocodiles km^{-1}) during a survey along the Phongola River in the 1980’s (Jacobsen 1984). Champion (2011) determined a “conservative estimate” of the dam population at 273 Nile Crocodiles, but the population could be considerably higher (Myburgh, pers. comm., CM Phongolo Nature Reserve). Champion (2011) recorded 30 nests during the 2009/10 nest season and the reproductive frequency of this population might be considerably higher compared to Lake St Lucia (Chapter 5) and Ndumo Game Reserve (Calverley and Downs 2014b), highlighting its conservation importance.

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

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

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

As a result of the depletion of Nile Crocodile populations and escalating threats to the species, their conservation status was classified as Vulnerable in the first South African Red Data Book on Reptiles and Amphibians (McLachlan 1978) and maintained as such in the second revision (Jacobsen 1988) as well as the Atlas and Red List of Reptiles (Marais 2014). In order to control trade, Nile Crocodile was listed as a CITES Appendix II species in South Africa under the ranching provision (Resolution Conf. 11.16) in 1994. Although no recent estimates are available for the total Nile Crocodile populations in South Africa, recent studies suggest that a number of populations are decreasing (Marais and Pooley 1991, Myburgh 2007, Ashton 2010, Botha et al. 2011, Combrink et al. 2011, Ferreira and Pienaar 2011, Woodborne et al. 2012, Calverley 2013, Calverley and Downs 2014b).

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

Regional threats to Nile Crocodiles

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

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

Study area: Lake St Lucia estuarine system

The Lake St Lucia estuarine system, the oldest protected estuary in the world (Whitfield et al. 2006) is situated in north-eastern South Africa in the province of KwaZulu-Natal (Fig. 1). At ~67 km in length, which includes the ~27 km long Narrows channel that connects the lake to the ocean, and an average of 6 km in width when filled to capacity, it is the largest estuarine system in Africa (Cowan 1997), but nonetheless very shallow with a mean depth of 0.98 m. Daily mean water temperature measured in the Narrows and Charters Creek during the four year study period (2009 to 2012) was 23.7°C ± 0.1 S.E., range 13.6 - 30.29 °C, but water temperatures vary across the lake, particularly with changing depth. Daily mean air temperature measured at St Lucia village was 21.5°C ± 3.4 SD, range 12.15 - 29.14 °C. The minimum and maximum water and air temperatures recorded during the study were 10.6 °C and 40.6 °C and 6.6 °C and 44.2 °C, respectively (Combrink, unpublished data).

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

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

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

In July 2002 the estuary mouth closed, with the exception of seven months in 2007, resulting in a constant salt load but dynamic salinity levels dependent on water volume (Taylor 2006). In 2003 as a result of below average rainfall and little input from the five streams, the lake divided in a number of compartments with varying salinities, increasing towards the north, and by June 2006 approximately 90% of the lake surface was exposed and dry (Whitfield and Taylor 2009). During this time most Nile Crocodiles were either concentrated in the south of the system in the Narrows, or they utilised freshwater seeps adjacent to swamp forests, often with associated burrows (Chapter 2). The removal of 5000 ha of exotic plantations on the Eastern Shores contributed to the rehabilitation of groundwater discharge and subsequent shoreline seepage creating favourable habitats (refugia). Vrdoljak and Hart (2007) suggested that such seepage during periods of low lake levels appears to provide a stable freshwater habitat for freshwater fishes providing a persistent supply of fresh water, even during times of extreme droughts. Good rainfall in December 2010, January, July and November 2011 as well as Cyclone Irina passing ~125 km offshore in March 2012 resulted in a restoration of water coverage throughout the lake system.

During March 2012 a beach spillway was established between the Mfolozi River and St Lucia estuary using a tracked excavator and on 6 July 2012 the Mfolozi River were re-linked with the St Lucia estuary after 60 years.

Aims and structure of the thesis

As the Lake St Lucia estuarine system contains the largest Nile Crocodile population in a single waterbody in South Africa, our main aim was to investigate their spatial and reproductive ecology and population status in order to formulate scientifically-based management recommendations. Our findings are presented in various chapters prepared as manuscripts so some repetition was unavoidable.

Chapter two provides an overview of historical Lake St Lucia Nile Crocodile surveys and presents a current estimate of the population based on diving and detectability correction factors. We discuss changes in crocodile emergence behaviour and distribution and how that correlates with seasonal variation and the availability of freshwater. We list capture methods per size class and discuss their effectiveness in different habitats. Captured crocodiles were permanently marked by removing a unique sequence of caudal scutes, additionally sub-adult and adults were colour marked with plastic tags for mark re-sight analysis.

In Chapter three we investigated diurnal and nocturnal movement patterns and activity levels of 18 Nile Crocodiles fitted with GPS-satellite transmitters in the lake system. We discuss diel, monthly and seasonal changes in movements and activity levels and investigate the function and significance of water temperature.

Chapter four provides insight into the home range and movements of Nile Crocodiles in Lake St Lucia. We estimated lifetime, yearly and seasonal home range sizes and core-use areas with kernel density estimation using ABODE. We found complex and varied home range patterns due to the topography and hydrologic heterogeneity of the shallow lake basin and feeder streams. We furthermore investigated home range overlap and discussed habitat features as drivers of spatial partitioning for sub-adults.

Chapter five provides an overview of the relative abundance and distribution of Nile Crocodile nests monitored in the lake system since 1982. Nest distribution reflects the spatial and temporal heterogeneity typical of St Lucia lake system, and we present the nine most important historical and present nesting areas. We show variation in female reproductive frequency and discuss changes in nest abundance and distribution in relation to freshwater availability, human disturbance, habitat transformation, invasive alien vegetation and food availability. As we captured nesting females on or adjacent to their nests during the nesting season, we investigated re-use of nest-sites. We conclude with an appraisal of Nile Crocodile recruitment in the Lake St Lucia estuarine system and suggestions for future research.

Chapter six investigates behaviour and movement patterns of nesting Nile Crocodile females during the nest guarding period in the Lake St Lucia estuarine system. Home range, nest-site selection, movement patterns, activity levels and nest fidelity of four nesting females are discussed.

Chapter seven provides insights into Nile Crocodile nest predation, hatchling liberation, nest abandonment and nest guarding activities of the nesting female. We consider aspects such as the distance between camera traps and the nest, the likely impact of the camera on females nest guarding activities, and predator identification and behaviour at the nest. We uniquely identified females based on their dermal pattern or unique features, described female movement at the nest-site and documented nest defence against on non-human intruders.

Chapter eight investigates Nile Crocodile homing behaviour and detailed movements of a female crocodile, previously captured in the lake system and fitted with a GPS-satellite transmitter. Subsequent to re-capture, we translocated her 40.3 km (straight-line distance) to False Bay, a completely different part of the system, where she was then released. The chapter presents detailed movements of the 136 days homing back to her capture location. Recommendations for future translocations are suggested.

Finally, chapter nine provides concluding remarks and management recommendations for the conservation of Nile Crocodile in the Lake St Lucia estuarine system.

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Caption for Figures

Figure 1. The Lake St Lucia estuarine system

Figures

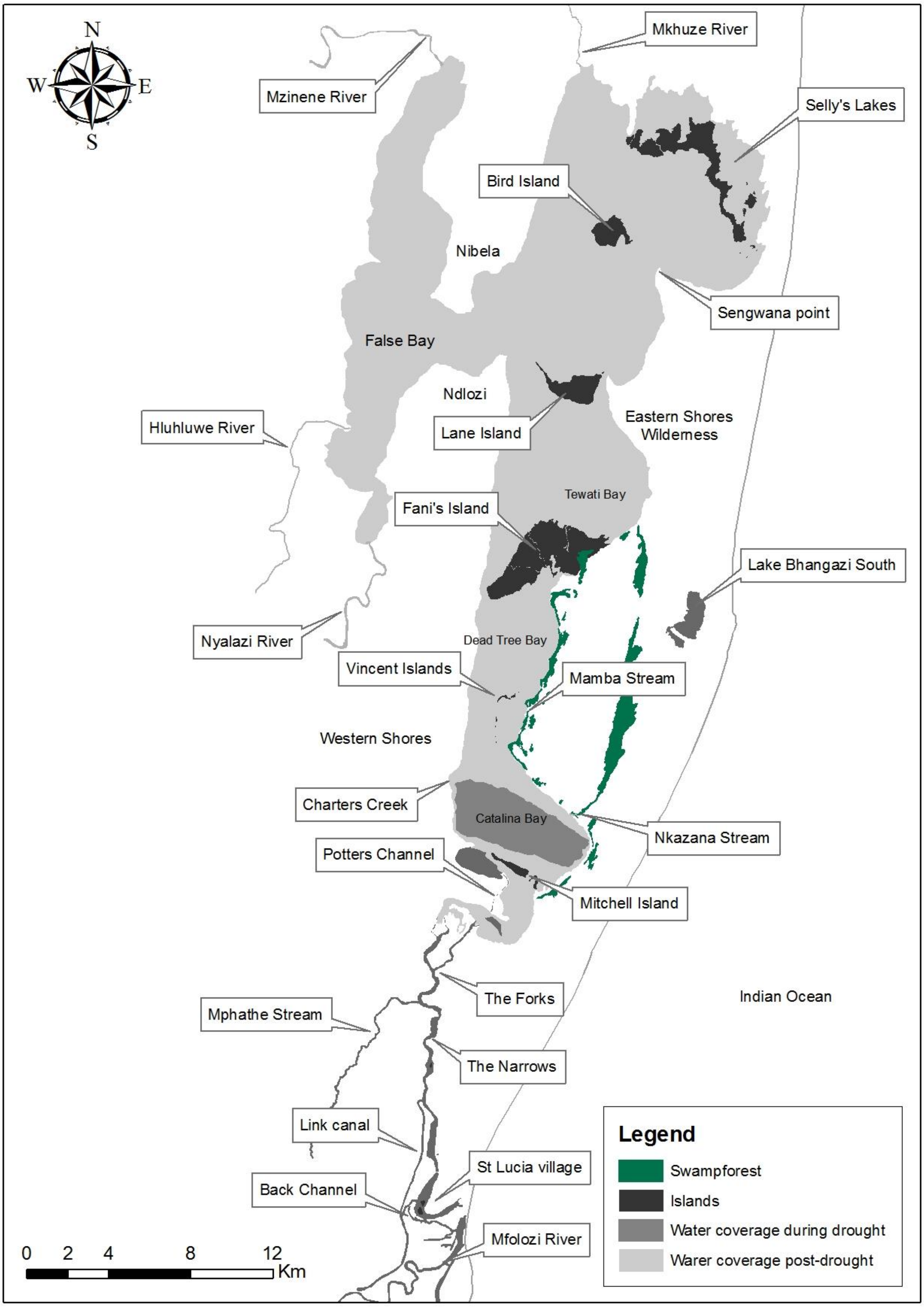

Figure 1. The Lake St Lucia estuarine system.

CHAPTER 2

Population size and distribution of Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

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ABSTRACT

Good estimates of population size are essential in conservation efforts, especially the management of rare or threatened species. Nile Crocodiles (*Crocodylus niloticus*) were once abundant in the Lake St Lucia estuarine system, until the arrival of the first European explorers precipitated declines through hunting and persecution. The depleted population was restocked from 1967 to 1976 and responded well to strict protection measures, with a mean annual increase of 13.0 % up to the early 1990s, stabilising thereafter.

Annual aerial surveys have been conducted most years since 1972, but crocodile diving behaviour (submerged bias) and observer bias were never quantified. To obtain correction factors, we used data from GPS-satellite transmitters attached to Nile Crocodiles, to augment aerial and spotlight survey parameters that couldn’t account for diving behaviour. We furthermore used two airplanes in aerial surveys to estimate observer bias. We estimated the lake system’s sub-adult/adult population at 858 crocodiles for 2013, and to account for interannual variance due to visibility bias, a mean estimate of 1005 ± 137 (95 % CI) for the period 2009 to 2013 was obtained.

Crocodiles were not distributed evenly throughout the system, but preferred low salinity aquatic habitat near the shoreline, sufficiently deep for cover and to enable movement. However, crocodiles utilised hypersaline areas for extended periods if freshwater seeps or shoreline wetlands were present. The estuary mouth closed in 2002 due to decreasing lake levels which herald the onset of a drought until 2011. Since 2004 freshwater intrusion from the nearby Mfolozi River through the Backchannels and Link canal reduced salinities in the ~27 km Narrows channel to a near freshwater state. This served as a refuge for most crocodiles during the drought when, at times, over 90 % of the lake was exposed and dry, or hypersaline. Spotlight counts in the Narrows indicated juvenile and sub-adult representation of 6.6 % and 19.9 %, respectively. These low cohort percentages are perhaps indicative of depressed recruitment due to the drought, but emergence ratio's for sub-adults suggested up to 54.0 % may be submerged (= invisible) during spotlight counts.

Large congregations formed during winter just south of the lake, with densities up to 372.9 crocodiles km^{-1}. This was seemingly a result of crocodile migration from hypersaline and dry conditions in the northern and central parts of the lake during the drought southwards.

The 2008 - 2013 aerial survey data suggests a notable declining trend. However, after correcting for submerged, observer and visibility bias, the population estimate for 2013 is comparable with 2003, the first year of the drought. This highlights the resilience of adult and sub-adult crocodiles at Lake St Lucia to perturbations such as a prolonged drought, as well as the importance of using correction factors for crocodile population estimates. Our correction factors will improve the accuracy of future aerial and spotlight surveys at Lake St Lucia, thereby facilitating a more effective management response to population stresses.

INTRODUCTION

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

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

The number of individual organisms at any given time in a population is a key metric in population biology (Williams et al. 2002). Even though the exact number of animals may be impossible to quantify, some knowledge of population size is often required for effective management (Leopold 1933, Bayliss 1987, Caughley and Sinclair 1994), especially when dealing with rare or threatened species (Primack 2000, Lancia et al. 2005). Uncorrected crocodile census techniques, such as aerial and spotlight surveys, are not useful estimators of absolute abundance due to visibility bias (crocodiles present but obscured by vegetation, inside a burrow, water turbidity), diving bias (the proportional time a crocodile is submerged) and observer bias (crocodiles in an observer's line of view and the number of crocodiles counted by that observer during a survey (Bayliss 1987, Shirley et al. 2012), each of which can significantly influence survey accuracy (Bayliss et al. 1986). However, if correction factors can be derived and applied to census data, crocodile surveys can provide more accurate information on the temporal and spatial distribution of the population and its response to physical and biological changes, increasing management effectiveness.

Despite a legacy of long term Nile Crocodile monitoring at Lake St Lucia of the longest monitored Nile Crocodile population, the proportion of present but undetected individuals during a given survey remains unquantified because supplementary information is required to estimate bias. We predicted that diving and observer bias cause substantial survey undercounting and that corrected estimates would result in a more accurate population estimate. Consequently, we aimed to obtain correction factors for diving bias using GPS-satellite transmitter data, and for observer bias by simultaneously counting crocodiles from two airplanes. These correction factors could then be applied to historical and present surveys.

MATERIALS AND METHODS

Study area

The Lake St Lucia estuarine system is situated in the north-eastern corner of KwaZulu-Natal province, South Africa (Fig. 1). It consists of a ~35,000 ha main lake basin, 6 km wide when filled to capacity, and a shoreline length of ~400 km (Taylor et al. 2006). The system is ~67 km in length including the Narrows, a ~27 km, 100-200 m wide tidal channel connecting the lake to the Indian Ocean.

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

The total survey distance for crocodiles is ~600 km, which include the shoreline length of the Narrows, streams, rivers, channels, Lake Bhangazi and all islands. The majority of the lake's shoreline is exposed with little vegetation, facilitating good observation of crocodiles from an airplane. However, streams and rivers flowing into the main lake are all heavily vegetated, making it difficult to count crocodiles from the air. Freshwater intrusions and seepage and their affiliated aquatic macrophytes (reeds and sedges such as *Phragmites australis* and *Juncus kraussii*) also obscure visibility. Additionally, the estuary mouth closed in 2002, and since 2004 salinities in the Narrows channel have decreased due to freshwater intrusion from the nearby Mfolozi River through the Backchannels and Link canal, leading to a sharp increase in shoreline vegetation and submerged macrophytes (e.g. *Stuckenia pectinata*), increasing visibility bias.

Lake St Lucia is a longitudinal, shallow waterbody with a mean depth of 0.98 m (Hutchison 1974), and features high turbidity due to wind effect and wave action (Taylor 2006). This impedes observing crocodiles in the water, and submerged crocodiles will be missed altogether.

Variations in catchment rainfall patterns, often between consecutive years, can have a considerable effect on lake levels and salinity, influencing the distribution and visibility of crocodiles and the accuracy of censusing. Historically, crocodiles were distributed from the Mkhuze River in the north, along the eastern shoreline and western shoreline south of Hell's Gate, Mphathe Stream and Narrows to the Mfolozi and Msunduzi Rivers in the south (Fig. 1).

During the last twenty years, human disturbance (e.g. increased settlements, small scale farming, water extraction and illegal gillnetting) especially in the northwest and southwest, led to a contraction of crocodiles away from the north and south. Therefore, connectivity with other Nile Crocodile populations in the region (e.g. Hluhluwe-iMfolozi and uMkhuze Game Reserves) is unlikely given increasing and extensive human disturbance and development along the feeding rivers. Refer to Chapter 1 for additional information on the study area.

Distribution and relative abundance

Aerial surveys

We conducted ten aerial surveys between 19 June 2009 and 13 June 2013 to record the distribution, relative abundance and seasonal movement pattern of crocodiles. Fixed-wing Cessna 182 (four-seater), a Bushbaby (two-seater) aircraft, and a Microlight Trike were used. The primary observer (Combrink) was present during all surveys and additional observers all had previous experience in crocodile aerial surveys. For the June (= winter) surveys, weather conditions were regarded as acceptable if wind speed was < 20 km/hour and cloud cover < 25 %. Aircraft departure always occurred after 10:00 in order to maximise the number of basking (= visible) crocodiles in the survey area (Downs et al. 2008). The position of each crocodile or group of crocodiles was marked with a GPS, and number of individuals recorded. Crocodile localities and the survey track were mapped in ArcView 9.3 (ESRI, Redlands, USA). Refer to Appendix 1 for survey routes flown during the study. The duration of each survey was recorded. Means ± standard errors are reported throughout.

In order to interpret historical crocodile distribution and movements in relation to the recent drought period, we obtained spatial and abundance records from journals, theses, published survey reports and maps from the former Natal Parks Board (now Ezemvelo), the Ezemvelo St Lucia research office and Ezemvelo St Lucia Crocodile Centre.

Spotlight surveys

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

Determining biases for aerial and spotlight surveys

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

We compared successful GPS-observations with unrecorded/unsuccessful, but scheduled "missed-observations" for the periods 10:00-14:00 ("day"), 19:00-01:00 ("night") and between months. These time periods are representative of the hours aerial and spotlight surveys were conducted, respectively. We summed the successful observations and missed-observations for day and night periods separately to obtain mean total and monthly emergence ratios. Factorial ANOVA was used to test for significant differences between months and time periods. Finally, we used the emergence ratios to estimate correction factors for diving bias during aerial and spotlight surveys.

Observer bias (the proportion of visible crocodiles in the observers field of view missed during a survey) was quantified through a double-counting technique (Magnusson et al. 1978, Hutton and Woolhouse 1989, Williams et al. 2002). Derived correction factors were used to estimate observer bias during past surveys and can be applied to future surveys using a single airplane, which is standard procedure for St Lucia crocodile surveys.

Population estimate

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

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

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

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

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

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

RESULTS

Distribution and relative abundance

Aerial surveys

The mean St Lucia sub-adult and adult crocodile count from 2009 to 2013 was 722 ± 35.6 (range: 113 - 819, Table 1). Overall, less crocodiles were counted in June 2013 (616) compared to June 2009 (819). The June 2011 (760) and 2012 (745) counts were similar, but more compared to the 670 crocodiles observed in June 2010 (Fig. 2).

Crocodiles were distributed throughout most of the lake system, albeit at low densities. By far the largest concentration was recorded south of the lake, in the Narrows (192 ± 55.8) and Potters Channel, a dredged extension of the Narrows (167 ± 25.2). On average, 448.0 ± 54.1, or 62.1 % of individuals, were concentrated in the Greater Narrows (Table 1), reaching a high of 82.1 % in 2010, in less than 2.0 % of the entire lake system. Crocodiles were also recorded in South Lake (117.2 ± 26.9; 16.2 % of mean total) and 87.2 ± 22.5 in North Lake (12.1 % of mean total), of which 70.8 % (62 ± 14.9 crocodiles) were found in Tewati Bay, a ~25 ha bay along the eastern shoreline fed by fresh seeping groundwater. Remaining parts of the system accounted for < 10 % of individuals, with areas containing, on average, > 30 crocodiles restricted to three freshwater shoreline seepage areas: Dead Tree Bay/Jubangoma (39 ± 10.9), Lake Bhangazi (31 ± 9.2) and Catalina Bay (32 ± 5.3). Very few crocodiles were found in the extreme north or south, or in False Bay (Table 1).

We recorded temporal variation in crocodile densities, consistent with previous findings (Pooley 1982b, Leslie 1997). As expected, more crocodiles were observed in June (winter basking behaviour), e.g. 670 in 2010 compared to 113 in January (summer) 2011, when most crocodiles were in the water and less visible or submerged (Table 1). Water temperature data support this; mean daily water temperature (10:00 to 14:00) varied significantly (One-way ANOVA: $F_{(22, 15444)} = 594.60$, $p = 0.00$) between winter (June 17.0 ± 0.1 °C) and summer (November 25.7 ± 0.2 °C, January 27.4 ± 0.1 °C). We counted less crocodiles during winter south of the lake (Greater Narrows) in 2013 (245) compared to 2012 (435) or 2009 (518). More individuals were observed in North Lake in 2013 (115) compared to 25 in 2010 and 68 in 2012 (Table 1).

The large proportion of crocodiles recorded south of the lake from 2009 to 2012, resulted in large basking congregations during winter. Exceptionally large congregations of > 200 individuals were counted in the Narrows and Potters Channel. Large basking formations in North Lake in 2003 (Tewati Bay = 192, Selly's Lakes = 203 and Fani's Island = 99) dispersed as the north and central parts of the lake dried out subsequently.

We noted changes between years in the size and location of basking congregations in the Narrows due to changing water levels (Fig. 3). Elevated (and cold) water levels during the 2010 winter flooded parts of a large 2009 basking area (199 crocodiles) just south of the Mphathe Stream confluence. Crocodiles moved north to Potters Channel, and basking crocodiles increased from 111 (2009), 163 (2010) to 261 and a density of 372.9 crocodiles km^{-1}, in 2011.

Diving bias during aerial surveys

The mean crocodile emergence/submergence ratio during the day (10:00 – 14:00) was 0.8 ± 0.04, which differed significantly throughout the year (One-way ANOVA: $F_{(11, 214)} = 15.427$, p = 0.000), with most crocodiles (93.7 % ± 0.04) emerged in June during winter and least (58.4 % ± 0.05, Table 3) in February during summer. June was the coldest month with mean water temperature 17.0 ± 0.1 °C, and air temperature 18.6 ± 0.2 °C (Fig. 4). We noted a strong inverse correlation (r = -0.95) between water temperature and diurnal crocodile diving behaviour (Fig. 5a).

The 3.0-3.5 m size class was most often emerged (85.6 % ± 0.03 %) with 2.5-3.0 m crocodiles the least (80.7 % ± 0.02 %), but these differences were not significant (One-way ANOVA: $F_{(3,222)} = 0.643$, p = 0.588, Fig. 5a and Table 3). June to August were the months with least variation in diving behaviour between size classes (Fig. 6a), with all sizes spending very little time submerged during the day (mean = 6.4 ± 0.8 % submerged). From November to February there was a marked divergence in the diurnal diving behaviour of different sized crocodiles, with > 4 m crocodiles being submerged most, followed by 2.0-2.5 m, then 2.5-3.0 m while 3.0-3.5 m individuals were emerged most often during a summer's day (Fig. 6a).

Spotlight surveys

Spotlight counts (n = 10) in the Narrows between June 2009 and June 2012 revealed temporal variation in crocodile density, with the lowest figure in January 2011 (2.2 crocodiles km^{-1}) and the highest (10.27 crocodiles km^{-1}) in July 2010 (Table 4).

We corrected spotlight counts for diving bias (Table 2) resulting in a range of 2.98 - 15.91 crocodiles km^{-1}. Water depth determined the most northern start/end point of each survey and this had a considerable effect on the length of the survey transect. Low water levels (0.47 m, measured at St Lucia bridge, Fig. 3) during the first survey on 19 June 2009 restricted the survey to 11.1 km, but as water depth increased to 0.82 m in the Narrows on 4 July 2011, we were able to extend the survey route to 20.3 km. The highest count was made in July 2010 when it was possible to include a large basking area just south of the Mphathe Stream confluence (129 crocodiles counted during the previous month’s aerial survey). During the June 2009 spotlight survey, water depth was not sufficient to include the Mphathe Stream confluence area, which might have increased the encounter rate. Increased water levels in July 2011 (0.80 m, Fig. 3) allowed the Mphathe Stream confluence area to be surveyed, but the high water level flooded the Mphathe Stream confluence area used the previous years and crocodiles moved north into Potters Channel in search of dry basking areas. The July 2011 encounter rate (11.98 crocodiles km^{-1}) was lower compared with the previous year (15.91 crocodiles km^{-1}), but it was possible to survey only 1.2 km (i.e. 50 %) of Potters Channel before it became too shallow. The largest basking congregation along Potters Channel was at the northern tip, which was too shallow to be included in the survey. It was not possible to survey the entire Potters Channel in a boat at night due to the shallow nature of the channel and impenetrable stands of *P. australis* in some areas. Dense stands of *P. australis* along the banks also prevented night foot surveys.

Diving bias during spotlight surveys

The mean emergence/submerge ratio of crocodiles during the night (18:00 – 02:00) was 0.55 ± 0.04 %, which differed significantly throughout the year (One-way ANOVA: $F_{(11,\ 214)}$ = 2.0855, p = 0.02). Most crocodiles (66.1 ± 0.05 %) were emerged in January (summer) and least (43.5 ± 0.04 %) during winter in June (Table 3), with a strong positive correlation (r = 0.93) between water temperature and nocturnal emergence behaviour (Fig. 5b).

We recorded size-related variation in nocturnal diving behaviour, with smaller crocodiles spending less time emerged than larger crocodiles, i.e. sub-adults (2.0-2.5 m) spent significantly less time (Tukey HSD test, p = 0.019) emerged (46.0 ± 0.03 %) compared with crocodiles > 4 m (61.5 ± 0.04 %, Fig. 6b and Table 3). Nocturnal diving behaviour for different size-classes showed least variation during May, September and January, with all crocodiles spending least time submerged in January (34.0 %, Fig. 6b). November was the month with most variation between the sizes classes.

Population estimate

During the simultaneous double count on 13 June 2013, 373 crocodiles were counted by *both* airplanes, 244 crocodiles *only* by the Cessna that flew anticlockwise around the lake and 115 *only* by the Bushbaby, flying clockwise. We corrected the raw count figures for diving bias using the diurnal June correction factor of 1.0627 (Table 2). This resulted in 396 crocodiles counted by *both* Cessna and Bushbaby, 259 crocodiles *only* from the Cessna and 122 *only* from the Bushbaby. We estimated the 2013 sub-adult and adult population for St Lucia at 858 crocodiles (variance = 171.87, s = 13.11, S.E. = 0.02, CV = 1.5 %).

We used the simultaneous aerial count results to obtain a detectability bias correction factor, i.e. 858 / 656 = 1.31. After correcting for observer/detectability bias, the 2009 to 2013 mean population was estimated at 1005 ± 137 crocodiles, 95 % C.I. (Table 1 and Fig. 7).

Using these correction factors we estimated the St Lucia Nile Crocodile population since 1972 (Fig. 7).

DISCUSSION

Distribution and relative abundance

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

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

Aerial surveys

Aerial counts have been conducted at St Lucia since 1972, and remains the most efficient method to cover the ~600 km survey area, of which large areas is too shallow for boat-based counts. The results emphasised the importance of aerial surveys in June, when water temperatures are at a minimum and crocodiles are most visible during the day while basking. During the study period (2009 - 2013) up to 82.1 % of crocodiles were recorded south of the lake, in the Greater Narrows area. This ~27 km channel never dried out, unlike the main lake where more than 90 % was exposed and dry in 2006 (Whitfield and Taylor 2009). Salinities in the Greater Narrows were low due to freshwater intrusion from the Mfolozi River, with suitable water depth for cover, courtship and mating, deep cool water during summer for thermoregulation, more fish relative to the main lake (Cyrus and Vivier, unpublished data) and dense shoreline stands (*P. australis*) providing shelter.

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

The number of crocodiles south of the lake peaked in 2010, but good rainfall (> 700 mm) in December 2010 and January 2011 resulted in a reconnection of previously isolated waterbodies and decrease in salinity. Crocodiles responded by moving north, and the 2013 count showed a 44 % decrease from the Greater Narrows and 69 % increase in South Lake and North Lake.

Diving bias during aerial and spotlight surveys

Crocodilian survey techniques (e.g. aerial and spotlight counts) are subjected to a number of biases affecting survey results (Bayliss et al. 1986, Bayliss 1987) and if unaccounted for, generally with correction factors, misleading results might preclude the most effective management response (Woodward and Moore 1993). Visibility bias occurs when a crocodile is present in the survey area but not visible to the observer (Bayliss 1987), while observer or detectability bias is the likelihood that an animal within an observer's field of view will not be seen (Caughley 1974, Ferreira and Pienaar 2011). A number of factors influence visibility bias, such as vegetation density, width and sinuosity of the river, sunlight reflection on the water, and the degree of wariness of the particular crocodilian population during spotlight surveys (Bayliss 1987). One of the most important factors affecting visibility bias is diving behaviour, i.e. submerged crocodiles not being visible to the observer the moment a survey craft (airplane or boat) travels over, or is in sighting proximity of the animal.

Crocodilians are aquatic ectotherms and water temperature plays an crucial role in their thermoregulation, with shallow surface water used to increase heat, whilst deeper water provides a refuge from high temperatures (Smith 1979). It has been noted that crocodilians becomes less active under cooler conditions and might therefore be spending more time submerged, reducing the probability of being counted (Woodward and Marion 1978, Hutton and Woolhouse 1989, Woodward and Moore 1993).

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

Spotlight surveys

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

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

Lake Sibaya (Combrink et al. 2011) and Lake Bhangazi 7.3 % (Combrink, unpublished data). The reasons for the elevated EO level in the Narrows might be a combination of wariness and habitat factors. The shallowness of the survey transects and impenetrable submerged macrophytes (*S. pectinata)* colonising extensive shoreline areas, often prevented the boat to approach a crocodile close enough for a size estimate.

The 19.9 ± 2.9 % mean sub-adult component was comparable with 16.0 % in the Panhandle of the Okavango Delta (Bourquin 2007), 21.6 % in Flag Boshielo Dam (Botha 2005), 27.4 % at Jozini Dam (Champion 2011) but considerably lower than 39.0 % in Lake Nyamithi at Ndumo Game Reserve (Calverley and Downs 2014). The Narrows is connected to the Mphathe Steam, the largest nesting area (mean = 18.2 ± 5.6 nests) during the study period (Chapter 3). Although not possible to estimate, it is suspected that a large proportion of these hatchlings will (as hatchings, yearlings or juveniles) disperse downstream into the Narrows, facilitated by strong flow subsequent to localised rainfall events. We predict a high survival rate of these young crocodiles due to dense shoreline vegetation lining the banks of the Mphathe Stream and Narrows, providing shelter and apparent food abundance such a small fish, amphibians and insects.

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

Population estimate

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

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

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

MANGEMENT RECOMMENDATIONS AND AREAS OF FUTURE RESEACH

- Continue with the annual winter aerial counts in June to record the relative abundance of crocodiles and their distribution.
- Lake level monitors have recently been installed in a number of areas. Given the apparent positive correlation between lake level and visibility/vegetation bias during aerial crocodile surveys, lake levels could now be quantified on the day of the aerial count and incorporated as a covariate in future count estimates.
- Partition the sub-adult component using photographic/videographic techniques from a slow-flying aerial platform, such as a double-motorised paraglider. The sub-adult proportion in the Narrows was estimated at 19.9 ± 2.9 % during spotlight counts, but it would be valuable to validate this figure with data for the entire population.

- Quantify the effect of airplane speed and visibility/vegetation bias during high lake levels using a slow-flying aerial platform, such as a double-motorised paraglider. This should preferably be conducted a close as possible to the annual aerial survey and the obtained ratio could be used as an additional “speed” correction factor in future surveys.
- The proportion of juvenile crocodiles (non-hatchlings: 0.4 - 1.5 m, ~1 - 4 years of age) is unknown at Lake St Lucia. They are not observed during aerial surveys due to their size and preference of vegetated habitats. This is an important segment as they represent recruitment and will affect future abundance. Estimate juvenile abundance through a mark-recapture programme by setting traps in nesting and adjacent areas.

CONCLUSIONS

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

By using emerge/submerge ratios from GPS-transmitters attached to crocodiles, we found that 6.3 % of crocodiles were submerged (= invisible) during a winter (June) aerial survey, 33.9 % during a summer (January) spotlight survey, increasing to 56.5 % in winter

(June). Observer bias accounted for 30.7 % crocodiles missed by observers from a second airplane during a simultaneous survey in winter (June). We corrected aerial and spotlight counts for these biases and estimate the 2013 adult and sub-adult population at 858 crocodiles and a mean (2009 to 2013) population estimate of 1005 ± 137 crocodiles (95 % CI).

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

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

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I acknowledge the former Natal Parks Board, (now Ezemvelo KZN Wildlife), for conducting annual crocodile aerial surveys over many years, in particular the role of Tony Pooley and Dave Blake during the formative years. I thank Ginger Skinner and Greg Nanni (Natal Parks Board and Ezemvelo) for their significant role as pilots, flying virtually all the counts through the years. I thank Donovan Barton-Hobbs for flying a number of aerial surveys during the study period (2009 to 2013), a well as Lawrence Munro (Ezemvelo) and Tony Gibson (double motorised paraglider). I acknowledge Mark Robertson, past CM of the Ezemvelo St Lucia Crocodile Centre for his huge contribution to this study, especially with supplying boats and outboard motors for fieldwork. I thank Dirk Rossouw, Ezemvelo CM Mfabeni Eastern Shores, for his support and involvement with the study.

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Caption for Figures

Figure 1. Nile Crocodile aerial surveys at the Lake St Lucia estuarine system: 2009 - 2013

Figure 2. Adult and sub-adult crocodiles counted during aerial surveys at the Lake St Lucia Estuarine system: 1972 - 2013. Arrow (1) indicates a 13.0 % growth from 1972 - 1993. Arrow (2) indicates an apparent stabilisation phase, possibly as a result of density dependent mechanisms and arrow (3) a notable decline in the counts. The perforated circles (4 - 11) indicate years where the low count was possibly a function of sub-optimal survey conditions (i.e. mostly high lake levels increasing visibility bias) and thus not a reflection in the actual population.

Figure 3. Monthly water level (cm) measured at the St Lucia bridge during the study period. Note that this level reflects the Narrows and not the main lake basin.

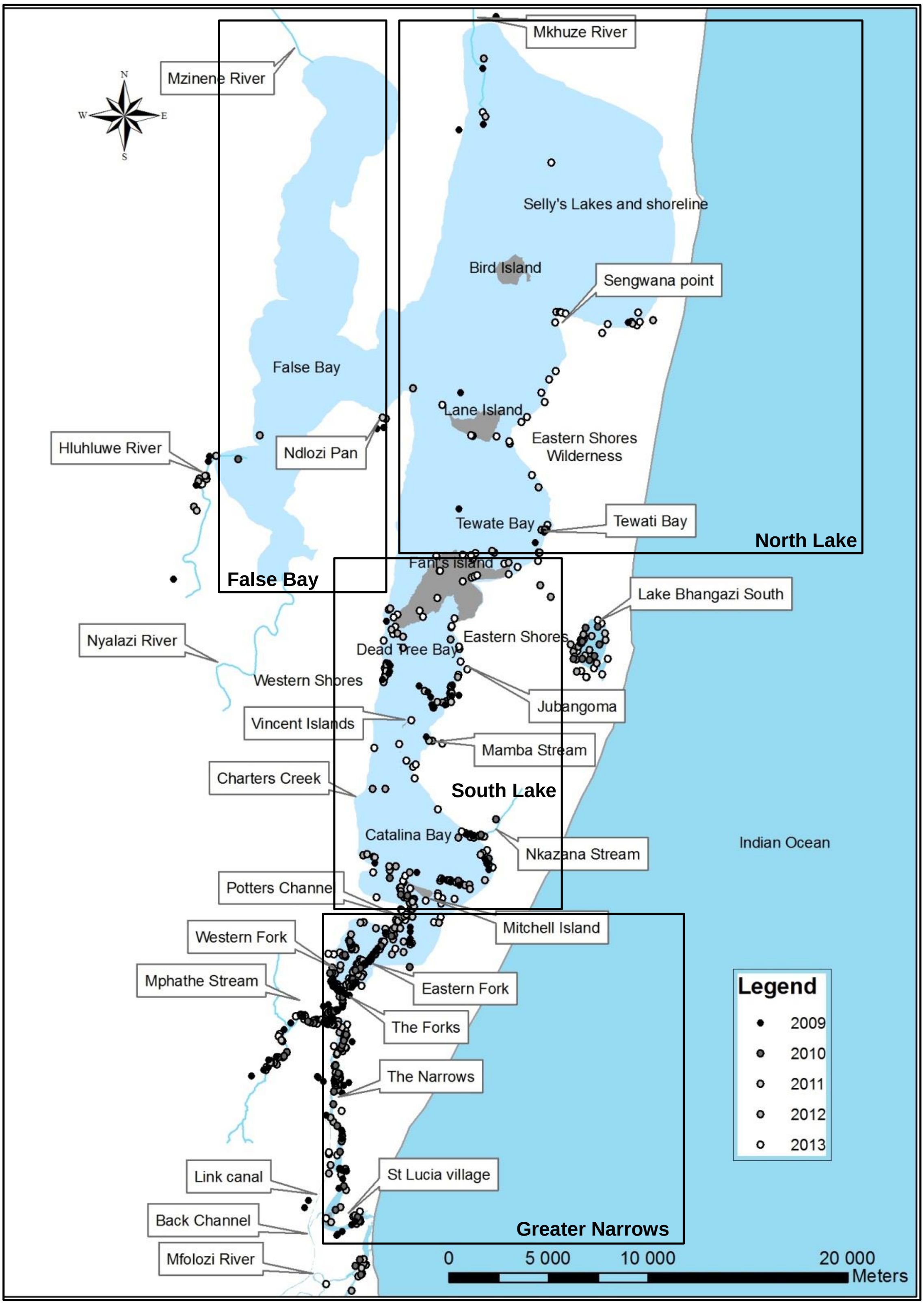
Figure 4. Mean daily water and air temperatures from 0800 - 14:00 at Lake St Lucia during the study period.

Figure 5. Strong inverse correlation (r = -0.954) between water temperature and emergence ratio of crocodiles during the day (a) and strong positive correlation (r = 0.934) between water temperature and emergence ratio of crocodiles at night (b).

Figure 6. Monthly diurnal (a) and nocturnal (b) emergence ratios for Nile Crocodiles at St Lucia.

Figure 7. Estimated Nile Crocodile population at Lake St Lucia, based on diving and detectability bias correction factors. Black bars represent raw count data, grey bars represent submerged bias and observer/detectability bias, and the figure on top of each bar represents the 5 year mean estimate.

Figures



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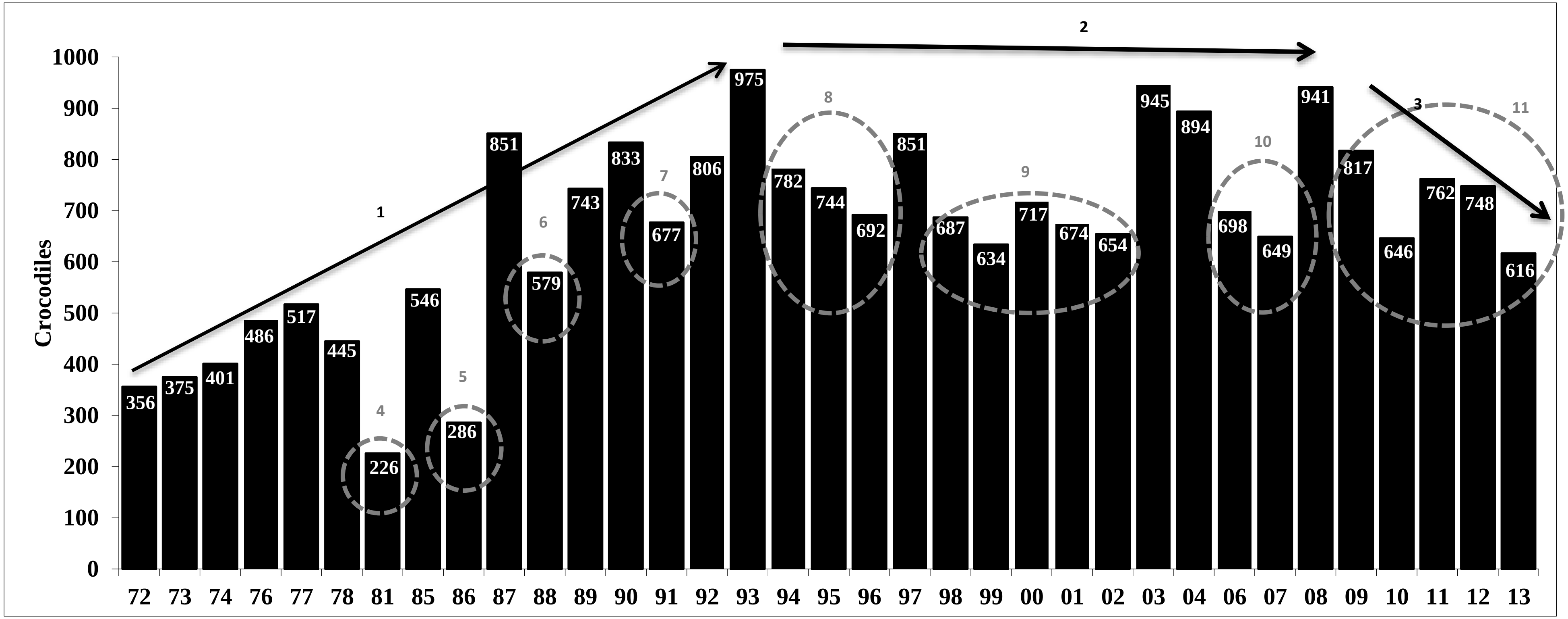

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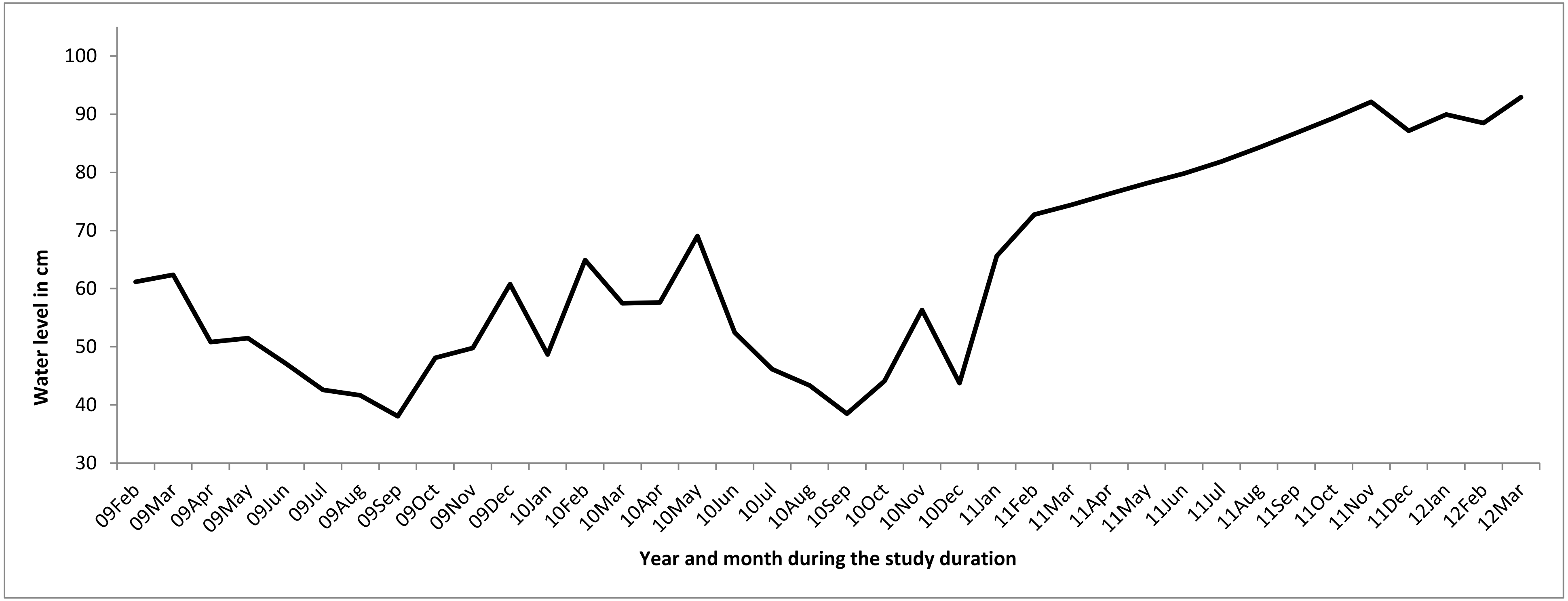

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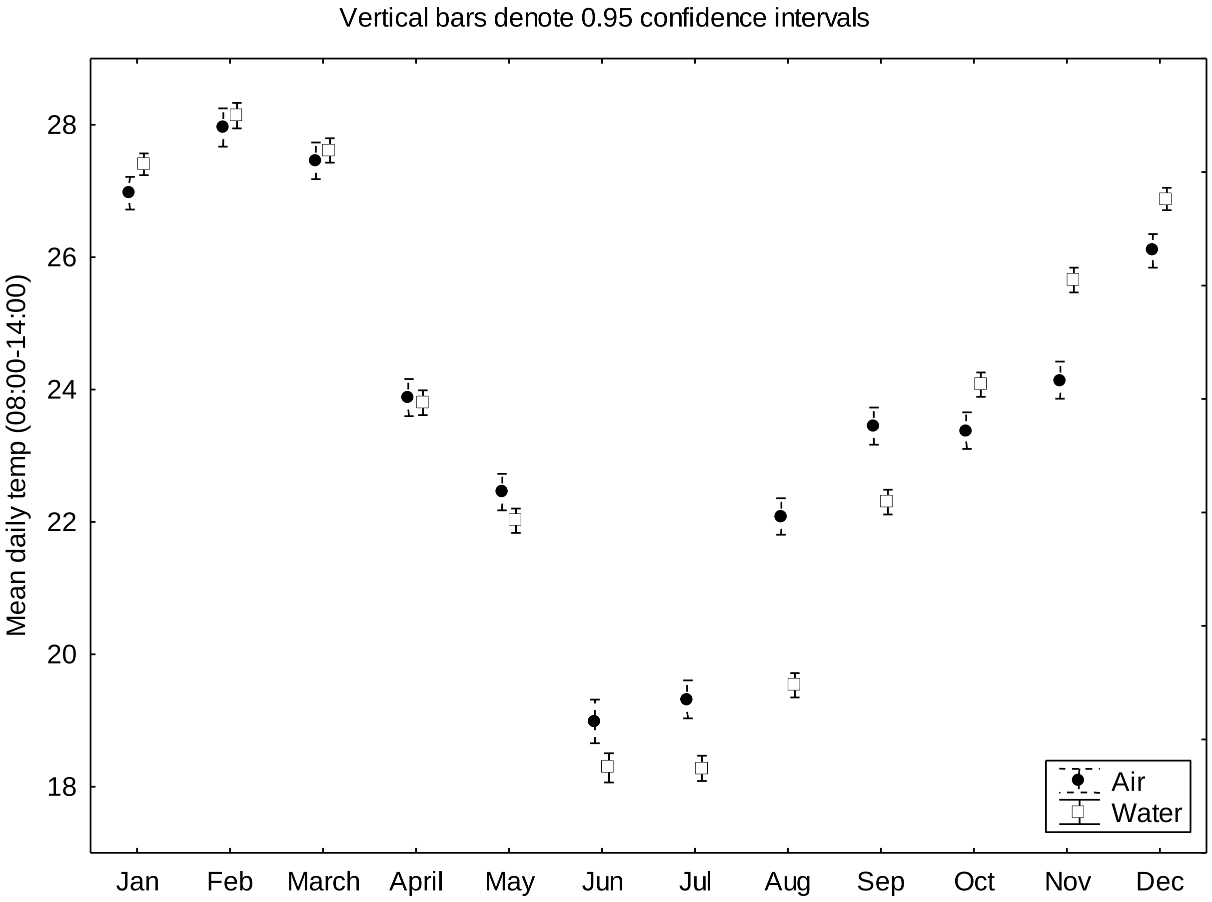

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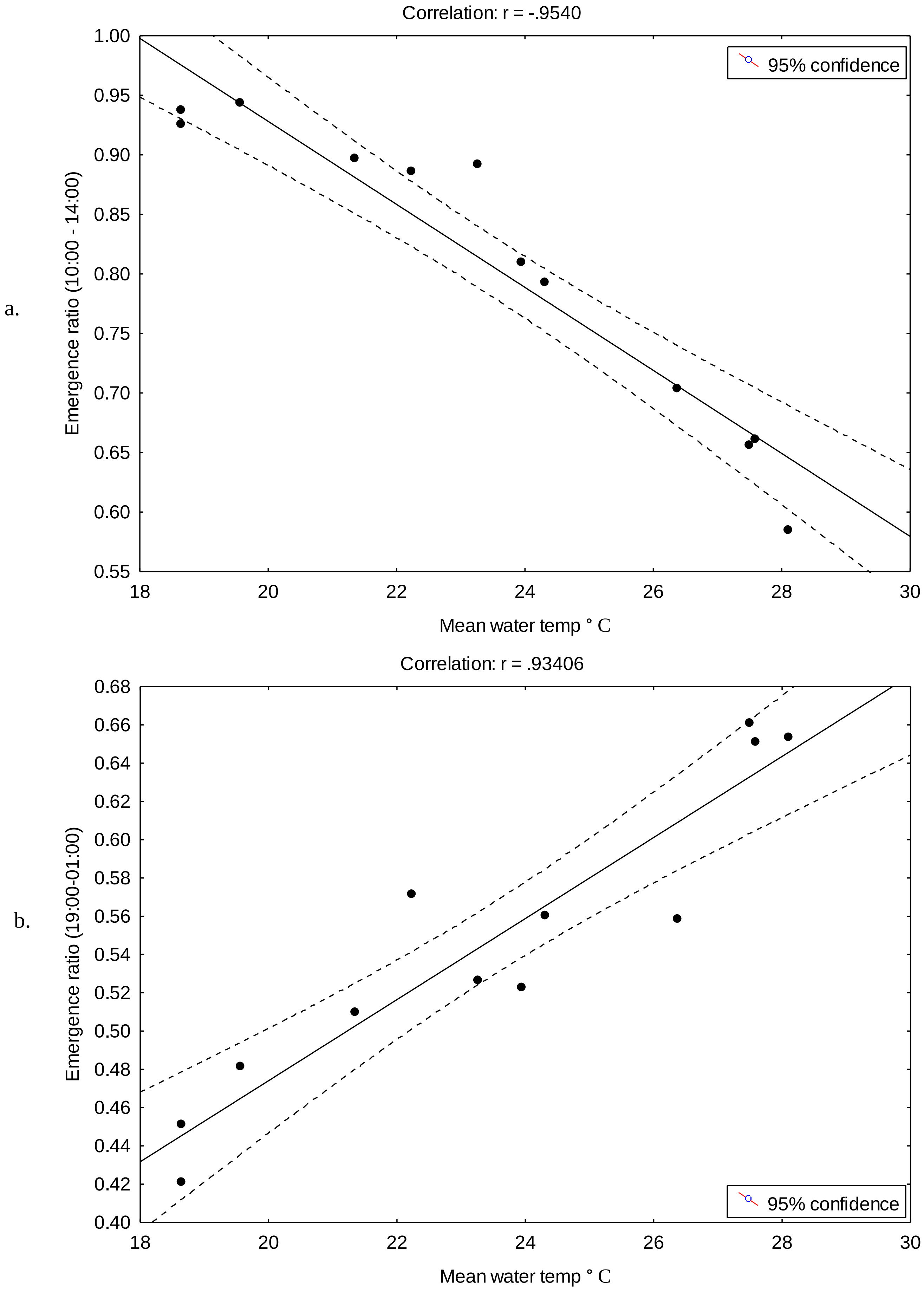

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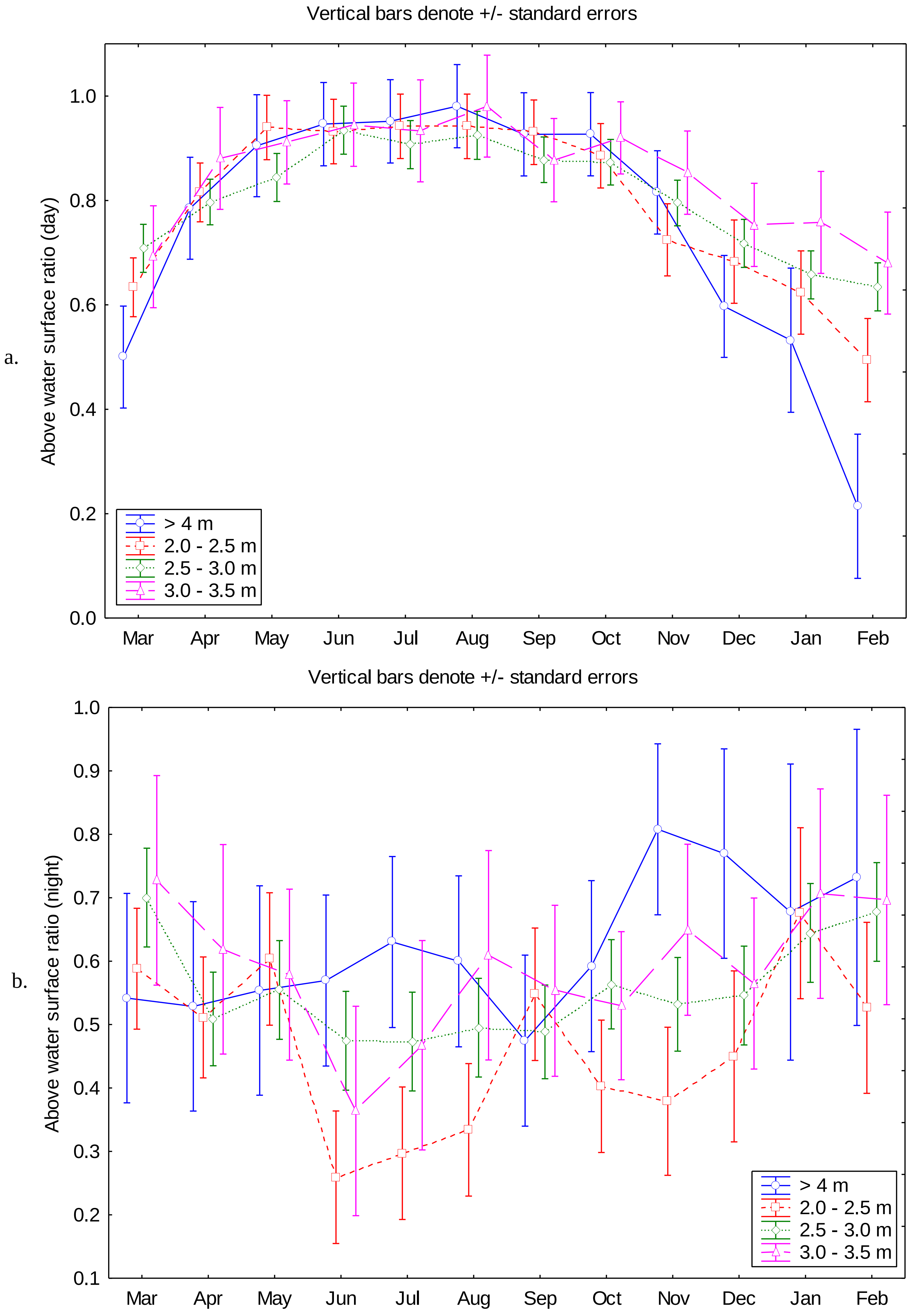

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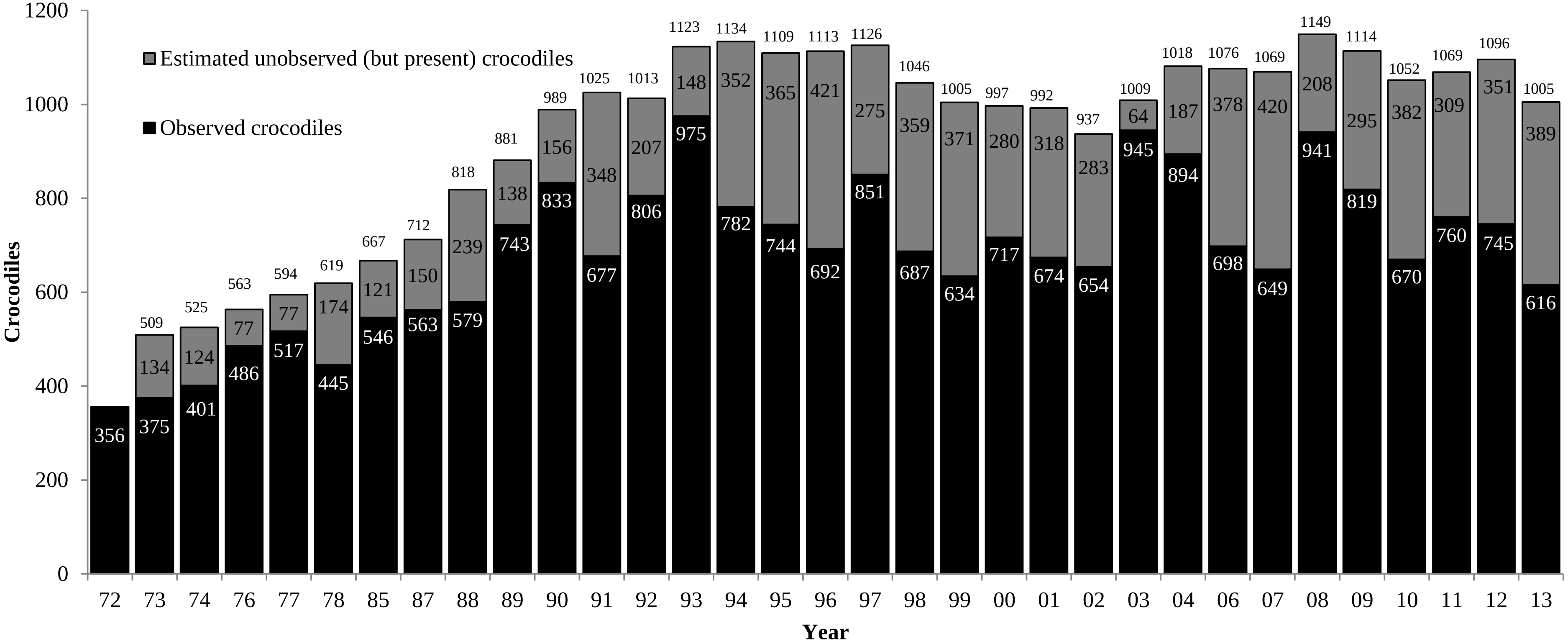

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Captions for Tables

Table 1. Crocodile aerial counts at the Lake St Lucia Estuarine system 2009 - 2013

Table 2. Day and night emergence ratios of Nile Crocodiles with water and air temperatures

Table 3. Spotlight surveys in the Narrows: 2009 - 2012

Tables

Table 1. Nile Crocodile aerial counts at the Lake St Lucia estuarine system 2009 - 2013

Area	**19 Jun ‘09**	**12 Sep ‘09**	**29 Nov ‘09**	**10 May ‘10**	**22 Jun ‘10**	**22 Jan ‘11**	**22 Jun ‘11**	**14 Jun ‘12**	**13 Jun ‘13**	**Mean June count**
Msunduzi River	0	0	0	1	1	0	0	2	0	1
Mfolozi River	12	2	5	4	4	0	3	2	10	6
Link canal	2	0	0	0	0	0	0	1	2	1
South of St Lucia estuary	**14**	**2**	**5**	**5**	**5**	**0**	**3**	**5**	**12**	**8**
Narrows	345	239	139	86	281	30	137	168	27	192
Eastern Fork	57	95	0	49	88	7	70	82	20	63
Western Fork	5	18	0	5	16	5	21	30	27	20
Potters Channel	111	107	0	116	165	1	261	155	144	167
Brodies crossing	0	0	0	0	0	0	3	0	27	6
Greater Narrows (Estuary)	**518**	**459**	**139**	**265**	**550**	**43**	**492**	**435**	**245**	**448**
Mphathe Stream	12	36	37	1	24	1	23	24	28	22
eSingeni wetland	0	4	0	0	1	0	0	0	0	0
Makakatana Bay	0	0	0	8	4	2	0	16	4	5
Mitchell’s Island	0	0	0	0	0	0	0	0	12	2
Catalina Bay	24	28	39	75	16	31	39	40	11	26
Fani’s Island - Catalina Bay	22	0	0	0	0	0	0	0	5	5
Nkazana Stream	11	5	9	0	5	0	6	11	32	13
Ndhlozi point – Fani’s island	0	1	1	0	0	1	17	40		11
Mamba Stream	1	5	5	1	2	2	6	3	0	5
Dead Tree Bay & Jubangoma	52	16	5	0	0	7	38	42	65	39
Fani's Island	1	1	0	38	0	4	0	0	48	10
South Lake	**111**	**56**	**59**	**122**	**27**	**47**	**106**	**152**	**189**	**117**
Tewati Bay	116	107	61	30	25	2	61	57	51	62
Lane island	32	0	0	0	0	0	0	0	26	12
Sengwana	0	0	0	0	0	0	0	0	29	6
Eastern Shores pans	0	0	0	0	0	0	0	2	0	0
Selly's lakes	1	25	10	0	0	0	9	5	7	4
Mkhuze River	8	3	0	7	0	0	3	4	2	3
North Lake	**157**	**135**	**71**	**37**	**25**	**2**	**73**	**68**	**115**	**88**
Lake Bhangazi South	0	54	26	51	38	15	54	40	22	31
False Bay	0	0	0	0	0	0	0	0	0	0
Hluhluwe River	5	0	0	5	0	2	5	15	5	6
Ndhlozi Pan	2	7	8	1	0	3	4	6	0	2
False Bay area	**7**	**7**	**8**	**6**	**0**	**5**	**9**	**21**	**5**	**8**
Total raw counts	**819**	**753**	**345**	**478**	**670**	**113**	**760**	**745**	**616**	**722**
Est. incl. diving bias correction (*)	**869**	**830**	**416**	**532**	**712**	**152**	**808**	**792**	**655**	**796**
Est. incl. observer bias correction (**)	**1140**				**933**		**1058**	**1037**	**858**	
Population estimate (5 year mean)	**1114**				**1052**		**1069**	**1096**	**1005**	

*** Diving bias correction factors: Jan = 1.34, May = 1.11, June = 1.06, Sep = 1.10, Nov = 1.21**

**** Population estimate include observer/detectability bias correction factor of 1.31 for June**

Table 2. Day and night emergence ratios of Nile Crocodiles with water and air temperatures

Month	Day 10:00-14:00	Mean air temp °C	Mean water temp ° C	Night (19:00-01:00)
January	0.656 ± 0.05	25.05	27.50	0.661 ± 0.05
February	0.584 ± 0.05	25.62	28.10	0.654 ± 0.05
March	0.661 ± 0.04	25.10	27.59	0.651 ± 0.04
April	0.810 ± 0.04	21.61	23.95	0.523 ± 0.04
May	0.886 ± 0.04	20.44	22.23	0.571 ± 0.04
June	0.937 ± 0.04	16.99	18.64	0.435 ± 0.04
July	0.895 ± 0.04	17.17	18.65	0.451 ± 0.05
August	0.911 ± 0.04	18.78	19.57	0.492 ± 0.05
September	0.874 ± 0.04	20.45	21.35	0.516 ± 0.04
October	0.874 ± 0.04	21.44	23.26	0.529 ± 0.04
November	0.793 ± 0.04	22.22	24.31	0.560 ± 0.04
December	0.704 ± 0.05	24.24	26.38	0.559 ± 0.04
Mean	0.7988 ± 0.04	21.59	23.46	0.5508 ± 0.04

Table 3. Spotlight surveys in the Narrows: 2009 to 2012

Date	Crocodiles observed	Juveniles <1.5 m	Sub-adults 1.5-2.5 m	Adults >2.5 m	Eyes Only	Survey route (km)	Encounter rate	Diving correction	Total crocodiles	Encounter rate crocodiles/km
19 June 2009	62					11.11	5.6	57.88	98	8.81
01 July 2010	150	17	33	50	50	14.60	10.3	54.9	232	15.91
05 October 2010	144	25	30	11	78	16.50	8.7	47.36	212	12.86
23 November 2010	75	3	17	10	45	10.88	6.9	43.97	108	9.92
11 January 2011	44	0	6	15	23	19.80	2.2	33.88	59	2.98
02 February 2011	92	5	27	25	35	17.60	5.2	34.65	124	7.04
29 March 2011	92	8	28	19	37	16.70	5.5	34.9	124	7.43
04 July 2011	157					20.30	7.7	54.9	243	11.98
16 February 2012	95	3	10	41	41	15.90	6.0	34.65	128	8.05
21 June 2012	109	3	10	15	81	18.30	6.0	57.88	172	9.40

CHAPTER 3

Movements and activity of Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

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ABSTRACT

Understanding the movement ecology of a species can have important management implications for its conservation. Despite crocodilians being apex predators, important ecosystem indicators, and sometimes responsible for conflict with humans or livestock, there have been relatively few detailed studies on movement and activity levels. We investigated the movements and activity of 18 Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa, from 2009 to 2012. We used satellite transmitters with sufficient daily positional fixes to give detailed activity and movements at spatial and temporal scales.

The overall activity level of Nile Crocodiles at Lake St Lucia was 41.0 %, and it differed significantly throughout the day. There was a significant seasonal effect on activity and Nile Crocodiles were most active during autumn (52 %) and least active during winter (30.47 %). We found a positive correlation between crocodile size and crocodile daily movements at Lake St Lucia. The mean daily movement was 1244 m and it differed significantly between individual crocodiles. The daily movements of adult males were the largest for all crocodiles, did not differ much from adult nesting females, but were larger than adult non-nesting females and sub-adults. Adult Nile Crocodiles moved more at night, but sub-adults moved significantly more during the day.

There was a seasonal difference in crocodile movement. Water temperature correlated with mean monthly crocodile movement, and the correlation was stronger for sub-adults than adults. Overall, the longest movements were made during autumn and the shortest in winter.

About 60 % of total daily movements were < 1 km per day, but for sub-adults this was 96 %. Adult males made the longest total daily movements between 1-5 km’s, but nesting females proportionally made most movements > 5km.

This study highlights the need for more field research on crocodilian activity and movements at similar detailed spatial and temporal resolution. This would allow for comparison across populations and species for a more complete interpretation of their biology, ecology and life history.

Keywords: Movements, activity, Lake St Lucia, Nile Crocodile, *Crocodylus niloticus*

INTRODUCTION

The movement of organisms is a complex process that depends on the individual’s ability to perform tasks, as well as the nature of the landscape on which it moves (Getz and Saltzc 2008). Movement is often a result of short-term objectives such as survival, maintenance and reproduction, or it may be influenced by longer term fitness implications such as population extinction (Holyoak et al. 2008). Therefore, knowledge of the movements and distribution of animals precede insight and understanding of fundamental population processes (Hutton 1989). Understanding movement ecology is important for a number of reasons; most importantly it is seen as a crucial component of climate change, habitat fragmentation, biological invasions and the spread of pests and diseases (Nathan et al. 2008). In particular, information of the daily and seasonal movement patterns, space use and activity ranges will increase understanding of crocodilian responses to hydrological patterns and restoration processes (Mazzotti et al. 2009) salinity tolerances (Pooley 1982a, Taplin and Loveridge 1988, Leslie and Spotila 2000), drought conditions, habitat preferences (Webb et al. 2009), diel rhythms (Cloudsley-Thompson 1964, Brien et al. 2008) and biological processes such as breeding and nesting (Hutton 1989).

The first crocodilian movement study using radiotelemetry was in the late 1960’s (Joanen and McNease 1970) and signified a major advancement in recording movement and spatial data over conventional capture-recapture techniques. It was now possible to locate tagged animals at regular intervals and concurrently record other variables such as habitat use. However, despite significant work on space-use and movement patterns, crocodilian radio telemetry studies were constrained to a large degree by their remote habitats, shy and cryptic nature, semi-aquatic existence, nocturnal activity patterns, and sensitivity to the presence of field researchers. Significant advancements in transmitter technology enabled the use of satellite technology, allowing crocodilians to be studied remotely for the first time

(Botha 2005, Read et al. 2007, Strauss et al. 2008, Campbell et al. 2013). A variety of satellite tracking technologies are available today, and the choice is a function of functionality and cost (Thomas et al. 2011). So far, two satellite systems have been used in published crocodilian studies; Argos-satellite (Read et al. 2007, Campbell et al. 2010, Campbell et al. 2013) and GPS-satellite (Strauss et al. 2008)..

The Argos satellite doppler-based system uses a platform transmitter terminal transmitting a pulse detected by the Argos polar-orbiting satellites located ~800 km above the earth. The data are downlinked and processed at the Argos processing centres. The accuracy of each location point is assessed to specific classes, ranging from 350 m to >1000 m (Argos user manual) and the researcher receives the data via the Argos system (Thomas et al. 2011). Conversely, GPS tracking devices receive transmissions from a constellation of ~24 satellites 20 000 km above the earth (NAVSTAR). When four or more satellites are in view, GPS provides a location accuracy of < 30 m. Data is transferred to the researcher using one of several options, for instance GSM (Global System for Mobile Communication), Iridium, Globalstar or Geostationary systems. We used a GSM module and received the positional data as a SMS (short message) via a GSM mobile phone network, stored on a server. The transmitter was interactive and could receive SMS commands, for instance, to change the interval at which location information is transmitted (Sundell et al. 2006).

Two other systems make use of a Store on board (SOB) functionality. The SOB system stores the data on the transmitter to be downloaded when the transmitter detaches from the animal at a pre-set time, and for data to be retrieved using the recapture system the animal needs to be physically recaptured in the field (Thomas et al. 2011).

Satellite based recording systems, have the ability to record large amounts of detailed temporal and spatial information, with seemingly little disturbance to the study animal, apart from the initial capture stress and the presence of the transmitter on the crocodile. The significant data increase allowed for more detailed analysis and understanding. Despite these improvements, there have been relatively few crocodilian movement studies (Table 1) compared with many other vertebrate taxa.

The Nile Crocodile is one of the largest extant crocodilian species and recognised as a top predator in both aquatic and adjacent terrestrial ecosystems throughout its range. Since Cott’s (1961) seminal work half a century ago, a large and growing body of literature has evolved on the biology, ecology, behaviour and management of the species, but very few detailed results on movements or activity have been presented and long term datasets are lacking.

Despite popular misconception, movements and periodic prolonged sustained activity seems to be associated with all life stages of the Nile Crocodile, subjected to season, water level, salinity, feeding opportunities, cover, human disturbance and reproductive state. Pooley (1969) described a clear and predictable seasonal movement pattern of Nile Crocodiles from the Phongola River in South Africa to seasonal pans in the adjacent floodplain during summer. As water levels decreased in winter, pans dried out and reduced water levels combined with increased human disturbance resulted in crocodiles moving back to the Phongola River and the disturbance free permanent pans within Ndumo Game Reserve. Pooley (1969) also documented seasonal movements between winter basking areas and summer nesting areas in Lake St Lucia and noted movements from the main lake into rivers or freshwater seepage areas during late winter when salinities increased (Pooley 1982a). Swanepoel (1999) recorded Nile Crocodile movements in the Olifants River between Kruger National Park and Moçambique, with downstream movements corresponding with high water levels (December/January) and upstream movements in April, during reduced river flow. Whitfield and Blaber (1979) and Pooley (1982) recorded crocodile movement in Lake St Lucia from North Lake and the lower Mfolozi and Msunduzi rivers coinciding with the

Striped Mullet (*Mugil cephalus*) migration and concentration in the Narrows during February to June**.** Leslie (1997) documented an extensive movement event of ~120 km for a tagged Nile Crocodile from the St Lucia Backchannels up the Mfolozi River. Botha (2005) recorded movements of larger crocodiles from the Olifants River into Flag Boshielo Dam during winter and back to the river at the onset of summer with rising water levels.

Crocodilians are mainly aquatic, but Kofron (1993) described terrestrial movements of juvenile Nile Crocodiles between the Runde River and temporary ponds during the wet season. Pooley (1982b) noted an increase of crocodiles in irrigation canals, farm dams and ponds during times of droughts when wetland areas were drying out.

Leslie (1997) recorded tidal facilitated movements of hatchlings in the St Lucia Narrows and a 21.5 km movement by a 395 cm male using capture-recapture methods. She tracked an adult female for 85 days over a 6 km stretch in the St Lucia Narrows. Although the number of VHF resightings was low, it provided some insight into short-term movements of Nile Crocodiles at Lake St Lucia.

Using remote monitoring technology, we studied Nile Crocodile movements and activity in the Lake St Lucia system. This resulted in a large quantity of spatial movement data over an extended time period. We anticipated that the outcome would facilitate insights into movement and activity patterns for different sex and size classes with varying season and lake water levels. We hypothesized that water temperature would influence both activity and movements of crocodiles, and that some individuals or size classes might exhibit elevated activity levels, but with a low frequency of longer total daily movements. We expected a number of novel findings, which should translate into more effective management of Nile Crocodiles in the Lake St Lucia estuarine system.

AIMS

Movements and activity patterns are two fundamentally important, but poorly understood components of the life history of Nile Crocodiles at Lake St Lucia. The overall aim of this study was to obtain sufficient spatial and temporal information in order to increase our understanding of these complex and dynamic processes for improved conservation management. The sub-aims were:

- To determine activity levels for the different size, sex and reproductive classes throughout the day, per month and between seasons.
- To determine diel movement patterns for the different size, sex and reproductive classes throughout the day and between seasons.
- To determine diurnal and nocturnal movement patterns for the different size, sex and reproductive classes and between seasons.
- To determine total movements per day for the different size, sex and reproductive classes and between seasons.

MATERIALS AND METHODS

Study area

The Lake St Lucia estuarine system is situated in the KwaZulu-Natal province of north-eastern South Africa (Fig. 1). At ~60 km in length, which includes the ~27 km long Narrows channel that connects the lake to the ocean, and an average of 6 km in width when filled to capacity, it is the largest estuarine system in Africa (Cowan 1997), but nonetheless very shallow with mean depth of 0.98 m . It is a dynamic system driven by varying environmental and ecological processes, each occurring at differing spatial and temporal scales (Taylor 2006). Please refer to Chapter 1 for a more comprehensive description of the study area.

Capture methods and transmitters

We used a combination of capture techniques to maximise success under diverse habitat conditions. The preferred capture technique was noosing, i.e. securing a self-locking cable around the crocodile's head, but detachable harpoons, treble hooks and traps were also used. We used GPS-satellite transmitters (African Wildlife Tracking) in combination with a GSM download system, while one GPS-satellite transmitter transmitted data via the Iridium system. Units were attached to crocodiles subcutaneously with orthopaedic stainless steel wire. Capture methods, transmitters and transmitter attachment are described in Appendix 2 and Appendix 5 respectively.

Partitioning of seasons

The Nile Crocodile is an aquatic ectotherm and ambient temperature plays a crucial role in thermoregulatory behaviour (Cott 1961). Temperature gradients in water are often sharp with deep water providing a refuge from high temperatures while shallow surface water are used for heat gains (Smith 1979). Past aerial surveys at Lake St Lucia indicated considerable seasonal variation in basking behaviour, peaking in winter while during summer most crocodiles bask very little (Pooley 1982a, Leslie 1997). In order to analyse movement and activity, we used water temperature to partition a calendar year into four unequal length seasons. This allowed for comparisons with other crocodilian studies, as most authors referred to seasons in their discussion (Joanen and McNease 1970, Joanen and McNease 1972, Taylor et al. 1976, Goodwin and Marion 1979, Taylor 1984, Kushlan and Mazzotti 1989, Hocutt et al. 1992, Rootes and Chabreck 1993, Botha 2005, Bourquin 2007, Calverley 2010, Champion 2011, Calverley 2013).

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

Movement analysis

Prior to analysis, Greenwich Mean Time (GMT) data were converted to South African local time, GMT + 2 h. Despite some seasonal variation in daylight, for the purpose of the analysis we defined the period 06:00 to 18:00 as "day" and 18:00 to 06:00 as "night". The displacement between two successive GPS points x_1y_1 and x_2y_2 was calculated using the following equation: 1000 x (6371.1 x ((2 x asin (sqrt ((sin((radians(y_1) - radians(y_2))/2)^2) + cos (radians (y_1)) x cos (radians(y_2)) x (sin((radians(x_1) –radians (x_2))/2)^2)))))). Displacements between GPS point locations were considered an interval along the shortest path connecting them. Therefore, displacements should be considered a minimum, as the actual distance would not have been a direct line.

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

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

Activity levels

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

Mean daily movement (MDM)

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

Diel movement patterns

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

Nocturnal and diurnal movements

Nocturnal and diurnal movements of Nile Crocodiles were determined at St Lucia. Despite some seasonal variation in daylight, for the purpose of the analysis we defined the period from 06:00 to 18:00 as "day" and from 18:00 to 06:00 as "night". We accounted for scheduled, but unrecorded GPS duty cycles. We fitted the data to P-P plots in order to check for normality, and non-normal distributions were logarithmic transformed. Kolmogorov-

Smirnov and Shapiro-Wilk normality tests were used determine if the transformed data was appropriate for parametric tests. Normally distributed datasets were analysed in using One-way and Factorial ANOVA.

Total daily movements

We investigated total daily movements as an additional indicator of Nile Crocodile activity. We calculated total daily movements as the sum of successfully recorded displacements and mean values for unrecorded scheduled displacements, over a 24 h period. Total daily movements were allocated to one of six categories; 0-1 km, 1-2 km, 2-3 km, 3-4 km, 4-5 km and > 5km and proportions were determined representing the % daily movement for each crocodile per movement category. For crocodiles that were tracked over seasons, we calculated the proportion of daily movements within each season according to the six categories. These were analysed using RMANOVA.

Statistical analyses were conducted in Statistica 7.1 (Tulsa, Ok, USA). Results are presented as means ± standard error (S.E.).

RESULTS

Transmitters

We attached 20 transmitters to 19 Nile Crocodiles from 16 September 2009 to 3 March 2011 in the Lake St Lucia estuarine system (Fig. 1 and Table 1). Female 447 never entered the GSM network to download data. The mean field data days per transmitter was 397 ± 61, range: 50 – 1111. The mean GPS fixes per transmitter was 3129 ± 457, range: 491 – 9063. We have knowledge of a single transmitter (AG 301) which became detached from a crocodile after 535 days. Three transmitter-fitted crocodiles have been recaptured to date, 297, 555 and 1070 days subsequent to transmitter attachment. None of the recaptured animals showed any sign of infection at the attachment site.

Activity levels

Diel pattern

The overall activity level (proportional displacements > 20 m, irrespective of the length of the displacement) of Nile Crocodiles at Lake St Lucia was 41.0 %, and it differed significantly throughout the day (X^2 = 1364.93, df = 5, p = 0.00, n = 18, Fig. 2). After a period of low activity (30 %) during late morning (10:00 to 14:00), activity increased to 36 % during the afternoon (14:00 to 18:00) and continued to increase to a maximum of 46 % during the early evening (18:00 to 22:00). Between 22:00 and 02:00 activity decreased slightly to 45 %, continued to decrease to 44 % from 02:00 to 10:00 (Fig. 2 and Table 2). Lake St Lucia Nile Crocodiles displayed a bimodal activity pattern with low activity (< 37 %) from 10:00 to 18:00 and high activity (> 44 %) from 18:00 to 10:00 (Fig. 2).

The overall activity level for adult males was 44 %, non-nesting females 51 %, nesting females 35 % (excluding the nesting summer season = 42 %) and sub-adults 30 %. Activity levels of adult males, non-nesting and nesting females differed significantly (p = 0.00) throughout the day (Fig. 3a), but temporal variation for sub-adults was not significant.

Monthly variation

We found a significant positive correlation between crocodile monthly activity and water and air temperatures, with water temperature (r = 0.798, p = 0.002) correlating slightly stronger than air temperature (r = 0.773, p = 0.003), Fig. 4. Crocodiles were > 50 % active from Jan. to April when water and air temperatures were high, peaking in March (58.8 %). From April to June crocodile activity reflected the sharp decline in air and water temperatures which reached a minimum of 18.3 °C in June and July. Minimum overall activity level (27.9 %) was recorded in August when the largest difference between mean water and air temperature was recorded, suggesting that the relative difference between water and air temperature was a more important predictor of inactivity than water or air temperature *per se*. The sharpest increase in crocodile activity occurred between Aug. (27.9 %) and Sep. (46.9 %). Subsequent to a marginal activity decreased during October, activity levels increased again for Nov. and Dec., as did water and air temperatures (Fig. 4).

Non-nesting females (n=3) were most active among all crocodiles and activity peaked in Jan. (82 %, Fig. 5a), decreasing to 72.2 % in Feb. Nesting females (n=4) also showed a decrease from Jan. to Feb., but at very low activity levels due to nest guarding activities (Fig. 5a). Conversely, both adult males (n=7) and sub-adult (n=3) activity increased from Jan. to Feb., with sub-adult activity reaching a maximum in Feb. (73.5 %) which was the highest recorded activity of all crocodiles for that month (Fig. 5a).

Adult male activity peaked in March (68.3 %, Fig. 5a) and after March all crocodiles, except nesting females, decreased in activity with sub-adults the lowest in June (18 %), and adult males and non-nesting females in July (28.7 % and 27.1 % respectively). Activity levels of nesting females increased sharply from Feb. (20.9 %) while nest guarding to a maximum of 63.1 % in April during the post-nesting period (Fig. 5a).

The activity of all crocodiles increased sharply from Aug. to Sep., apparently in response to a similar sudden increase in water temperature from 19.5 °C to 22.3 °C. All crocodiles, except nesting females, displayed a somewhat lower activity level during Oct. while nesting females continued to increase, reaching a second annual peak in activity during Oct. before activity decreased towards December due to nesting. Sub-adult activity increased very sharply from 25.0 % in October to 60.1 % in November.

Seasonal variation

There was a significant seasonal effect on activity (X^2 = 1967.08, df = 3, p = 0.00 Fig. 3b and Table 2) and as expected Nile Crocodiles were least active during winter (31 %) with the lowest activity level (17 %) recorded during late morning (10:00 to 14:00) in winter. Spring activity (41 %) was comparable with mean annual activity (41 %), but during summer activity was considerably higher (45 %), with crocodiles being most active in autumn (52 %). The highest recorded activity period was early evening (18:00 to 22:00) in autumn (58 %), Table 2.

The diel activity rhythm throughout the seasons followed a similar pattern with crocodiles being least active during late morning, followed by increased activity during the afternoon, peaking during the early evening. Thereafter activity levels stabilised or decreased slightly until there was a sudden decrease in activity during late morning (Fig. 6).

Seasonal variation in activity levels for adult males, non-nesting and nesting females and sub-adults were all significant (p = 0.00), with crocodiles most active in summer and least active in winter, except nesting females, Table 1 and Fig. 3b. Nesting females were most active in autumn (57 %) and least active during the summer nesting period (26 %, Table 2).

Mean daily movement (MDM)

The relevant descriptive statistics for the 19 Nile Crocodiles tracked from 16 Sep 2009 to 20 October 2012 in the Lake St Lucia estuarine system are summarised in Table 1. They include overall levels of activity (%), mean, median and largest daily movements, number of data points, field transmitter days and days moved > 20 m and > 100 m.

We found a positive correlation between crocodile size and MDM (Pearson's r = 0.888, n= 15, p = 0.00). MDM of Nile Crocodiles at St Lucia was 1244 ± 161 m and there was a significant difference between crocodiles (One-way ANOVA: $F_{(17, 6767)} = 92.90$, p = 0.00, Fig. 7a). Female 601 (293 cm TL) moved the longest daily distances (2854 ± 66 m, median 2331 m) and Male 533 (204 cm TL), a sub-adult and smallest individual in the study, the shortest (213 ± 94 m, median 97 m Table 1, Fig. 7a).

The largest study animal, Male 520 (413 cm TL from the Mphathe Stream) MDMs were the longest (2178 ± 247 m, median 1996 m) of adult males, and Male 501 (316 cm TL) MDMs the shortest (906 ± 235 m, median 469 m, Fig. 7a and Table 1). However, they were both tracked for a relative short duration, 50 and 55 days respectively. Considering the five adult males tracked for more than 200 days, the MDMs of Male 504 from Lake Bhangazi was the highest (1936 ± 75 m, median 1587 m) and Male 121 from Catalina Bay the lowest (1592 ± 110 m, median 493 m). The MDMs of adult males (1712 ± 34 m, n = 7) were the highest of all crocodiles, did not differ significantly from adult nesting females (1606 ± 36, n = 4), but were significantly different (Factorial ANOVA: $F_{(3, 7013)} = 252.19$, p = 0.00) from adult non-nesting females (919 ± 46 m, n = 4) and sub-adults (294 ± 52 m, n = 3), Fig. 8.

Sub-adult MDMs were significantly different from each other (One-way ANOVA: $F_{(2, 1031)} = 31.88$, p = 0.00). The largest, Female 534 (212 cm TL), moved the most (334 ± 18 m, median 270 m), followed by Male 503 (208 cm TL, 311 ± 82 m, median 156 m). The smallest study animal, Male 533 (204 cm TL), made the shortest movements (213 ± 22 m, median 97 m).

Diel movement patterns

The diel movement pattern showed a definite rhythm and crocodile movements per time period differed significantly throughout the day (One-way ANOVA: $F_{(15, 34395)} = 45.05$, p=0.00, n = 18, Fig. 9a). Crocodiles moved the least (115 ± 5 m) during late morning 10:00-

14:00, increased movement (174 ± 6 m) during the afternoon 14:00-18:00, and peaked (289 ± 6 m) during the early evening (18:00-22:00). Between 22:00-02:00 movements decreased somewhat (258 m ± 6 m) and stayed relatively constant during the early morning hours (02:00-06:00: 247 ± 6 m and 06:00-10:00: 243 ± 6 m) before a sharp decline in the late morning (Fig. 9a).

The diel MDM pattern of adult males and nesting females showed much higher variability and a preference for nocturnal movements compared to non-nesting females and especially sub-adults (Fig. 9b). Sub-adults moved significantly less without any preference to a particular time period. Nesting females made significantly longer movements than adult males during very early morning, afternoon and early evening, but adult males moved significantly more during the late morning (Fig. 9b). Non-nesting females moved significantly less than adult males and nesting females throughout a 24 h day, except during late morning, but movements were not significantly different to nesting females (Fig. 9b).

Diurnal and nocturnal movements

Overall, Nile Crocodiles moved significantly more at night (753 ± 12 m) than during the day (554 ± 12 m, Factorial ANOVA: $F_{(1, 13560)} = 24.76$, $p = 0.00$, Fig. 7b and Fig.10). This was true for both females (706 ± 16 m at night; 509 ± 16 m in the day, One-way ANOVA: $F_{(1, 7376)} = 9.3186$, $p = 0.00228$) and males (808 ± 17 m at night; 607 m ± 17 m in the day, One-way ANOVA: $F_{(1, 6182)} = 15.79$, $p = 0.00007$).

Adults moved significantly more at night (864 ± 13 m) than during the day (625 ± 13 m, One-way ANOVA: $F_{(1, 11492)} = 51.66$, $p = 0.00$). Similarly, adult males and females were significantly more mobile at night compared to the day (nocturnal male movement 981 ± 21 m; diurnal male movements 728.1 ± 20.66, One-way ANOVA: $F_{(1, 4922)} = 29.44$, $p = 0.00$;

adult females nocturnal movements 776 ± 17 m, diurnal movements 547 ± 17 m; One-way ANOVA: $F_{(1, 6568)} = 22.84$, $p = 0.00$).

Sub-adults moved significantly (One-way ANOVA: $F_{(1,2066)} = 24.123$, $p = 0.00$) more during the day (161 ± 7 m) than at night (133 ± 7 m).

Monthly movements

Overall, the monthly MDMs differed significantly throughout the year (RMANOVA: $F_{(11, 88)} = 3.1761$, $p = 0.00$, Fig. 11). We also found considerable temporal variation between the different crocodile groups (Fig. 5b). Water temperature significantly correlated with mean monthly crocodile movement, and the correlation was stronger for sub-adults (Pearson's $r = 0.852$, $p = 0.00$ Fig. 12a) than adults (Pearson's $r = 0.799$, $p = 0.002$ Fig. 12b).

Sub-adult MDMs per month were longest in Feb. (534 m, Fig. 5c), while adult males and non-nesting females' MDMs per month were the highest in March, 2302 m and 1461 m respectively. After March all crocodiles, except nesting females, daily movements decreased with each month and sub-adults and adult males moved least in June (148 m and 1094 respectively), non-nesting females in July (431 m) and nesting female in Aug. (704 m). The mobility of nesting females were severely restricted during the nest guarding period (Dec. to Feb., Fig. 5b).

Nesting female movements increased rapidly subsequent to the nesting period, reaching a maximum of 2531 m during May, most likely to improve condition before winter. Thereafter mobility decreased sharply, reaching a low in Aug. The MDM of all crocodiles, except sub-adults, increased between Aug. and Sep. (Fig. 5b) while sub-adults remained the same before a continued increase from Oct. to Feb (Fig 5c).

Seasonal movements

There was a significant seasonal difference in the MDMs of crocodiles (One-way ANOVA: $F_{(3, 6705)} = 88.241$, $p = 0.00$, Fig. 13a). The longest movements were made in autumn (1730 ± 59 m), followed by summer (1449 ± 34 m) and spring (1351 ± 49 m), while crocodiles least mobile during winter (948 ± 41 m). Tukey HSD post-hoc analysis revealed that movements during summer were significantly longer than winter movements. Spring mobility was significantly less than autumn, while winter movements were significantly lower than all other seasons (Fig. 13a).

Nesting females were most mobile during autumn (2529 ± 95), which was significantly more than all other crocodiles (Fig. 13b). Movements of nesting females during summer and winter and summer and spring were not significantly different, but spring movements (1597 ± 81 m) were significantly ($p = 0.00$) more than winter (1135 ± 66 m, Fig. 13b). The movements (MDM) for adult males during autumn (1938 ± 95 m), spring (1754 ± 76 m) and summer (1920 ± 54 m) were not significantly different, but winter (1290 ± 67 m) was significantly less. Adult non-nesting female movements during autumn (938 ± 134 m), spring (960 ± 122 m) and summer (1094 ± 75 m) were not significantly different, but movements during winter (610 ± 95 m) were significantly less (Fig. 13b). Sub-adults were significantly less mobile than all other crocodiles throughout the year. Sub-adult movements during winter (135 ± 95 m) and summer (398 ± 84 m), summer and spring (241 ± 117 m), and winter and autumn (282 ± 147 m) were significantly different, but mobility between autumn and spring, autumn and summer, and spring and winter were not significantly different (Fig. 13b).

Daily movements per distance category

We investigated daily movements per distance category as an additional indicator of movement. On average, most crocodiles (61.0 ± 5.7 %) moved < 1 km per day, 16.7 ± 2.3 %, 1-2 km, 10.0 ± 1.8 % 2-3 km, 5.2 ± 1.1 % 3-4 km, 3.0 ± 0.7 % 4-5 km, and 4.0 ± 1.0 % > 5 km per day, (Fig. 14a).

The proportion of daily movements differed significantly between adult males, non-nesting females, nesting females and sub-adults (RMANOVA: $F_{(15, 70)} = 7.18$, $p = 0.00$, Fig. 14b.). Adult non-nesting females made significantly more movements in the 0-1 km category per day (67.7 ± 8.1 %) compared with adult males (44.9 ± 6.1 %), but daily movements of non-nesting and nesting females (59.2 ± 7.8 %) were not significantly different. Almost all (96.4 ± 9.0 %) daily movements of sub-adults were < 1 km per day, significantly more than all other crocodiles (Fig. 12b).

The proportions of movements in the 1-2 km category were similar for adult males (22.1 ± 2.6 %) and non-nesting females (20.3 ± 3.5 %) with nesting females somewhat less (13.5 ± 3.5 %) and sub-adults significantly less (2.6 ± 4.0 %).

Adult males made the longest daily movements > 1 km but < 5 km’s, as nesting females proportionally made most movements > 5 km (7.5 ± 1.5 %). Only 5.19 % of non-nesting females were > 3 km per day, compare to nesting females’ 17.6 %.

DISCUSSION

Transmitters

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

Activity levels

The paucity of literature describing crocodilian activity levels reflects the difficulty in obtaining detailed spatial information of this aquatic predator, often in very remote and inaccessible areas. The overall temporal pattern confirms elevated nocturnal activity levels for Nile Crocodiles. However, during summer when water temperatures are high, the clear distinction between nocturnal and diurnal activity levels became diffused.

Nile Crocodiles are bimodally active at Lake St Lucia with a period of low activity (< 37 %) from 10:00-18:00 and high activity (> 44 %) from 18:00-10:00. Diel activity levels varied significantly and the seasonal variation in activity patterns was seemingly an interchange between water and air temperatures and solar radiation. Crocodiles were least active during winter with very little activity from 10:00-18:00, coinciding with winter basking behaviour (Combrink, pers. obs., Downs *et al.* 2009). Crocodiles returned to the water at night to escape the cool air temperatures (Chapter 2) with subsequent increased activity, especially during early evening when body temperatures are still elevated from basking. During summer when water temperatures were high, crocodiles were not reliant on solar radiation to elevate body temperatures and therefore seldom came ashore to bask, with an associated subsequent decrease in activity variance throughout the day.

Variation in monthly crocodile activity followed changes in water and air temperatures, except for nesting females. Their activity levels were strongly influenced by nest guarding activities, resulting in decreased activity during the summer nest period, followed by a rapid increase in post-nesting activity, possibly to improve condition, as water temperature decreased towards winter.

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

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

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

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

Brien (2008) recorded activity level of the Estuarine Crocodile during winter (cool dry season). Adult males seem to be somewhat more active (45.3 % and 44.8 %) compared with this study (mean 36.6 %), and they found a similar trend for a single sub-adult (22.7 %) compared with 13.8 % for this study. Winter activity levels of Estuarine Crocodile (mean 31.3 %) were remarkably similar to mean winter Nile Crocodile levels in this study (30.5 %).

Both studies recorded an adult female as the most active individual during winter, with Estuarine Crocodiles (51.5 %) and Nile Crocodiles (60.9 %).

Mean daily movement

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

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

Sub-adults were confined to specific shallow and vegetated habitats adjacent to the main and much deeper channel of the Narrows. They very seldom ventured into the deep water of the main channel possibly due to predation risk by larger crocodiles (Chapter 4). Of the three sub-adults, the smallest individual was the least mobile while the largest sub-adult made the longest daily movements. It seemed like habitat features, such as topography, affected adult movements as well. There was a general pattern that crocodiles confined to narrower and structurally complex parts of the system such as Mphathe Stream and the Narrows had a lower MDM, while crocodiles in main Lake St Lucia and Lake Bhangazi were making longer daily movements (such as 1086 m for a 402 cm male in a ~61 ha section of the Narrows, 1935 m for a 406 cm male in a ~220 ha freshwater lake, 444 m for a 270 cm non-nesting female along a 4.5 km freshwater stream and 1222 m for a 240 cm non-nesting female in the Narrows and Catalina Bay). Large parts of Lake St Lucia were completely dry for the first part of this study period. With increased rainfall and freshwater input from the Mfolozi River, water levels increased, which led to a range expansion of some crocodiles into previously dry parts of the lake, resulting in increased daily movement.

Kay (2004) found MDM of Estuarine Crocodile adult females in the lower Ord estuary, northern Australia, much lower (<1 km) compared with this study, but movements might have been restricted due to possible nesting activities in summer. The maximum daily movement recorded by a female was 10 100 m compared with 14 507 m for a Nile Crocodile (Female 601, Table 1) in this study. This was also considerably more than the previously recorded Nile Crocodile daily movement of 2 900 m at Lake Ngezi, Zimbabwe (Hocutt et al. 1992). Adult male Estuarine Crocodile movements (1578 m, range 600 – 3300 m) were somewhat less but related to movements in this study (1708 m, range 905 – 2178 m). The maximum daily movement recorded for a male (4.3 m) Estuarine Crocodile was 23 300 m moving downstream, and it was possible that a current or tidal effects could have facilitated the high rate of movement (Kay 2004). Read (2007) recorded a maximum daily movement of 30 400 m for a 4.5 m Estuarine Crocodile in the ocean homing back to its capture location. This remarkable movement rate was only possible due to Estuarine Crocodiles adopting behavioural strategies to use the momentum of favourable surface currents. This strategy required very little active swimming, reduced the daily energy budget and facilitated increased dispersing potential (Campbell et al. 2010). The maximum daily movement for Nile Crocodiles recorded in the Lake St Lucia system was 17 389 m by a 2.7 m female, also homing back to its capture location (Chapter 8).

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

Diurnal and nocturnal movements

Cott (1961) noted that Nile Crocodiles is nocturnally aquatic, but Hutton (1989) was able to determine the extent of behavioural differences between diurnal and nocturnal movements at Lake Ngezi. Overall, the mean nocturnal movement at Ngezi was 660.0 m, somewhat less than the 752.5 m for this study. However, Nile Crocodiles at Lake Ngezi were seemingly much less active during the day (73.16 m) compared to this study (554.02 m), while most Ngezi crocodiles moved > 20 m on less than 40 % of days (Hutton 1989). At St Lucia crocodiles moved > 20 m 92.0 % of days and > 100 m 65.6 % of days. Hutton (1989) noted that juveniles at Ngezi were more strictly nocturnal compared to adults. At St Lucia sub-adults were significantly more active during the day. We suggest this may be a temporal intraspecific predation avoidance strategy and equates to ecological separation of sub-adult and adults. Cott (1961), Graham (1968) and Hutton(1989) noted ecological separation between juveniles and adults, and we propose a similar dynamic at St Lucia, at least in the Narrows where sub-adults were tracked.

Seasonal movements

A number of crocodilian studies have attributed differences in seasonal movements, for the most part, to changes in temperature (Chabreck 1965, Joanen and McNease 1972, Goodwin and Marion 1979, Hutton 1989, Kay 2004). At St Lucia water temperature significantly correlated with mean monthly crocodile movement, and the correlation was stronger for sub-adults than adults. At Lake St Lucia, crocodiles were most mobile during autumn and females were also most active during autumn. Adult males were equally mobile in summer (1920.17 ± 54.33) and autumn (1937.53 ± 95.07). Nesting female mobility peaked subsequent to the three month nest guarding period, possibly due to searching of optimal feeding opportunities before winter. *Alligator mississippiensis* adult males were most active during summer (MDM = 855 m) with almost no movements during winter at the den site (Joanen and McNease (1972). Daily movements (4000 m) for adult male Estuarine Crocodile during summer were high (Kay 2004), with movements during winter (1300 m) remarkably similar to winter movements for St Lucia adult males (1290.24 m ± 66.63). It appears the temperate distribution of the American Alligator has a restrictive effect on winter mobility whereas Estuarine Crocodile and Nile Crocodile are relatively more active during winter, with Nile

Crocodiles at St Lucia often undertaking long journeys to winter basking congregations (Combrink, pers. obs., Chapter 2).

Total daily movements

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

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

CONCEPTUAL FRAMEWORK

A general conceptual framework for movement ecology was outlined by Nathan *et al.* (2008). They proposed three basic components related to the individual, i.e. internal state, navigation capacity and motion capacity, and a fourth component referring to external factors affecting its movement. Arrows indicated the direction of impact and the subsequent movement path feeds back to the internal and external components. We have presented a simplified conceptual framework for Nile Crocodile movement in the Lake St Lucia estuarine system (Fig. 15), based on these principals.

The most important external factors consisted of the physical environment or habitat and the diel and seasonal influence of water and air temperature. This affected the internal state, i.e. “why move”, of the individual crocodile as a result of three factors: nutrition, reproduction and social aspects. The internal state influenced both motion capacity and navigation capacity. The motion capacity consisted of swimming, overland walking if surface water was unavailable and in extreme circumstances and for very short distances, galloping.

Navigation capacity, i.e. “where to move”, consisted of hatchling dispersal from the natal area and juvenile and small sub-adult dispersal to the main lake. Nest site selection, territorial maintenance behaviour and homing instinct all were part of navigation capacity.

The actual movement path was a dynamic interplay of the external and internal factors affecting movement, the navigation capacity and motion capacity (Fig. 15).

MANAGEMENT CONSIDERATIONS

As a result of depleting populations and escalating threats, the Nile Crocodile is a threatened and protected species in South Africa, listed as Vulnerable (McLachlan 1978, Jacobsen 1988, Marais 2014). The Lake St Lucia estuarine system is host to the largest Nile Crocodile population within a single waterbody in South Africa and is the largest population in the province of KwaZulu-Natal. It is recognised that within the context of conserving a healthy and viable Lake St Lucia ecosystem, a specific management strategy is required for Nile Crocodiles (Taylor et al. 2007) which highlights research as a key objective to underpin management actions.

The general insights provided by this investigation will contribute to a more complete understanding of crocodile biology, ecology and life history. Specific information on diel, monthly and seasonal movement and activity levels will contribute to the survey and monitoring programme, a key management function. It will also support the dissemination of aspects pertaining to human-crocodile conflict, an important management component at St Lucia, as tourists and community members almost daily interact with shared natural resources such as water, fishing and reed harvesting.

Public and community education initiatives, another management objective, could incorporate aspects of the study in education programmes such as audio-visual material and posters as part of existing talks and interpretation at the St Lucia Crocodile Centre to stimulate interest in crocodile biology, ecology and conflict mitigation.

Crocodile activity and movements are such integral components of their overall ecology and life history that improved understanding of these aspects will indirectly inform numerous other management actions such as capture of damage-causing crocodiles, protection of key basking and breeding areas, and determining routes of law-enforcement foot and boat patrols at Lake St Lucia.

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Caption for Figures

Figure 1. The Lake St Lucia estuarine system, the largest estuarine system in Africa.

Figure 2. Temporal activity pattern (%) of Nile Crocodiles (n=18) in the Lake St Lucia estuarine system

Figure 3. Temporal (a) and seasonal (b) activity pattern of Nile Crocodiles in the St Lucia estuarine system.

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Figure 14. A general conceptual framework of movement ecology of Nile Crocodiles in the Lake St Lucia estuarine system based on the model of Nathan *et al.* 2008.

Figures

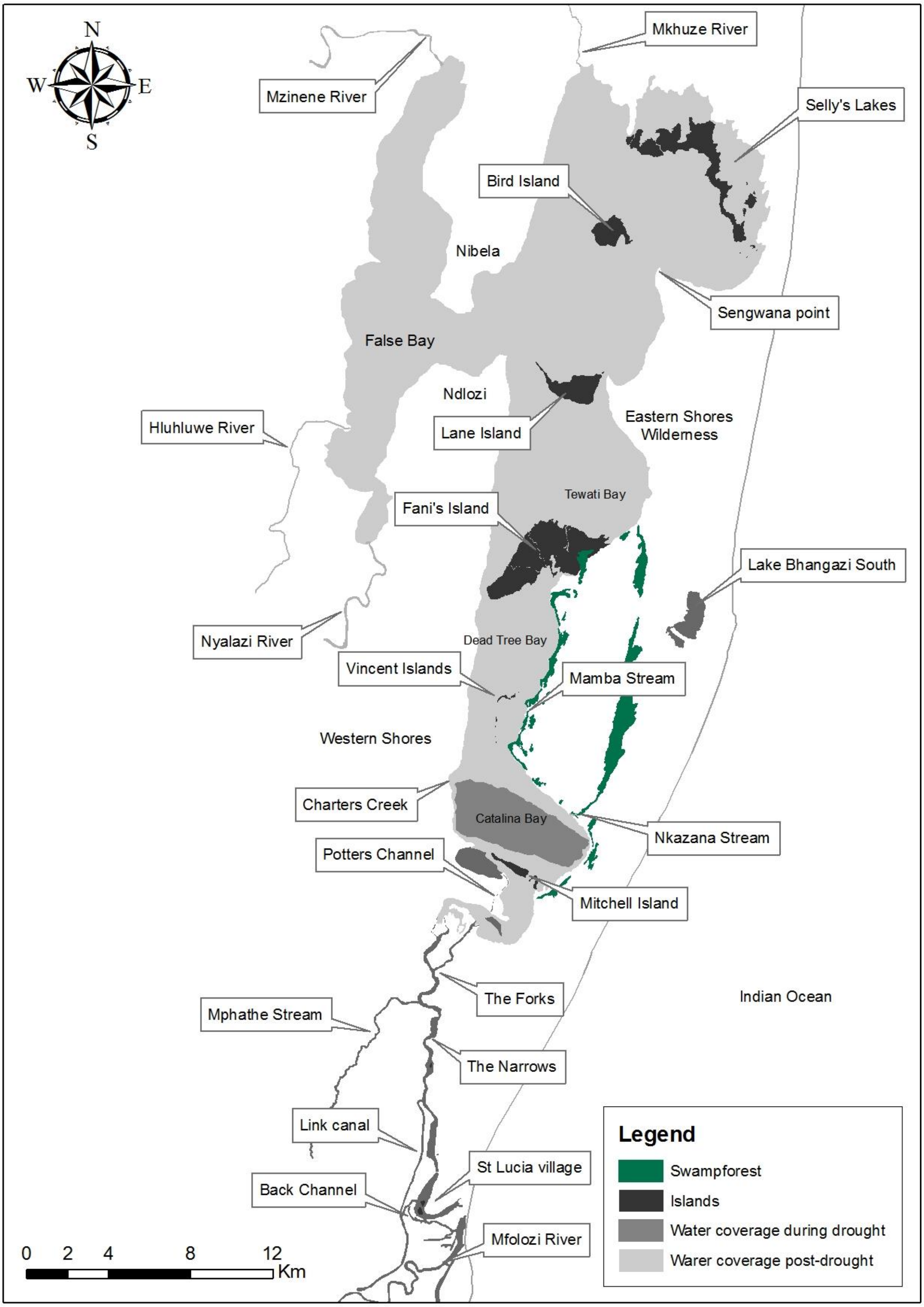
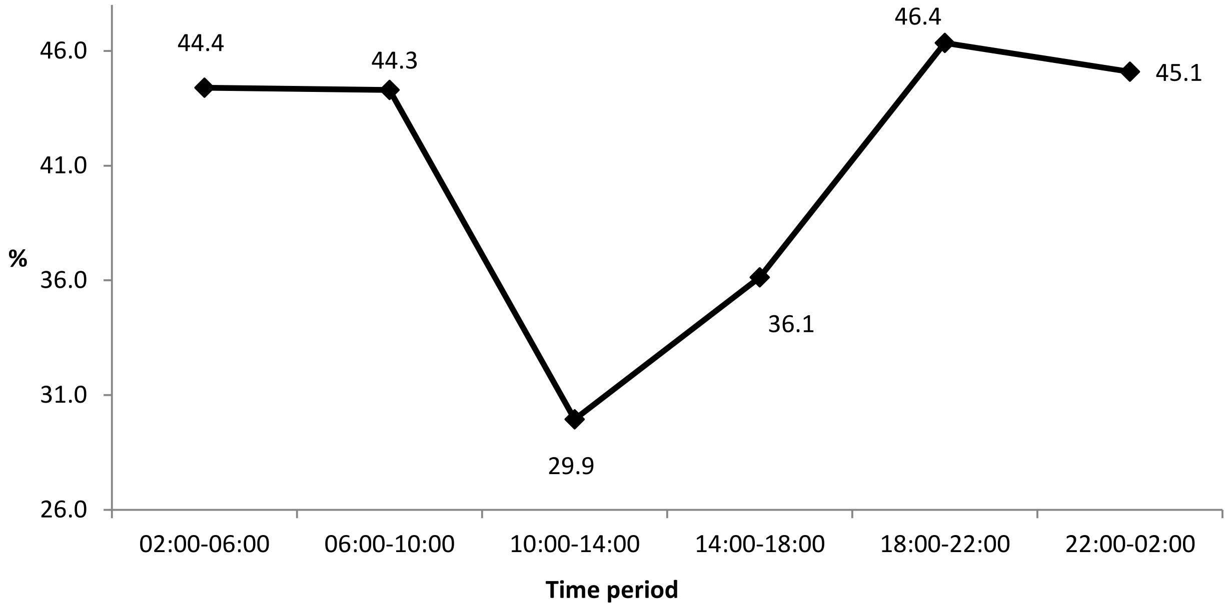


Figure 1. The Lake St Lucia estuarine system, the largest estuary in Africa.



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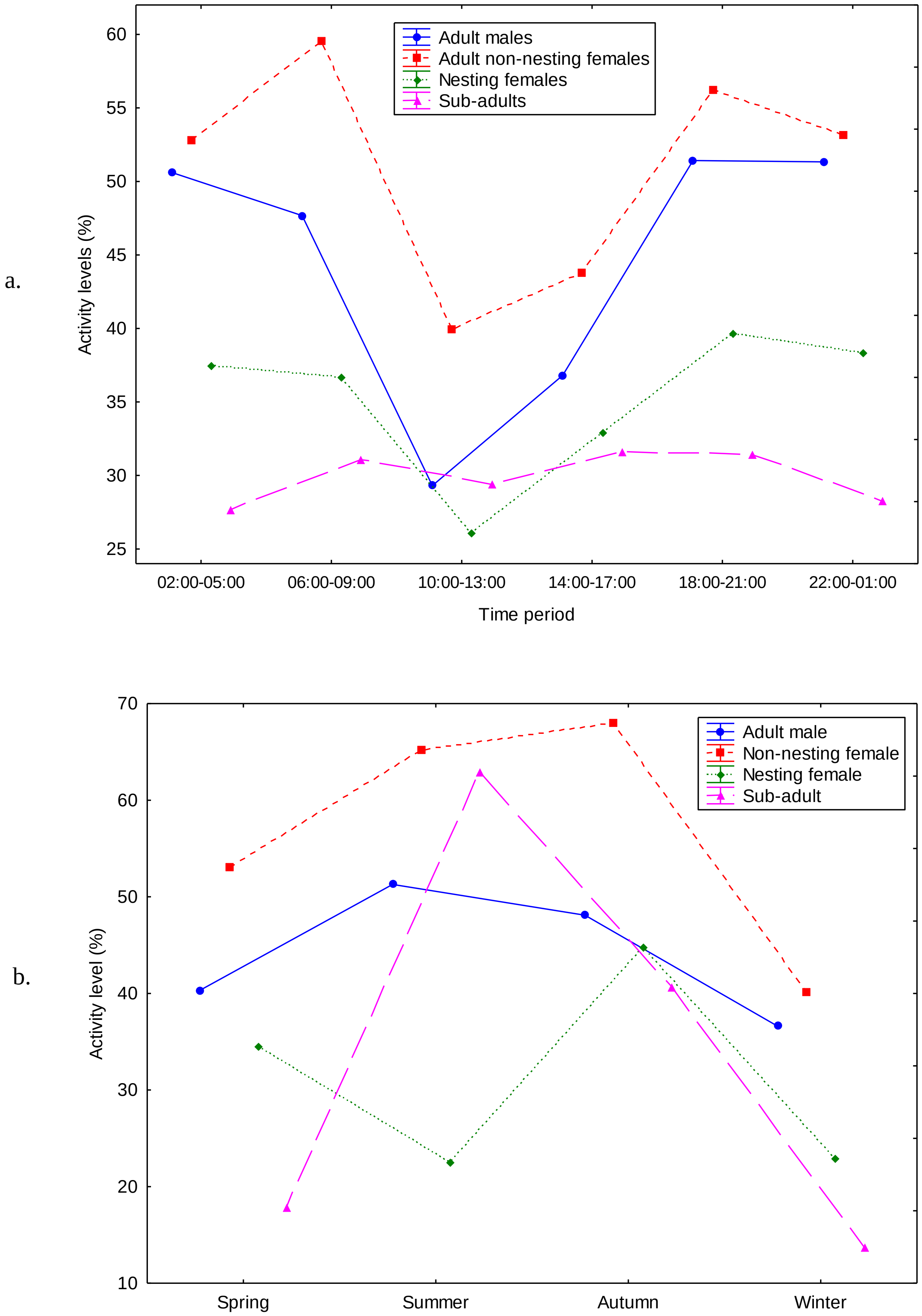


Figure 3. Temporal (a) and seasonal (b) activity pattern of Nile Crocodiles in the St Lucia estuarine system.

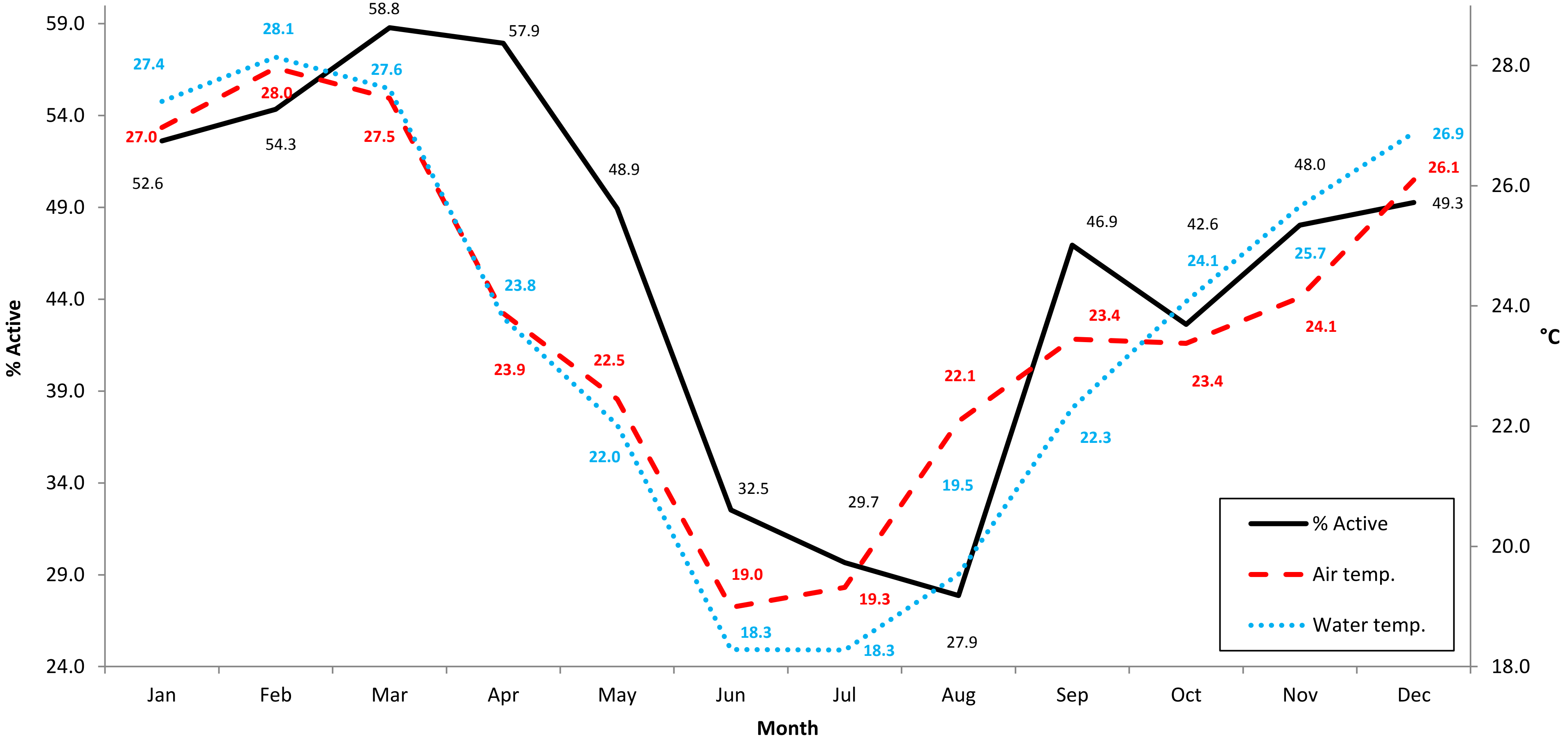
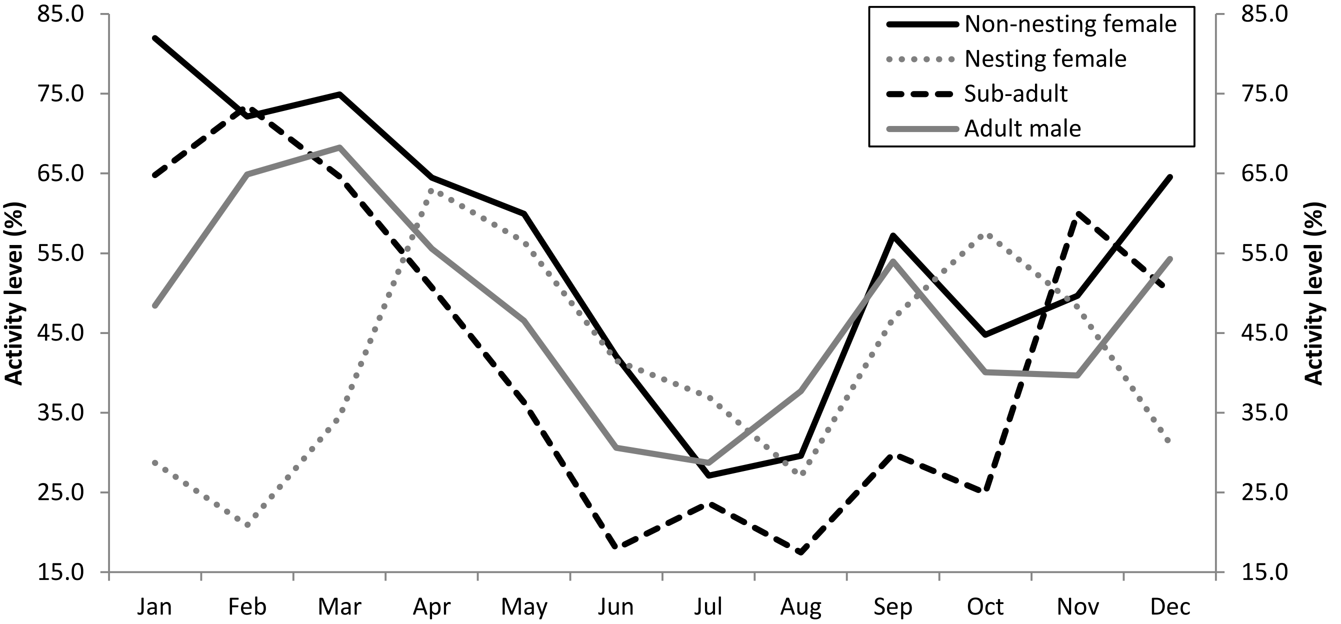


Figure 4. Mean Nile Crocodile activity levels (%), water and air temperatures at Lake St Lucia: 2009 - 2012.

a.



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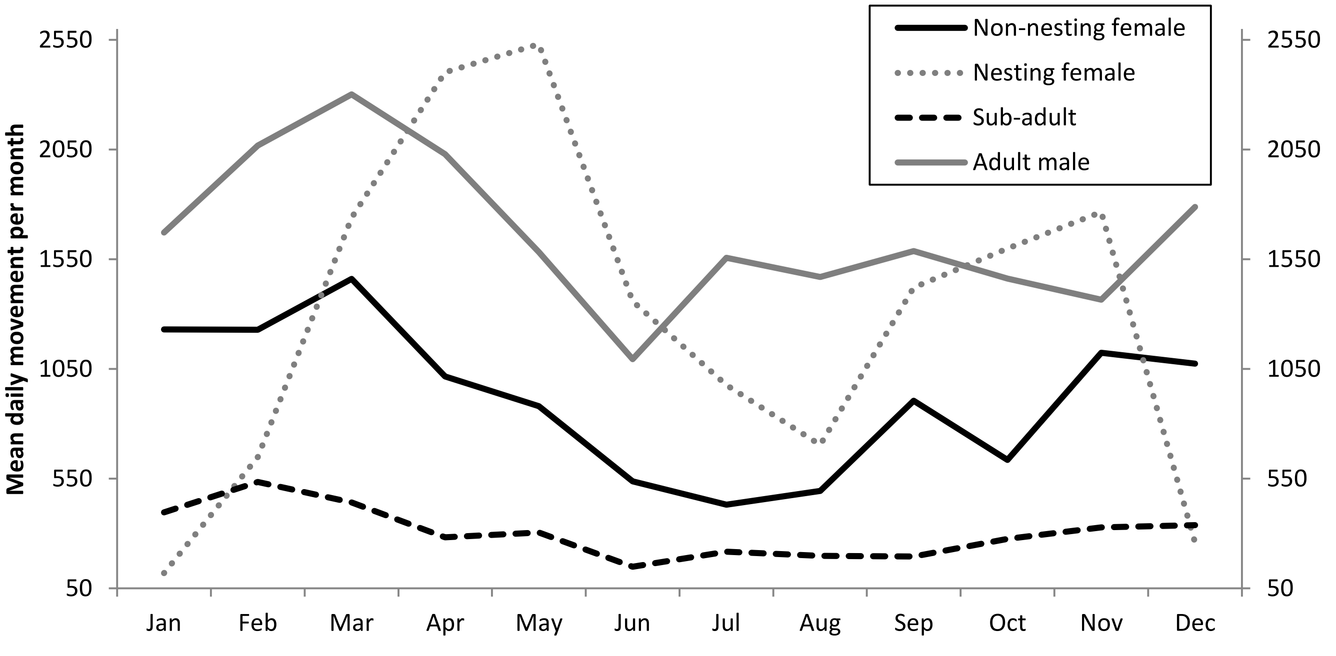


Figure 5. Monthly activity level (a) and mean daily movement (b) of Nile Crocodiles in the Lake St Lucia estuarine system.

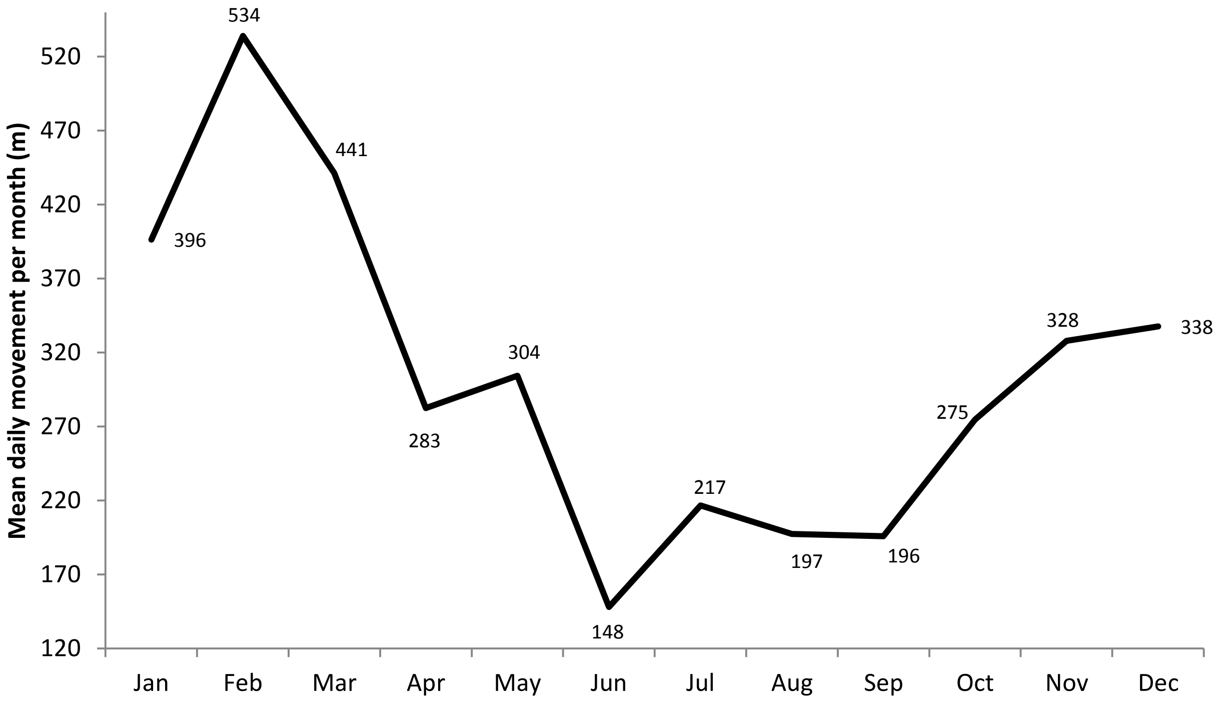
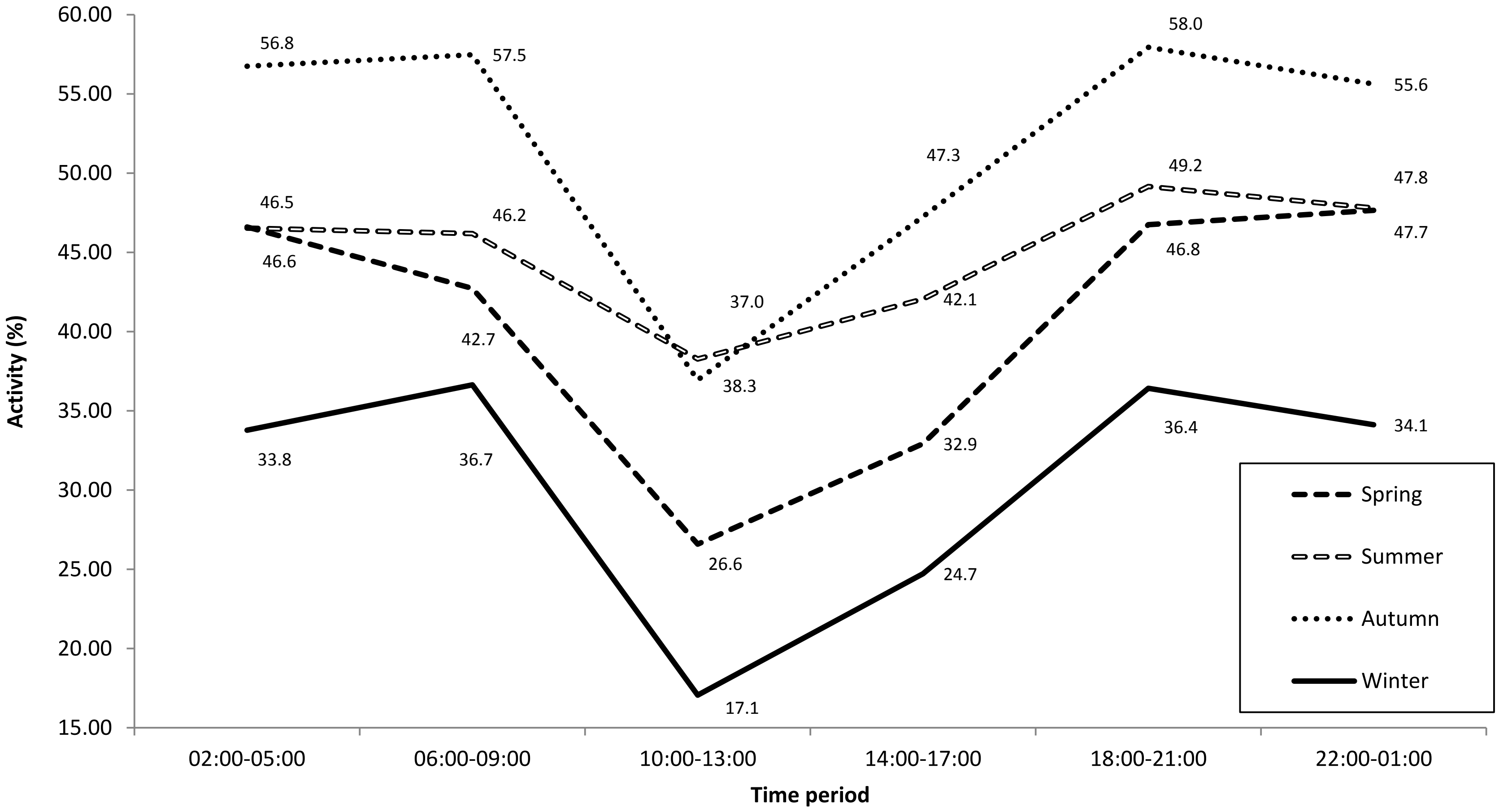


Figure 5c. Mean daily movement per month for sub-adult Nile Crocodiles (n=3) at Lake St Lucia.



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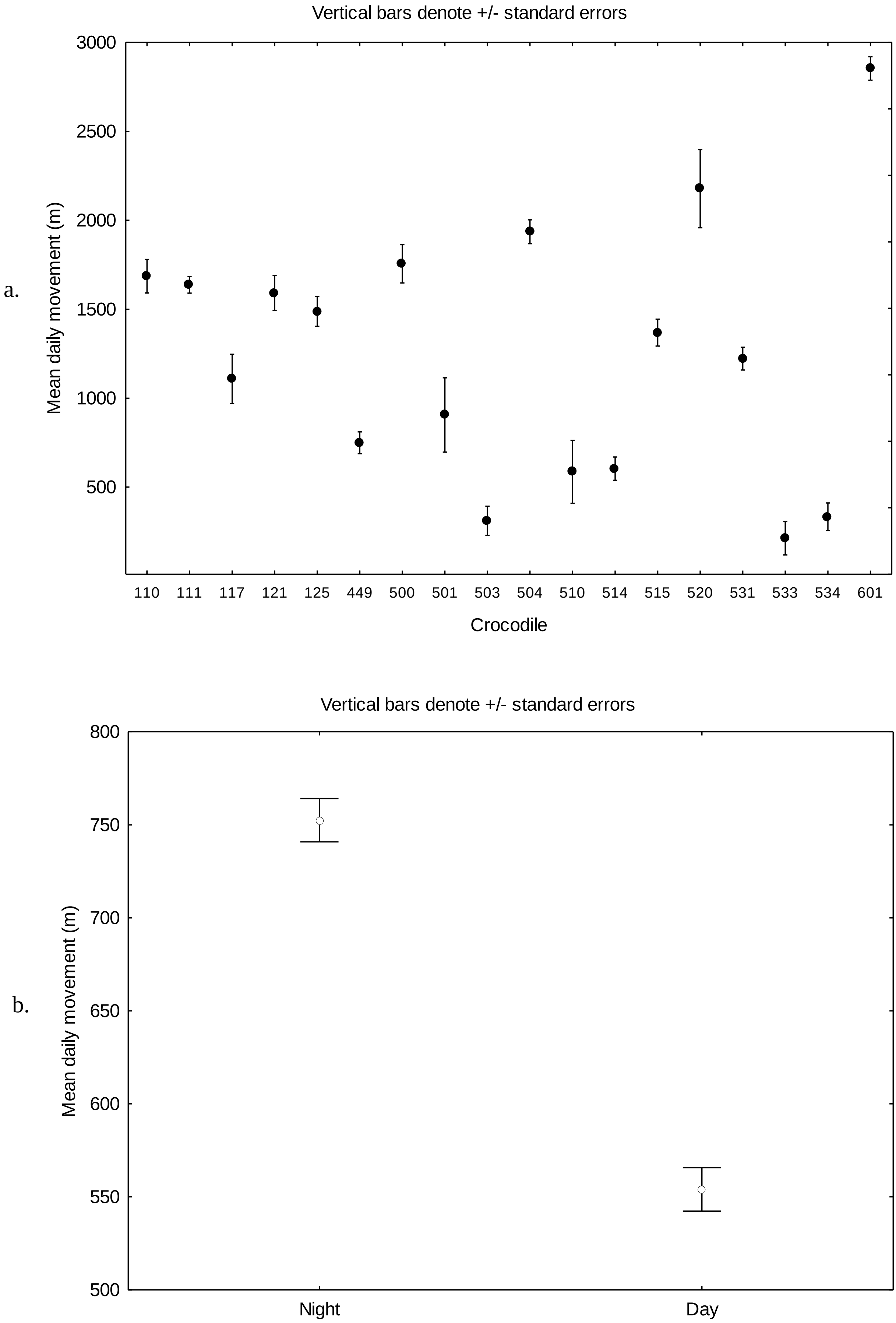

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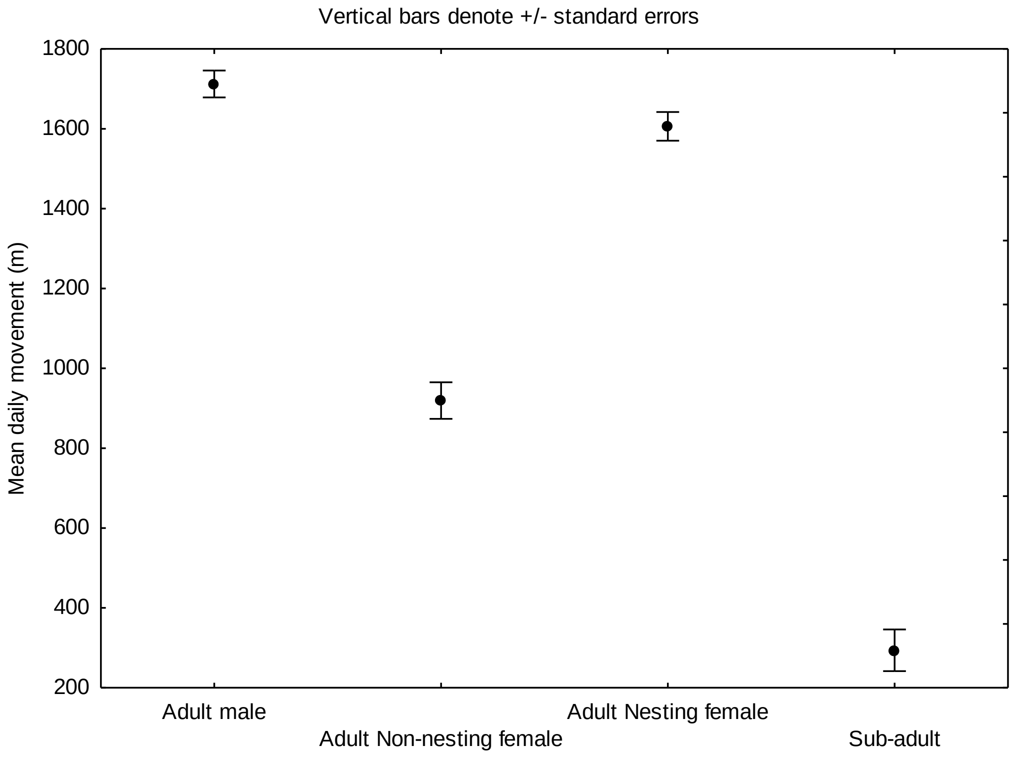

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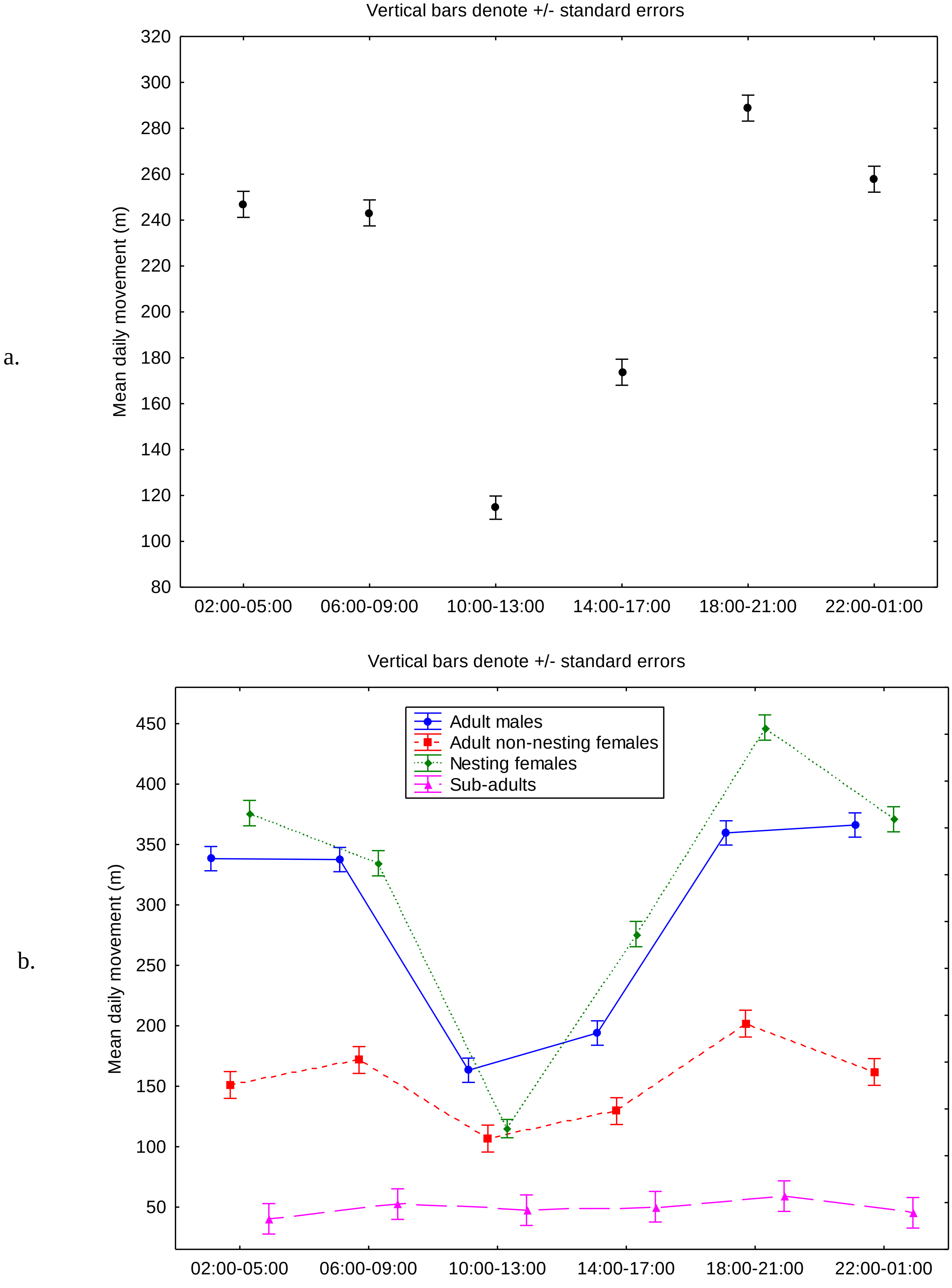

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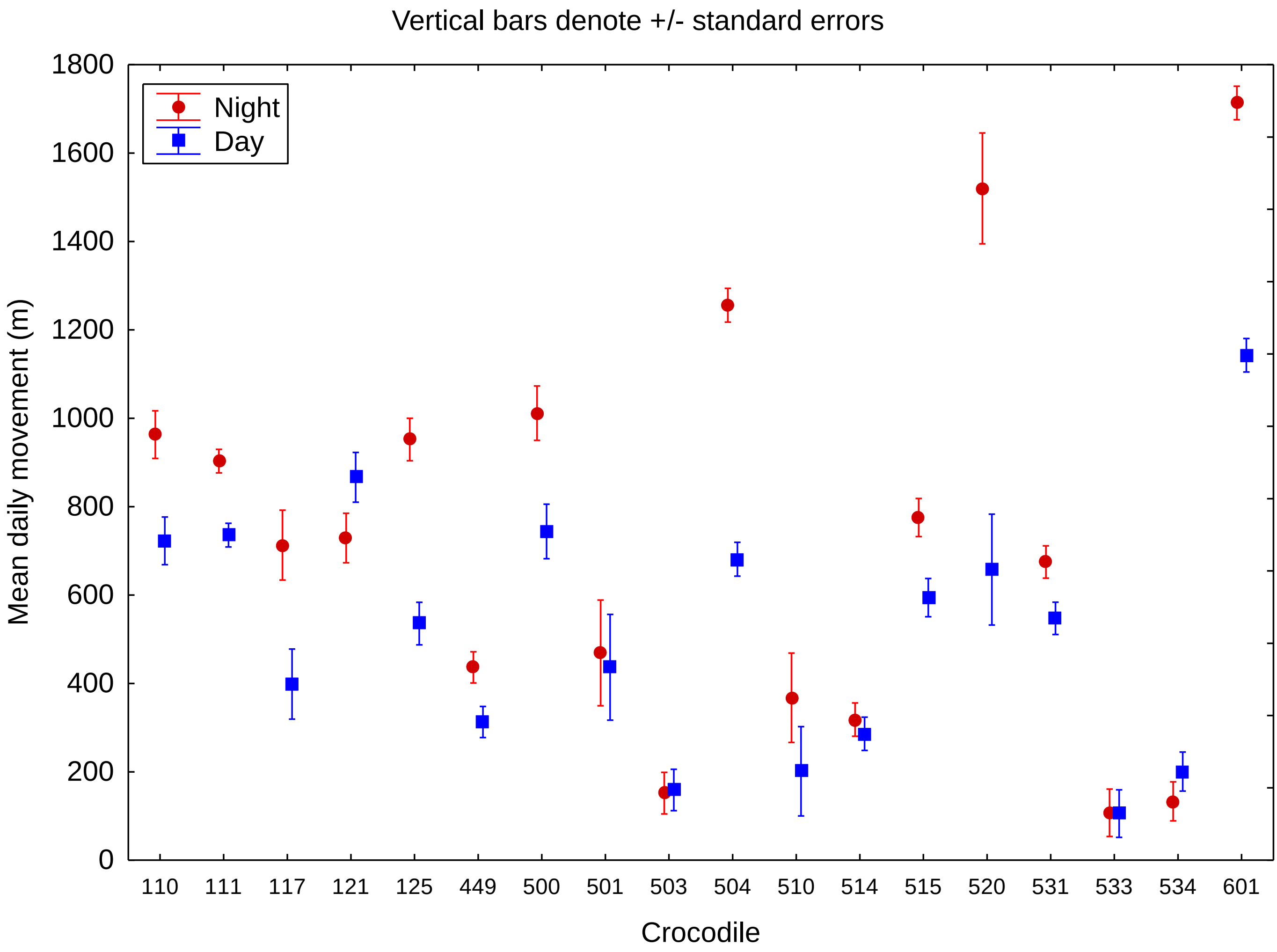

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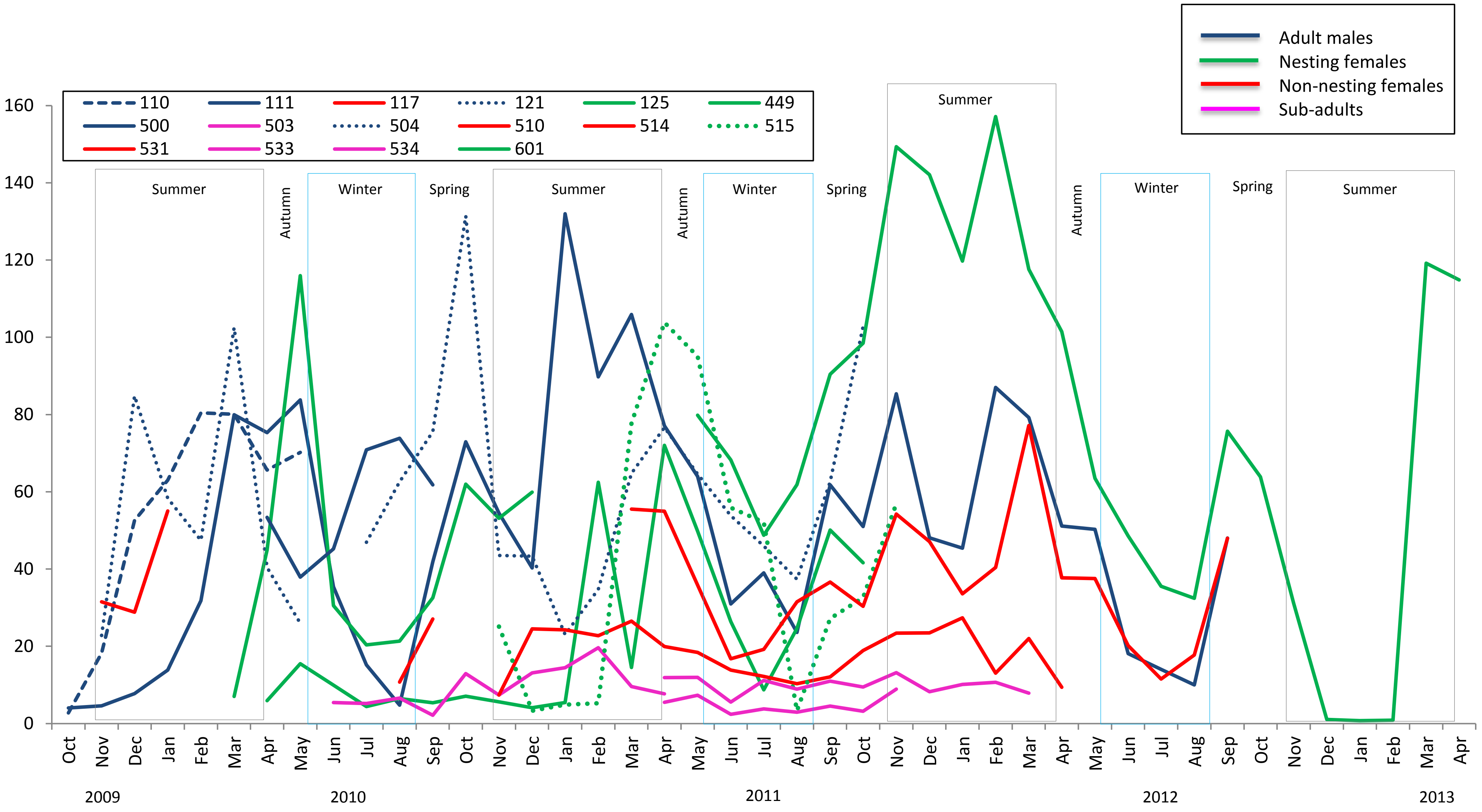
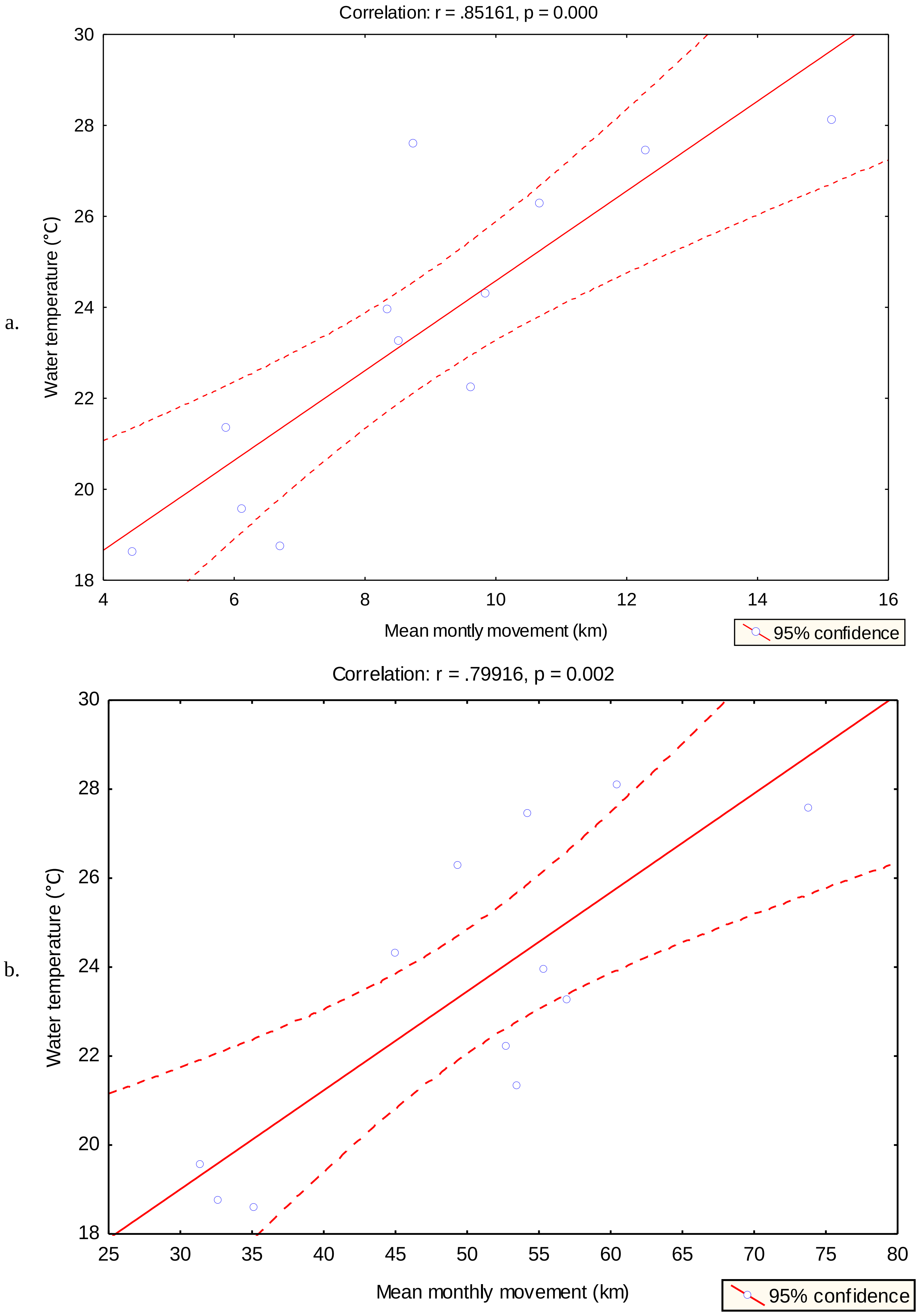


Figure 11. Total monthly movement (km) of 16 Nile Crocodiles in the Lake St Lucia estuarine system from Oct. 2009 – April 2013. The month that the transmitter was attached and stopped functioning was omitted, as well as individuals with less than four months of data.



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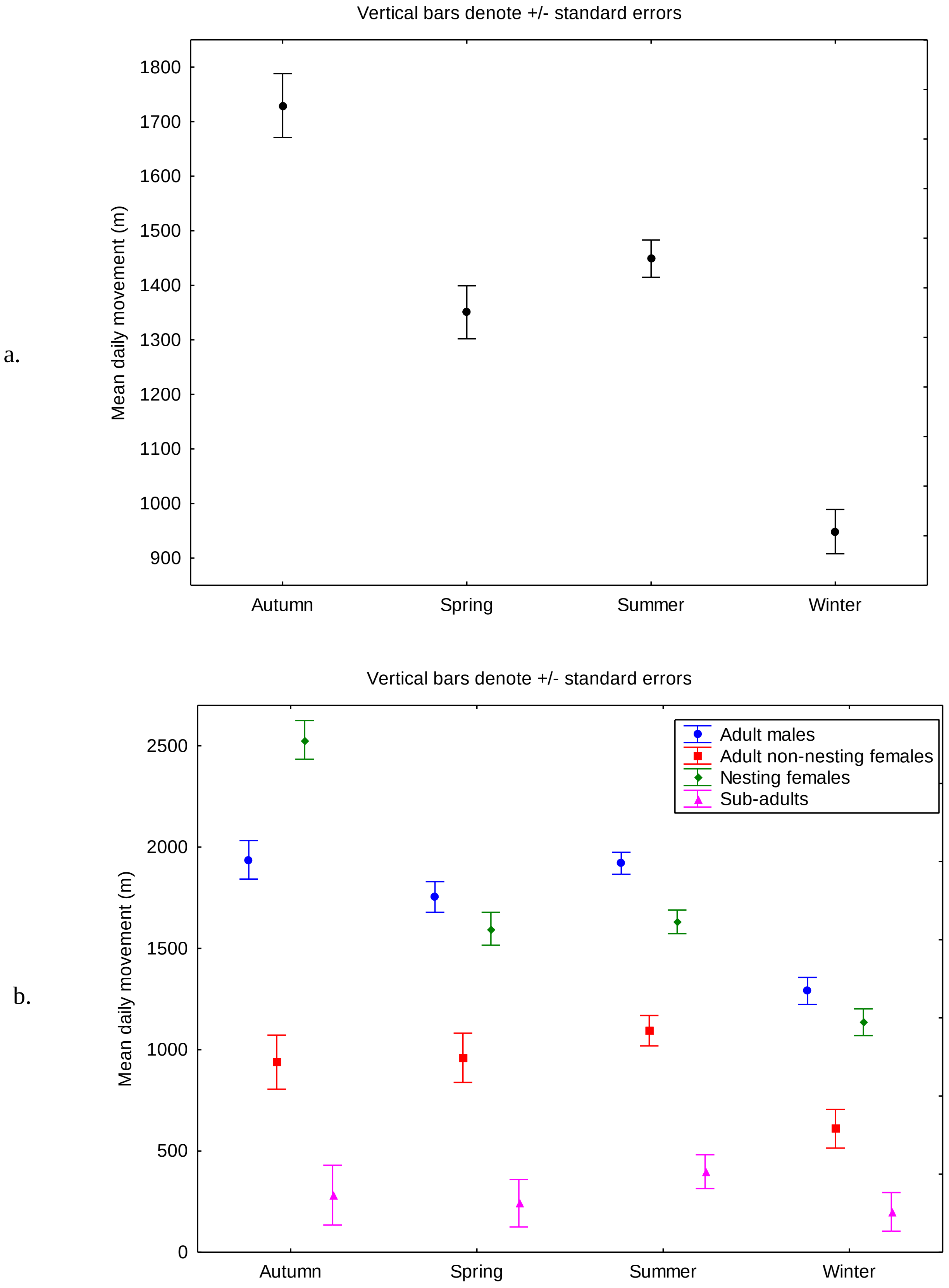

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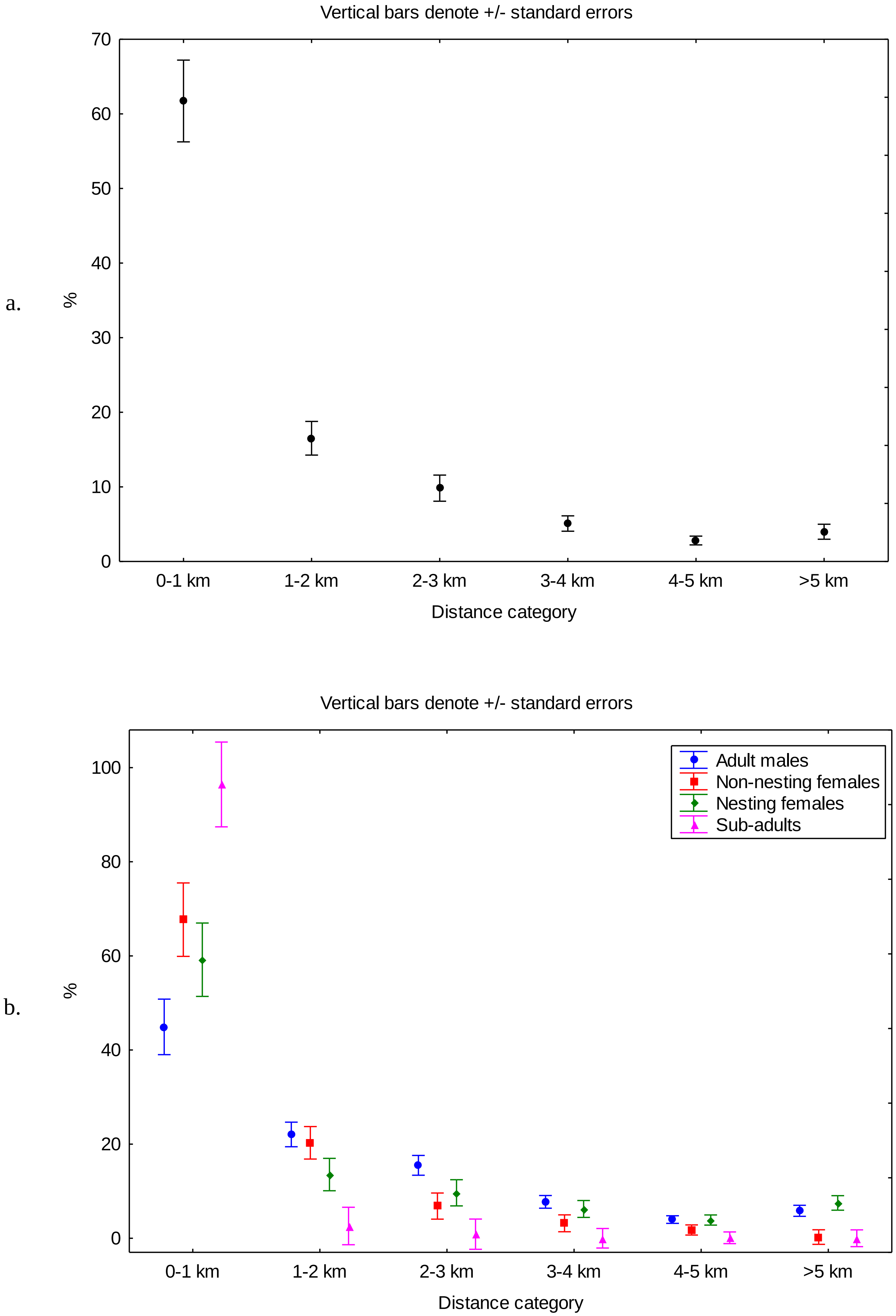

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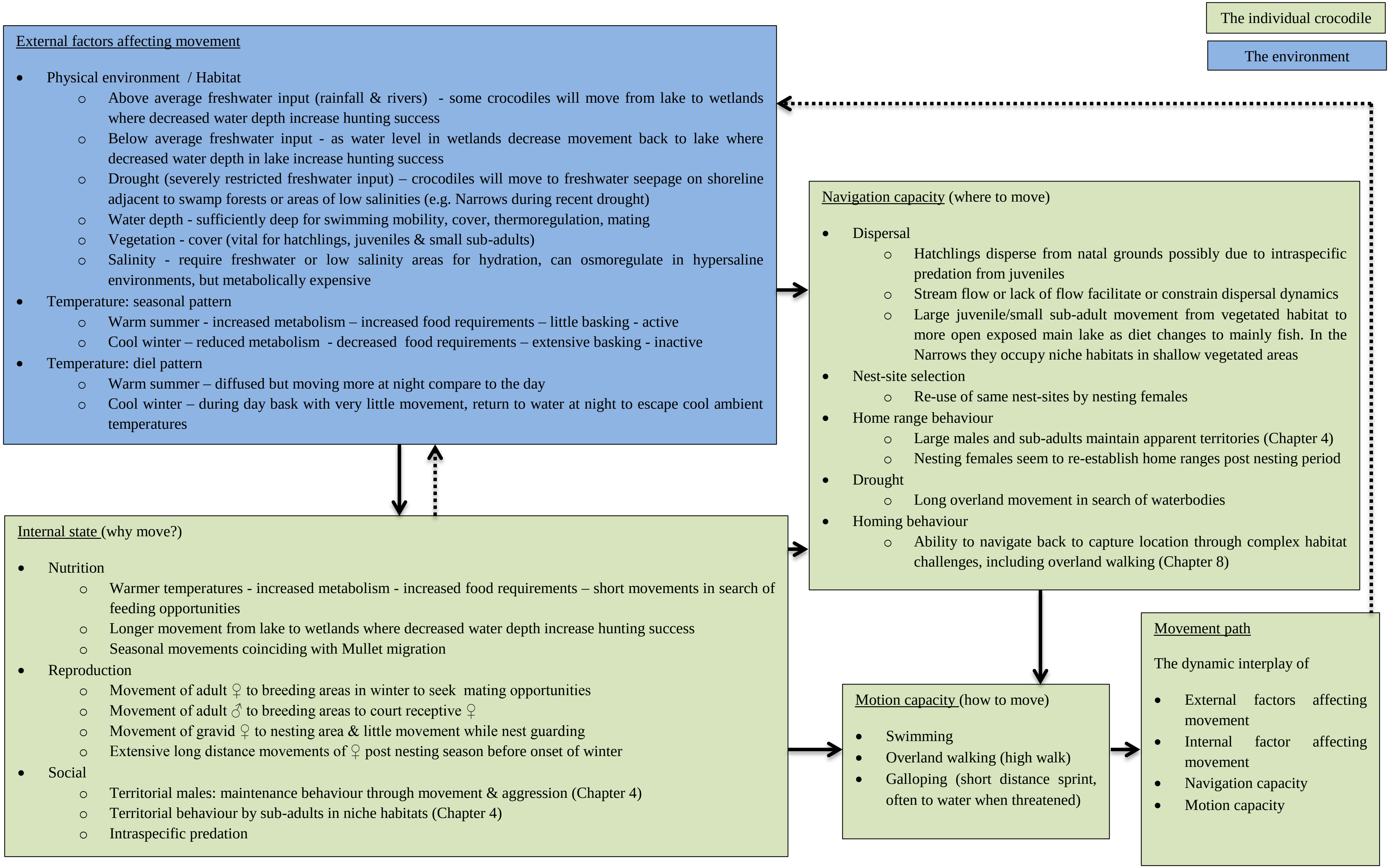

The individual crocodile

The environment

External factors affecting movement

- Physical environment / Habitat
    - Above average freshwater input (rainfall & rivers) - some crocodiles will move from lake to wetlands where decreased water depth increase hunting success
    - Below average freshwater input - as water level in wetlands decrease movement back to lake where decreased water depth in lake increase hunting success
    - Drought (severely restricted freshwater input) – crocodiles will move to freshwater seepage on shoreline adjacent to swamp forests or areas of low salinities (e.g. Narrows during recent drought)
    - Water depth - sufficiently deep for swimming mobility, cover, thermoregulation, mating
    - Vegetation - cover (vital for hatchlings, juveniles & small sub-adults)
    - Salinity - require freshwater or low salinity areas for hydration, can osmoregulate in hypersaline environments, but metabolically expensive
- Temperature: seasonal pattern
    - Warm summer - increased metabolism – increased food requirements – little basking - active
    - Cool winter – reduced metabolism - decreased food requirements – extensive basking - inactive
- Temperature: diel pattern
    - Warm summer – diffused but moving more at night compare to the day
    - Cool winter – during day bask with very little movement, return to water at night to escape cool ambient temperatures

Navigation capacity (where to move)

- Dispersal
    - Hatchlings disperse from natal grounds possibly due to intraspecific predation from juveniles
    - Stream flow or lack of flow facilitate or constrain dispersal dynamics
    - Large juvenile/small sub-adult movement from vegetated habitat to more open exposed main lake as diet changes to mainly fish. In the Narrows they occupy niche habitats in shallow vegetated areas
- Nest-site selection
    - Re-use of same nest-sites by nesting females
- Home range behaviour
    - Large males and sub-adults maintain apparent territories (Chapter 4)
    - Nesting females seem to re-establish home ranges post nesting period
- Drought
    - Long overland movement in search of waterbodies
- Homing behaviour
    - Ability to navigate back to capture location through complex habitat challenges, including overland walking (Chapter 8)

Internal state (why move?)

- Nutrition
    - Warmer temperatures - increased metabolism - increased food requirements – short movements in search of feeding opportunities
    - Longer movement from lake to wetlands where decreased water depth increase hunting success
    - Seasonal movements coinciding with Mullet migration
- Reproduction
    - Movement of adult ♀ to breeding areas in winter to seek mating opportunities
    - Movement of adult ♂ to breeding areas to court receptive ♀
    - Movement of gravid ♀ to nesting area & little movement while nest guarding
    - Extensive long distance movements of ♀ post nesting season before onset of winter
- Social
    - Territorial males: maintenance behaviour through movement & aggression (Chapter 4)
    - Territorial behaviour by sub-adults in niche habitats (Chapter 4)
    - Intraspecific predation

Motion capacity (how to move)

- Swimming
- Overland walking (high walk)
- Galloping (short distance sprint, often to water when threatened)

Movement path

The dynamic interplay of

- External factors affecting movement
- Internal factor affecting movement
- Navigation capacity
- Motion capacity

Figure 15. A general conceptual framework of movement ecology of Nile Crocodiles in the Lake St Lucia estuarine system based on the model of Nathan *et al*. 2008.

Caption for Tables

Table 1. Selected statistics of 18 Nile Crocodiles tracked from 16 Sep 2009 to 20 October 2012 in the Lake St Lucia estuarine system

Table 2. Activity levels for Nile Crocodiles at the Lake St Lucia estuarine system: 2009 to 2013

Tables

Table 1. Selected statistics of 18 Nile Crocodiles tracked from 16 Sep 2009 to 26 May 2013 in the Lake St Lucia estuarine system

Crocodile	**Transmitter**	**Size class**	**Size (cm)**	**Sex**	**Duty cycle**	**Data points**	**Field days**	**Activity (%)**	**DM > 20m (%)**	**DM > 100m (%)**	**MDM**	**MeDM**	**MxDM**
111	AG 170/303	A	295	♂	1, 4	9584	1344	49.0	97.8	84.7	1856	1107	15257
110	AG 169	A	349	♂	1, 4	3895	269	41.7	90.7	65.9	1686	1071	7565
121	AG 172	A	392	♂	1	2474	249	31.2	80.6	74.8	1592	493	11975
504	AG 301	A	406	♂	1, 4	4423	535	53.4	94.2	78.5	1936	1587	8723
500	AG 297	A	402	♂	1	2888	204	51.1	100.0	95.1	1756	1459	10081
520	AG 307	A	413	♂	2	491	50	57.6	92.0	86.0	2178	1996	6384
501	AG 298	A	316	♂	1	771	54	27.9	100.0	74.6	905	469	6998
		A		**♂**		**3504**	**386**	**44.5**	**93.6**	**79.9**	**1701**	**1169**	**9569**
514	AG 304	ANN	270	♀	1, 2, 4	2418	555	44.2	97.3	69.6	604	513	4626
531	AG 308	ANN	240	♀	4	1784	549	70.6	93.3	77.7	1222	927	9922
117	AG 171	ANN	283	♀	1	1147	126	58.5	98.4	76.0	1108	836	4871
510	AG 302	ANN	309	♀	1	1061	76	23.5	93.5	37.7	586	135	4575
		ANN		**♀**		**1603**	**327**	**50.9**	**95.6**	**65.3**	**880**	**603**	**5999**
447	AG 173	AN	273	♀	1	0	-	-	-	-	-	-	-
449	AG 296	AN	285	♀	1, 4	9063	634	17.7	93.4	48.0	749	208	7805
515	AG 305	AN	304	♀	1, 2	2750	392	40.0	91.0	53.3	1369	326	14355
125	AG 295	AN	289	♀	2, 4	4342	339	38.0	97.7	70.0	1488	786	9324
601	AG 503	AN	293	♀	4	2978	775	52.92	91.6	77.7	2490	1982	14894
		AN		**♀**		**4783**	**535**	**35.2**	**93.4**	**62.3**	**1524**	**826**	**11595**
		All		**♀**		**3193**	**431**	**42.0**	**94.5**	**63.8**	**1202**	**714**	**8797**
534	AG 306	SA	212	♀	4	1446	405	52.7	88.9	58.9	334	294	1540
503	AG 299	SA	208	♂	1, 4	4153	356	17.4	94.7	40.9	311	156	4211
533	AG 309	SA	204	♂	1, 4	896	273	36.1	76.2	28.6	213	97	2613
		SA				**2165**	**345**	**29.9**	**86.6**	**42.8**	**286**	**182**	**2788**
		Total				**3142**	**399**	**41.0**	**92.9**	**66.6**	**1244**	**802**	**8096**

A = Adult, ANN = Adult non-nesting female, AN = Nesting female, SA = Sub-adult, **# =** diurnal movement, i.e. 06:00 - 18:00, DM = days moved, MDM = mean daily movement, MeDM = median daily movement, MxDM = Maximum daily movement

Table 2. Activity levels for Nile Crocodiles at the Lake St Lucia estuarine system: 2009 to 2013

	All crocodiles	**Adult ♂**	**Non-nesting ♀**	**Nesting ♀**	**Sub-adults**
Overall	41.0	44.5	50.9	35.2 /42.0*	29.9
Spring	40.6	40.3	46.0	47.1	17.9
Summer	45.0	51.3	61.4	26.2	62.9
Autumn	52.0	48.1	59.5	57.3	40.7
Winter	30.5	36.6	32.5	29.3	13.8
02:00-06:00	44.4	50.6	52.8	37.5	27.7
06:00-10:00	44.3	47.7	59.5	36.7	31.1
10:00-14:00	29.9	29.3	39.9	26.1	29.4
14:00-18:00	36.1	36.2	43.8	32.9	31.6
18:00-22:00	46.4	51.4	56.2	39.7	31.4
22:00-02:00	45.1	51.3	53.2	38.3	28.3
Seasonal Chi-square	1364.93	1128.96	273.70	276.7	11.1
Seasonal df	5	5	5	5	5
Significance level	p = 0.00	p = 0.00	p = 0.00	p = 0.00	p = 0.05
Temporal Chi-square	1967.08	620.89	822.85	1815.61	1907.01
Temporal df	3	3	3	3	3
Significance level	p = 0.00	p = 0.00	p = 0.00	p = 0.00	p = 0.00
n	18	7	4	4	3

CHAPTER 4

Home range and movements of Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

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ABSTRACT

Nile Crocodiles (*Crocodylus niloticus*) are apex predators found in the lakes, wetlands, rivers, and estuaries of northeastern KwaZulu-Natal, South Africa. Despite their ecological and conservation significance, as well as infrequent conflict with humans, very little is known with regard to the species' spatial ecology, movements and home range behaviour. We investigated these aspects in the Lake St Lucia estuarine system using a subcutaneous attachment procedure to secure GPS-satellite transmitters to adult males, females and sub-adults. Transmitter longevity of 14 individuals were sufficient for seasonal comparisons. We corrected 55 173 observations for temporal submerge bias and unequal GPS capture schedules, removing 35 380 observations.

We estimated lifetime, yearly and seasonal home range size, and core-use areas with kernel density estimation using ABODE. Asymptote analysis confirmed the number of observations for most crocodiles were sufficient to describe their full range of movements.

Adult males median home range was 713.1 ha and core-use area 81.5 ha. Three size-related patterns emerged; transient (< 3 m TL), topographically confined (3.5-4 m TL) and "territorial" (> 4 m TL). Adult males revealed an inverse correlation between home range size and crocodile size, while adult female home range size were generally more homogeneous, with median home range size 400.8 ha and core-use area 106.9 ha. All nesting females displayed an explosive increase in mobility and space-use subsequent to the nesting period, and all adults, except one female in the central part of the lake, moved during winter to large congregations south of the lake during the drought.

Sub-adults occupied significantly smaller home ranges than adults (median = 22.9 ha; core-use area = 9 ha), which were habitat specific with strict spatial partitioning. They remained in shallow vegetated areas adjacent to deep water, avoiding the open deep water altogether. We hypothesised that limited sub-adult habitat in the Narrows might be an important density regulating mechanism at St Lucia.

We conclude that size, sex, reproductive status, and habitat (topography, hydrologic heterogeneity, and freshwater availability) are primary determinants of Nile Crocodile space-use and mobility in ecologically complex systems, and explain the widely variable home range patterns observed among individuals at Lake St Lucia.

Keywords: Home range, spatial ecology, movement, GPS-satellite tracking, Lake St Lucia estuarine system, Nile Crocodile.

INTRODUCTION

The Nile Crocodile (*Crocodylus niloticus*) is an apex predator found in aquatic ecosystems throughout northeastern KwaZulu-Natal province, South Africa. The Lake St Lucia estuarine system, part of South Africa’s first World Heritage Site, hosts the largest Nile Crocodile population in a single waterbody in South Africa. Despite the species’ ecological and conservation significance, as well as infrequent conflict with humans in Zululand, no information exists with regards to its spatial ecology and home range behaviour.

Crocodiles generally do not move randomly, but direct their movements to particular areas (Joanen and McNease 1970, Joanen and McNease 1972, McNease and Joanen 1974, Hutton 1989, Kay 2004, Brien et al. 2008, Campbell et al. 2013). Burt (1943) defined the area traversed by an animal during “normal” activities such as feeding, drinking, breeding, basking, and nesting, as its home range. However, Burt’s definition does not recognise that space use within a home range may vary (Kie et al. 2010), therefore Worton (1989) highlighted the importance of estimating the utilisation distribution (UD), also known as the distribution of an animal's position within its home range.

Home range strategies may influence life-history processes such as survival and growth (Jewell, 1966). In crocodilians, intraspecific predation is a fundamental population process (Cott 1961, Hutton 1989), which suggests spatial partitioning of different size classes may be a crucial factor in population dynamics (Hutton 1989).

To investigate animal movement patterns and space-use strategies, individuals have to be marked or uniquely identified for spatio-temporal information to be collected at appropriate levels. Mark-recapture provided an important tool for baseline crocodilian movement studies (Chabreck 1965, Webb and Messel 1978, Tucker et al. 1997, Bourquin 2007), and Tucker *et al.* (1997) estimated linear home ranges of Australian Freshwater Crocodiles (*C. johnstoni*). Advances in VHF technology allowed for higher data capture intervals and therefore more detailed estimates of home ranges (Joanen and McNease 1970, McNease and Joanen 1974, Hutton 1989, Kay 2004, Brien et al. 2008). Despite these advances, VHF tracking still requires the researcher to physically locate the study animal, a difficult undertaking due to crocodilians remote habitats, cryptic nature, semi-aquatic existence, nocturnal activity patterns and sensitivity to the presence of field researchers.

More recently, the development of transmitters with the ability to record accurate spatio-temporal datasets using remote GPS technology led to an increase in data collection. However, this has not been tested on Nile Crocodiles, apart from a pilot study (Botha 2005).

Despite the ecological significance of Nile Crocodiles as an apex predator, wide sub-Saharan distribution, and responsible for more human fatalities than any other animal in Africa (Lamarque et al. 2009), very little is known about the spatial ecology of the species. In addition to two published studies (Hutton 1989, Hocutt et al. 1992), home- or linear ranges of Nile Crocodiles have been estimated in the Lake St Lucia Narrows (Leslie 1997), Flag Boshielo Dam (Botha 2005), Panhandle of the Okavango Delta (Bourquin 2007) and Nyamithi Pan of Ndumo Game Reserve (Calverley 2013), but all were constrained by low sample size, limited data retrieval (mean daily observations = 0.78 ± 0.5, mean transmitter-days = 113.4 ± 34.9), lack of seasonal movement data, and/or premature transmitter detachment and/or failure. The problems of sufficient battery life and transmitter longevity are well-documented in past Nile Crocodile studies (Swanepoel 1999, Botha 2005, Bourquin 2007, Strauss et al. 2008, Champion 2011, Calverley 2013).

The aim of this study was to monitor adult males, females and sub-adults using GPS-satellite telemetry, thereby facilitating data collection at sufficiently high resolution for detailed movement behaviour and home range analyses over a number of seasons. We predicted sub-adults will occupy smaller home ranges, and that home range size of all crocodiles will be smaller during the cool winter season. In light of previous studies, we suspected considerable differences in space-use between males and females and strict spatial partitioning of large males. Due to the suitable longevity and high spatial accuracy of our transmitters, we also anticipated novel insights into the spatial ecology and natural history of the species. Finally, we sought to understand how this aquatic predator responds to the complex spatiotemporal ecological conditions present at the Lake St Lucia ecosystem.

MATERIALS AND METHODS

Study area

The Lake St Lucia estuarine system is situated in northeastern KwaZulu-Natal province, South Africa (Fig. 1). At ~67 km in length with an average width of 6 km when filled to capacity, it is the largest estuarine system in Africa (Cowan 1997). Lake St Lucia is a shallow system (mean depth = 0.98 m, Hutchison 1974), shaped by dynamic environmental and ecological processes at various spatial and temporal scales (Taylor 2006). Refer to Chapter 1 for a more detailed description of the study area.

Biotelemetry

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

Seasonal partitioning

Temperature is a critical factor in thermoregulatory behaviour, activity, and movement of ectotherms like the Nile Crocodile (Cott 1961). To analyse movements and home range behaviour, variation in water temperature was used for seasonal partitioning, allowing for comparison with other studies (Joanen and McNease 1970, Joanen and McNease 1972, Taylor et al. 1976, Goodwin and Marion 1979, Taylor 1984, Kushlan and Mazzotti 1989, Hocutt et al. 1992, Rootes and Chabreck 1993, Botha 2005, Bourquin 2007, Calverley 2010, Champion 2011).

Water temperature was collected every 30 min at Catalina Bay (Charters Creek Ezemvelo management jetty) and the Narrows (St Lucia Wilds jetty), as these sites were the only areas in the lake system sufficiently deep (i.e. > ~75 cm) throughout the study period. Data loggers (iButton DSL 1922 Thermochron temperature data loggers, Maxim Integrated, San Jose, USA) were secured to a pole in the water, 30 cm from the bottom. Thermochron monitors record time and temperature, and the data were stored on the device until uploaded in MS Excel for analysis. Temperature was accurate to ± 0.5 °C (http://www.maximintegrated.com). We calculated mean water temperature per week over three years.

Home range analyses

We used nonparametric kernel density estimation (Worton 1989) to estimate utilisation distributions and home ranges. All analysis were conducted using ABODE (Laver 2005), a kernel home range estimation for ArcGIS. The 95 % home range was contoured at 95 % of the volume of the density surface and the core-use area was calculated using Horner and Powell's (1990) statistical clumping core analysis to provide an objective delineation of core-use areas and not some arbitrary defined probability cut-offs (e.g. 50 % utilisation distribution). We used a biweight kernel, and the least-squares cross-validation (LSCV) was used for selecting the optimum bandwidth or smoothing parameter, which was fixed (as oppose to adaptive). Data was standardised to unit variance, which meant that h_{ref} was calculated from the standardised dataset (Laver 2005).

We conducted random asymptote analysis in ABODE to confirm that the sampling duration covered the full behavioural repertoire exhibited by each crocodile and to determine the minimum number of location estimates required to have a specific confidence in the sample. We furthermore conducted sequential asymptote analysis in ABODE to identify temporal dispersal events or significant sallies (Laver 2005).

Nile Crocodiles are semi-aquatic animals that spend most of their lives in or at the waters' edge (Cott 1961), utilising distinct ecological boundaries or topographical features. Home range estimates (95 % utilisation distribution) that include areas outside the lake, channel or stream boundaries were removed through scrutinisation high resolution orthophotos of the study area in ArcGIS 9.

Crocodilians spent a considerable proportion of their life submerged and seasonal variation in the submerge-emerge ratio has been recorded for the American Alligator (Woodward and Marion 1978, Bugbee 2008) and Nile Crocodiles (Chapter 2, this study). We calculated day/night and monthly submerged-emerged ratios of Nile Crocodiles using GPS-satellite transmitters and found significant temporal variation (Chapter 2), a potential bias in home range analysis. We subsequently corrected our dataset with the highest monthly diurnal (Feb = 0.58) and nocturnal submergence ratio (June = 0.44), removing 35 380 from the original 55 173 observations.

Area-use profiles

We constructed simple area profiles reflecting individual crocodile temporal use of the major topographic areas of the lake system. These profiles visually reflected the extent and variation of movements between these areas during their tracking duration.

RESULTS

We attached GPS-satellite transmitters to 19 crocodiles from 16 September 2009 to 3 March 2011. The transmitters of Male 520 and Male 501 malfunctioned prematurely after 50 and 54 days respectively, and Female 447 never entered the GSM network. Two females were captured on their nests and continued nesting activities subsequent to transmitter attachment. One of them, Female 449, continued to nest the following year, while two other females captured and secured with transmitters outside the nesting season, continued to nest during the study period.

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

Initial GPS-schedules were set to record a point-locality every hour, but this schedule was subsequently changed to 12 points in 24-hours and finally to every four hours. Prior to analysis, GPS-schedules were standardised to a four hour sequence.

Seasonal partitioning

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

All crocodiles

Adults displayed a significantly greater home range (adults 418.3 ha; sub-adults 22.9 ha) and core-use area (adults 103.3 ha; sub-adults 9.0 ha) compare to sub-adults (Mann-Whitney U Test, p = 0.016, Fig. 2).

Random asymptote analysis for Male 110, Male 121, Female 125, Male 500 and Female 503 (Fig. 3 - Fig. 7) indicated that all crocodiles reach an asymptote consistently within 5 % of the final home range size, after a mean of 490 ± 105 S.E. observations (fixes) or 81.7 days of tracking, based on the 6 observations per 24h transmitter schedule.

Adult males

Adult males occupied a median home range of 713.1 ha, and core-use area of 81.5 ha (Fig. 8 and Table 1). Three size-related patterns of home range behaviour emerged; transient (< 3 m TL), topographically confined (3.5 – 4 m TL) and territorial (> 4 m TL). We found a strong inverse correlation (r = 0.8741; p = 0.053) between home range size and crocodile size, for adult males.

Transient home range (< 3 m TL)

Male 111, the smallest adult male (295 cm TL), moved 2311.6 km during the 1344 tracking days (MDM = 1856 ± 60 m). His mean annual home range size during the four years was 1378.8 ± 248.8 ha, the largest of all adult males (Table 1). He displayed extensive interannual home range variation, both in size and distribution (Fig. 9), doubling from 702.0 - 1449.7 ha from the first to the second year, and increased from 1462.9 - 1901.0 ha from the third to the fourth (n = 249 days) year. Temporally, his annual home ranges shifted latitudinally, from the Narrows (south of the main lake) to Catalina Bay (southern lake) and Dead Tree Bay (central lake). This transient behaviour was expedited by increased water levels from January 2011, re-linking Catalina Bay and Dead Tree Bay.

Topographically confined home range (3.5 – 4.0 m TL)

The home ranges of Male 110 (350 cm TL) and Male 121 (392 cm TL) were 713.1 ha and 860.2 ha respectively (Table 1), considerably smaller than Male 111 (1378.8 ± 248.8 ha). Their home ranges were mainly restricted to Catalina Bay (Fig. 10), with 121’s main basking area on the southwestern shoreline (Fig. 10b) and 110’s on the southeastern shoreline (Fig. 10a). Both males journeyed from Catalina Bay, but at different times of the year. Male 110 moved 13 km south down the Narrows during the last two weeks of April, coinciding with the annual Striped Mullet (*Mugil cephalus*) migration (Whitfield and Blaber 1979). He spent most of the time at two large winter basking congregations. Male 121 journeyed 14 times from his core-use area along the southwestern shoreline to the Nkazana Stream, a small perennial stream flowing into Catalina Bay in the northeast (Fig. 10b). In total, he utilised the stream 49.5 % of the time. The mean salinity of Catalina Bay during the tracking period was 51.9 ± 2.5 psu and both crocodiles established core-use areas at fresh water sources, Male 110 mainly used shoreline seepage pools while Male 121used the Nkazana Stream.

Territorial behaviour (> 4 m TL)

Home ranges of the two largest adult males, Male 500 (200.5 ha; Fig. 11a)) and Male 504 (121.2 ha; Fig. 11b), were significantly smaller compared to adult males < 4 m (Mann-Whitney U Test, $p < 0.05$). These large males were most active and mobile of all males (Table 1 Chapter 3), and their mean daily movements (MDM) were significantly more compared to other adult males (One-way ANOVA: $F_{(1, 2526)} = 13.83$, $p = 0.0002$). Elevated mobility within a small home range, suggested territorial maintenance behaviour.

Male 504 was restricted to Lake Bhangazi, a ~200 ha freshwater waterbody ~5.8 km east of Lake St Lucia (Fig. 11b). He moved on two occasions, three days and 14 days respectively, south through a connecting stream to the adjacent Mfabeni swamp, following good rainfall and stream flow.

Season

Although home ranges and core-use areas exhibited large seasonal variation, they were not significantly different. Home ranges was twice as large in summer (747.2 ha) compare to winter (294.0 ha). Core-use areas were 130.5 ha in summer compare to 75.1 ha in winter (Table 2). Variation (i.e. interquartile range) of home ranges and core-use areas were much larger during summer compared to winter (Table).

Male 500 (> 4 m TL) journeyed during winter on three separate occasions to large basking congregations (Fig. 11a). These journeys were between June and August, which coincides with the period when Nile Crocodile males have viable sperm (Kofron 1990).

Adult females

Adult females occupied a median home range of 400.8 ha, and core-use area of 106.9 ha (Table 1, Fig. 8).

Home ranges of Female 531, 601 and 515 were restricted mostly to the Narrows channel and were quite similar in size (range: 357 – 426 ha; Table 1). Female 514 occupied the smallest home range (37.0 ha), mainly upstream from a weir in the Mphathe stream (Fig. 12a). Female 125, which nested along the Nkazana Stream, occupied the largest home range, 1988.7 ha, utilising large sections of Dead Tree Bay, Catalina Bay and the Narrows (Fig. 12b).

Female 531, the smallest adult (240 cm) in the study, occupied a large home range of 426 ha (Table 1). She utilised her core-use area (No. 1 in Fig. 14a) 76 % of the time and embarked on five journeys, 25 days on average. The three journeys during the 2011 winter were to sites of known basking congregations in the Eastern Forks and Potters Channel (X. Combrink, pers. obs.), possibly for courtship and mating. She stayed the following summer in her core-use area and during 2012 autumn moved to Catalina Bay for 64 days.

The home range of Female 449 was severely restricted during her first year when Dead Tree Bay was almost completely dry and she utilised a 21.6 ha freshwater refuge area along the shoreline (Fig. 13a). The water level in the bay increased at the end of her first tracking year after 725 ml of rain in Dec. 2010 and Jan. 2011 (Ezemvelo, unpublished data), which led to an increased home range the second year of 745.2 ha (Fig. 13b).

Season

Home ranges of adult females showed almost no seasonal variation (summer = 190.5 ha; winter = 198.0 ha), but core-use areas were larger in winter (79.3 ha) than summer (52.2 ha).

Home ranges and core-use areas showed very little variation (i.e. interquartile range) both during summer and winter (Table 2).

Sub-adults

Sub-adults occupied a median home range of 22.9 ha, and core-use area of 9.0 ha (Table 1). Male 533, the smallest sub-adult (204 cm TL) and study animal, occupied the smallest home range (18.4 ha), in the Narrows. He made four short journeys south, on average 1.3 days and 270 m in duration. His habitat preference was vegetated shallow areas adjacent to the main deep channel. He favoured the eastern shoreline (87.4 % of observations) over the western shoreline (12.6 % of observations) Male 533 was least mobile (MDM = 213 m) with an activity level of 36.1 %, Table 1.

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

Male 503 (208 cm) occupied the largest home range (118.4 ha) of all sub-adults. He mainly used two areas, a large winter area (~1.1 ha), and ~910 m south a second area (~0.5 ha) consisting of a vegetated shallow area adjacent to the main channel (Fig. 14b). He also used a third area (~0.3 ha) where the Narrows fork, ~2.7 km north for one week. During late spring, he moved ~8.9 km down the Narrows to the Honeymoon Bend area. His home range in this area was much larger compared to the northern areas (~5.2 ha), staying in this area for the remainder of his tracking duration. Mean daily movement increased to 239 m coincident with warmer summer water temperatures.

Season

Home ranges (summer = 16.2 ha; winter = 18.2 ha) and core-use areas (summer = 5.9 ha; winter = 5.7 ha) of sub-adults suggests no seasonal variation, but low sample size prevent comparison.

DISCUSSION

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

At Lake St Lucia, we found a significance difference (Mann-Whitney U Test; $p = 0.016$) in home range size of adults (418.3 ha) and sub-adults (22.9). Core-use areas (adults = 103.3 ha, sub-adults = 22.9 ha) also differed significantly (Mann-Whitney U Test; $p = 0.024$). Adult male home range was much larger (713.1 ha) and biologically significantly different than adult females (400.8 ha). Seasonal differences were not significant for size or sex, but the median home range of adult males were twice as large in summer compare to winter. Adult female and sub-adult median winter home range were slightly larger in winter compare to summer.

Adult males

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

Campbell *et al.* (2013) described two discrete behavioural space-use strategies of male Estuarine Crocodiles (*C. porosus*) during the breeding and nesting season in the Wenlock River. They found that "nomadic" males (3.81 ± 0.08 m TL) did not display a stable total (95 % UD) home range but travelled extensively, comparable with Male 111, while "site-fidelic" males (4.17 ± 0.14 m TL) were characterised by a stable home range within discrete sections of the river, comparable with the larger males (110, 121 and 500) in this study. Campbell *et al.* (2013) found Estuarine Crocodile maintained larger home ranges and core-use areas compared to Nile Crocodiles in this study (905 ± 80.7 ha and 410 ± 36.7 ha compared to St Lucia Nile Crocodiles 713.1 and 81.5 ha respectively). Overall, Estuarine Crocodile males were more mobile (MDM 4156 ± 884 m) compared to Nile Crocodile males in this study (1701 ± 60 m), but this may have been facilitated by tidal current flow.

Kay (2004) found his smallest Estuarine Crocodile male (253 cm TL) in the Ord River occupied the largest mid-stream linear range (87 km) which did not stabilise at the end of the study, similar to transient Male 111. His largest male (434 cm) was most mobile (3300

± 6500 m S.D.), a trend also noted for St Lucia males, but at much higher rates sustained by current flow (Kay 2004). Ord River Estuarine Crocodile males did not appear to be site fidelic to any particular section of river, but the low number of observations per study animal (mean = 32) preclude more complete understanding.

Adult females

Adult females occupied biologically significant smaller home ranges compared to adult males, and they were generally less variable. It furthermore seemed that habitat and topography might be a significant factor limiting home range size. Generally, females in the main lake (125 and 449 during her second year) maintained larger home ranges than females mainly restricted to the Narrows (531, 601 and 515) and Female 514, restricted to the small Mphathe Stream, occupied the smallest home range. During the drought Female 449's home range was concentrated within a small freshwater refugia, but as lake levels increased, she moved from the shoreline into the bay, significantly increasing her home range.

We suspect that import resources such as freshwater seepage areas, preferred hunting/feeding areas and basking/mating sites (especially during winter), are spatially more dispersed in the main lake, compared to the Narrows, which seemingly facilitates larger home ranges.

The absence of home range size differentiation between summer and winter could be attributed to winter movements to basking/mating areas of all females, except Female 449, and restricted space use in summer on the nest for four nesting females.

Sub-adults

Home range and core-use areas of sub-adult Nile Crocodiles at St Lucia was significantly smaller than adults. All transmitter-fitted sub-adults were captured in the Narrows and they were very habitat specific, partial to shallow, well vegetated areas adjacent to the deep channel and strictly territorial with no overlap between neighbouring sub-adults (Fig. 15).

Hutton (1989) found small and localised home ranges of 10 ha (100 % isopleth) at Lake Ngezi for Nile Crocodiles < 2.2 m, considerably smaller than the 22.9 ha median home range of the present study. His findings that large sub-adults abandoned their home ranges and moved throughout much of the available habitat were not recorded at St Lucia. Nonetheless, the sub-adults in this study were possibly still too small to disperse, although exploratory behaviour was recorded for Female 531, a small (240 cm) adult.

Calverley (2013) recorded somewhat smaller sub-adult total home ranges (15.2 ± 10.8 ha) in a Lake Nyamithi of Ndumo Game Reserve than this study (22.9 ha median).

Brien *et al.* (2008) recorded the home range for a sub-adult male Estuarine Crocodile (171 cm) during winter at Seven Mile Waterhole. His home range was 1.2 ha and core-use area 0.1 ha, much smaller than this study’s median home range and core-use area of 18.2 ha and 5.9 ha respectively. The MDMs of sub-adult Nile Crocodiles at St Lucia (199 ± 17 m) were also higher compared with the Seven Mile Waterhole Estuarine Crocodile male (137 m) as well as the maximum daily movement (Nile Crocodile = 2023 m, Estuarine Crocodile 1075 m).

CONCLUSION

Despite being the largest, most dangerous and widely disturbed crocodilian in Africa, very little scientific data is available on the spatial ecology and home range behaviour of Nile Crocodiles, with all previous studies focusing on lacustrine or lotic systems.

Typical of all estuaries, the Lake St Lucia estuarine system is spatio-temporally dynamic as well as the largest estuarine system on the continent. The inherent physical and biological variability was exacerbated by a prolonged drought, followed by rapid restoration of water-levels within the tracking duration of a number of study crocodiles. This resulted in behavioural adaptations in spatial ecology and home range behaviour, reflecting the variability of the physical and biological environment.

Asymptote analysis confirmed that the number of observations for most crocodiles were sufficient to describe their full range of movements, but we recorded transient behaviour of a young adult male, gradually moving northwards subsequent to the restoration of water levels.

Adult males revealed a negative correlation between home range size and crocodile size, while adult female home range size were generally more homogeneous. All nesting females displayed an explosive increase in mobility and space-use subsequent to the nesting period, and we hypothesized that this behaviour was in response to a need to increase body condition before the onset of winter.

All adult crocodiles moved during winter to large congregations that formed south of the lake during the drought period (Combrink, pers. obs.). We hypothesized that this was driven primarily by reproductive requirements and not thermoregulatory needs. Since early 2011, lake-water levels were restored, resulting in a decrease of these winter congregations.

Sub-adults occupied significantly smaller home range than adults, which were habitat specific. They remained in shallow vegetated areas adjacent to deep water, avoiding the open deep water altogether. It is likely that this limited sub-adult habitat in the Narrows might be an important density regulating mechanism at St Lucia.

During the drought large parts of the western, northern and central lake dried out or became hypersaline and too shallow to facilitate crocodile movement. Crocodiles either moved south to Catalina Bay where sufficiently deep water expedited movement and other activities (e.g. basking and feeding), providing they had access to freshwater seepage along the eastern shoreline of the bay. Aerial data suggests that most crocodiles moved even further south to the low salinity Narrows channel. However, some remained in the central region and were restricted to freshwater shoreline seepages areas, or refugia inside swampforest bordering the eastern shoreline. As water levels increased, former areas were rapidly colonised and movement levels increased.

We conclude that size, sex, reproductive status and habitat influenced Nile Crocodile space-use and movements, resulting in complex and varied home range patterns, not surprising given the dynamic nature of estuaries, especially during times of perturbations.

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Caption for Figures

Figure 1. The Lake St Lucia estuarine system.

Figure 2. Home ranges (a.) and core-use areas (b.) of adult males and adult female Nile Crocodiles at St Lucia.

Figure 3. Home range analysis for Crocodile 110, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 200 fixes (observations).

Figure 4. Home range analysis for Crocodile 121, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 400 fixes (observations).

Figure 5. Home range analysis for Crocodile 125, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 800 fixes (observations).

Figure 6. Home range analysis for Crocodile 500, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 400 fixes (observations).

Figure 7. Home range analysis for Crocodile 503, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 650 fixes (observations).

Figure 8. Home range (a.) and core-use area (c.) of adult males and females in the Lake St Lucia estuarine system.

Figure 9. Home ranges and core-use areas of transient Male 111 over the four years tracking duration. Year 1 = a, year 2 = b, year 3 = c and year 4 = d.

Figure 10. Home ranges and core-use areas of Male 110 (a.) and male 212 (b.) in Catalina Bay.

Figure 11. Home ranges and core-use areas of Male 500 (a.) and Male 504 (b.).

Figure 12. Home ranges and core-use areas of Female 514 (a.) and Female 125 (b.).

Figure 13. Home range and core-use areas of nesting Female 449.

Figure 14. Home range and core-use areas of Female 531 (a.) and Female 503 (b.).

Figure 15. GPS-observations of sub-adult in the Narrows channel. Both (a.) and (b.) illustrating strict spatial partitioning and a preference of shallow vegetated areas adjacent to the main deep Narrows channel, and a avoidance of the deep open water of the channel.

Figures

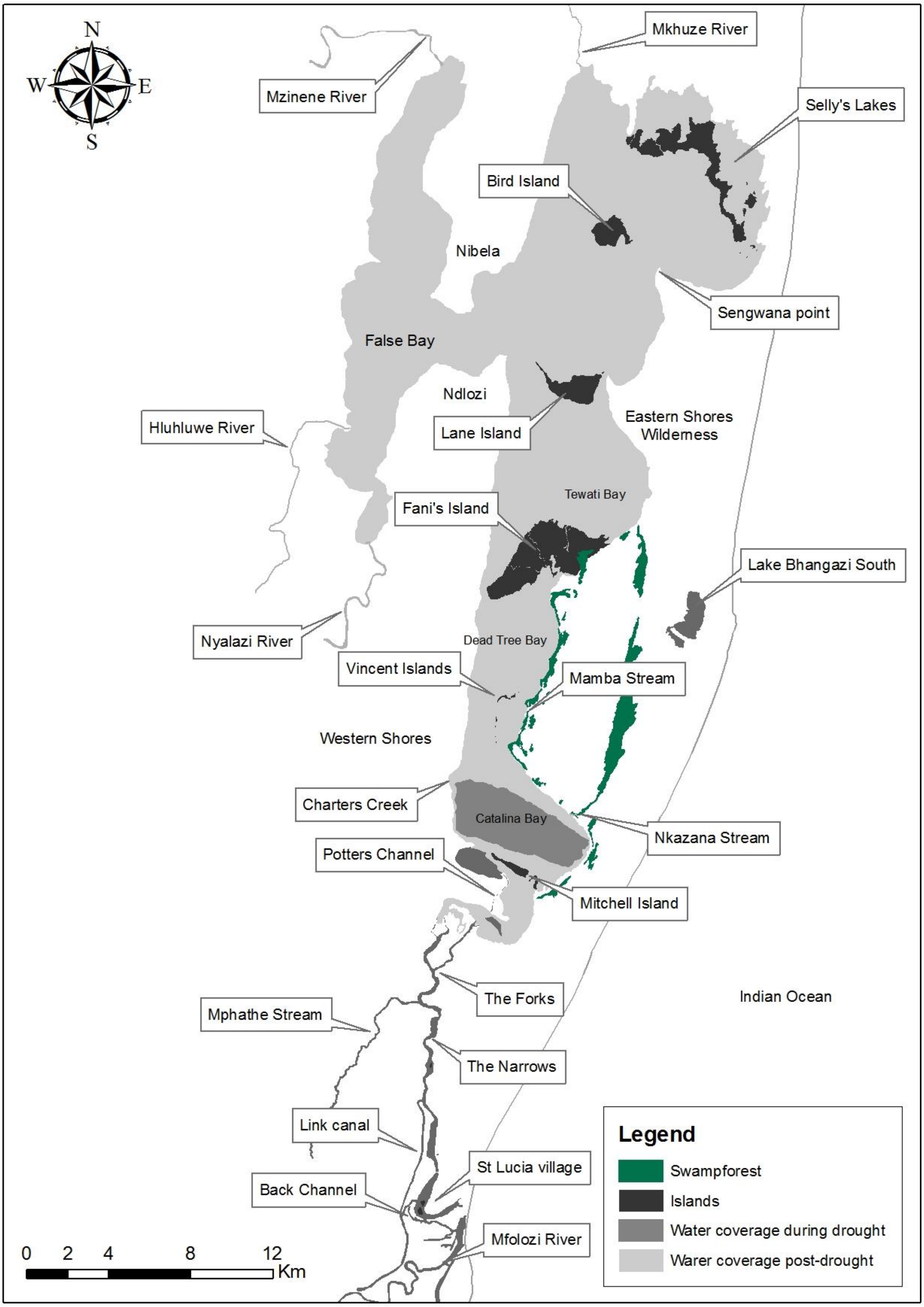

Figure 1. The Lake St Lucia estuarine system.

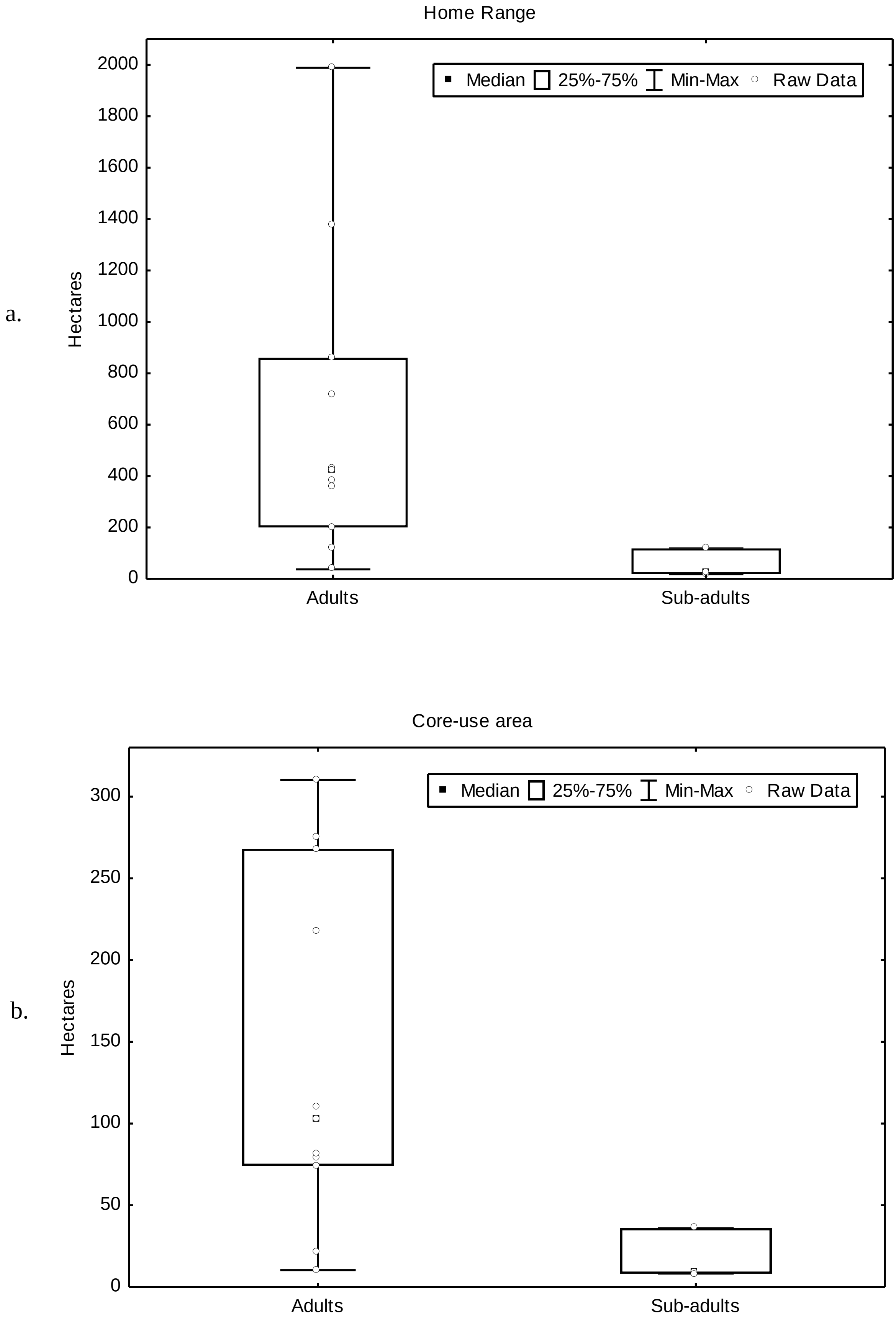

Figure 2. Home ranges (a.) and core-use areas (b.) of adult and sub-adult Nile Crocodiles at St Lucia.

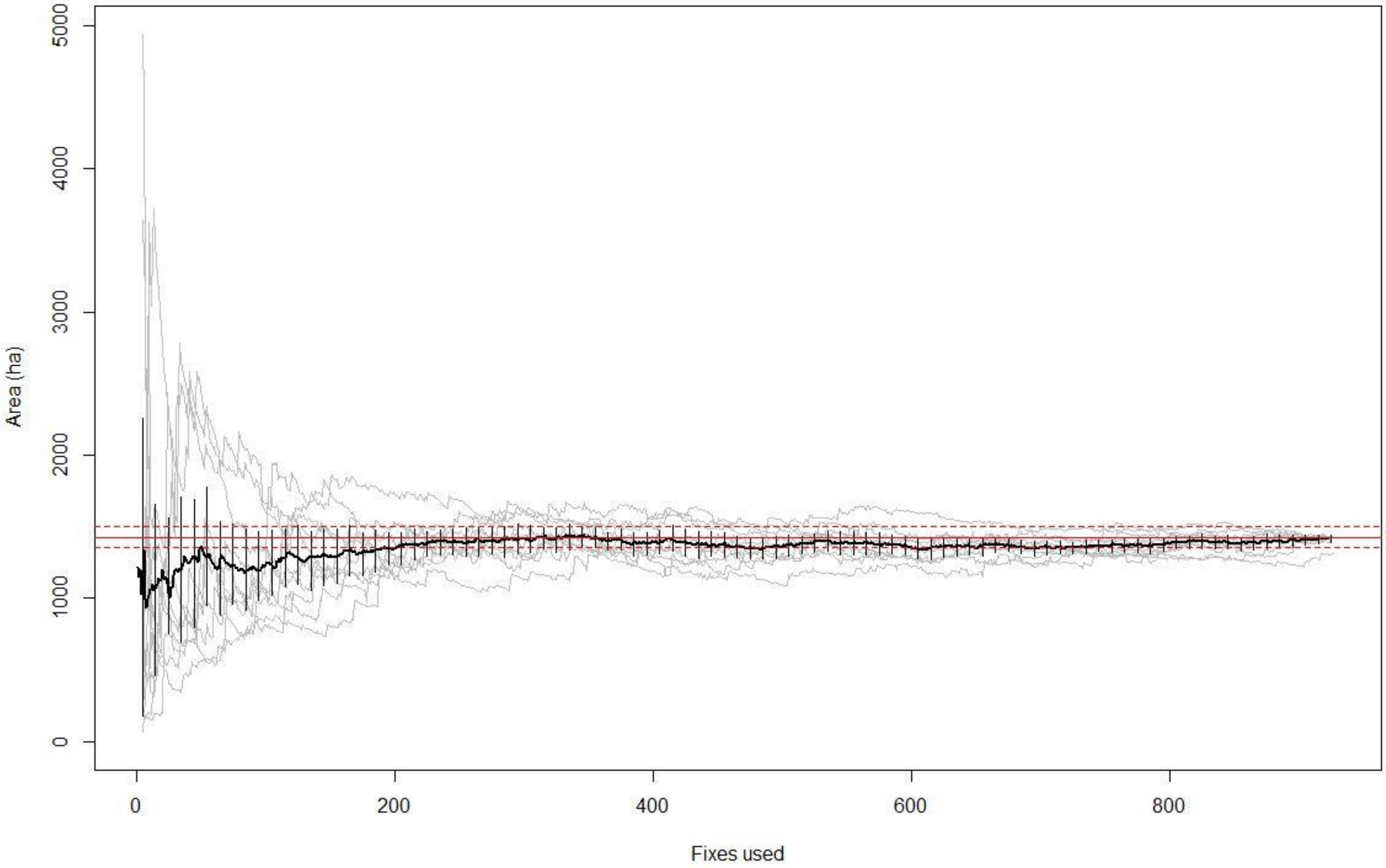

Figure 3. Home range analysis for Crocodile 110, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 200 fixes (observations).

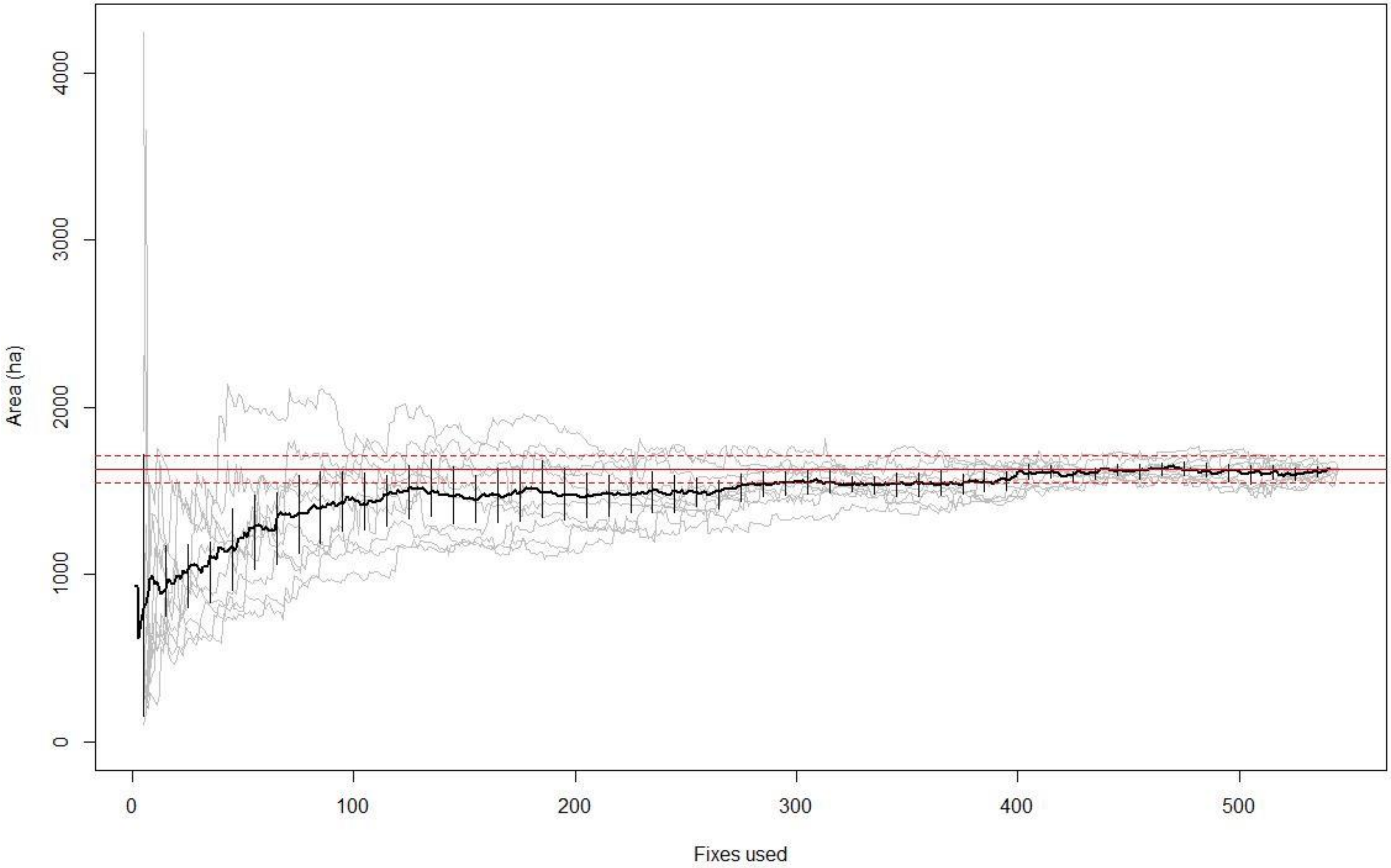

Figure 4. Home range analysis for Crocodile 121, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 400 fixes (observations).

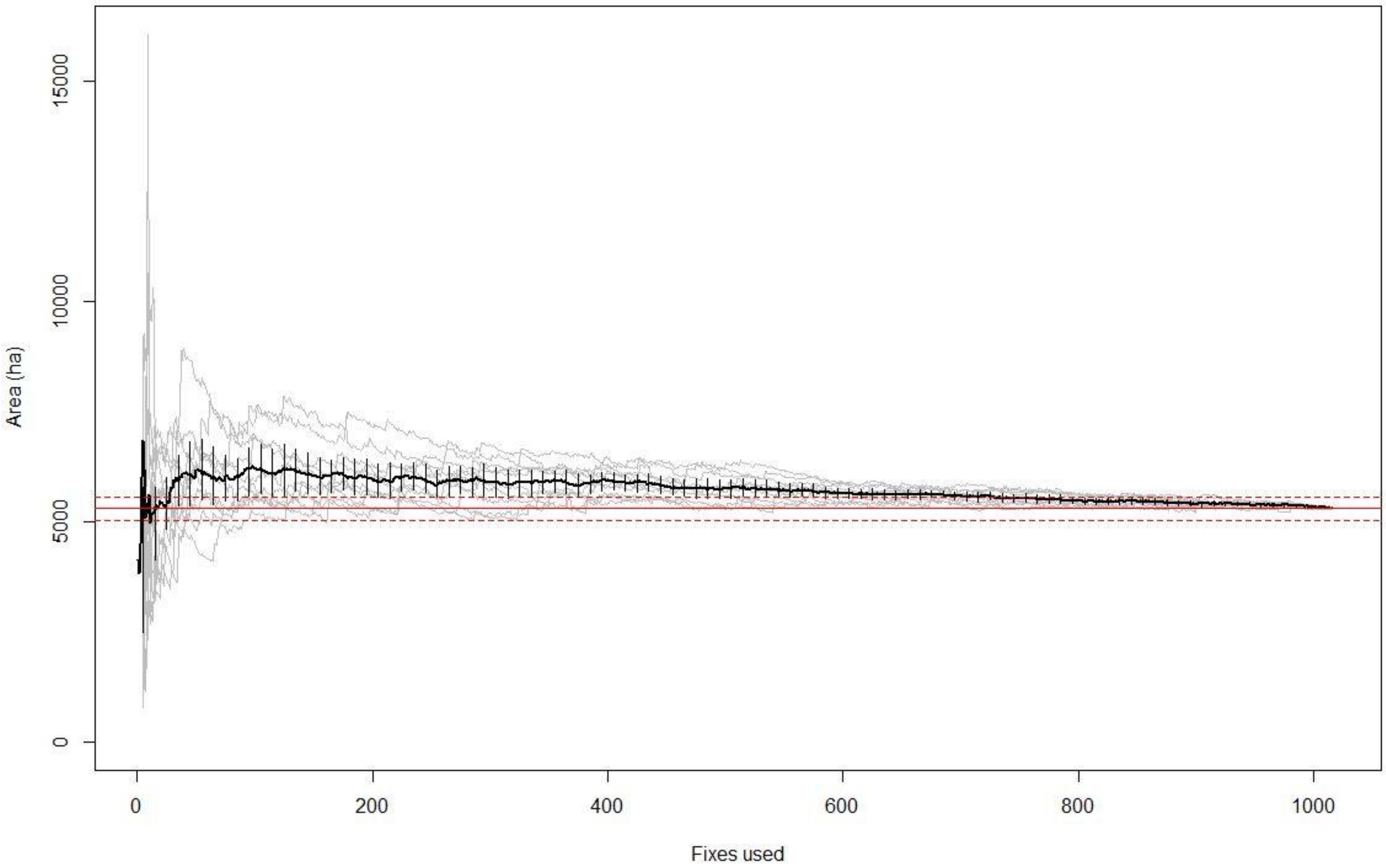

Figure 5. Home range analysis for Crocodile 125, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 800 fixes (observations).

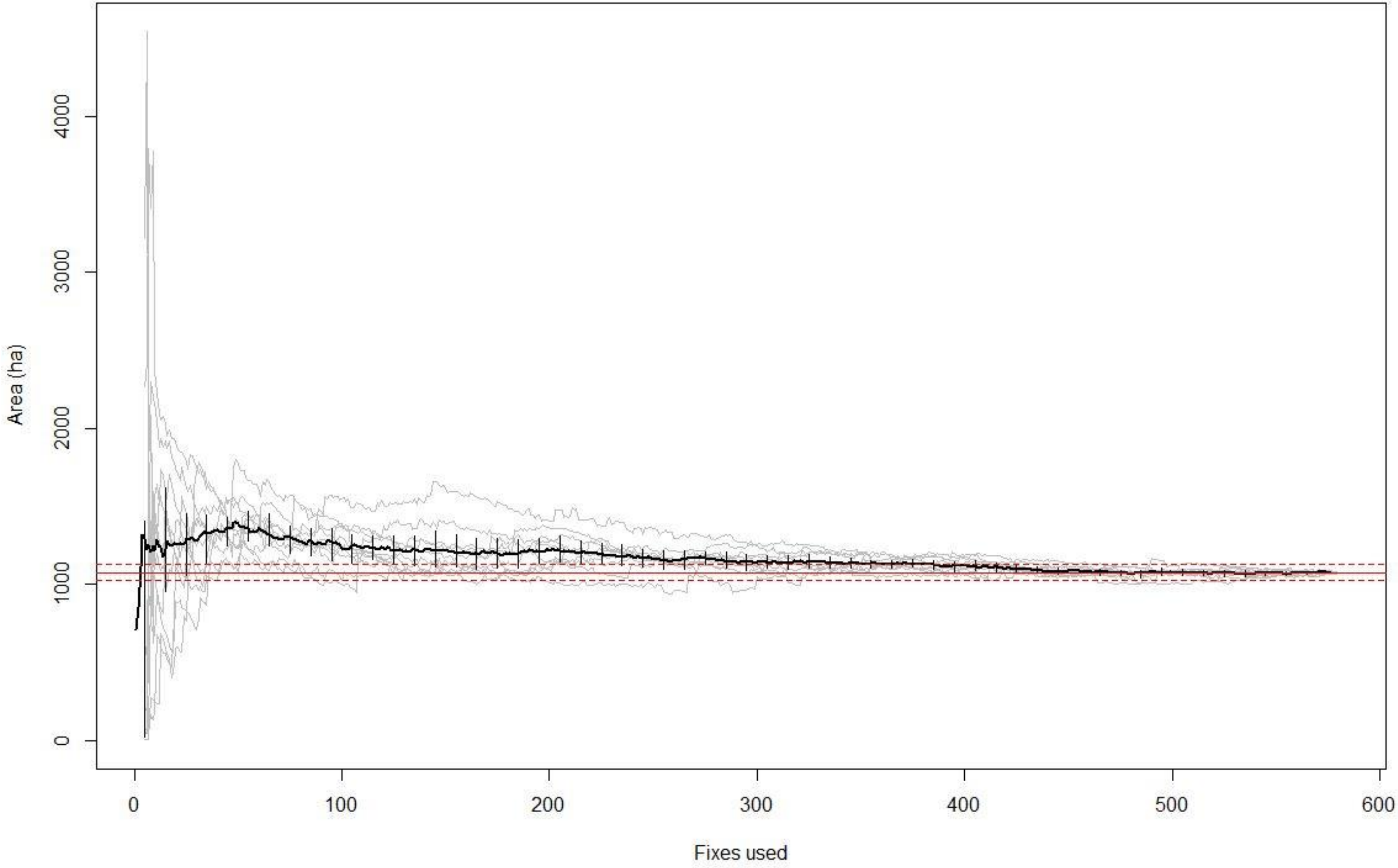

Figure 6. Home range analysis for Crocodile 500, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 400 fixes (observations).

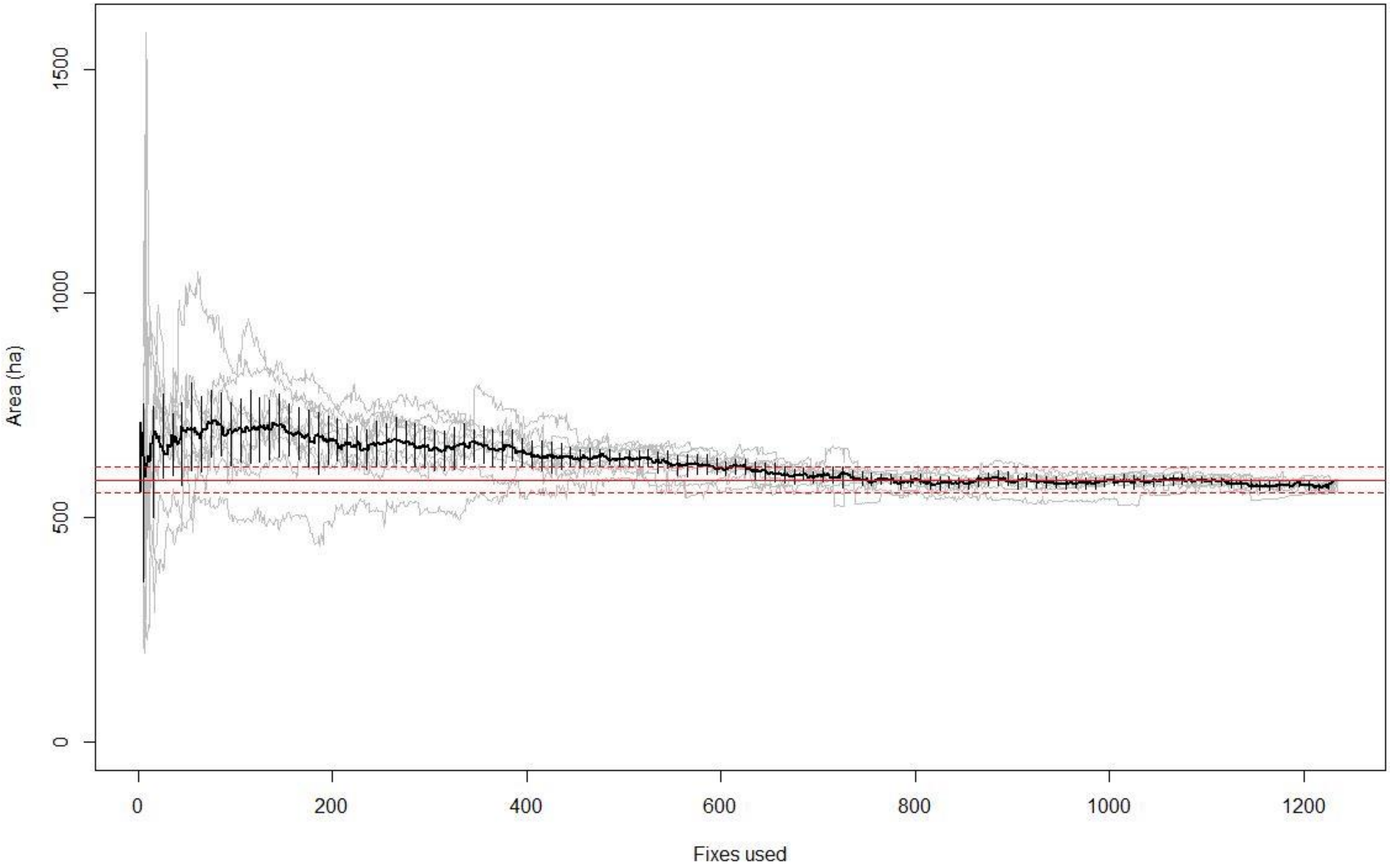

Figure 7. Home range analysis for Crocodile 503, indicating 10 random simulations (grey lines) of kernel asymptotes and their mean 95% CI function (black bars, every 10th observation selected for better visual display). Mean kernel home range (black) reach an asymptote consistently within the 5% (dashed red line) of the final home range size (red line) after approximately 650 fixes (observations).

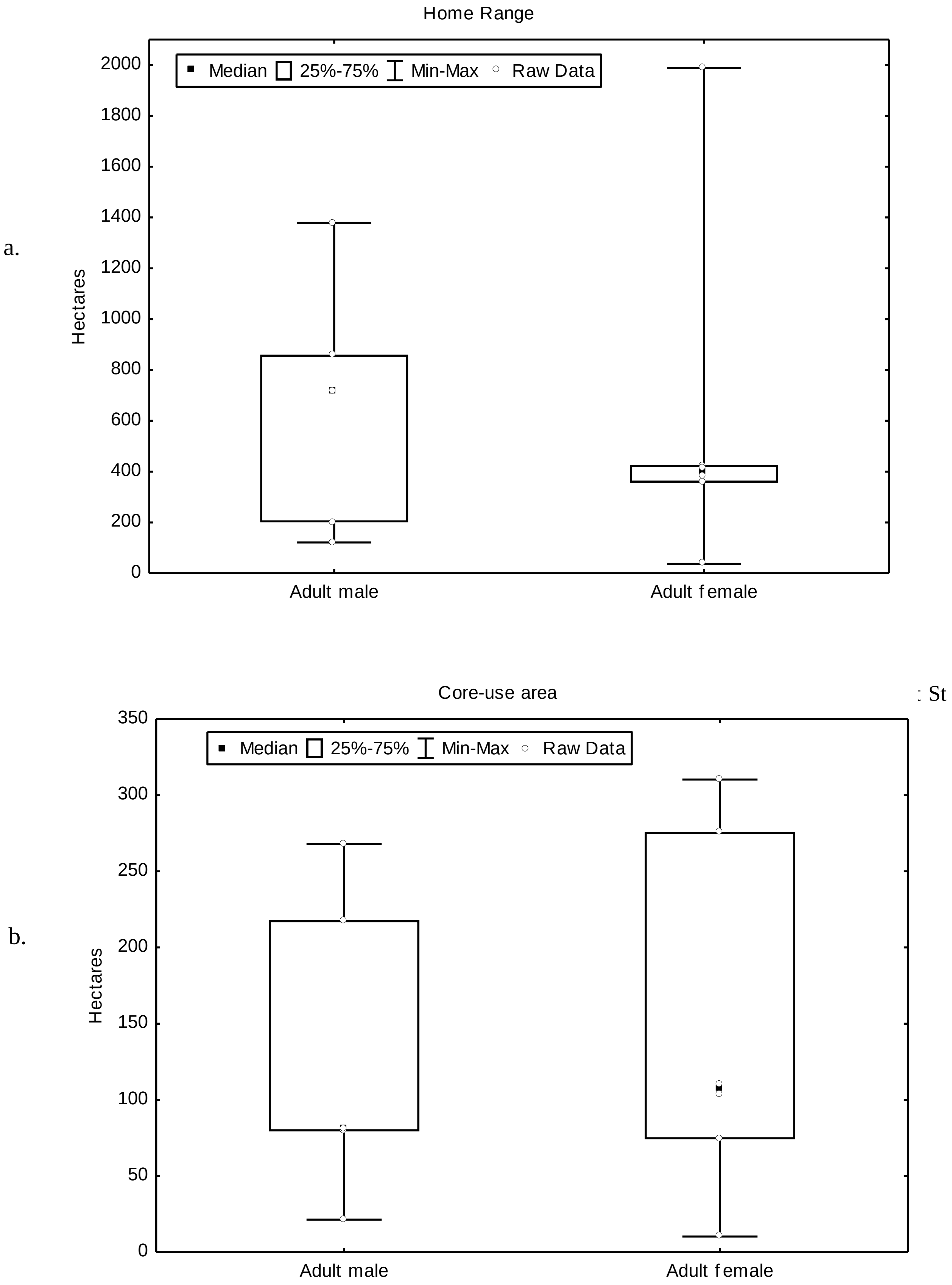

Figure 8. Home range (a.) and core-use area (b.) of adult males and females in the Lake St Lucia estuarine system.

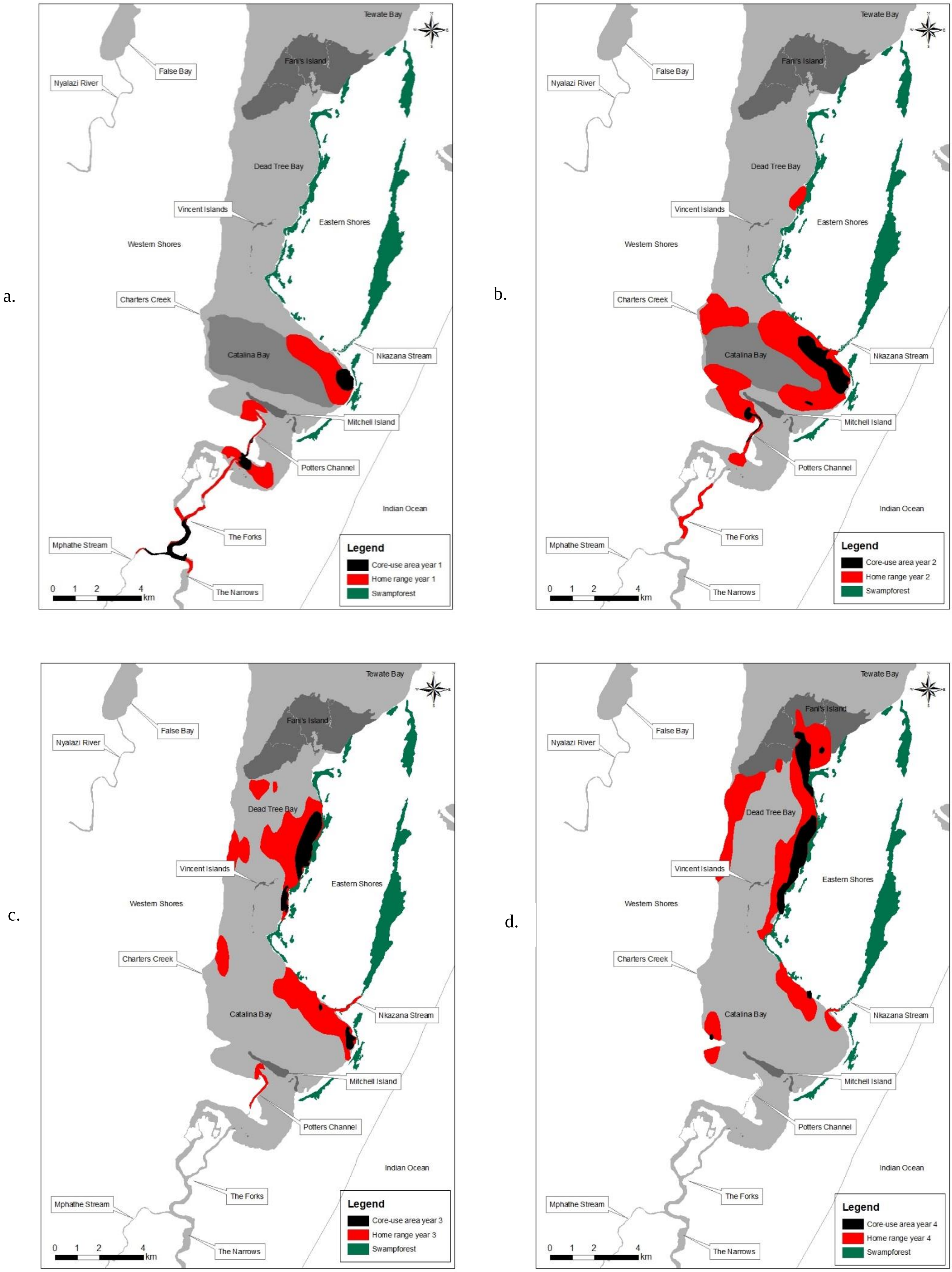

Figure 9. Home ranges and core-use areas of transient Male 111 over the four years tracking duration. Year 1 = a, year 2 = b, year 3 = c and year 4 = d.

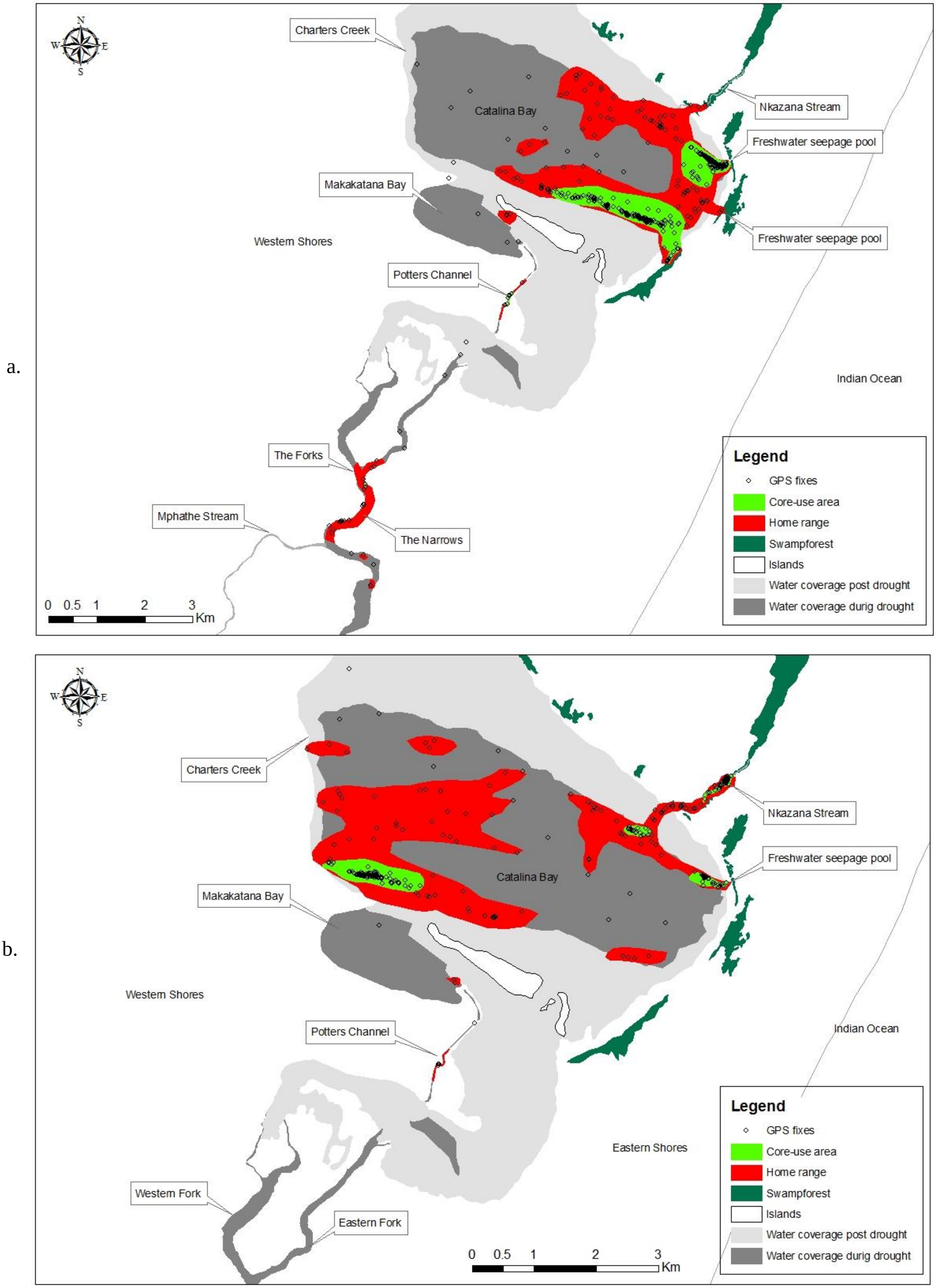

Figure 10. Home ranges and core-use areas of Male 110 (a.) and Male 121 (b.) in Catalina Bay.

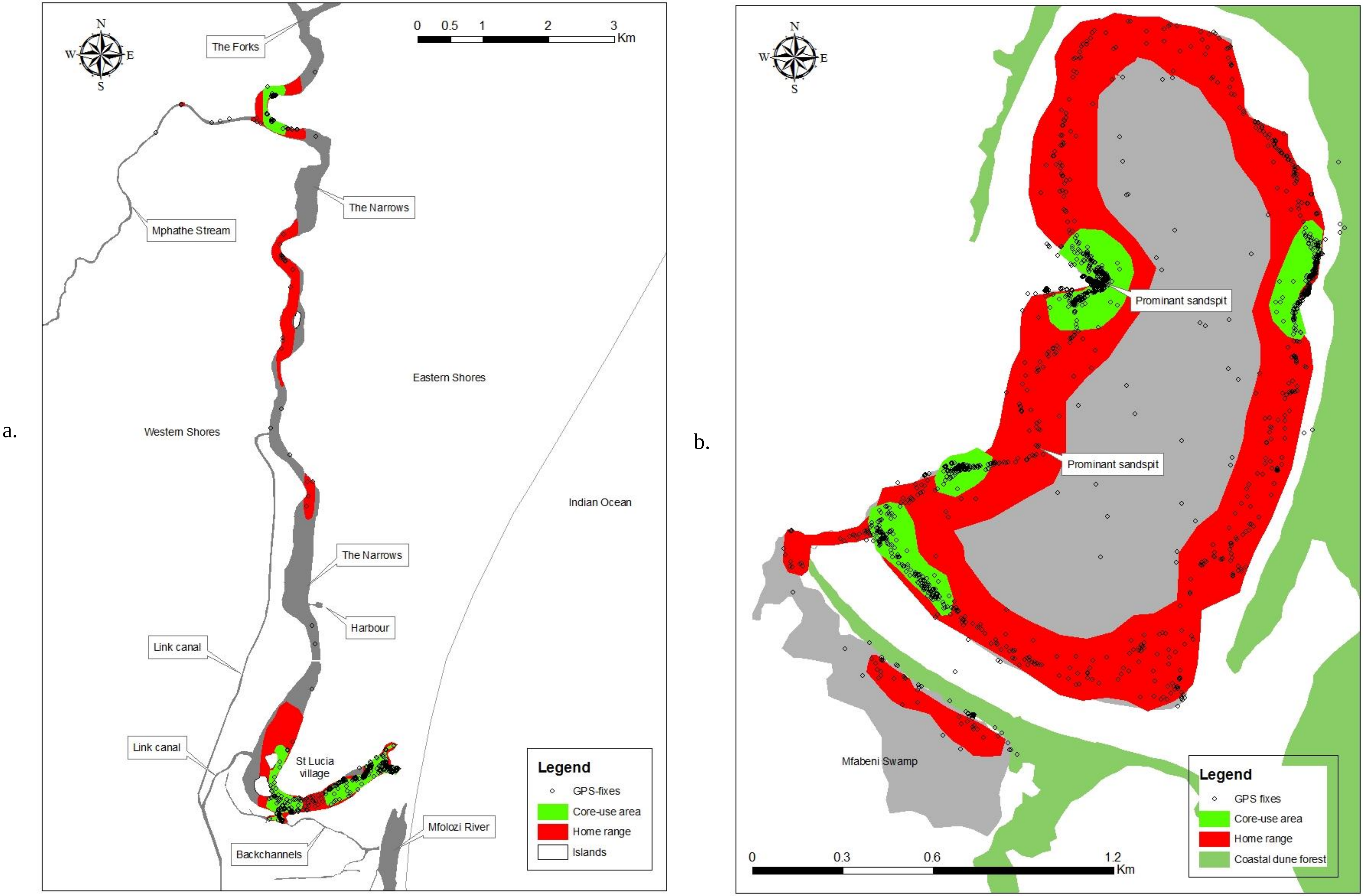

Figure 11. Home ranges and core-use areas of Male 500 (a.) and Male 504 (b.).

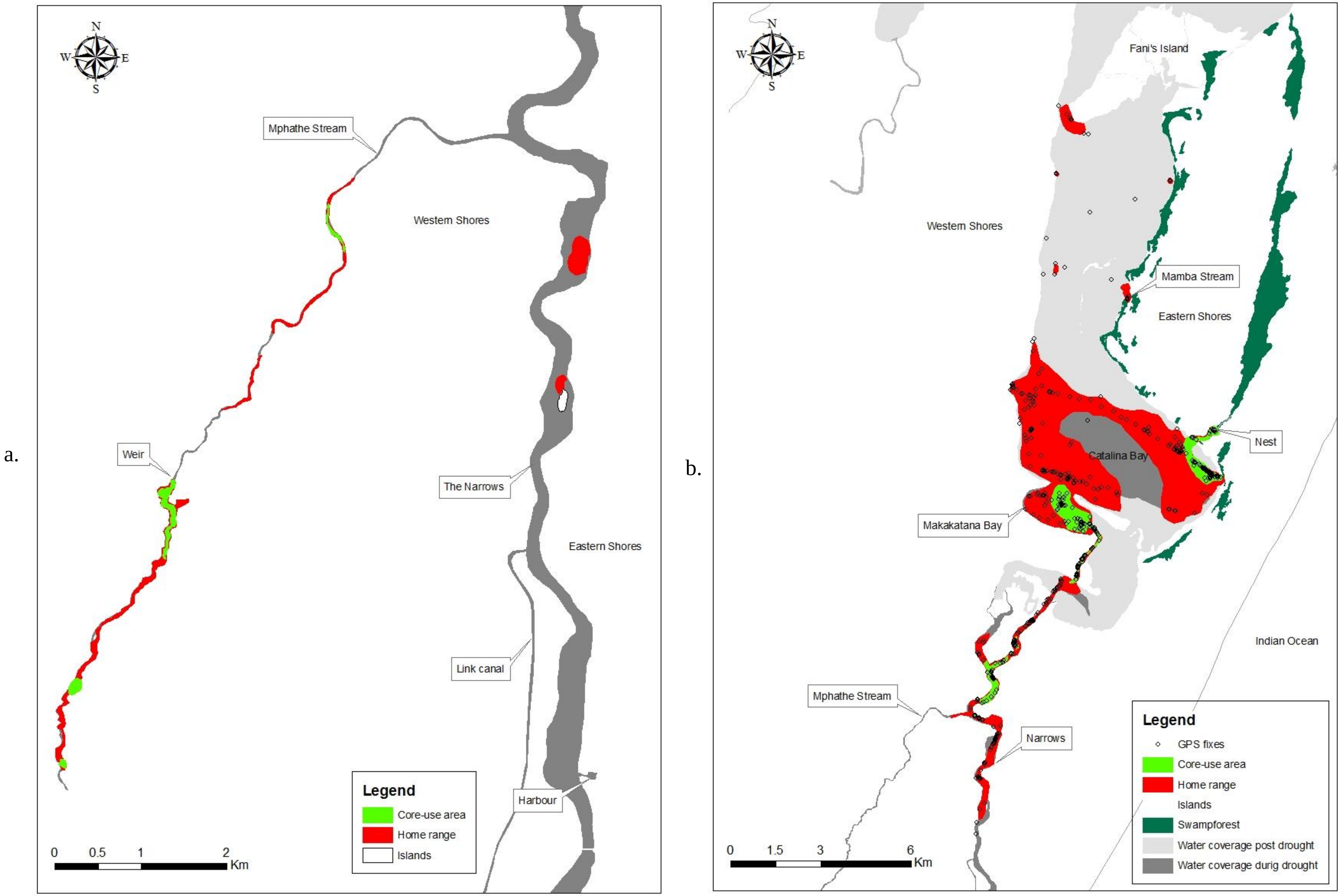

Figure 12. Home ranges and core-use areas of Female 514 (a.) and Female 125 (b.).

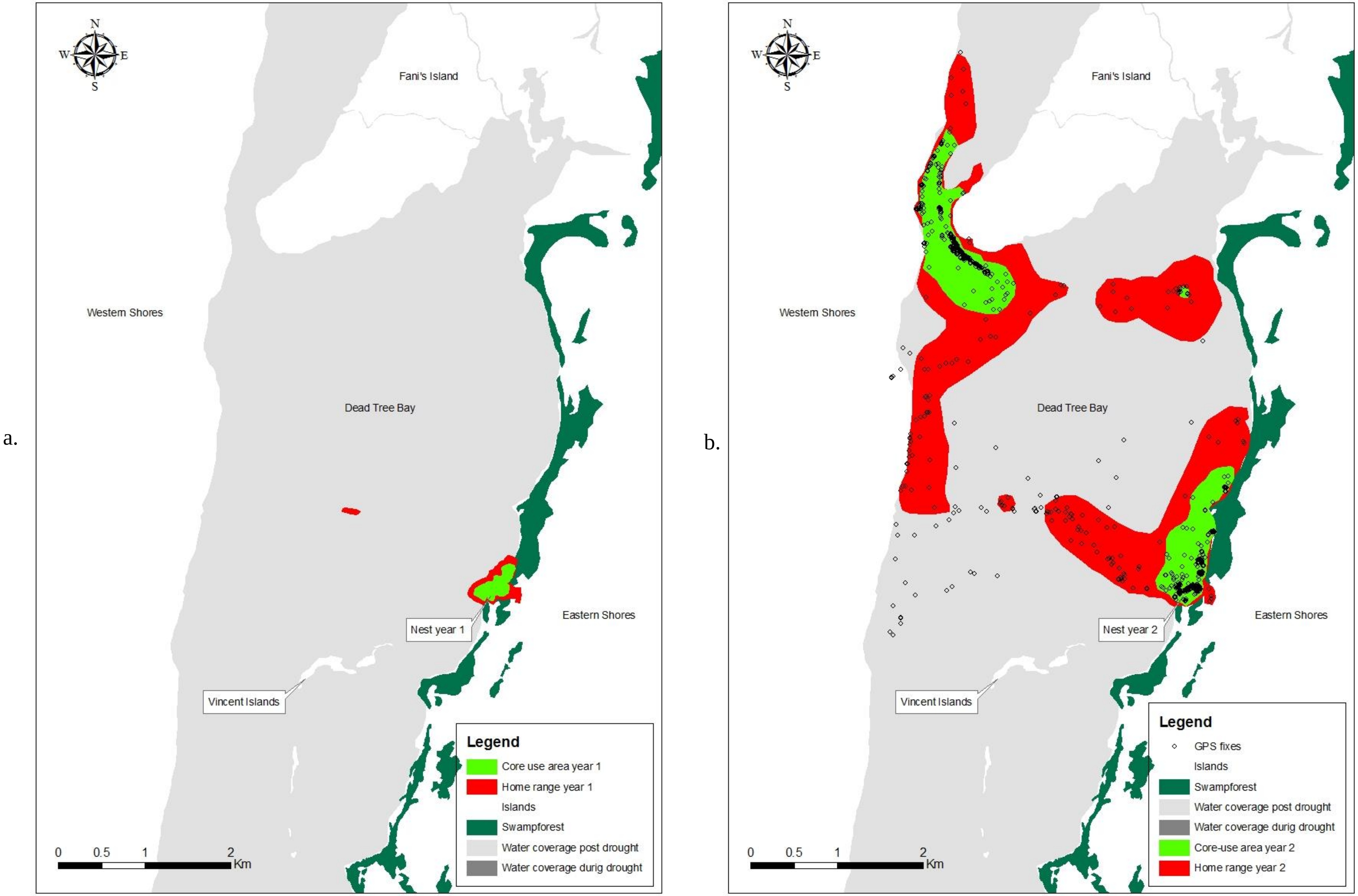

Figure 13. Home range and core-use areas of nesting Female 449.

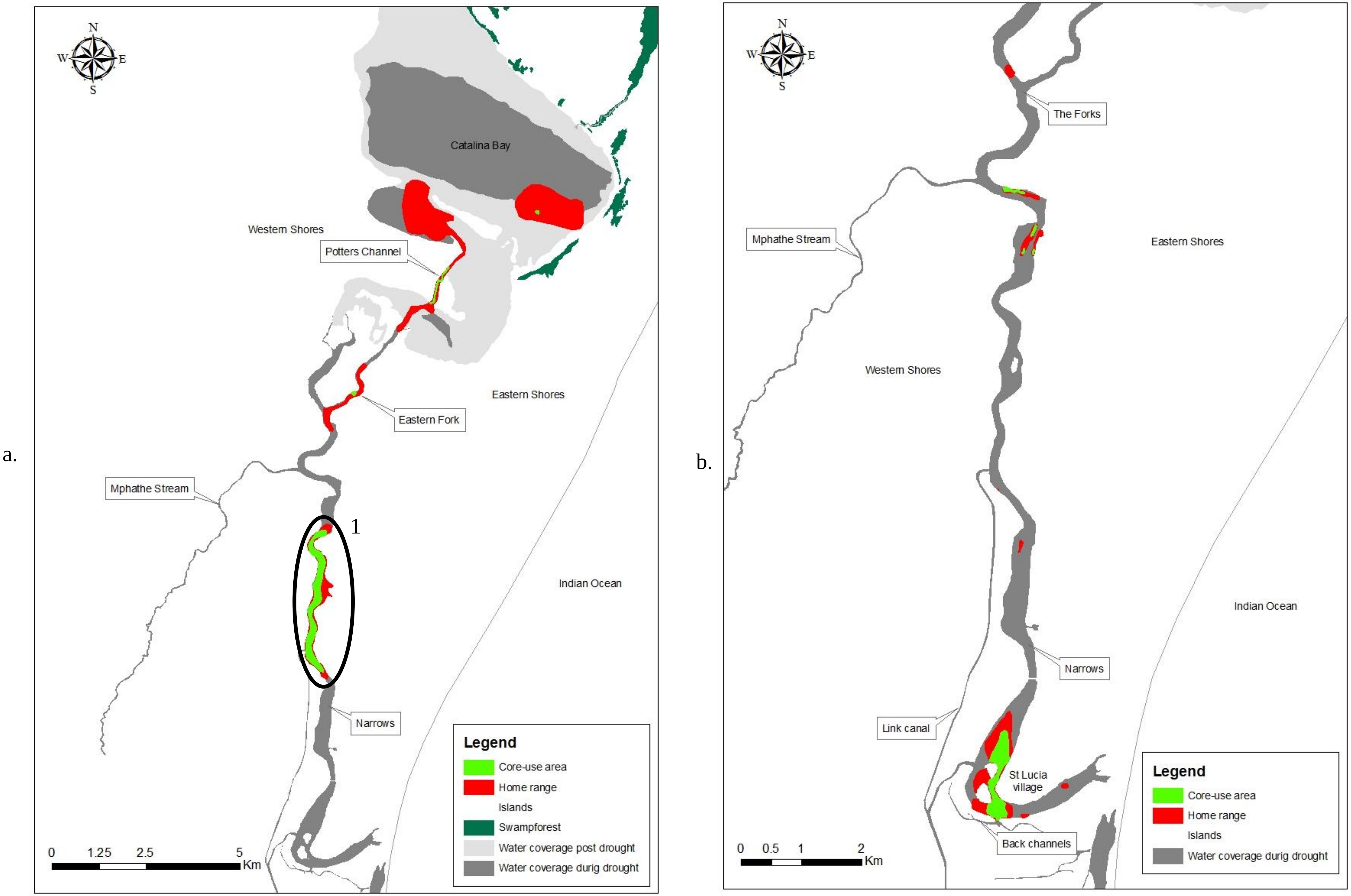

Figure 14. Home range and core-use areas of Female 531 (a.) and Female 503 (b.).

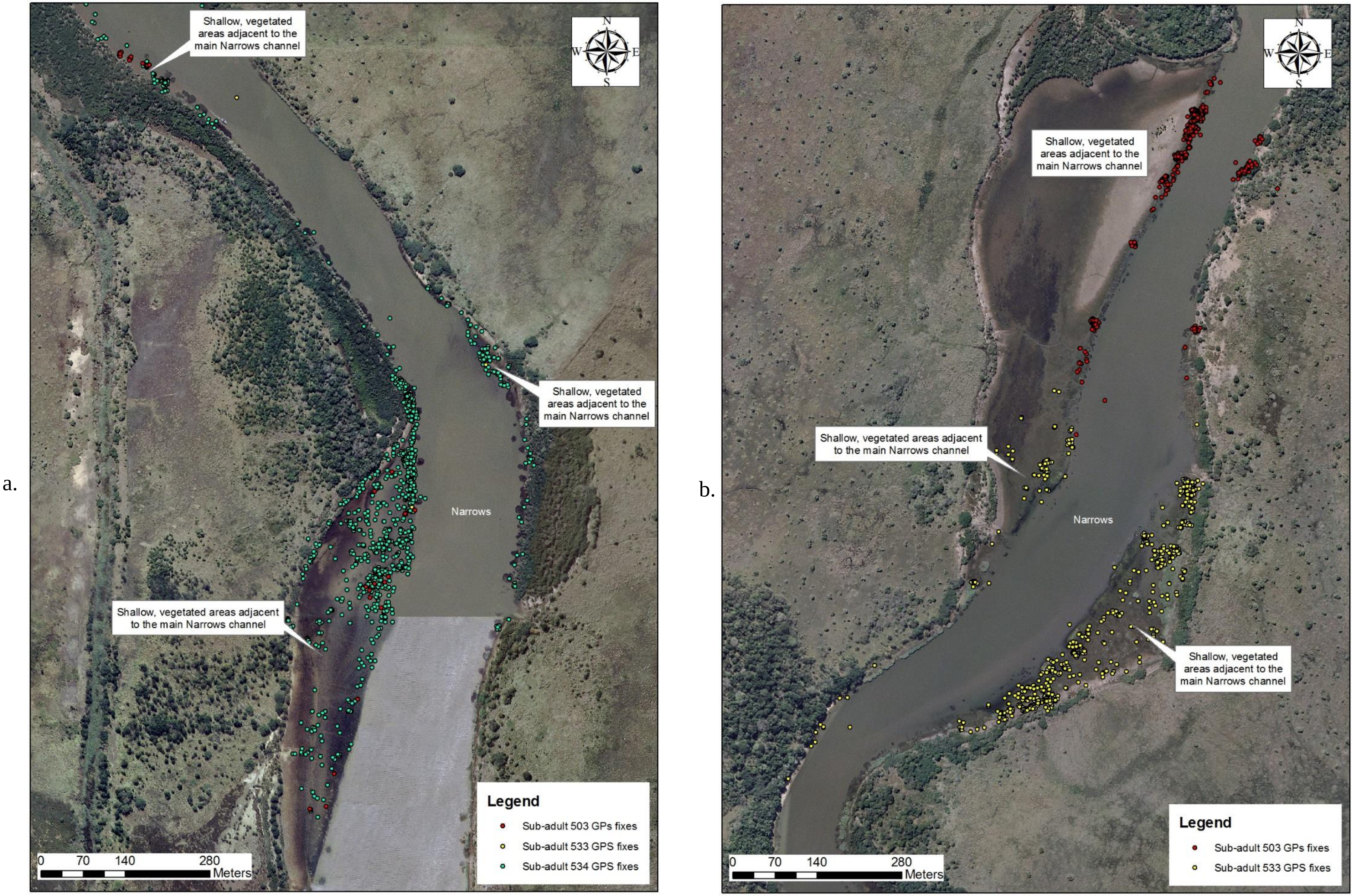

Figure 15. GPS-observations of sub-adult in the Narrows channel. Both (a.) and (b.) illustrating strict spatial partitioning and a preference of shallow vegetated areas adjacent to the main deep Narrows channel, and a avoidance of the deep open water of the channel.

Captions for Tables

Table 1. Annual home range and core-use area size, no. of core areas and daily movements of Nile Crocodiles at Lake St Lucia.

Table 2. Seasonal home range and core-use area size of Nile Crocodiles at Lake St Lucia.

Tables

Table 1. Annual home range and core-use area size, no. of core areas and daily movements of Nile Crocodiles at Lake St Lucia.

Crocodile	Size (cm)	Home range (ha)	Core (ha)	No of core areas	Mean DM	Median DM
111 *	295	1378.9	268.1	5	1856	1095
110	349	713.1	217.9	4	1686	1071
121	392	860.2	79.3	4	1592	493
500	402	200.5	81.5	3	1756	1459
504 *	406	121.2	21.4	4	1936	1587
Adult males median		**713.1**	**81.5**			
Adult males IR range		**659.7**	**138.6**			
531 *	240	426.0	103.3	4	1222	927
514 *	270	37.0	10.3	4	604	513
449 *	285	383.4	110.6	2	749	208
125	289	1988.7	310.2	5	1488	786
601 *	293	418.3	275.8	3	2490	2331
515	304	357.0	74.2	3	1369	326
Adult females median		**400.8**	**106.9**			
Adult females IR range		**69.0**	**201.6**			
533	204	18.4	9.0	2	213	97
503	208	118.4	35.9	4	311	156
534	212	22.9	8.2	4	334	294
Sub-adult male median		**22.9**	**9.0**			
Sub-adult IR range		**100.0**	**27.7**			

* Mean home range and core-use area calculated due to data > 1 year

Table 2. Seasonal home range and core-use area size of Nile Crocodiles at Lake St Lucia.

Crocodile	**Size (cm)**	**Home range (95%)**	**Home range**	**Core**	**Core**
		Summer	**(95%)**	**Summer**	**Winter**
111	295	1510.0	411.6	293.8	75.1
110	349	383.1	-	119.5	-
121	392	1111.2	-	141.4	-
500	402	-	294.0	-	75.1
504	406	131.3	54.6	37.8	11.2
Adult males median		**747.2**	**294.0**	**130.5**	**75.1**
Adult males IR range		**1053.4**	**357.0**	**139.0**	**63.9**
531	240	271.1	119.3	74.3	56.4
514	270	70.3	8.5	19.4	4.8
449	285	95.6	173.1	12.4	92.2
125	289	1616.1	822.9	95.3	108.3
601	293	159.4	223.0	48.6	123.9
515	304	221.5	282.3	55.8	66.3
Adult females median		**190.5**	**198.0**	**52.2**	**79.3**
Adult females IR range		**175.5**	**163.0**	**54.9**	**51.9**
533	204	16.2	4.9	5.9	2.4
503	208	48.8	18.2	19.6	7.2
534	212	10.9	26.7	3.5	5.7
Sub-adult male median		**16.2**	**18.2**	**5.9**	**5.7**
Sub-adult IR range		**37.9**	**21.8**	**16.1**	**4.8**

CHAPTER 5

An overview of Nile Crocodile (*Crocodylus niloticus*) nest abundance and distribution in the Lake St Lucia estuarine system, South Africa

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ABSTRACT

Reproductive output is one of the key primary population processes responsible for changes in population size. The relative abundance and distribution of Nile Crocodile (*Crocodylus niloticus*) nests have been monitored at the Lake St Lucia estuarine system for more than three decades, mean nest count 1982 to 2013 = 76.19 ± 6.42, range: 29 - 141. The macro-level heterogeneity of nesting habitat reflected the spatio-temporal diversity of the Lake St Lucia system, and is possibly unique within a single Nile Crocodile population. Changes in nest abundance and distribution were related to increased anthropogenic disturbance and habitat transformation in the northern and southern parts of the lake. Hydrological variability, especially reduced freshwater input and availability during a prolonged drought combined with the state of the estuary mouth (i.e. closed or open), affected prey densities. This resulted in considerable variation (6.9 % - 56.4 %) of reproductive frequency. Surveys efficiency improved through the years and annual survey effort is now recorded facilitating improved interpretation of count data. However, the ratio of present, but unrecorded nests remains unquantified. Nest counts were low during the study period (2008/9 to 2012/13) and only three areas revealed more than five nests, on average. All nests were located close to freshwater streams or seepage areas. A limited paraglider survey over a ~20 km distance revealed nests missed during the foot survey, highlighting the potential of this method, especially over terrain where conventional foot surveys were difficult, such as forests and thickets. We recorded burrowing behaviour associated with nesting; in all cases when nearby water was too shallow for cover, and nesting females entered those burrows when disturbed. We captured 12 nesting females on or adjacent to nest-sites during the 2009/10 nesting season and confirmed re-use of the exact same nest-site. Other females oviposited in nest-sites occupied by different females during previous years. The Lake St Lucia Nile Crocodile population is the largest estuarine nesting population and largest monitored and possibly most stable (i.e. unaffected by flooding) nesting population in South Africa. Insights into the abundance and distribution of crocodile nests while understanding how threats, such as anthropogenic disturbance, lead uptake by the ingestion of fishing sinkers and alien invasive plants might affect rates of reproduction, can inform management actions to mitigate such threats timeously.

Keywords: Reproduction, Nest surveys, nest distribution, Lake St Lucia estuarine system, conservation. *Crocodylus niloticus*

INTRODUCTION

The Nile Crocodile (*Crocodylus niloticus*) is a threatened species in South Africa, assessed as Vulnerable on the Red Data List in 1978, 1988 and 2013 (McLachlan 1978, Jacobsen 1988, Marais 2014), that requires national protection (Van Schalkwyk 2007). The overall conservation philosophy in the iSimangaliso Wetland Park is to maintain healthy and viable ecosystems. However, it is recognised that within this context, a specific management strategy is required for Nile Crocodiles (Taylor et al. 2007). It highlights monitoring as a necessary and important tool (Wallace et al. 2013) to detect a decline in the population or nesting effort early enough, so that management actions can be instituted to conserve the population (Taylor et al. 2007).

The key to understanding many of the biological aspects of crocodilians lies in the study of their reproduction (Webb 1977). To better understand population dynamics it is necessary to monitor the relative abundance and distribution of crocodilian nests. Although nest surveys focus on a single segment of the population, it is important as it relates directly to the future of the population. Knowledge of the relative abundance and distribution of crocodile nests in an area and how threats are impacting on breeding activities can institute management actions to mitigate their consequences. Although nest surveys were conducted in a number of populations (Modha 1967b, Graham 1968, Hutton 1984, Games 1990, Hartley 1990, Graham et al. 1992, Swanepoel et al. 2000, Botha 2005, Shacks 2006, Champion 2011, Combrink et al. 2011, Calverley 2013), nesting trends are difficult to assess but invariably will follow population declines. Crocodiles are long-lived, slow growing species often with low reproductive frequency. A population monitoring programme which over-emphasise the adult component and under-emphasise the nesting component could be deceptive as the population might appear stable, but may have a reduced reproductive success, resulting in an ageing population prone to a rapid collapse as the old reproductive animals might all die within a relative short time. Nile Crocodile populations have been depleted throughout much of their range and extirpated from at least three countries: Israel, Algeria and Comoros (Fergusson 2010). It is likely that all breeding populations outside areas of strict protection will decline in the future while some populations within formally protected areas are facing similar pressures (Combrink et al. 2011).

Although some aspects of Nile Crocodile reproductive ecology at Lake St Lucia were investigated from 1959 to 1978 (Pooley 1982a), nest surveys have been conducted since the 1980's, resulting in one of the longest monitored crocodile populations in Africa. At first surveys merely reported on the number of nests, apparent predation levels and maps indicated the general nest areas. The Lake St Lucia system is extensive, e.g. the ~35 000 ha lake has a shoreline of ~400 km (Taylor et al. 2006), and there numerous adjacent wetlands, streams, rivers and pans surrounded by potentially suitable nesting areas. Staff limitations prevented systematic coverage of all known nesting areas during the early years and survey effort was often not documented. In an effort to expand survey effort beyond the known nesting areas, especially to incorporate suitable, but unsurveyed areas, aerial surveys for nests were introduced in the early 1990's (Anderson 1993, 1994) and although nests were recorded, they were mostly from known nest areas. These surveys were conducted from fast (>100 km^{-1}) flying fixed-wing airplanes and were discontinued as they did not significantly add to the foot survey data.

With advancements in technology, especially Global Positioning System (GPS) units, it was possible to record nest location with higher accuracy (Leslie 1997) and produced high resolutions maps in Geographic Information Systems. More recently, efforts were initiated to reinstate the marking nest-sites as well as photographing and identify nesting females, when possible. A twin-seater motorised paraglider was tested and this survey craft has the ability to operate at speeds as low as 5 km^{-1} at whatever height required, providing a stable aerial platform for counting and recording crocodile nests. Survey effort, a key variable when interpreting nest survey data, can now be quantified with the use of CyberTracker, a GPS based electronic integrated monitoring system.

AIMS

As reproductive output is one of the key primary population processes responsible for changes in population size, the aim of this chapter was to describe and quantify trends in nesting success in recent decades of the St Lucia Nile Crocodile population. To achieve this, the sub-aims were:

- To synthesise historical (1959 to 1978) and recent (1982 to 2008) information (maps, reports and other literature) relating to crocodile nesting.
- To determine the relative abundance and distribution of Nile Crocodile nests for the period 2009 to 2013.
- To increase the coverage of the annual Ezemvelo foot survey area by including suitable, but historically unused nesting habitat, which would normally be excluded from the annual foot survey.
- To increase survey effort from a vertical plane over extensive swamp forests along the eastern shoreline.
- To estimate the population’s reproductive frequency.
- To confirm re-use of nest-sites.

METHODS

Study area

The Lake St Lucia estuarine system is situated in the north-eastern KZN province of South Africa. It is the largest estuarine system in Africa (Cowan 1997, Whitfield 2013). Historically, the Mfolozi River and St Lucia Estuary shared a common mouth, but accelerated sediment accumulation (primarily from the Mfolozi) promulgated a decision to manually separate the mouth of the Mfolozi in 1952. In 1956, a separate mouth was opened for the St Lucia estuary (Taylor 2011).

In recent years the lake has been affected by a drought. In July 2002 the estuary mouth closed, and with the exception of seven months in 2007, (Taylor 2006) remained closed until, in 2013 an artificial channel linking it to the Mfolozi River, and hence to the sea, was excavated. In 2003 as a result of below average rainfall and little input from the five streams, the lake divided in a number of separate compartments. Each compartment having a different salinity, increasing towards the north. By June 2006 approximately 90 % of the lake surface was exposed and dry (Whitfield and Taylor 2009). Good rainfall in December 2010, January, July and November 2011 as well as Cyclone Irina passing ~125 km offshore in March 2012, resulted in a restoration of water coverage throughout the lake system (see Chapter 1 for a more comprehensive study area description). Thus, for virtually the full period of this study (2009 to 2013) the lake was affected by extreme and atypical conditions.

Historical data: 1959 to 2008

Theses, reports, memorandums, nest recording sheets and published literature, both scientific and popular, were used to obtain historical information on Nile Crocodile nesting at Lake St Lucia from 1959 to 2008.

Aerial surveys (2008/9 to 2011/2)

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

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

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

Nest effort

Nest effort, or reproductive frequency, is the proportion of mature females in the population that are nesting each year. It is an important parameter to estimate as it provides information on the reproductive segment of the population and might reveal other factors (e.g. rainfall, nutrition, social pressure) affecting reproduction.

We calculated nest effort (E) of Nile Crocodiles using a method described by Chabreck (1966) and adapted by Leslie (1997) for use at Lake St Lucia.

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

N = population estimate

X = nest estimate

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

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

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

We estimated the population N from winter aerial surveys. To account for visibility bias we estimated diving and detectability bias (Chapter 2). We calculated X based on summer nest surveys, multiplied by 1.1 as we estimate that 10 % of the nests are missed during the survey. We used F = 0.5049, the female to male ratio determined in the capture study. We estimated the sub-adult component of the population based on size estimates obtained during 10 spotlight surveys to be 19.86 %. Although the study included capture data from 2009-2012, we included 1982 to 2013 nest and aerial survey data (Ezemvelo, unpublished data) for comparative purposes. Years where nest and aerial surveys were not conducted or incomplete, were excluded from the analysis then solved the equation for E.

Re-use of nest-sites

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

Use of burrows

We recorded crocodile burrowing behaviour at Lake St Lucia. Burrows associated with nesting activities were noted during nest surveys.

Identification of nesting females

Scute marking

We captured nesting females during the 2009/10 nesting season and each female was uniquely marked by clipping the caudal verticils with a sharp knife using a numbering system based on Australia's Queensland Parks and Wildlife Service (Kay 2004).

Colour-coded caudal tags

We attached 36 x 58 mm colour-coded flexible plastic tags (TAGEM, Ramsay Engineering) during the 2009/10 nesting season to nesting females. A sequence of first three, then later four, colour-coded tags was used to uniquely mark each female and tags were attached to both side of the tail, usually the first three or four single caudal verticils. See Appendix 4 for tag attachment method.

RESULTS AND DISCUSSION

Historical data: 1959 to 2008 - overview

The Nile Crocodile population at Lake St Lucia is the most southern viable nesting population (Leslie and Spotila 2001). It is also the largest estuarine nesting population throughout its range and largest recorded and apparently most stable (i.e. unaffected by flooding) nesting population in South Africa.

The Nile Crocodile has a well-defined breeding and nesting season at St Lucia, with oviposition during November and December and hatching from January to March (Pooley 1982a, Leslie 1997). It is therefore convention when reporting the results of a nest survey to include both the year of oviposition and hatching, e.g. 2008/9. Females seem to select nesting areas based on a number of specific physical requirements, i.e. sufficient vegetation close to the nest to provide cover and shade to the guarding female, fresh water for hydration and deep enough to provide the female with cover and suitable as a nursery site for hatchlings (Pooley 1969, 1982a). The distance between the nest and nearest fresh water varied considerably, but the presence of freshwater is a key requirement for nesting. Pooley (1982a) recorded a distance of 15 - 50 m between the lake and Otoneni, the main nesting area. The distance between nests and fresh water along the Nkazana Stream were determined by the distance of the forest edge from the stream, as females nested on the forest edge for sufficient sunlight. Nests along the Mphathe Stream tend to be relatively close to, and well elevated above, the stream and some of the furthest nests (max. 182 m) from water were recorded at eSingeni (Combrink, unpublished data), where females nested adjacent the a wetland. The majority of St Lucia nests were constructed on well drained soils, but Pooley (1982a) also mentioned nests in alluvial clay and decomposing vegetation in the Mkhuze Swamps, as well as in the Link canal on levees created by dredger spoil consisting of pebbles, fine sand, shell fragments and clay. Some nesting areas along the Mphathe Stream were high in clay content while others in this area contained a high proportion of organic material. Fawcett (1987b) conducted a study using a number of multivariate statistical techniques to analyse a suite of nest-site parameters (e.g. distance to fresh water and shade, height above nearest water, etc.). He found a high variability among nest-sites and suggested that St Lucia crocodiles are more flexible with regards to nest site selection than previously thought.

Pooley (1982a) recorded the average Zululand Nile Crocodile clutch size as 45 eggs (range: 18 - 73) from a sample of 132 clutches. Egg collection data from 92 nests along the Link Canal and Backchannels of the St Lucia estuary from 1988/89 to 1994/95 revealed a mean clutch size of 48.15 ± 1.08 eggs (range: 18 – 76; Ezemvelo unpublished data).

Results from artificial Nile Crocodile nest studies show that incubation duration in Zululand ranges from 84 to 98 days, depending on temperature (Pooley 1969). Leslie (1997) found under constant incubation temperatures that warmer temperatures within the viable range lead to shorter incubation times (e.g. 82.2 days at 31°C to 69.9 days at 33°C) and confirmed a female : male : female pattern of temperature-dependent sex determination. Exclusive females were produced at 31.0 °C, 70 % females were produced at 31.5 °C, whilst the majority of males were produced at 32.0 °C, 32.5 °C and 33.0 °C the intermediate incubation temperatures. Low hatching success at 34 °C and 35 °C resulted in small sample sizes, but females dominated at these temperatures. Leslie and Spotila (2001) found that soil temperatures 25 cm deep in shaded areas at the Mphathe Stream were 5.0 - 6.0 °C cooler than open sunny areas. However, the mean incubation temperature for two nests at the Mphathe stream was only 0.8 °C cooler compared to mean incubation temperatures for all nests where temperature were recorded over the entire incubation duration (Leslie 1997). This suggests that although soils may be much cooler in deep shaded areas, crocodiles generally tend to avoid such areas for oviposition.

Hutton (1987) and Leslie (1997) conducted Temperature Sex Determination (TSD) studies with Nile Crocodiles. Leslie found that the upper and lower pivotal temperatures for Nile Crocodiles were 34.5 °C and 31.7 °C respectively. Although Hutton did not incubate eggs above 34.0 °C, he noted that hatching success in Zimbabwe was 69.0 % at 34.0 °C as oppose to Leslie’s results at St Lucia where the mean hatching success (over two nesting seasons) at 34.0 °C was 38 %. This apparent difference in hatching success between the populations in Zimbabwe and St Lucia, might indicate a possible relationship between geographic variation and sex determination (Maciejewski 2006) as the St Lucia population represents the southernmost viable nesting population for Nile Crocodiles (Leslie and Spotila 2001), possibly resulting in animals that are more adapted for cooler conditions and less able to develop at high temperatures (Leslie 1997). Nile Crocodile nest incubation occurs during the summer rainfall period and hatching coincides with relatively high lake and stream levels (Pooley 1982a). When development of the embryos is complete, the hatchlings vocalise from their egg chambers, which stimulates the female to unearth the eggs (Graham 1968, Pooley 1969, 1977). This action by the female is crucial, and failing to liberate the hatchlings will result in complete nest mortality (Graham 1968, Pooley 1969, Combrink, pers. obs.). Pooley (1969) recorded female assistance with nest opening in all nests examined in Zululand, Hutton (1984) mentioned the inability of hatchlings to liberate themselves from the ground after hatching and Graham (1968) believed this action by the female was more important to hatchling survival than any other function of the female during incubation. Pooley (1962) noted during incubation studies of eggs taken from St Lucia nesting grounds that up to three quarters of hatchlings will use their egg tooth, situated on the upper tip of the crocodile snout, to first puncture and then tear the tough internal membrane that protects the embryo. The hatchlings will yelp continuously. The female will actively assist the hatchings by picking them up with her jaws and transporting them in her buccal cavity to water. Pooley (1977) recorded behaviour in a semi-captive environment where both male and female assisted in liberating hatchlings from their eggs by gently rolling the egg between the palate and tongue, cracking it open. Hatchlings initially remain together, while being guarded by the female, but it seems like dispersal from the nursery area is subjected to local conditions at the nursery area, e.g. dispersal facilitated by stream flow might be much more rapid (e.g. Mphathe and Nkazana stream) as oppose to much more sedentary behaviour from hatchlings in a small wetland areas (e.g. shoreline wetland areas at Dead Tree Bay).

Historical data: 1959 to 2008 – nest surveys

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

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

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

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

Historical data: 1959 to 2008 – relative nest abundance

The results of nest surveys since 1982 are shown in Fig. 2. Some years represent incomplete surveys and are indicated with white bars. Hatching success for 1984 (1983/84 nest season) was possibly zero as virtually all nests were flooded by Tropical Cyclone Domoina (Taylor and Blake 1986).

During the 1981/82 Nile Crocodile nesting season, Pooley counted 125 nests (Fig. 2), but survey intensity was not recorded (Taylor and Blake 1986). The 1984/85 surveys were incomplete, and nests were recorded only at Ndhlozi Pan and Otoneni-Ngema (Taylor and Blake 1986). The 1985/1986 survey recorded 101 nests while 131 nests were recorded the following year (Fawcett 1987a) and 123 nests in 1988/89. Nest surveys were conducted more regularly during the 1990’s and the number of nests recorded per survey also increased, from 74 in 1990/91 to 141 in 1998/99. The 1998/99 count (141) was the highest number of nests ever recorded. The number of recorded nests decreased during 2000 and 2001 (97 and 91 nests) and increased marginally to 113 nests during the 2001/2 survey. From 2003 - 2008, i.e. during the drought period and estuary mouth closure, nest numbers decreased to record low figures, mean = 52.0 ± 1.87. Leslie (1997) recorded decreased nesting during the drier years between 1994 to 1997, and suggested that the availability of fresh water had a direct effect on nest effort.

During the 2007/08 nesting season, 73 nests were counted, an increase of 49 % compared to the previous year. The estuary mouth opened in March 2007 due to Cyclone Gamede and seawater poured in for a number of weeks. The connection between the lake an ocean was re-established for six months before closing again in August 2007, with the lake approximately 75 % full and salinities throughout at that of seawater (Cyrus et al. 2010). We suspect that the influx of seawater and resultant increase of fish diversity and abundance created improved feeding opportunities with consequential increased nest effort.

Although Nile Crocodile nesting surveys have been conducted at St Lucia since 1982, the interpretation of the results are confounded by the absence of survey effort, visibility bias (i.e. an unknown proportion of nests will always be overlooked during the survey), observer bias (i.e. the ability of identifying a nest is related to the skill and experience of the observer), the magnitude of potential nesting areas, limited manpower and wide fluctuations in nest effort. Nonetheless, nest survey effort has increased through the years but since 2000 the index in relative abundance indicated a decreasing trend, especially since the onset of the drought in 2003. We suspect that declining food resources was the most important contributor to the significant decrease in nesting since the drought. It furthermore suggests that despite an increase in game reintroductions to the Eastern and Western Shores of Lake St Lucia, crocodiles are seemingly still reliant on fish as a primary source of protein. An current study (Warner et al. in prep.) is investigating Nile Crocodile feeding ecology at St Lucia using stable isotope analysis. We are expecting the results to elucidate the relative importance of game compared to fish in the diet of St Lucia Nile Crocodiles.

Historical data: 1959 to 2008 – nest distribution

Nile Crocodiles do not nest throughout the entire lake system, but select and utilise specific areas which they often re-use (Pooley 1969). New nests are infrequently recorded (Ezemvelo unpublished data, Combrink, pers. obs.). Refer to a comparison of historical nest recorded by Pooley as well as in the recent past (1982 to 2008, Fig. 1).

Nile Crocodile nests have been recorded from the very north of the Mkhuze Swamps to the extreme south of the Mfolozi River. No nesting activities have ever been recorded along the shoreline of False Bay or the Western Shores, except for Ndhlozi Pan, a small (~5.14 ha) waterbody on the northern tip of Ndhlozi Peninsula and a single nest record (1999) just south of Charters Creek (Myhill, pers. comm.). Recently, two nests were discovered in 2011 and hatchlings in 2012 along Potters Channel (Fig. 3). Most nesting occurred along the eastern shoreline with the major nesting areas the Mkhuze River, Otoneni-Ngema, Jubangoma, Mamba Stream, Ndhlozi Pan, Nkazana Stream, eSingeni, Mphathe Stream, the Backchannels and Link Canal.

It seemed that despite the required nest-habitat characteristics present at all the nesting areas at Lake St Lucia, the macro-level heterogeneity of nesting habitats within a single population are possibly unique. This warrants a more detailed discussion of the different nesting areas:

i. Mkhuze River

The Mkhuze River, especially where it flows into Lake St Lucia, was a major nesting areas at Lake St Lucia during the 1960’s and 1970’s with an estimated 20 nests per year (Pooley 1982b) (Fig. 1). Pooley (1982b) also mentioned the role of Demezana and Mpempe Pans further north as an apparent important crocodile recruitment source for the lake. By the early 1980’s, resource use such as reed cutting and fishing, combined with burning and general disturbance from nearby communities, led to a decline in crocodile basking and nesting activities. Nest numbers fluctuated between zero and eight nests from 1982 to 1989, and no nesting has been recorded since 1989.

ii. Otoneni- Ngema

Historically, Otoneni-Ngema was the largest and most important nesting area with numerous nests, often in close proximity (Fig. 1). Pooley (1982a) recorded 45 nests at Otoneni and 21 at Ngema during a single year. Otoneni is situated in the Eastern Shores Wilderness area, east of Lane Island and extends along the lake shoreline in a north-easterly direction. Ngema is northeast of Otoneni, and is separated by a few hundred meters of open grassland. The general area is characterised by *Phragmites* reeds growing along the shoreline as a result of freshwater seepage, 30 - 40 m from the shoreline and to the east a belt of coastal forest parallel to the shoreline. During very wet years, e.g. 1957, 1963, 1970, 1996 and 1997 crocodiles were nesting east of the forest patches close to freshwater pans. As freshwater seepage decreased and pans dried out, nesting decreased. In 2001/02, 10 nests were recorded in this area, which decreased to nine in 2002/03. During the winter of 2003 all the pans dried out and no nesting were recorded from 2004 to 2008. Surface water in these pans were a good predictor of crocodile nesting as nesting females require freshwater for hydration and nursery areas for their hatchlings.

iii. Jubangoma

Jubangoma falls within the southern section of the Eastern Shores Wilderness and consists of a large forest patch to the east of Fani’s Island (Fig. 1). The southernmost tip the forest is narrow (~100 m) and as it extends to the north for ~1.6 km, it broadens out to ~600 m. The main nesting area is to the east of the forest in close proximity to pans and wetland areas.

These pans may dry out during years of low rainfall years and during such conditions females tend to avoid this area. From 1999 to 2002, this was an important nesting area with an average of 17 ± 2.20 nests. In 2002/03, five females nested here and up to 2008 no nesting has been recorded.

iv. Mamba Stream

Mamba Stream is situated on the Eastern Shores, just to the east of Vincent Islands (Fig. 1). The actual seepage stream is situated almost at the top of a narrow stretch of coastal forest (~80 m) that extends in a south-north direction, parallel to the shoreline. From 1986 to 1989 Mamba Stream was the most important nesting area with a mean of 26 ± 1.68 nests. Communal nesting in 1987/88 (6 nests) and 1988/89 (8 nests) have been observed, with some nests only 0.5 m apart (Pullen 1989). During the 1985/86 and 1986/87 surveys, 28 nests were found, 21 in 1988/89, 21 in 1998/99 and 10 in 2001/02. Since the start of the drought in 2003, surprisingly few crocodiles have nested here. Four nests were recorded in 2002/03 and three in 2005/06, although in 2007/08, 14 nests have been recorded.

v. Ndhlozi Pan

Ndhlozi Pan is situated at the northern tip of Ndhlozi Peninsula (Fig. 1). The northern shoreline is separated from the main lake by a forested elevated ridge, with open sandy patches. Most nests were recorded within these open sandy areas. The highest number of nests recorded here was 12 in 1996/97, the previous year 11 nest were found, 11 in 1998/99 and nine in 2001/02. Since the start of the drought the number has decreased to four in 2002/03, eight in 2006/07 and one in 2007/08 with no nesting from 2004 to 2006.

vi. Nkazana Stream

The Nkazana Stream is situated on the Eastern Shores and it drains water from the Mfabeni Swamp into the northeastern shoreline of Catalina Bay. It is a consistent source of freshwater, even during the most severe droughts. During the drought of 1970, 37 crocodiles were translocated here from the Mkhuze Swamps, as it was the only freshwater stream flowing (Pooley 1982a). The Nkazana Stream was one of the most stable nesting areas in the lake system, both during years of high rainfall as well as during the recent drought period (2002 to 2012). The lowest number of nests recorded was three during 2007/08 and the highest 22 in 1985/86.

vii. eSingeni wetland

eSingeni wetland is situated on the Eastern Shores, northeast of The Forks (Fig. 1). It is characterised by a wetland area (~41.9 ha) and ~1.7 km long from east to west, and is bordered on the western and northern side by an elevated sandy ridge with coastal scrub forest and open sandy patches. Although much of the wetland is not permanently inundated with water, a small water body, ~1.5 ha, usually contains surface water. Crocodiles nest north and east of the wetland. The first nest records (19) were recorded in 1998/99. In 1999/2000, 32 nests were recorded and this figure decreased to 19 and 20 in 2000/01 and 2001/02 respectively. eSingeni seemed to be largely unaffected by the recent drought although nesting decreased to eight nests during 2002/03, but doubled to 16 in 2004/05. In 2006/07 nine nests were recorded which increased to 16 in 2006/07 and decreased once again to seven in 2007/08. A possible explanation for the interannual variation is that nests were easily overlooked in this area. The nesting area is extensive and densely vegetated with small open patches where nests are located, which makes it difficult to cover systematically. It is likely that crocodiles nested here prior to the 1998/99 survey.

viii. Mphathe Stream

The Mphathe Stream flows into the Narrows from the Western Shores, south of the main lake. Historically, extensive surrounding exotic tree plantations within its relative small catchment have had a negative impact on the water budget (Pooley 1982a) and subsequent stream flow. As a result of the forestry activities, an alien plant species, Triffid Weed, has invaded the area along parts of both riverbanks. This invasive species transformed numerous open sunny nesting banks into dense impenetrable thickets. Leslie and Spotila (2001) have demonstrated that the soil temperature at the average depth of a crocodile nest (25 cm) have resulted in the lowering of soil temperatures with 5.0 to 6.0 °C. If nests are excavated in such areas this cooling effect may affect the sex ratios of crocodile embryos and possibly reduce their survival. However, the mean incubation temperature for two nests at the Mphathe stream was only 0.8 °C cooler compared to mean incubation temperatures for all nests where temperature were recorded over the entire incubation duration (Leslie 1997). This suggests that although soils may be much cooler in deep shaded areas, crocodiles tend to avoid such areas for oviposition.

During the 1980's the stream was a low density nesting area, with maximum of five nests recorded per year. In 1994 nests increased to 10 with 14 in 1995/6, eight in 1998/99 and two nests in 2000/01. Since the onset of the drought nesting increased significantly and 26 nests were recorded in 2004/05 and 22 in 2005/06. During 2005/06, the 22 nests made up more than 47 % of the total known nesting for the entire lake system. Nesting increased to 28 in 2007/08. During the prolonged drought this stream was the most important nesting area in the system.

ix. Backchannels and Link Canal

The Backchannels and Link Canal are situated in the southernmost extremity of the lake system. The Link Canal was excavated between the Mfolozi River and the Narrows and is ~11 km. It has very steep banks due to the dredger spill and it is on these banks that crocodiles nested. The water is fresh and *Phragmites* reeds as well as alien invasive vegetation lined the banks. The Backchannels are situated just south of Honeymoon Bend in the Narrows and link the Narrows with the Mfolozi River in an east-west channel. This channel is dominated by mangrove and crocodiles nested in protected open and sandy areas. Nesting was first recorded here in 1981/82 with 17 nests in the Backchannels and 10 in the Link Canal. In 1985/86, 21 nests were recorded in the Backchannels and three in the Link Canal. From 1987 nesting decreased in the Backchannels with 20 recorded during that year, 12 in 1987/88, eight in 1988/89 and the last year that nesting were recorded here was five nests in 1989/90.As nesting decreased towards the latter half of the 1980's in the Backchannels, nesting activity increased in the Link Canal from three in 1985/86 to 10 in 1986/87. This figure almost doubled in 1988/89 (18) and increased further to 21 in 1991/92 and again almost doubled to 39 in 1993/94. The Backchannels and Link canal used to be the most important nesting areas in the southern lake system, with an average of 26.17 ± 2.88 nests recorded from 1982 to 1995. During 1996 an estimated 20 female crocodiles were snared and killed and a number of egg clutches were removed from the Link canal (Leslie 1997). Subsequent to this event, nesting decreased to an average of 1.65 ± 3.32 two nests per year, for the period 1996 to 2011 (Combrink et al. 2013). In 1999/2000, 14 females returned to nest here, but between 1999 and 2008 the highest number of nesting females in the area was two.

From 1988/89 to 1994/95, 92 clutches (4430 eggs) were removed by staff from the Ezemvelo St Lucia Crocodile Centre. These nests were regarded as "doomed" due to high clay content and strong possibility of being flooded and eggs were incubated at the Crocodile Centre. No records exist of hatchlings being released back into the lake system and this might have had a considerable negative impact on crocodile recruitment in the system.

x. Other nesting areas

Other, less important areas where crocodile nesting have been recorded were Msunduzi River (south of the St Lucia estuary), wetlands northeast of St Lucia town, the Narrows, Potters Channel, Mfazana Pan, eastern and northeastern shoreline of Catalina Bay, Lake Bhangazi South and pans just to the north of Lake Bhangazi South, Tewati Bay area, Sengwana and Selleys Lakes (Ezemvelo, unpublished data).

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

Six possible new Nile Crocodile nest-sites were recorded on 1 February 2009. Four potential nests were observed in the Dead Tree Bay area, all in small open areas surrounded by thick forest that would have been impossible to detect during a foot patrol. Two possible new nests were recorded in the Catalina Bay area, one ~500 m north of the Nkazana stream inflow and one ~1.3 km south of the Catalina Bay public jetty. Nest-sites were also observed at Nkazana Stream, the Forks area in the Narrows and the Mphathe Stream.

During the aerial survey (Jan. 2011) nine nests were counted in total. Extensive potential nesting areas, especially in the Tewati Wilderness Area, were covered but no nesting activities recorded.

During a paraglider survey we covered the area from Jubangoma to Mamba Stream, to a point ~2.6 km further south. The survey distance was ~20 km and the duration 66 minutes. Thirteen nests or likely nest-sites were identified from the air and eight nests were confirmed during a subsequent foot patrol. A number of possible nest-sites recorded from the paraglider above the forest canopy, especially in the Jubangoma area, could not be located on foot, as a result of the dense closed canopy forest, and subsequent lack of navigation with the GPS.

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

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

Ezemvelo surveys recorded 29, 80, 32, 61 and 60 nests during the 2008/09 to 2012/13 nesting seasons, over 14 areas at Lake St Lucia (Table 1 and Fig. 3). Nest densities were overall low and only three areas revealed more than five nests, on average, i.e. the Mphathe Stream (mean 18.2 ± 5.62), eSingeni (mean 12.6 ± 2.01) and Nkazana Stream (mean 7.8 ± 1.39). The highest count of 80 nests is lower compared to the average of 102.93 ± 7.17 nests for the 21 year period prior to the St Lucia estuary mouth closure and drought (1982 to 2002) and the 29 nests in 2009 was the lowest nest count for Lake St Lucia ever recorded. The average nest count since the onset of the drought (2003 to 2011) was 53.22 ± 5.55 nests. All nests were associated with nearby freshwater and therefore no nesting was recorded in the Eastern Shores Wilderness area, as seasonal pans and wetlands were still dry. During the 2013 nesting survey two nests were recorded along the Eastern Shores shoreline, one at Ngema (Fig. 3).

Since 2007 we recorded increased fluctuations between successive years (i.e. 49, 73, 29, 80, 32, 61), as oppose to a more stable period from 2003 to 2007 (i.e. 54, 54, 49, 49), see Fig. 2. Furthermore, in the four years prior to the drought and mouth closure (1999 to 2002), the average nest count was 110.5 ± 11.18 nests. This decreased to 52.0 ± 1.87 nests for the first four years since the drought and estuary mouth closure (2003 to 2007). In March 2007, the sea broke through the estuary mouth due to Cyclone Gamede. Seawater flowed in for weeks before the mouth closed naturally during August 2007, with the lake approximately 75 % full and salinities throughout at that of seawater (Cyrus et al. 2010). We suspect that the massive influx of seawater linking the three remaining isolated water bodies of the (mostly dry) lake, combined with the six months of re-connectivity with the sea (i.e. healthy open estuary) led to improved feeding opportunities for crocodiles. The following nesting season (2007/08) nesting increased to 73 nests, 80 nests were recorded for the 2009/10 season, which decreased to 60 nests recorded in 2011/12. We hypothesise that improved nutrition resulted in the higher number of females nesting in 2008, but as females seldom nest in consecutive years (Kofron 1990), there was a decrease in 2009 but a high proportion of females once again nested in 2010.

Changes in nest distribution and relative abundance: 1982 to 2013

Nile Crocodiles at Lake St Lucia generally prefer to re-use the same nest areas (Pooley 1969). However, during the past three decades there have been dramatic changes in the relative abundance and distribution of nests at St Lucia, seemingly determined by human disturbance, illegal killings, water coverage and the availability or lack of freshwater (Fig. 4).

Human disturbance (reed harvesting, small scale agriculture, fishing and burning) at the confluence of the Mkhuze River and Lake St Lucia resulted in the abandoning of all nesting since 1989. This used to be a major nesting area during the 1960's and 1970's with an estimated 20 nests per year (Pooley 1982b).

Human disturbance, combined with illegal killings of nesting females (Leslie 1997) south of the St Lucia estuary (Mfolozi River, Backchannels and Link Canal), resulted in a decline from an average of 28.8 ± 2.80 nests (1982 to 1989) to 0.70 ± 0.26 nests (2002 to 2013), Fig. 4.

The decline in nest numbers adjacent to North Lake from 31.75 ± 4.49 nests (1982 to 2002) to 2.6 ± 1.28 nests (2003 to 2013) was seeminly due to the drought (2003 to 2012) and subsequent drying out of the entire North Lake, with only a few small areas of freshwater seepage along the shoreline (e.g. Tewati Bay).

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

Nest effort

Estimates of nest effort at Lake St Lucia varied from 56.4 % (1987) to 6.9 % (2009) over the 32 year period (Fig. 5 and Table 2) with a mean of 22.92 ± 2.63 %. Seemingly, the two best predicting factors for nest effort were the dynamic interaction between food availability and rainfall (Fig. 6). Abundant feeding opportunities apparently resulted in a higher proportion of reproductive females during a particular year while restricted food availability (e.g. indirect effect due to estuary mouth closure and less fish entering the lake or direct effect during severe droughts when lake level contracts while becoming hypersaline at the same time) had the opposite effect. A high proportion of reproductive females should result in high nest effort, but only when abundant freshwater sources are available. Females will select nest-sites close to freshwater (streams, ephemeral pans or wetlands) for hydration during nest guarding as well as to ensure a nursery area for hatchlings. If spring rainfall (September and October) was late, or below average, some females will arrest reproduction possibly by reabsorbing developing egg follicles (Fig. 6).

We estimated nest effort since 1982 and indicated mean lake salinity values for the two months preceding nesting, as well as annual rainfall (Fig. 5). The first two years (1981/82 and 1986/87 nest surveys) were the highest ever recorded. That might have been due to general low levels of disturbance and illegal killings and good food availability, especially Striped Mullet (*Mugil cephalus*) and low lake salinities, especially in 1987.

The next period of elevated nest effort was from 1996 to 2002, again during high rainfall low lake salinities. Subsequently to that and during the recent drought with periods of hypersalinity, nest effort decreased to record low levels. During the recent drought the estuary mouth was closed for almost the entire period. It seemed likely that the status of the estuary mouth (i.e. open or closed) had an indirect effect (open mouth facilitate healthy estuarine functioning and increased food abundance) on nest effort (Fig. 6). The mean nest count prior to estuary closure (1982 to 2001) in 2002 was 103.07 ± 7.7 nests, while during the period when the estuary mouth was closed (2003 to 2012) nesting significantly decreased to 53.56 ± 5.92 nests (t = 4.48, d.f. = 21, p = 0.001). In March 2007 the estuary reconnected to the sea for six months and nesting increased from 49 (pre-mouth opening) to 73 (post-mouth opening) nests.

Physical properties of nest-sites

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

Use of burrows

We recorded Nile Crocodiles using burrows at five localities, eSingeni (two), Nkazana Stream (19), Mamba Stream (two), Dead Tree Bay (six) and False Bay Park (one) and recorded the use of the burrows with camera traps (Fig. 7). All localities, except Mphophomeni Pan (in False Bay Park), are known nesting areas and we have observed nesting females entering nearby burrows when disturbed. At Nkazana Stream, nine burrows are associated with nest-sites, and two burrows at eSingeni, Mamba Stream and Dead Tree

Bay have been used by nesting females during the nesting season. In all areas, burrows were excavated where the adjacent water, e.g. stream (Nkazana) or freshwater seepage (eSingeni, Mamba Stream and Dead Tree Bay) was too shallow to facilitate adequate cover for the nesting female. Burrows possibly serve as important microhabitats for female thermoregulation as burrow temperatures are more stable than ambient temperatures in summer. Crocodile burrows are used by males and females during the non-nesting season, and different individuals have been observed using the same burrow over time.

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

Identification of nesting females

Scute marking and attaching colour-coded caudal tags

We captured 12 nesting females on or adjacent to their nest-site during the 2009/10 nesting season (Table 3). Additional five mature females were caught (22 October & 19 November 2009) in the Nkazana Stream, a known nesting area at the onset of the nesting season and the following year (23 October 2010) a female in the Mphathe Stream. A tagged nesting female, colour code OOB was recorded next to her nest during the 2013 survey along the shoreline of Catalina Bay, adjacent to the Nkazana Stream. She was captured in the Nkazana Stream on 6

May 2009, 1317 days before the re-sighting, and fitted with coloured plastic caudal tags. The tags were in good condition with minimal fading of colour and little algae coverage.

Scute marking and attaching colour-coded caudal tags were effective methods for unique identification. Not wanting to cause additional disturbance, we did not returned to check on the tagged females, so the likely tagging effect on the animal's nesting behaviour was not noted. However, all females that were fitted with caudal tags and transmitters, returned to their respective nests to continue with nest guarding activities (Chapter 6).

When nesting females can be uniquely identified and re-sighted in subsequent years, important biological and ecological spatial and temporal information such as reproductive frequency, growth, body condition and changes in nest-site usage can be recorded and monitored.

Reuse of nest-sites

During the 2009 nesting survey, 11 nest-sites (38 %) were reused. In 2011, 24 nest-sites (30 %) were reused, 13 from 2009. During the January 2011 survey 20 of the 26 nest-sites, 77 %, were reused, five from 2010 and three from 2009. During the 2012 survey 46 of the 58 nests were reused, a total of 79 %. Ten nests were from 2011, 23 from 2010 and four from 2009.

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

CONCLUSIONS

The Nile Crocodile population at the Lake St Lucia estuarine system represents the most southern viable nesting population throughout the species' range. It is also the largest estuarine nesting population and largest recorded and possibly most stable (i.e. unaffected by flooding) nesting population in South Africa.

Although some aspects of Nile Crocodile reproductive ecology at Lake St Lucia were investigated from 1959 to 1978 (Pooley 1982a), nest surveys have been conducted since the 1980's, making it one of the longest monitored Nile Crocodile populations in Africa. The mean number of nests recorded at St Lucia from 1982 to 2013 was 76.19 ± 6.42. Historically, large nesting areas were distributed from the very north of the system next to the Mkhuze River, along the eastern shoreline, Mphathe Stream, and the Link canal, Backchannels and Mfolozi River in the very south. Increased anthropogenic disturbance and habitat transformation north and south of Lake St Lucia resulted a shift in nest distribution, contacting towards the protected eastern shores.

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

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

MANAGEMENT RECOMMENDATIONS

- Nesting females, especially those nesting far from water, are particularly vulnerable to illegal killings. The killing in 2013 of a female at eSingeni, the second largest nesting area on the eastern shores during the nesting period, highlighted this threat. Field rangers should patrol the boundary of large known nesting areas for suspicious signs and activity from November to March.
- St Lucia crocodiles tend to re-use the same nest-sites during periods of similar rainfall and salinity, the GPS position of every previously used crocodile nest-site should systematically be checked during surveys. As new nests are discovered, they should be added to the database and checked in subsequent years. Therefore, survey effort should theoretically increase slightly every year. Survey routes will be pre-planned and uploaded on a GPS which will ensure more effective integration of new staff that might not be familiar with the survey area, as well as minimise disorientation or losing direction.
- Cybertracker, an integrative GPS information system that records the actual route followed during the survey, also have the capacity to capture GPS locations of nests together with a suite of pre-selected nest parameters should be incorporated as a standard

method during nest surveys. This will increase efficient capturing of survey effort, a vital aspect of post-survey analysis and interpretation, and will also allow for a post-survey audit, if required.

- Each active nest-site should be photographed in order to monitor bush encroachment and the presence of Triffid Weed. The presence of Triffid Weed should be recorded and due to their vegetative development and immense seed production, plants must be manually removed on an annual basis, before June/July, prior to flowering and seed dispersal (Leslie 1997).
- When a female is encountered on/next to her nest, her tail section should be photographed for subsequent identification. Uniquely identified females that are re-sighted in subsequent years provide important biological and ecological information such as reproductive frequency and nest-site fidelity.

RECOMMENDATIONS FOR FUTURE RESEARCH

- One of the key unknown aspects of any crocodile nest monitoring programme is the proportion of present, but unrecorded nests in the population. In order to estimate this ratio we suggest using a double motorised paraglider. This survey craft has the ability to operate at speeds as low as 5 km-1 at whatever height required, providing a stable aerial platform for improved coverage of all potential nesting habitat. We expect the paraglider to locate more nests compare to the conventional foot survey and this ratio of paraglider count to foot patrol count could serve as a future correction factor.
- Mapping of all potential nesting areas, linked to hydrological patterns. This will inform management of important areas during the nesting period and allow researchers to ground truth some of these areas to check if we are missing nests.

- Investigate the role and importance of temperature sex determination in wild crocodile nests at Lake St Lucia. During incubation the developing embryo is subjected to a number of factors that will determine its survival and consequent contribution to the dynamics of the population. While predation, flooding and nest abandonment are some of the obvious causes of egg mortality, none plays a more important role in the development, body size, frequency of abnormalities, post-hatching growth, survivorship, thermoregulation patterns and sex of the newborn hatchling than incubation temperature (Hutton 1984; Deeming & Fergusson 1989; Webb and Cooper-Preston 1989; Thorbjarnarson 1990).

- Conduct a double shift, pulsed temperature experiment at the St Lucia Crocodile Centre to determine the temperature sensitive period for the Nile Crocodile.
- Investigate nest temperature and sex of hatchlings for a number of nests at the St Lucia Crocodile Centre. This will require keeping hatchlings up to an age where that can be sexed with 100 % certainty. Leslie (1997) found even at 14 months of age there were obvious males and females but there were also a large number of individuals that showed cliteropenis characteristics of both males and females.
- Research and survey activities will result in some degree of disturbance to nest guarding females and the aim is always to minimise the time spent at/near the nest. However, the attachment of three transmitters to nesting females (Chapter 6) as well as setting and checking 19 camera traps (Chapter 7) at crocodile nests with no evidence of nest abandonment and very little of subsequent predation, suggest the strict policies for crocodile researches at nests could be relaxed to allow for more research activities at wild crocodile nests at Lake St Lucia.

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Caption for Figures

Figure 1. Nile Crocodile nest records by Pooley (1959 - 1978) and more recent (1982 - 2008) at Lake St Lucia.

Figure 2. Index of relative nest abundance of Nile Crocodiles at the Lake St Lucia estuarine system: 1982 – 2013. It is not certain if a nest survey was conducted in 1984, but it is reasonable to assume that all nests would have been flooded due to Tropical Cyclone Domoina. The open bars represent years of incomplete surveys.

Figure 3. Nile Crocodile nests recorded at the St Lucia estuarine system from 2008/9 to 2012/13

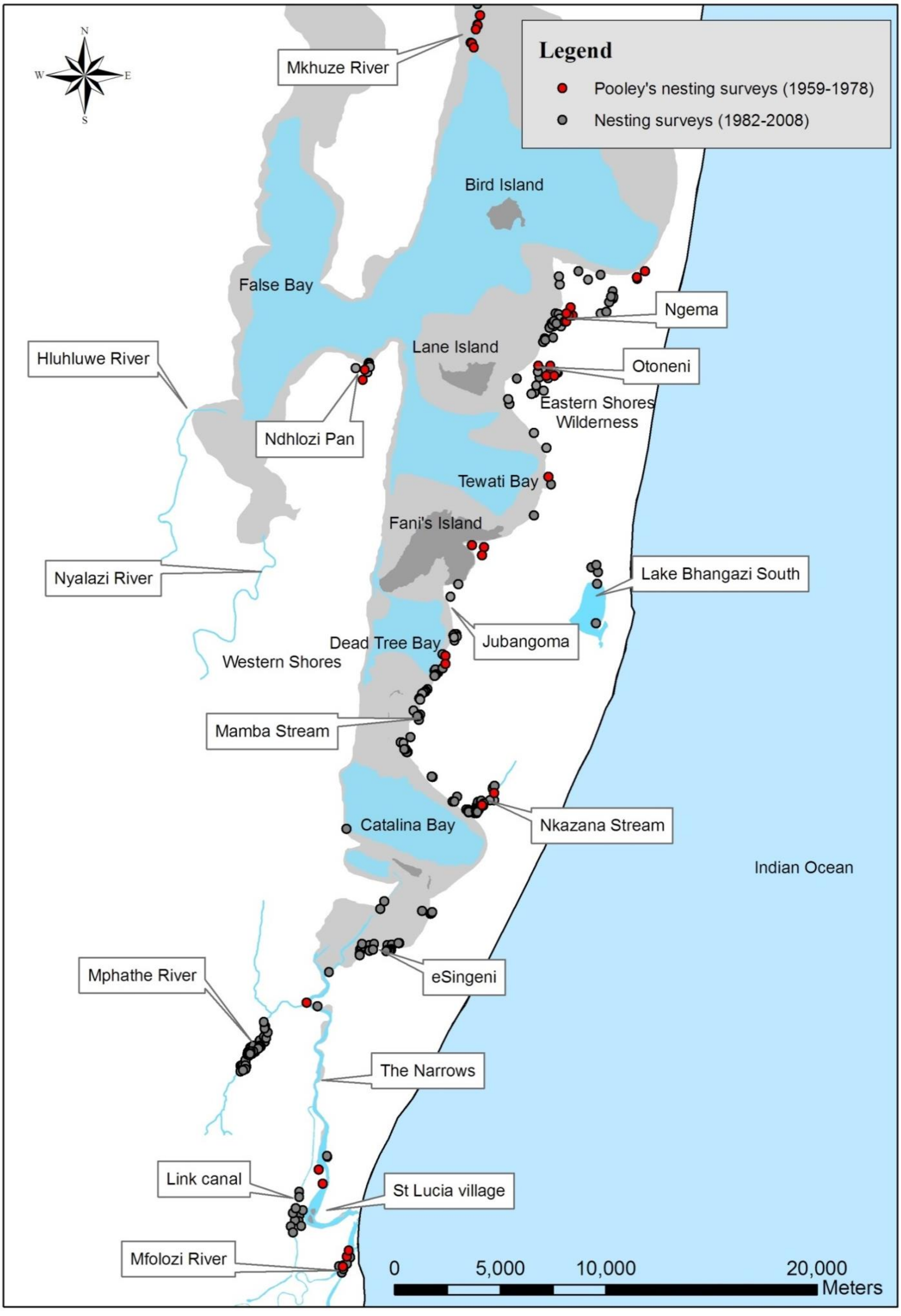
Figure 4. Temporal changes in Nile Crocodile nest distribution in the Lake St Lucia Estuarine system from 1982 to 2013. The period 2003 to 2013 included most of the recent drought.

Figure 5. Nest effort of Nile Crocodiles at Lake St Lucia on the primary y-axis. In (a.) the mean lake salinity during the months preceding nesting (Sep. and Oct.) are displayed on the secondary y-axis. In (b.) the annual rainfall during the year of nesting are displayed on the secondary y-axis.

Figure 6. A simplified hypothetical conceptual modal of Nile Crocodile nest effort dynamics at Lake St Lucia

Figure 7. Nile Crocodile burrows and burrowing behaviour at the Lake St Lucia estuarine system.

Figures



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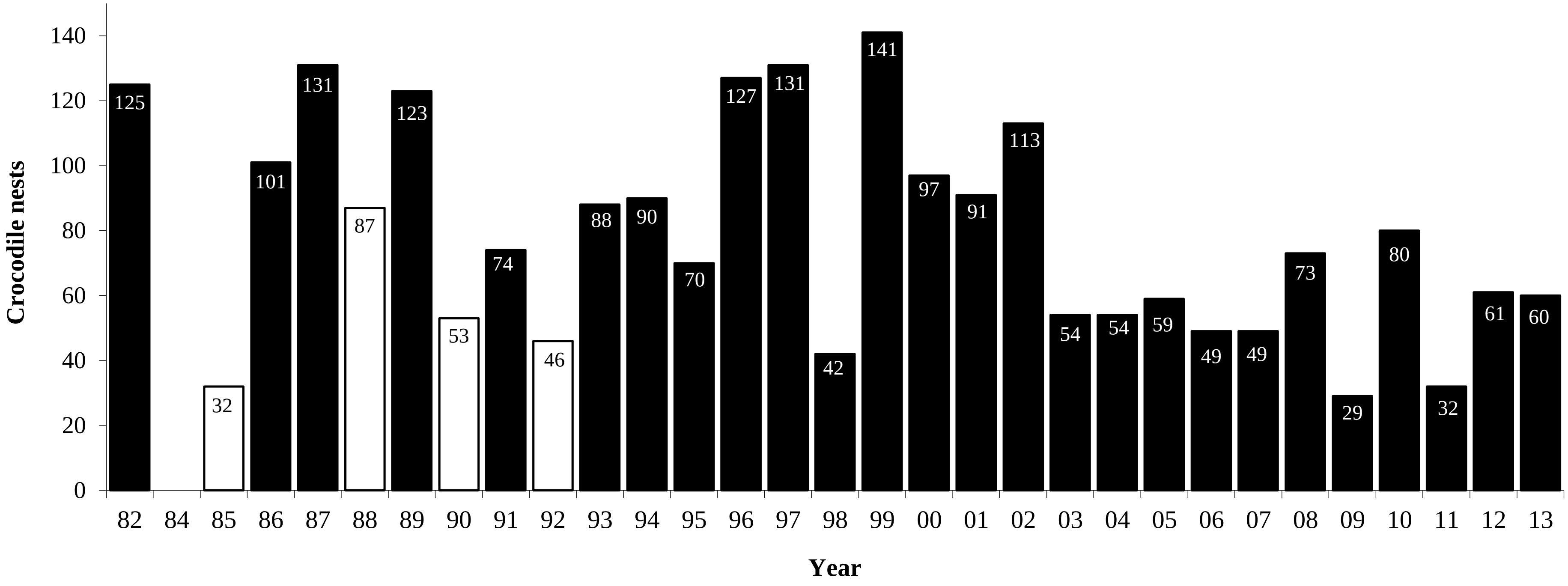

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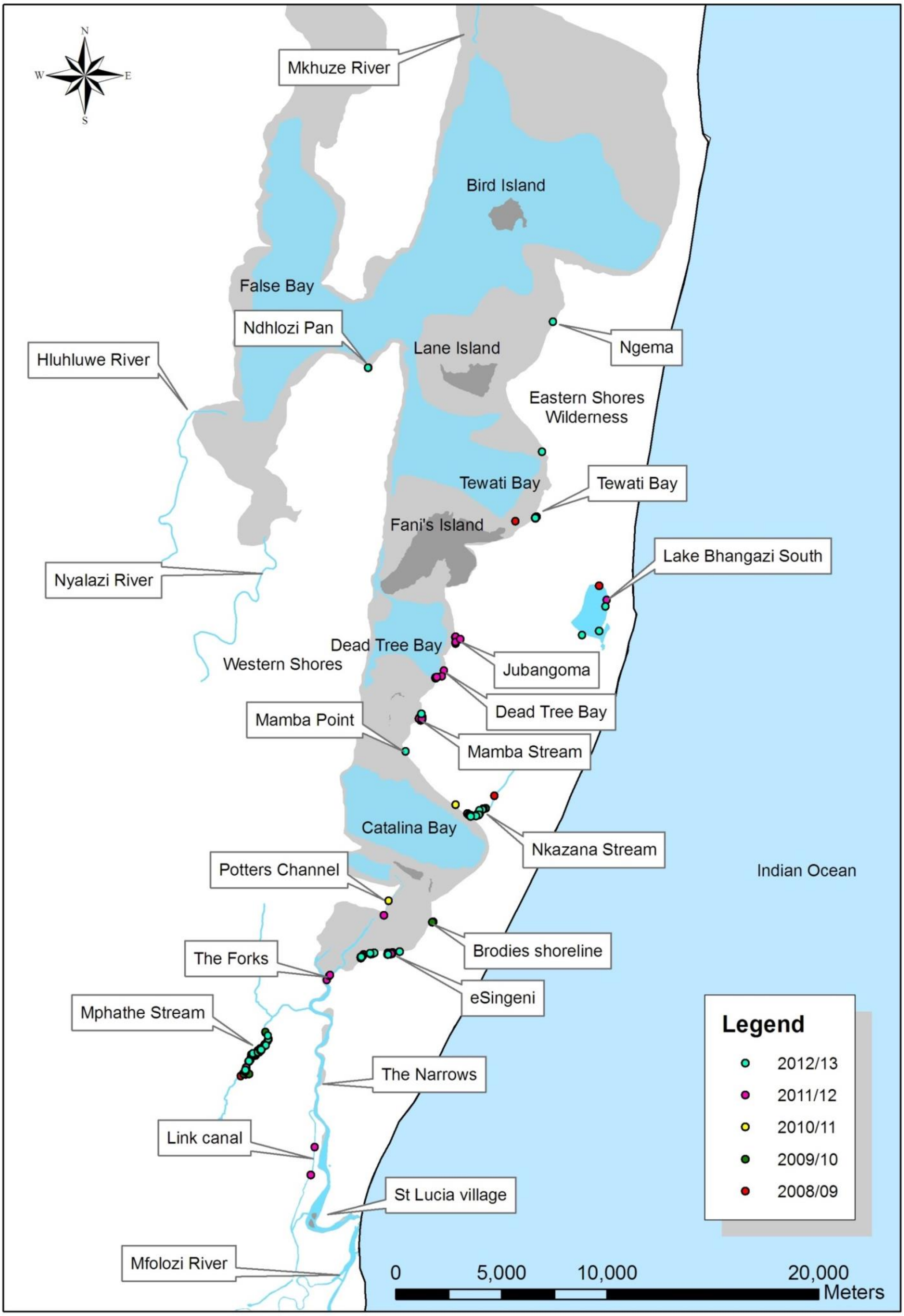

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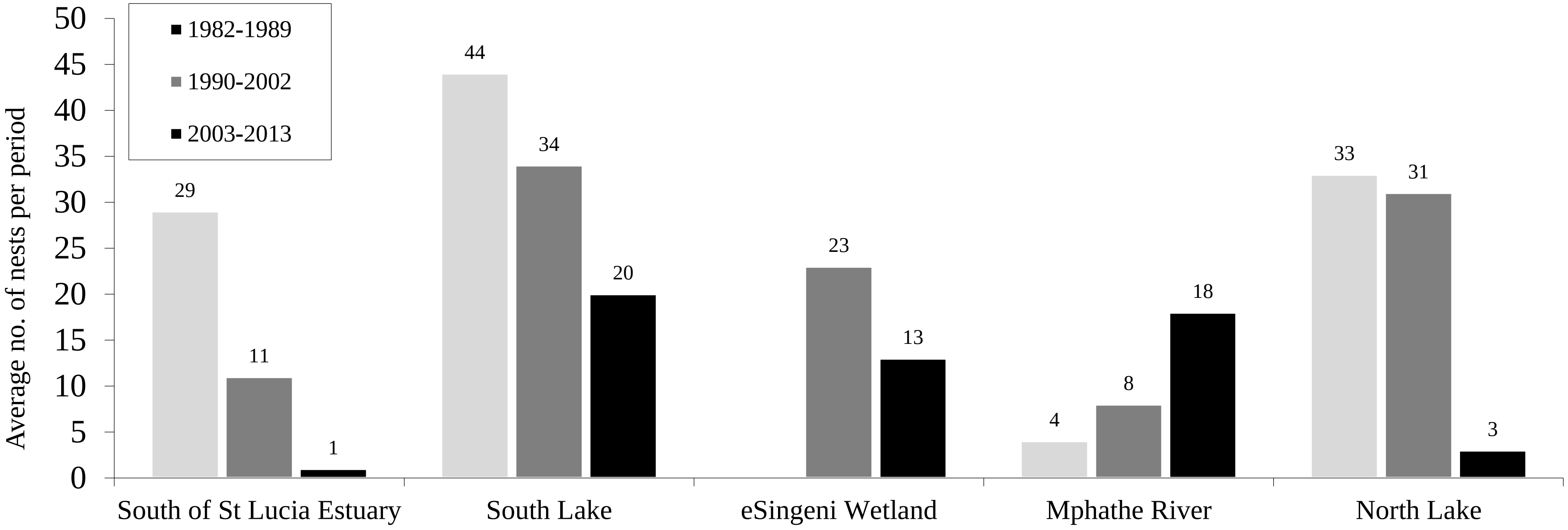

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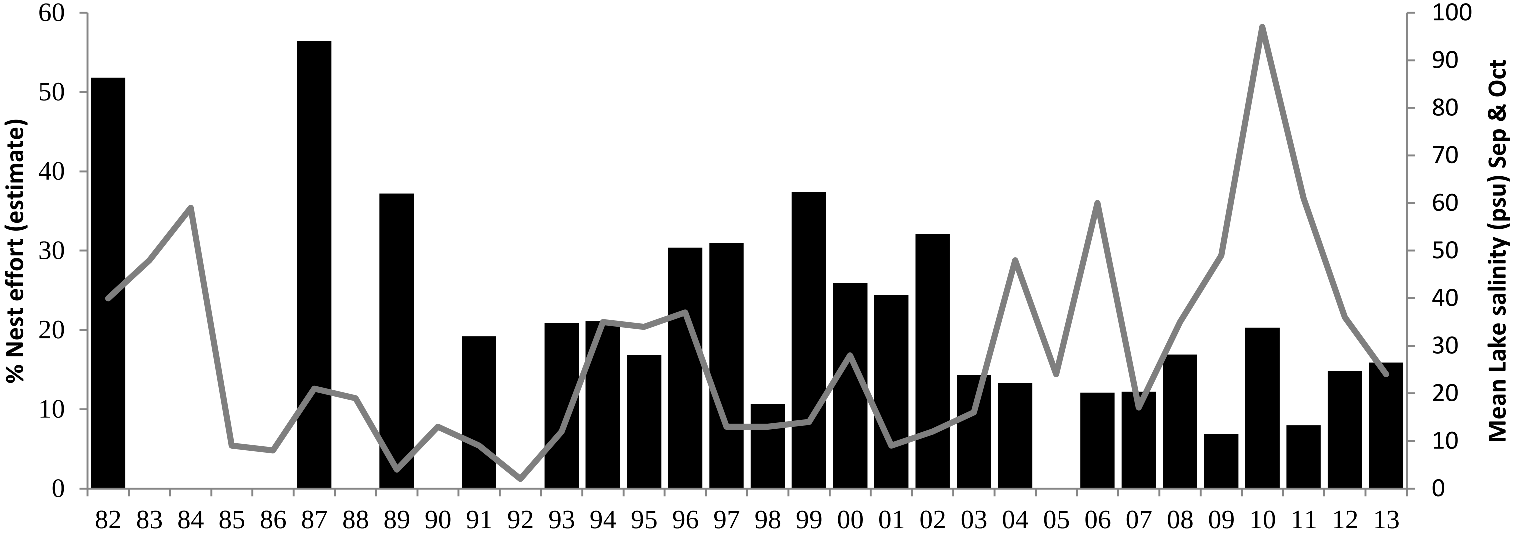
a.



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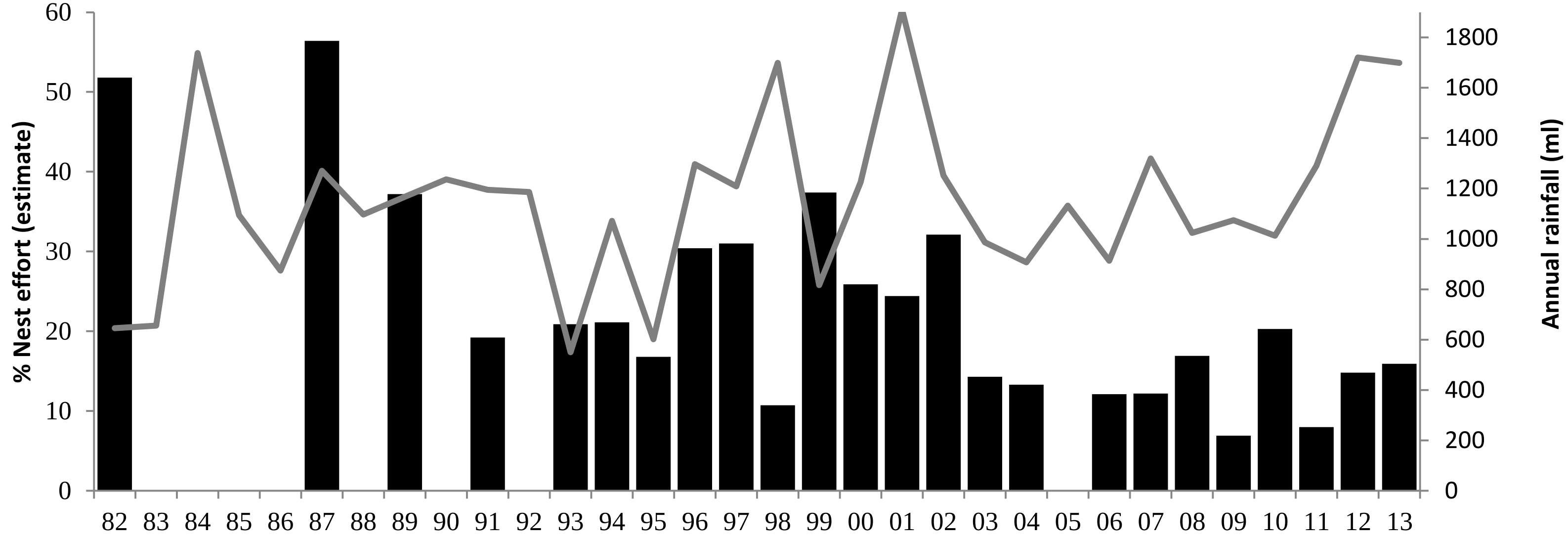

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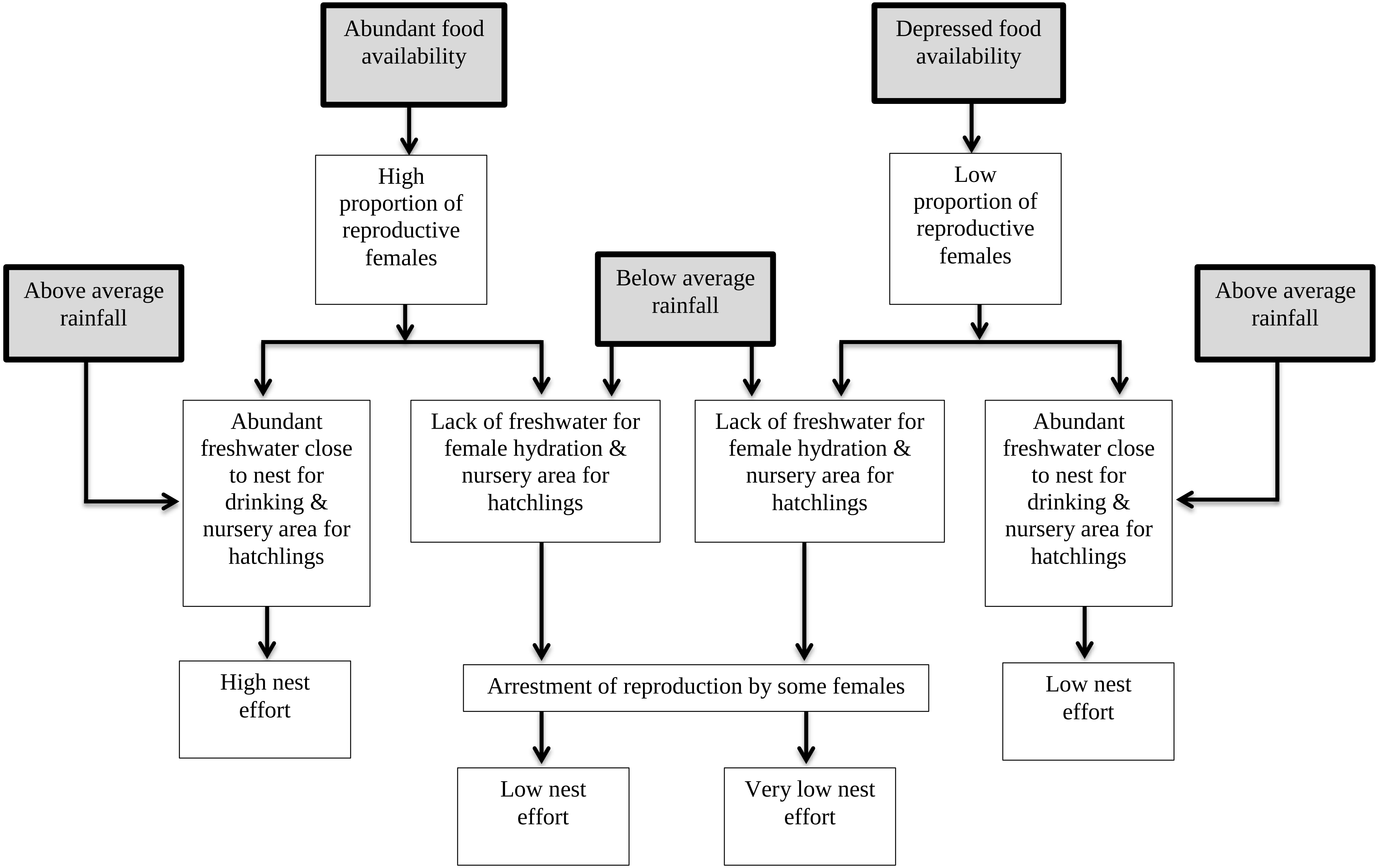

Figure 6. A simplified hypothetical conceptual model of Nile Crocodile nest effort dynamics at Lake St Lucia

eSingeni burrow near nest

Mamba Stream burrow near nest

Crocodile entering Nkazana Stream burrow

Crocodile captured in burrow at Nkazana Stream

Crocodile exiting a Nkazana Stream burrow

Nkazana Stream burrow near nest

Figure 7. Nile Crocodile burrows and burrowing behaviour at the Lake St Lucia estuarine system

Caption for Tables

Table 1 – Nile Crocodile nests recorded in the St Lucia estuarine system 2008/9 – 2012/13

Table 2 Nest effort of Nile Crocodiles in the Lake St Lucia estuarine system: 1982 - 2013

Table 3 Nesting females captured on/next to their nest-sites in the Lake St Lucia estuarine system

Tables

Table 1 – Nile Crocodile nests recorded in the St Lucia estuarine system 2008/9 – 2012/13

Area	**2008/09**	**2009/10**	**2010/11**	**2011/12**	**2012/13**	**Mean ± S.E.**
Link Canal	0	0	0	2	0	0.4 ± 0.4
Mphathe Stream	12	38	4	18	19	18.2 ± 5.62
Narrows (Forks)	0	0	1	4	0	1.0 ± 0.77
Narrows (St Lucia village)	0	0	1	1	0	0.2 ± 0.24
Potters Channel	0	0	2	1	0	0.6 ± 0.4
Catalina Bay eastern shoreline	1	0	0	0	0	0.2 ± 0.2
eSingeni	11	18	6	13	15	12.6 ± 2.01
Nkazana Stream	3	10	8	7	11	7.8 ± 1.39
Mamba Stream	0	6	5	5	2	3.6 ± 1.12
Dead Tree Bay	0	3	1	3	0	1.4 ± 0.68
Jubangoma – Tewati Bay	0	5	2	4	6	3.4 ± 1.08
ES Wilderness	1	0	1	1	2	1.0 ± 0.32
Ndhlozi Pan	0	0	0	1	1	0.4 ± 0.24
Lake Bhangazi	1	0	1	1	4	1.4 ± 0.68
Total	29	80	32	61	60	52.40 ± 7.87

Table 2 Nest effort of Nile Crocodiles in the Lake St Lucia estuarine system: 1982 - 2013

Year	**Population count**	**Population estimate**	**Adult estimate**	**Adult female estimate**	**Nest estimate**	**Nest effort estimate**
1982	226	643	515	265	138	51.8
1987	563	619	496	256	144	56.4
1989	743	881	706	364	135	37.2
1991	677	1025	822	423	81	19.2
1993	975	1123	900	464	97	20.9
1994	782	1134	909	468	99	21.1
1995	744	1109	889	458	77	16.8
1996	692	1113	892	460	140	30.4
1997	851	1126	902	465	144	31.0
1998	687	1046	838	432	46	10.7
1999	634	1005	805	415	155	37.4
2000	717	997	799	412	107	25.9
2001	674	992	795	410	100	24.4
2002	654	937	751	387	124	32.1
2003	945	1009	809	417	59	14.3
2004	894	1081	867	446	59	13.3
2006	698	1076	862	444	54	12.1
2007	649	1069	857	441	54	12.2
2008	941	1149	921	474	80	16.9
2009	819	1114	893	460	32	6.9
2010	670	1052	843	434	88	20.3
2011	760	1069	857	441	35	8.0
2012	745	1096	878	452	67	14.8
2013	616	1005	806	415	66	15.9

Table 3 Nesting females captured on/next to their nest-sites in the Lake St Lucia estuarine system

Crocodile	**Date caught**	**Area**	**TL mm**	**SVL mm**	**Unique scute code**	**Tag colour ***	**Transmitter**
130	2009/10/22	Nkazana Stream	2834	1522	LH2 RH3 V9	WOG	
131	2009/10/22	Nkazana Stream	3222	1782	LH2 RH4 V2	GWO	
453	2009/11/19	Nkazana Stream	2618	1412	LH5 RH4 V6	OWG	
436	2009/11/19	Nkazana Stream	2744	1510	LH5 RH4 V7	BGG	
439	2010/01/02	eSingeni – at nest-site	2650	1408	LH5 RH4 V10	GWB	
440	2010/01/02	Nkazana Stream – at nest-site	2740	1454	LH5 RH5	BWW	
441	2010/01/03	Nkazana Stream – at nest-site	2906	1560	LH5 RH5 V2	GOW	
442	2010/01/07	eSingeni – at nest-site	2922	1608	LH5 RH5 V3	WGG	
443	2010/01/07	eSingeni – at nest-site	2840	1528	LH5 RH5 V4	OGW	
444	2010/01/08	eSingeni – at nest-site	2820	1522	LH5 RH5 V5	WGB	
445	2010/01/08	eSingeni – at nest-site	3068	1640	LH5 RH5 V6	BWG	
446	2010/01/15	eSingeni – at nest-site	3164	1680	LH5 RH5 V7	WYB	
447	2009/12/10	eSingeni – at nest-site	2774	1564	LH5 RH5 V8	GBW	AG 173
448	2010/02/01	eSingeni – at nest-site	3004	1688	LH5 RH5 V9	BYG	
125	2010/02/09	Nkazana Stream – at nest-site	2892	1614	LH2 RH3 V6	GBB	AG 295
449	2010/03/05	Dead Tree Bay – at nest-site	2848	1564	LH5 LH6 LH7 LH8 LH9 V10	OYB	AG 296

CHAPTER 6

Nesting behaviour of female Nile Crocodiles (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

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ABSTRACT

While nesting biology and ecology have been investigated for a number of Nile Crocodile (*Crocodylus niloticus*) populations, virtually no information is available on the behaviour and movement patterns of nesting females during the nest guarding period. In this study, home range, nest-site selection, movement patterns, activity levels and nest fidelity of four nesting females were investigated. Gravid females seemingly selected winter basking/breeding areas close (351 ± 2 m) to nest-sites. Females did not move directly to the site of oviposition, but apparently considered other potential and or historic nest-sites as well. Mean home range and core-use area of nesting females were 8539 ± 4752 m^2 and 4949 ± 3302 m^2 respectively. Mean home range (0.85 ha) was significantly smaller than the mean home range of non-nesting females (108.4 ha) during the nesting season. Activity levels and mean daily movements while nesting were 8.1 ± 2.5 % and 213 ± 64 m respectively and increased to 47.9 ± 11.7 % and 2176 ± 708 m during the post-nesting period. Overall levels of nest fidelity were 82.8 ± 11.7 %, 78.1 ± 15.9 % during the day which increased to 87.3 ± 7.8 % at night.

The highest nest fidelity recorded during incubation was 99.7 % over a 96 day period. Nest abandonment (including non-transmitter female nests) was recorded for six nests of which three were abandoned before the end of incubation. Of the post-incubation nests at the Mphathe Stream, partial embryonic development was recorded in one nest and no development in two nests, possibly a result of cool incubation temperatures. GPS-satellite data from nesting females are elucidating spatial and behavioural patterns during the nest guarding period and providing novel insights into this important event.

INTRODUCTION

Key to understanding many of the biological aspects of crocodilians lies in the study of their reproduction (Webb 1977), but behavioural aspects such as nest fidelity, movements, activity and space-use of females while nest-guarding, are generally poorly documented for most species. Pooley (1962) and (1969) published the first detailed data on Nile Crocodile incubation and made a significant contribution to understanding the social dynamics of the species through his experiments and observations, despite captive conditions. Through careful field observations, Modha (1967) documented basic social behaviour of breeding (courtship and mating) and nesting wild Nile Crocodiles at Lake Turkana, while Kofron (1993) described social behaviour of Nile Crocodiles at the Chipinda Pools, during a drought.

Advances in VHF telemetry allowed for increased monitoring of spatial activities and movements over extensive periods (Joanen and McNease 1970). The spatial ecology of nesting females has been documented for the American Alligator (*Alligator mississippiensis)* see (Joanen and McNease 1970, Goodwin and Marion 1979, Taylor 1984, Rootes and Chabreck 1993), American Crocodile (*C. acutus*) see (Kushlan and Mazzotti 1989) and Nile Crocodiles, see (Hutton 1984, 1989, Hocutt et al. 1992).

However, detailed investigations into spatial and movement ecology and activity levels of wild nesting females using VHF is constrained by their remote habitats and sensitivity to disturbance by field researchers. The use of transmitters with the ability to record sufficiently large and accurate spatio-temporal datasets using Global Positioning Systems (GPS)-satellite technology over a number of seasons, led to a significant increase in data, enabling more detailed analysis.

AIMS AND PREDICTIONS

Female Nile Crocodiles invest 84 to 98 days, depending on soil temperature (Pooley 1969), guarding their eggs. During this period they are vulnerable on land, often far from water (Pooley 1969, Fawcett 1987) and generally not feeding (Pooley 1982a). Little information is available on Nile Crocodile female movements and behaviour while nest guarding, therefore our aim was to use GPS-satellite transmitters to collect information remotely at adequate temporal and spatial scales for analysis of these parameters. It was expected that females would occupy small home ranges and show considerable levels of site fidelity, possibly higher at night than during the day based on detectable ventral imprints early in the morning often on nests encountered (Combrink, pers. obs.). We predicted that females would move between the nest and freshwater for drinking, but that overall activity levels would be low.

MATERIALS AND METHODS

Study area

The Lake St Lucia estuarine system is situated in north-eastern KwaZulu-Natal province of South Africa. At ~60 km in length, which includes the 20 km long Narrows channel that connects the lake to the ocean, and an average of 6 km in width when filled to capacity, it is the largest estuarine system in Africa (Cowan 1997), but nonetheless very shallow (mean depth of 0.98 m (Hutchison 1974). It is a dynamic system driven by varying environmental and ecological processes, each occurring at differing spatial and temporal scales (Taylor 2006). A more detailed description of the study area is presented in Chapter 1.

Biotelemetry

We captured three nesting Nile Crocodile females on/very close to their nests on 10 December 2009 at eSingeni, 9 February 2010 at Nkazana Stream and 5 March 2010 at Dead Tree Bay (Fig. 1). GPS-satellite transmitters (Africa Wildlife Tracking) download via the Global System for Mobile Communication (GSM) were subcutaneously attached with orthopaedic stainless steel wire and 100 kg breaking strain nylon to the nuchal rosette area. Two females (515 and 601) were captured and fitted with transmitters outside of the nesting season and continue to nest during the 2010/11 and 2012/13 nest seasons. Refer to Appendix 2 for a description of capture methods, and Appendix 5 for transmitter attachment procedure.

Data analysis

Prior to analysis, data in Greenwich Mean Time (GMT) were converted to South African local time, GMT + 2 h. The displacement between two successive GPS points X_1Y_1 and X_2Y_2 was calculated using the following equation: 1000 x (6371.1 x ((2 x asin (sqrt ((sin ((radians(X_1) – radians (Y_2))/2)^2) + cos (radians (Y_1)) x cos (radians(Y_2)) x (sin((radians(X_1) –radians (X_2))/2)^2)))))). Displacements between GPS-observations were considered an interval along the shortest path connecting them and therefore displacements were considered a minimum distance travelled. We investigated fine-scale movements through analysis of total and mean daily movement rates. Results are presented as mean ± standard error (S.E.).

Nest-site fidelity

Nest-site fidelity, or nest attendance, was defined as the proportional time a nest-guarding female was < 25 m from her nest. In order to assess nest-site fidelity and investigate likely differences between day and night, we determined the proportion of GPS-observations < 25 m from the nest for the total day and night period. In order to compare daily levels of nest fidelity with daily movement rates, we calculated mean daily movements and mean daily distance moved from the nest.

Activity levels

We determined activity levels of nesting females by investigating displacements between four hourly GPS-observations, i.e. six over a 24 h period. We defined displacements < 20 meters as zero movement, i.e. no activity and displacements of > 20 meters as a movement event, irrespective of the length of the movement. The distance of 20 m was used to account for accuracy limitations of the GPS-satellite transmitter. A submerged transmitter was unable to record a GPS point and this had to be accounted for otherwise scheduled but unrecorded GPS duty cycles would spatially inflate the value of the first successfully recorded displacement. Therefore, if one or more consecutive scheduled GPS recordings were unsuccessful (i.e. submerged transmitter), we calculated the mean value for the unrecorded schedules and if these were less than 20 m, they were considered to represent zero movement. However, if the unrecorded displacement value(s) were > 100 m, it was considered a movement event, irrespective of the number of consecutively missed GPS schedules. We determined the proportion of times a nest-guarding female moved (i.e. being active), or did not move (i.e. inactive) over a 24 h period.

Home range analysis

We used nonparametric kernel density estimation (Worton 1989) to estimate home ranges of nesting females during the nesting period. We also estimated home ranges of non-nesting females during the same period. All analysis were conducted using ABODE (Laver 2005), a kernel home range estimation for ArcGIS. The 95 % home range was contoured at 95 % of the volume of the density surface and the core-use area was calculated using Horner and Powell's (1990) statistical clumping core analysis to provide an objective delineation of core-use areas and not some arbitrary defined probability cut-offs (e.g. 50 % utilisation distribution). We used a biweight kernel, and the least-squares cross-validation (LSCV) was used for selecting the optimum bandwidth or smoothing parameter, which was fixed (as oppose to adaptive). Data was standardised to unit variance, which meant that h_{ref} was calculated from the standardised dataset (Laver 2005).

RESULTS

A total of 4519 GPS-observations were recorded while females were nest guarding or guarding hatchlings subsequent to nest liberation (Table 1). Female 447 never entered the GSM network to download data. Females 125 and 449 were captured on their nests so the dataset for that season is incomplete. Female 449 continued to nest the following (2011/12) nest season but abandoned her nest after two months for reasons unknown. Female 515 and 601 were captured outside the nesting season and nest during subsequent nest seasons with complete datasets.

Basking/breeding location and freshwater availability

It was possible to determine winter basking/breeding locations prior to nesting for Female 449 and Female 601, which were close (~350 m and ~353 m) to the nest-site the following nest season. In contrast, Female 125 moved around continuously throughout the winter of 2010 following nesting without residing at particular basking/breeding areas. She did not nest the following summer. Likewise, Female 601 did not nest the summer of 2011/12 and during the preceding winter's basking/breeding period she showed no fidelity to any specific basking/breeding area, but instead moved throughout her home range in the Narrows. However, during the winter basking/breeding season (June-August 2012) prior to nesting, she was inactive (movement < 20 m between GPS-observations) for 60 % of the time and 97 % of this at one particular location, ~350 m from the site used for nesting during the following nesting season. Her mean daily movements (MDMs) during the winter basking/breeding period preceding nesting were significantly less compared to the previous year when she did not nest ($t = 2.24$, d. f. = 182, $p < 0.05$).

All nesting females' nests were situated within or bordering on home ranges occupied during the non-nesting season. The availability of nearby freshwater was seemingly the most important predictor of a nesting-site, as other requirements (open, exposed area with sandy substrate, sufficiently elevated with nearby shade) were available at numerous locations within their non-nesting home ranges. Female 449 and 125 nested close to freshwater (shoreline seepage and stream respectively) in their home ranges, while Female 515 nested adjacent to the freshwater Mphathe Stream within her non-nesting home range. Female 601 did not nest adjacent to the low salinity Narrows channel mostly utilised during the non-nesting season, but selected her nest-site ~360 m away near the freshwater Mphathe Stream, and specifically relative close (~90) m to an ephemeral pan.

Nest-site selection

GPS-observations of transmitter-fitted females during the non-nesting season (Females 515 and 601) as well as Female 449 during the 2010/11 nest season, provided information relating to nest-site selection.

Female 449

On 10 December 2010 just after 20:00, she walked overland ~90 m from a shoreline wetland to the location that would become her 2010/2011 nest-site. Before 01:00 the next morning she moved back to the wetland. The next day after 21:00, she moved in a southerly direction ~150 m through dense swamp forest to a previously recorded crocodile nest-site on the forest edge. She stayed here ~14 h before returning to the shoreline wetland, and almost immediately walked ~70 m along the shoreline and arrived at her 2010/11 nest-site. After six h she moved back to the wetland area, and returned the next day to the same site for a third time, but this time settled at the site for oviposition (Fig. 2).

Female 515

On 11 November 2010 (after 20:00) she moved from the Mphathe Stream ~6660 m into the Narrows and north up the Eastern Fork and into a very small (2-3 m wide) channel leading to eSingeni, a major nesting area. By 06:00 the next morning, and ~160 m from the nearest recorded historical nests at eSingeni, she turned around and headed back to the Mphathe Stream. We suspect that the reason she turned around was that the particular site earmarked for oviposition was already occupied by another, possibly larger, female. She moved back to the Mphathe Stream and on 15 November arrived after 18:00 at her nest location. After staying for a few h she moved upstream ~1730 m, turned around and moved passed her nest-site for ~1160 m, turned back upstream once again and arrived at her nest-site 16:00 on 16 November 2010 (Fig. 3).

Female 601

During the afternoon of 9 November 2012 she walked overland ~170 m from the Mphathe Stream in a southerly direction to an ephemeral pan and returned to the stream. Three days later she left the Mphathe Stream and walked ~40 m in a northerly direction to an apparent suitable nest area (i.e. open, sandy substrate close to, but elevated above the stream). She returned to the stream a few h later and moved to the same area the next day, at the same time, also to return once again after a few h. She repeated this behavioural pattern during the following two days. However, the following day (16 November) she moved ~270 m upstream, and then overland for ~380 m. The first ~170 m was open but the remaining distance was through a ~200 m forest area. Her nest-site was on the eastern edge of the forest (Fig. 4).

Nesting home range size and movements

The mean home range of nesting females was significantly smaller (0.85 ha) than non-nesting females (108.41 ha) during the nesting season (t = 3.34, d.f. = 6, p = 0.01).

Female 449 occupied the largest home range of all nesting females, 14973 m^2 (1.5 ha) in 2009/10 and 24217 m^2 (2.4 ha) in 2010/11. In 2009/10 she mostly moved between the nest and a wetland, ~190 m away and the following year, she excavated her nest ~75 m from her 2009/10 nest-site, and mainly moved to freshwater shoreline seepage in front of her nest. Her MDMs during both years were similar, 378 m and 327 m, although she was much more active (16.7 %) during 2009/10 compared with 2010/11 (6.8 %), which also resulted in a smaller core-use area, 6391 m^2 (0.64 ha), in 2010/11 compared with 17300 m^2 (1.73 ha) in 2009/10 (Table 1).

The nesting home range of Female 125 was 1457 m^2 (0.15 ha), which also incorporated an area in the Nkazana Stream ~45 m below her nest. Her core-use area while nest-guarding was 288 m^2. While nesting she was 8.3 % active with a MDM of 194 m, which increased significantly (One-way ANOVA: $F_{(1, 338)} = 35.535$, $p = 0.00$) to 1716 m subsequent to the nesting period.

Female 515 had a nesting home range of 1850 m^2 and core-use area of 567 m^2, similar to the core ranges of Female 449 in 2010/11 and 601 (Table 1). Her MDM prior to nesting was 1208 m, which decreased to 131 m while nesting. Following the nesting period it increased to 3648 m. Her pre- and post-nesting MDM was not significantly different ($p = 0.50$), but nesting and post-nesting MDM was significantly different (RMANOVA: $F_{(1, 393)} = 31.659$, $p = 0.00$).

Female 601 was most site fidelic of all nesting females, with MDM of 28 m and activity level of 0.6 %. Her nesting home range and core-use area was 198 m^2. Mean daily movements of her pre-nesting (2795 m), nesting (28 m) and post-nesting (3954 m) periods were all significantly different: One-way ANOVA $F_{(2, 772)} = 90.68$, $p = 0.00$. Her activity levels increased from 0.6 % while nesting to 77.1 % for the post-nesting period (n = 70 days).

Nest-site fidelity and movements during nest guarding

Female 125

Female 125 was captured on 9 February 2010 ~45 m downstream of her nest in the Nkazana Stream. She returned to her nest 46 h following her release in the stream (Fig. 5). She remained on or next (i.e. < 25 m) to her nest for 91.4 % of the time, while most of the remaining observations indicated her position in the stream, ~45 m away. She was marginally more on the nest at night (92.1 %) than during the day (90.7 %, Table 1) and made 45 excursions between her nest and the stream during the 51 days nesting. Her longest continued absence from the nest was two days and 2 h. After transmitter attachment her movements increased for a four day period before she settled at the nest (Fig. 6). The following month was characterised by high levels of nest fidelity, although from 11 March she spend proportionally more time in the stream than at her nest. We suspect hatching occurred after 21:00 on 22 March. By 22:00, she was in the stream and returned to the nest only on three brief (1-3 h) occasions from 23 to 25 March. She stayed in the stream below her nest supposedly guarding the hatchlings for nine days and 22 h, before moving downstream into Catalina Bay on 3 April 2010.

Female 449 (2009/10 nest season)

Female 449 was captured next to her nest on 5 March 2010 at Dead Tree Bay, fitted with transmitter and released at the site of capture (Fig. 2). She returned 24 h later to her nest. She remained on or next to her nest 36.9 % of the time, while the majority of the time spend from the nest was ~185 m away in a small shoreline wetland. She spent considerable more time on the nest at night (56.4 %) compared to 15.3 % during the day (Table 1). She made 15 excursions between the nest and the wetland in total. The longest continued duration at/next to her nest was 38 h, while the longest continued absence from the nest was two days and seven h. On 16 March she left the nest between 04:00-05:00 and moved to the wetland. She returned between 19:00-20:00 that evening but after 3 h moved from the nest for the last time. By 00:00, she was in the wetland area where she stayed for 24 h before moving to a swamp forest refuge site ~130 m away. We suspected the nest was predated on 16 March, while she was in the wetland.

Female 449 post-nesting movements

During the post-nesting period she utilised two areas, almost exclusively. The first and most important was a refuge area within closed canopy swamp forest, ~68 m southeast of the shoreline (Fig. 2). The second site was a small shoreline wetland area on the edge of the swamp forest, open and fully exposed to sunlight. This site received freshwater seepage from the adjacent forest. The female stayed at the swamp forest refuge subsequent to nesting for more than two months (18 March to 28 May 2010) and then moved to the open wetland area on the forest edge 28 May 2010, possibly for better basking opportunities during the cool winter. She stayed here for more than 10 weeks, almost without moving, until 8 August 2010. She then moved back to the swamp forest refuge for 5 weeks (8 August to 17 October) and returned to the open wetland site for another two weeks (17 October to 3 November) before returning one again to the swamp forest refuge for a final week, until 7 November 2010.

On 8 November 2010 she moved ~60 m from the swamp forest site to another small wetland on the shoreline where she stayed for 11 days until 19 November, before returning to the swamp forest refuge. On 7 December 2010 she moved ~140 m to a shoreline wetland.

(2010/11 nest season)

On 13 December 2011, she settled on her nest. GPS acquisition success during the nest guarding period was 99.0 %. She remained on/next to her nest 89.9 % of the time, while 10.08 % was away mostly moving into Dead Tree Bay and a nearby wetland, the same wetland used the previous year. She was on/next to her nest 87.5 % during the day and 92.5 % at night and made 26 excursions between the nest and the bay or wetland. The longest continued duration at/near her nest was 43 days and 12 h. During this period she was recorded once (23 December 2010, 01:00) on the shoreline, ~35 m from her nest, presumably to rehydrate. Her longest continued absence from the nest before she eventually abandoned the nest on 05:00 on 12 February 2011 was 19 h.

She showed high levels of nest fidelity until 24 January (Fig. 7). The following week was characterised by increased movements onto the shoreline, possibly as good rains were filling up the previously dry Dead Tree Bay in front of the nest. The only extensive and directed movement was made on 30 January to an area ~462 m from the nest. She continued to guard her nest with very little movements the following week but on 8, 10 and 11 January made extensive movements into the bay, always returning to her nest again. She abandoned her nest the next day for unknown reasons.

Female 515

We caught female 515 in a trap in the Mphathe Stream on 23 October 2010, outside of the nesting season. We attached a transmitter and released her in the stream at the capture site. On 17 November she settled at her nest-site (Fig. 3). GPS-observations indicated her position on/next to the nest 96.6 % in total, 95.7 % at night and 97.6 % during the day. It is unclear when the nest hatched as she continued to stay in the area until 24 March. Her movements did increased after 90 days and it is possible that the female continued to use this area before finally moving into the Narrows and south to the St Lucia estuary mouth, a distance of ~17.5 km, Fig. 8.

Female 601

She was captured on 9 April 2011 in the southern section of the Narrows. She did not nest the following nesting season but settled at her nest-site on 16 November 2012 ~451 m south of the Mphathe Stream, on the eastern side of a forest patch (Fig. 4). She was the most nest fidelic of all females, 99.7 % on/next (i.e. < 25 m) to her nest during the following 97 days. Only two movements were recorded away from her nest, one of ~94 m to an ephemeral pan

(Fig. 9) although it was possible that more return journeys of less than 4 h (the transmitter's duty cycle) were made to the pan for drinking.

She started liberating her hatchlings in the early hours of 21 February 2013 and by 04:00 that morning her position was recorded at the edge of the ephemeral pan, ~94 m away. At 08:00 she was back at her nest, presumably to check or collect more hatchlings and four h later she position was recorded at the nest once again. By 16:00 she returned to the pan and for the next 20 days she stayed at the edge of the pan, presumably guarding her hatchlings almost without any noticeable movement in the pan. Of the 121 observations, 99.2 % were recorded in the depression that formed most likely as a result of her immobility and duration (Combrink, pers. obs.). A number of eggshells were found in the depression, which indicated that some hatchlings were possibly transported from the nest completely or partially within the egg. On 13 March, after guarding her hatchlings for 20 days, she walked ~440 m north to the Mphathe Stream, and moved east into the Narrows and south into the St Lucia estuary.

Female range during the pre and post-nesting period

We found considerable variation in the use and apparent importance of female nest-areas. It seemed that Female 125's use of the Nkazana Stream was mostly restricted to the nesting season. After departing from the stream on 4 April 2010 she returned to her nest-site on three very brief occasions, 19 October, 9 November and 13 November. The last two visits were during the time when gravid females select nest-sites, but GPS-observations confirmed she did not nest during the 2010/11 season. Her post-nesting movements were typical of most nesting females and were characterised by sudden and dramatic increased daily movements, which decreased after a few weeks at the onset of winter and cold water temperatures (Fig. 10).

The only exception to this post-nesting increased mobility was Female 449 at the end of her 2010 nesting, when she, unlike the other nesting females, did not return to the estuary or lake following nesting. Dead Tree Bay was too shallow to facilitate movement so instead she moved to a refuge within the adjacent swamp forest where she remained for most of the time, except during winter when she moved to an open area on the shoreline adjacent to a seepage pool. Consequently, her post-2009/10 nesting MDM decreased to 240 m and activity levels to 7.2 % in the period between 2009/10 nesting and 2010/11 nesting (Table 1). She continued to nest the following year as well and activity level and MDM while nest-guarding were 6.8 % and 327 m respectively. Water levels increased in Dead Tree Bay sufficiently for crocodile movement and her post-nesting movements were typical again in that she moved extensively from February to April post-nesting (activity 48.64 % and MDM 1324 m, Table 1) which was significant compare to the previous year (One-way ANOVA: $F_{(3, 631)} = 55.06$, $p = 0.00$, Table 1).

Female 515 nested adjacent to the Mphathe Stream but also continued to use the stream extensively during the pre- and post-nesting periods, with 74.7 % of all GPS-observations recorded from the stream.

Female 601 also nested near the Mphathe Stream, although she utilised the adjacent Narrows extensively (78.1 %) during the non-nesting season.

Sequential asymptote analysis of home ranges for Female 125, Female 449, and Female 601 indicate explosive increases in space-use immediately subsequent to nesting (Fig. 11). Due to the ongoing drought at the end of Female 449's first nesting event, she was restricted to a small freshwater refuge. During her second nesting event, 725 mm of rain restored water levels in the lake (Fig. 11).

Nest abandonment

Female 449 abandoned her 2010/11 nest on 11 February 2011. She re-visited the nest on two occasions, 13 February (< 2 h at the nest) and 1 March (< 3 h at the nest). We checked the nest on 7 March and found dried carcasses of four hatchlings in a slight depression on the nest. Leaves had settled on the nest and it was evident that the female had not been back for a few weeks, which corresponded with the GPS-satellite data.

While photographing the area, hatchlings vocalised from within the nest cavity, possibly as a response to our movements. As it was evident that the female was not going to return, we opened the nest and liberated 37 eggs, 22 live hatchlings and 15 non-viable eggs. As we released the hatchlings in a nearby (~105 m) shoreline wetland, they started vocalising which immediately attracted a few other, slightly larger, hatchlings in the pool. We suspect they were the hatchlings from the top nest layer as the closest other known nest was 1950 m away.

Nest abandonment has also been recorded during this study on five other occasions. On 7 April 2010, subsequent to the nest incubation period, we excavated two abandoned nests at the Mphathe Stream monitored by camera traps. We found 38 eggs in the first nest, with no embryonic development and 42 eggs in the second nest, with partial development of 16 embryos (mean total length = 224.1 ± 7.1 mm) and 26 eggs with no development. On 10 April 2012 we excavated an abandoned nest at the Mphathe Stream monitored by a trap camera and found seven eggs, with no embryonic development. In March 2012 we recorded nest abandonment with two camera traps at the Mphathe Stream following a flooding event subsequent to tropical storm Irina. The female never settled back on the nest after the flood but visited the nest once on 12 March 2012 for 10 minutes. On 18 March 2012 the nest was predated by a Marsh Mongoose (*Atilax paludinosus*) and subsequently by Water Monitor (*Varanus niloticus*), refer to Chapter 7.

On 12 March 2012 while photographing egg remains at a nest at Mamba Stream hatchlings vocalised from a nearby (~4 m) nest almost completely colonised with vegetation. As it was evident that the female abandoned the nest, we opened the nest and found 32 eggs containing 25 hatchlings and 7 non-viable eggs.

DISCUSSION

Basking/breeding location and freshwater availability

It seemed that the reproductive state of Female 449 and Female 601 influenced the location of the winter basking/breeding area, in that they selected winter basking/breeding sites close to sites that were used for nesting during the subsequent nesting season. Webb *et al.* (1977) suggested that Estuarine Crocodile (*C. porosus*) females in Arnhem Land, might select their dry season (winter) habitat based on suitability for nesting the subsequent wet (summer) season, with access to fresh water a prerequisite. It is plausible that reproductive females at St Lucia establish the presence of water levels during the winter dry season and if suitable surface water is available, return in early November to nest.

Kay (2004) and Campbell *et al.* (2013) described movements of mature Estuarine Crocodile females of up to 62 km and 54 km's respectively to suspected nesting habitat during the wet season in the Ord and Wenlock Rivers, and suggested it was due to sub-optimal nesting habitat in their dry-season range.

Basking behaviour, where crocodilians respond behaviourally to cool water temperatures, raising body temperature above water temperature (Hutton 1987a), was noted by (Mcllhenny 1935, Smith 1979) when air temperature exceeded water temperature. At Lake St Lucia, crocodiles congregate during the cool winter months (Pooley 1982a, Leslie 1997) in areas of suitable basking habitat, i.e. open level areas close to sufficiently deep water with salinities low enough for drinking. Courtship and mating (breeding) of wild Nile Crocodiles in Zimbabwe during winter coincided with follicle growth and vitellogenesis in females from April to mid-Aug., while males had viable sperm from mid-May to mid-Sep. (Kofron 1990). Detoeuf-Boulade (2006) recorded the reproductive cycle of the Nile Crocodile in the Okavango Delta also during winter and it is reasonable to assume this would be similar at St Lucia.

Nest-site selection

The physical requirements for a crocodile nest at St Lucia are well documented (Pooley 1962, 1982a, Fawcett 1987, Leslie 1997) and nests are often used by the same or other females in subsequent years (Pooley 1962, Combrink and Robertson 2012, Chapter 5) supposedly when certain environmental conditions (e.g. lake levels, rainfall patterns and the state of the estuary mouth, i.e. open or closed) are relative stable. However, new nests have been recorded infrequently (Combrink and Robertson 2012).

All gravid females seemed to have considered other suitable or previously used sites for nesting prior to final selection and it seemed as if the general area were well known to the females. For instance, the route Female 601 navigated to her nest-site was ~400 m away from the stream and the last ~200 m was through dense forest. We found old eggshells at this site and it seems reasonable to assume that she knew this site from past nesting events. It also seemed plausible that her visit to the ephemeral pan on 9 November was to assess water levels in the pan. She eventually nested ~90 m from this pan and guarded her hatchlings in this pan for 21 days.

We suspect capture stress at Female 449’s 2009/10 nest resulted in her not re-visiting or considering that nest for re-use. Kushlan and Mazzotti (1989) found that excessive disturbance of American Crocodile (*Crocodylus acutus*) females at their nests resulted in changes of nest-sites in subsequent years.

It is possible that Nile Crocodiles has a cognitive map of high valued areas within their range, such as previous nest-sites, free of disturbance, freshwater seeps, streams etc. It furthermore seems that females make decisions and consider other potential/recent sites if initially inspected nest-sites are occupied, unfavourable or associated with a previous stress or disturbance, such as a capture event. It also seems likely that reproductive Nile Crocodiles assessed water levels of earmarked nest areas during the winter breeding/basking period.

Female 601 nested furtherest from water and displayed the highest nest fidelity. Conversely, females that nested closer to water moved more between the nest and water with resultant lower levels of nest fidelity and improved predation opportunities for egg predators (Chapter 5).

Home range size and movements

Hutton (1989) found that most mature Nile Crocodile females at Lake Ngezi maintained small (15 ha) home ranges near their nest-sites, although one female occupied a home range in the lake but moved to the river for nesting. Lake St Lucia nesting females maintained much larger home ranges during the non-nesting season (786.85 ± 400.81 ha, Chapter 4), but the home range and core-use area were much smaller compare to Nile Crocodiles at Ngezi, 0.85 ha and 0.49 ha respectively. All St Lucia nesting females all showed explosive increased movement and home range extensions (providing sufficiently deep water for movement) just after the nesting period, similar behaviour noted by Hutton for female N78 (301 cm) at Ngezi.

Campbell *et al.* (2013) reported mean home range of 650 ± 244.78 ha and MDM of 977.78 m for suspected nesting females, much larger compared to confirmed nesting Nile Crocodile females at St Lucia of 0.85 ± 0.48 ha and MDM of 212 ± 64 m. It is likely that the movements and home ranges of suspected Estuarine Crocodile nesting females in the Wenlock River were seasonal movements, or that the low duty cycle (twice daily) of the GPS-Argos observations were too low for constructing more accurate (i.e. smaller) home ranges during nesting.

Rootes and Chabreck (1993) found no difference in home range size between American Alligator (*Alligator mississippiensis*) nesting and non-nesting females, unlike this study where significant differences were recorded. Their home range estimates of nesting American Alligator was considerable larger 17.8 ± 16.9 ha compared to St Lucia nesting females, but mean daily movement of American Alligator much less, 27.3 ± 14.1 m, compared with this study, 211.64 ± 63.77 m. This might be a result of their tracking regime or relative low VHF observations, i.e. 195, compared to this study's 4519 GPS-observations. The American Alligator seemed less nest fidelic (68.8 % ± 5.8 S.D.), compared to St Lucia females (82.8 ± 11.7 %).

Joanen and McNease (1970) found similar home ranges (1.06 ha) during incubation for American Alligator, compare to our study, and with similar MDM (24.08 m) reported by Rootes and Chabreck (1993) for American Alligator. It is likely that the lower intensity VHF tracking regime (411 observations in total) was overestimating range size and underestimating movement's rates.

Alligators moved the most and hold the largest range size during the courtship and breeding period (Joanen and McNease 1970, Rootes and Chabreck 1993), which seems to be the opposite with female Nile Crocodiles in this study that were least active during the winter basking/breeding period and most active just after nesting.

Nest-site fidelity and movements during nest guarding

Despite variation between females, very high levels of nest fidelity were recorded (mean = 82.8 %) with Female 601 most nest fidelic (99.7 %). The lowest recorded fidelity was 36.6 % for female 449 during her 2009/10 nest season. It is possible that capture stress contributed to the high proportion of observations (63.4 %) away from the nest, of which the majority came from a wetland ~185 m from the nest. Of the 36.6 % observations on/near the nest, 15 % was during the day and 56.4 at night, i.e. of all observations < 25 m from the nest, 79.8 % were recorded at night. She nested the following year and nest fidelity was 89.9 % (87.5 % in the day and 92.5 at night). Capture stress did not affect all females equally. Female 125 maintained high levels of nest fidelity (91.1 %) for the remainder of nesting, with very little variation between day (90.7 %) and night (92.1 %) fidelity levels. It is also evident that transmitters attached to Female 449, Female 515 and Female 601 did not interfere with subsequent breeding or nesting activities.

Nest-guarding against egg predators during embryonic development and nest liberation at the end of incubation are both essential activities by the female to ensure hatchling survival. Levels of nest-site fidelity or nest attendance reported in this study were very high compare to other studies on American Alligator, 7.6 % (Joanen 1969), 14.9 % (Deitz and Hines 1980), 43 % (Kushlan and Kushlan 1980), but non used GPS-satellite transmitters, and the use of marsh buggies or air-boats required for most alligator nesting investigations probably results in underestimates of frequencies of attendance (Deitz and Hines 1980). Webb *et al.* (1977) reported close nest attendance of Estuarine Crocodile females in Arnhem Land, based on observed female tracks near the nest. Deitz and Hines (1980) found that high levels of nest-site fidelity had a significant effect on hatching success when predation is likely and experiments conducted by Kushlan and Kushlan (1980) also suggested that nest attendance can be an effective defence against predators such as racoons increasing reproductive success. They argued that nest guarding has been effective against predators in the alligator's evolutionary history.

Female range during the pre and post-nesting period

Hutton (1989) reported that most nesting Nile Crocodiles at Ngezi were found throughout the year close to their nesting areas in the river as this was the only suitable nesting area. He suggested a dominance hierarchy between females for nest-site use and the smallest nesting female moved from the lake to the river for nesting, and back subsequent to the nest season.

Transmitter-fitted females at Lake St Lucia seemed to nest within or at the margin of their home-ranges during the non-nesting season and the presence of freshwater at earmarked nest areas during the dry season was apparently an important nest requirement for reproductive females. Due to the variability of freshwater input, which seemed to conform to a cyclical wet/dry pattern of about 10 years (Tyson and Preston-Whyte 2000), food availability (presence, density, distribution or absence of the annual Striped Mullet (*Mugil cephalus*) migration) and human disturbance, shifts in nest-site distribution seems to reflect the biological and physical variability typical of the St Lucia system. The inherent variability might be one of the key determinants of the low reproductive frequency recorded at St Lucia (Chapter 5).

Nesting habitat in the Lake St Lucia system seemed to be abundant in the southern parts in the system, especially adjacent to freshwater streams. However, we suspect competition for nest-sites in the central and northern parts of the lake during drought periods when access to freshwater refugia is limited. However, we have observed communal nesting (five nests) at the onset of the recent drought period ~60 m within swamp forest at Dead Tree

Bay, but in subsequent years some of those females have apparently moved away or did not nest.

Campbell *et al.* (2013) suggested that female Estuarine Crocodiles in the Wenlock River might select breeding areas based on the best resources within productive river sections, in order to build up fat-stores for egg gestation and nesting. The Nile Crocodile breed during the cool dry season (Hutton 1989, Kofron 1990) when water temperature and metabolic rate are low (Pooley and Gans 1976, Huchzermeyer 2003) and therefore little if any feeding. We suspect at St Lucia breeding (courtship and mating) areas during the winter dry season are selected based on the close proximity of suitable nest areas and it is possible that reproductive females assess the potential of suitable nest-sites based on the presence of freshwater levels at the time. If suitable surface freshwater is available, she might return in early November to nest, providing adequate levels of freshwater or the presence of a burrow nearby.

The largest range extensions and daily movements of nesting females at St Lucia were just after the nesting period. We suspect this was reflecting a need for good feeding opportunities following the 12-15 weeks of limited/no feeding while nest guarding and perhaps the necessity to re-establish home ranges subsequent to the absence while nesting. Prior to the estuary mouth closure in 2002, the Striped Mullet (*Mugil cephalus*) migration from the ocean north through the Narrows during mid-April to mid-May every year coincided with the time when nesting females were moving from their nests or nursery areas and an increase of crocodiles have been recorded in the Narrows during this time of year (Whitfield and Blaber 1979, Pooley 1982b). All nesting females, except Female 449 at Dead Tree Bay in the central part of the lake, moved into the Narrows immediately following their nesting event, possibly in search for shoaling *M. cephalus*.

Nest abandonment

It is likely that Female 449’s 2010/11 clutch consisted of two or three layers of eggs, separated by a middle layer of sand, as noted by Pooley (1969) and Combrink (2005) at Lake St Lucia. The top layer would have been shallower than the deeper eggs and exposed to higher soil temperatures during the day. This would have resulted in accelerated embryonic development and decreased incubation time (Leslie 1997), relative to the cooler eggs below.

When the female re-visited the nest on 1 March, the hatchlings in the top layer might have picked up her movements near the nest and vocalised to be liberated (Pooley 1969). We suspected that she might have moved the hatchlings to the nearest nursery area, ~105 m along the shoreline and very close to her swamp forest refuge site. She apparently never returned to the nest to collect the remaining hatchlings, or the four that were dead found on the nest were at that stage slightly deeper and not exposed, nor fully developed and therefore not responding to her presence. Later they managed to opened the egg from the inside with their egg-caruncle (Pooley 1962) and crawled out from the loose shallow sand to the surface, but probably died from exposure and dehydration. Combrink (2005) measured sand surface temperatures at a Nile Crocodile nest as high as 50 °C.

The estimated incubation time from nest occupation on 13 December (based on GPS-observations) and suspected oviposition to 7 March was 84 days. This is the lower incubation estimate for Zululand (84 to 98 days) by Pooley (1969). Leslie (1997) recorded Nile Crocodile incubation duration of 69.9 days at constant temperature of 33 °C. It is possible that the female liberated the first layer after 78 days incubation (13 December 2010 to 1 March 2011).

Little is known about the incidence or extent of nest abandonment at St Lucia. Pooley (1969) recorded infertile eggs in seven of 75 nests, but it is not clear if the entire or only a proportion of the clutch were infertile. Hutton (1987b) documented nest abandonment at

Ngezi using VHF radiotelemetry and noted a decrease in nest attendance after ~100 days and after ~110 days most females deserted their nests. Ngezi is a high altitude lake where cooler temperatures skewed sex ratios in favour of females and caused elevated levels of embryonic mortality (Hutton 1987b). He observed one instance (0.93 %) of early nest abandonment at Ngezi, while Modha (1967) recorded 1.32 % early nest abandonment and 3.29 % total nest abandonment. Of the four abandoned nests at St Lucia, two along the Mphathe Stream were in partially shaded areas and it is possible that cool temperatures resulted in total and partial failure of embryonic development in the two nests. Leslie and Spotila (2001) found that temperatures in some nests along the Mphathe Stream at St Lucia were well below the viable range and may have resulted in skewed sex ratios, partial or total embryonic failure.

CONCLUSIONS

This is the first study to investigate detailed crocodilian nest behaviour using GPS-satellite monitoring and the first to describe Nile Crocodile nesting home range. It seemed that the reproductive state of females influenced the location of the winter basking/breeding area close to earmarked nest-sites in order to assess the potential suitability of freshwater availability at the time. Gravid females considered other suitable or historicly used sites for nesting prior to final site selection and it seemed as if the general area were well known to the females. It is possible that navigation of nesting females might be governed by a cognitive map of high valued areas within their range, such as previous nest-sites, free of disturbance close to freshwater. Lake St Lucia nesting females maintained large home ranges during the non-nesting season but nesting home range and core-use areas were very small compare to other crocodilian species as well as Nile Crocodiles at Lake Ngezi, although this could only be a function of our detailed GPS-satellite data. Lake St Lucia nesting females showed increased mobility and range expansion just after nesting, possibly driven by the need to maximise feeding opportunities before winter and re-establishing home ranges. Despite variation between females, very high levels of nest fidelity were recorded. Nest-guarding against egg predators as well as liberation at the end of incubation are both essential activities by the female to ensure hatchling survival. Transmitter-fitted females at Lake St Lucia seemed to nest within or at the margin of their home-ranges during the non-nesting season which possibly suggest an abundance of suitable nesting areas at Lake St Lucia, especially in the southern parts in the system, adjacent to freshwater streams. However, we suspect competition for nest-sites in the central and northern parts of the lake during drought periods although communal nesting has been observed here during in the past while Mullet population were abundant. Little is known about the incidence or extent of nest abandonment at St Lucia. Of the four abandoned nests, two along the Mphathe Stream were in partially shaded areas and it is possible that cool temperatures resulted in total and partial failure of embryonic development.

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Caption for Figures

Figure 1 – The Lake St Lucia estuarine system.

Figure 2 - Nest-sites of Female 449 at Dead Tree Bay during the 2009/10 and 2010/11 nest seasons.

Figure 3 – Nest-site of Female 515 at the Mphathe Stream during the 2010/11 nest season.

Figure 4 – Nest-site of Female 601 at the Mphathe Stream during the 2012/13 nest season.

Figure 5 – Nest-site of Female 125 at the Nkazana Stream during the 2009/10 nest season.

Figure 6 – Mean daily movements (black) and mean movements from the nest (grey) of Female 125 during the nesting period.

Figure 7 – Mean daily movements (black) and mean movements from the nest (grey) of Female 449 during the 2010/11 nest season.

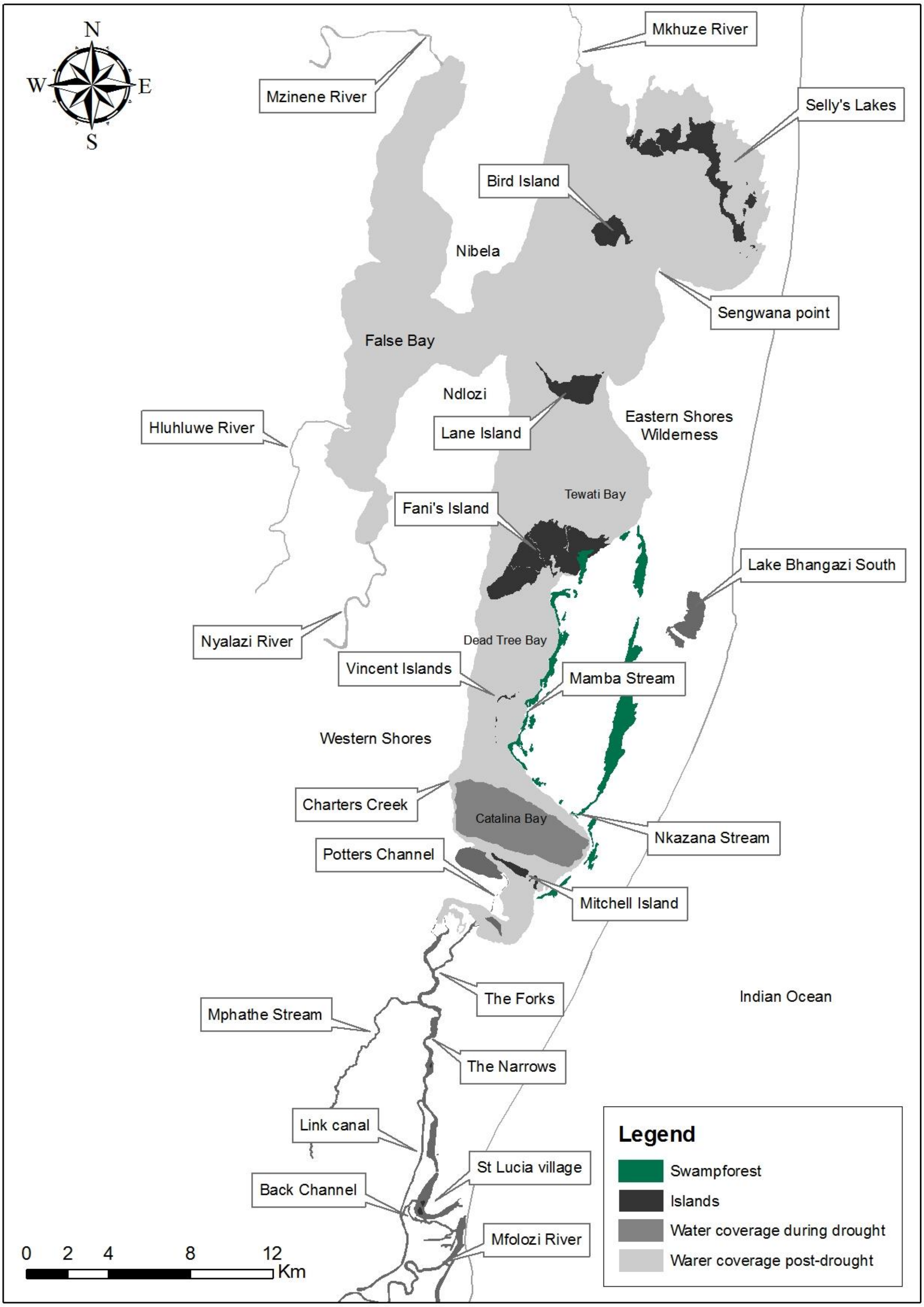
Figure 8 – Mean daily movements (black) and mean movements from the nest (grey) of Female 515 during the nesting period.

Figure 9 – Mean daily movements (black) and mean movements from the nest (grey) of Female 601 during the nesting period. Subsequent to liberating her hatchlings on 21 Feb., she moved to an ephemeral pan, ~90 m away from the nest.

Figure. 10 - Monthly movements of nesting Nile Crocodile at the Lake St Lucia estuarine system. The square brackets indicate the nest period of individual females, while the perforated ovals indicate post nest movements. The warm wet summer is from 8 Nov. to 7 April and cool dry winter 22 May to 31 Aug.

Figure 11. Sequential asymptote analysis of home ranges for nesting Female 125 (a.), nesting female 449 (b.) and nesting Female 601 (c.). Home ranges of all three females indicate explosive increases in space-use immediately subsequent to nesting. Note that due to the ongoing drought at the end of Female 449’s first nesting event, she was restricted to a small freshwater refuge. During her second nesting event, 725 mm of rain restored water levels in the lake.

Figures



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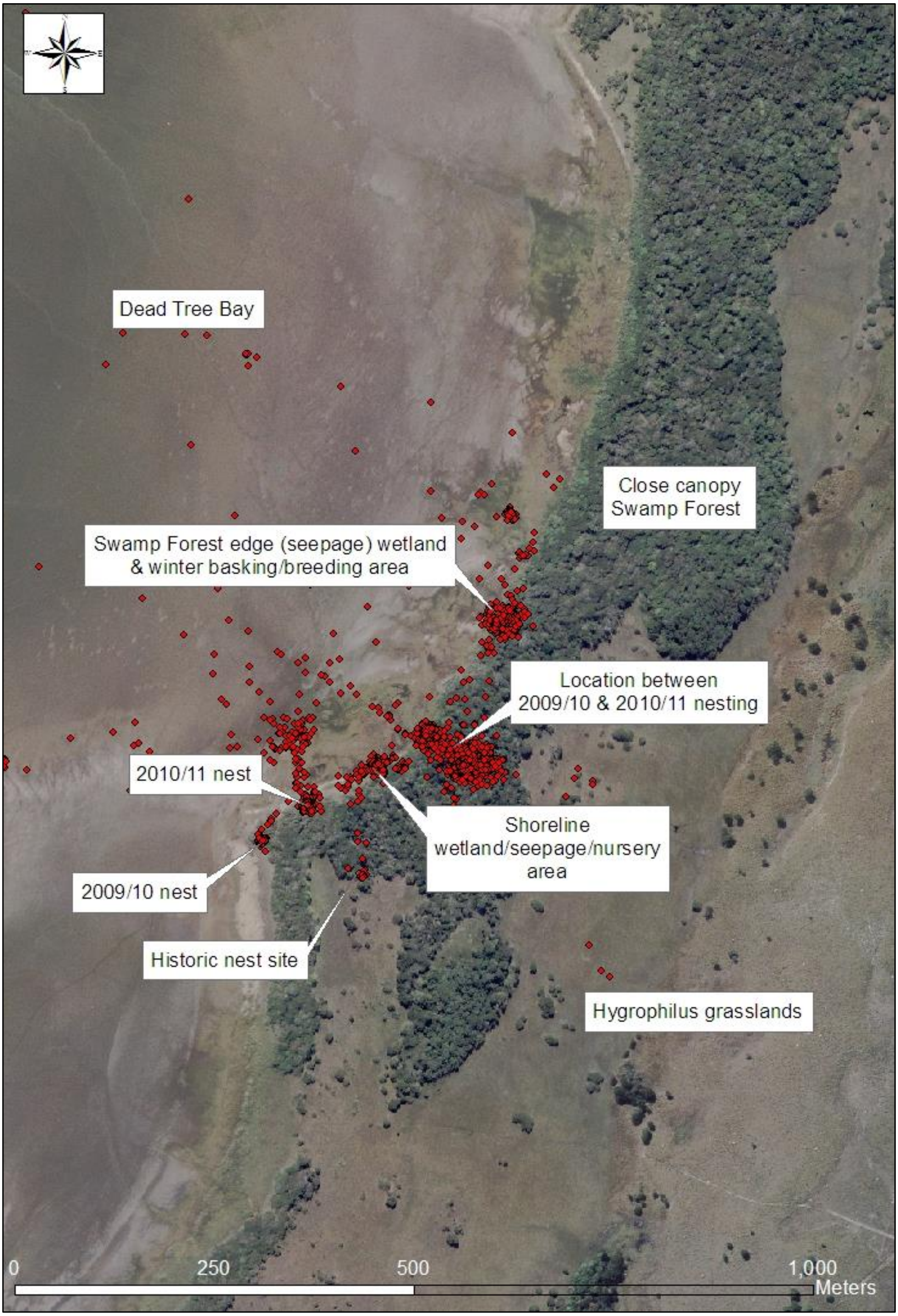

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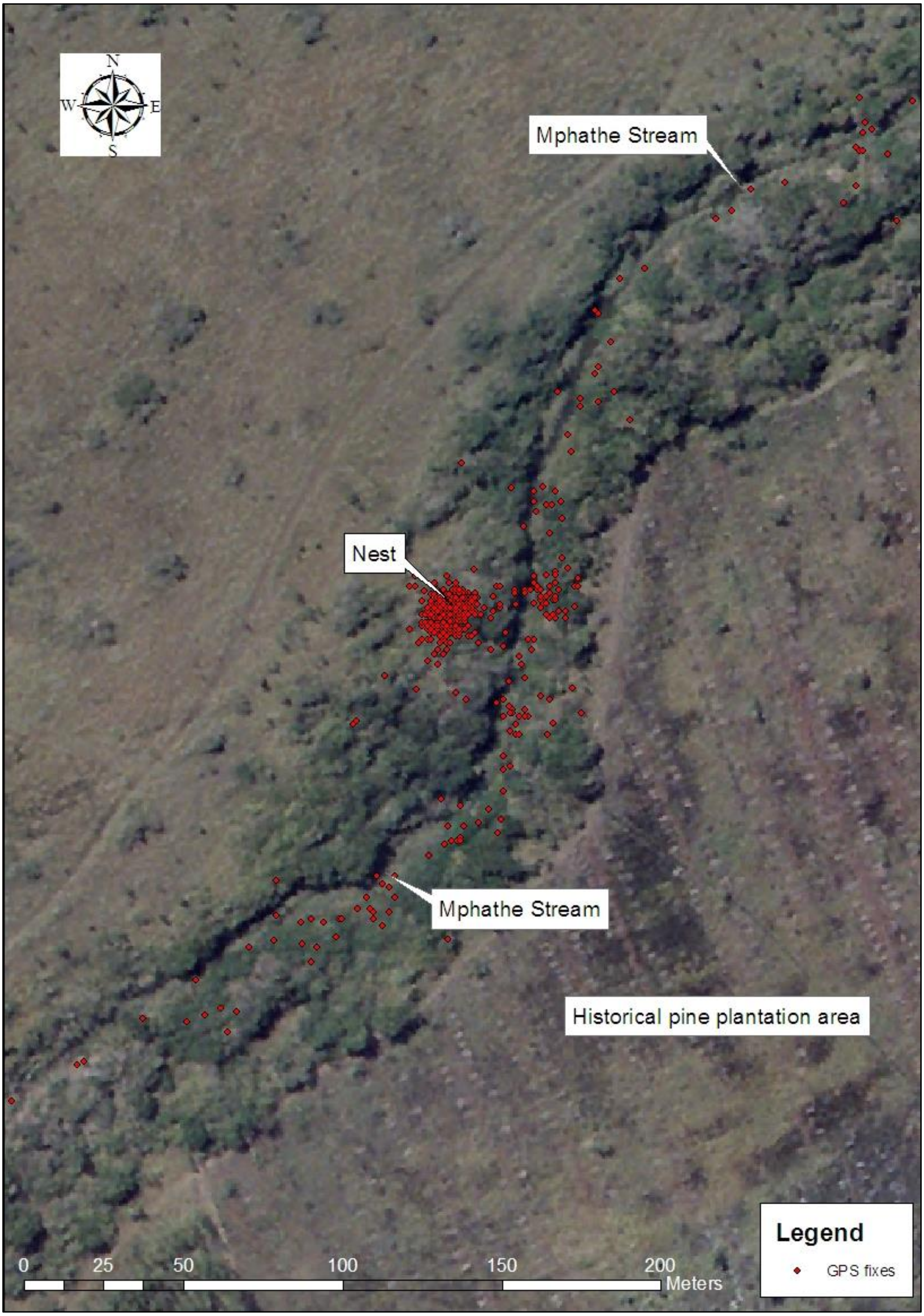


Figure 3 – Nest-site of Female 515 at the Mphathe Stream during the 2010/11 nest season.

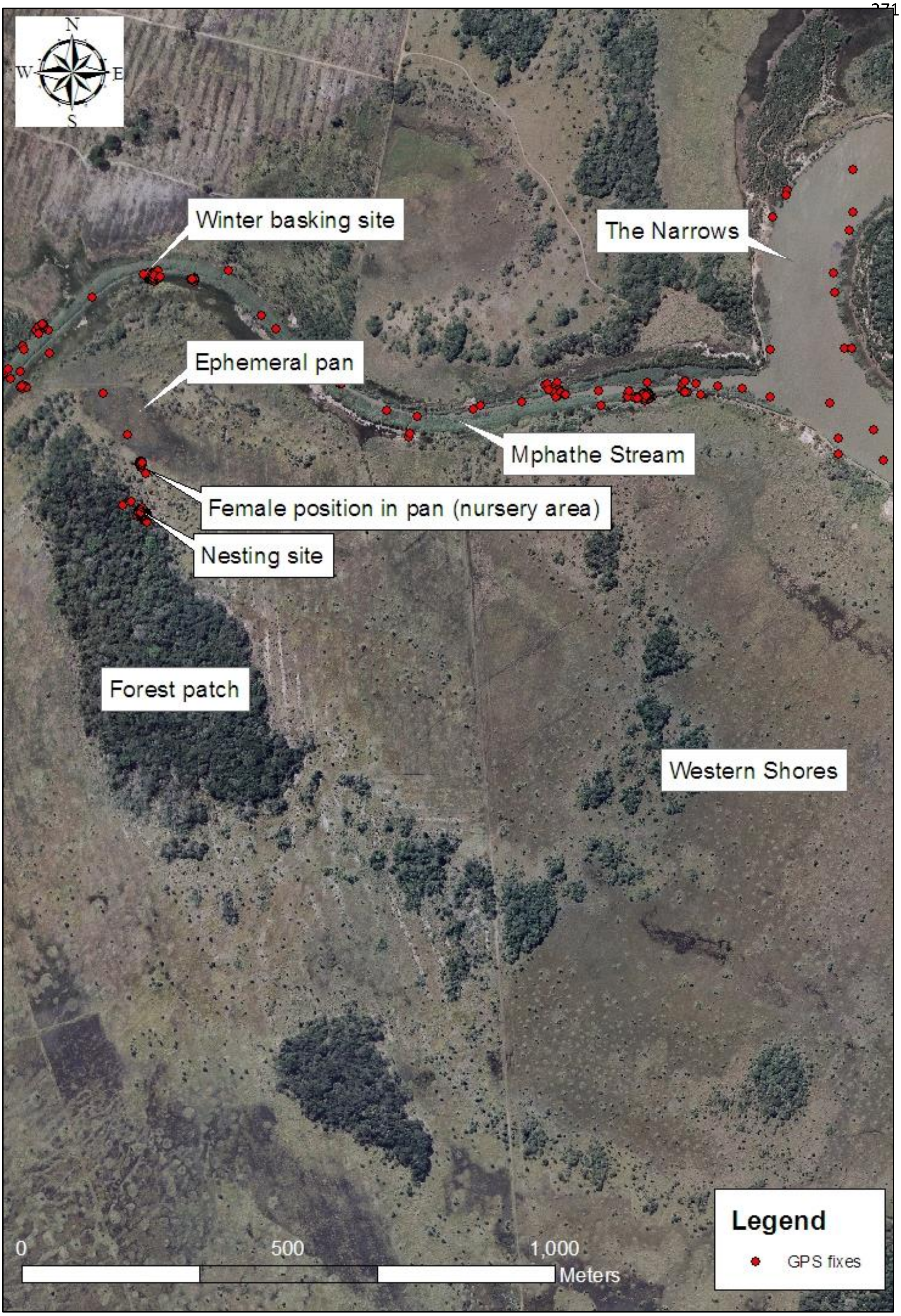


Figure 4 – Nest-site of Female 601 at the Mphathe Stream during the 2012/13 nest season.

Figure 5 – Nest-site of Female 125 at the Nkazana Stream during the 2009/10 nest season.

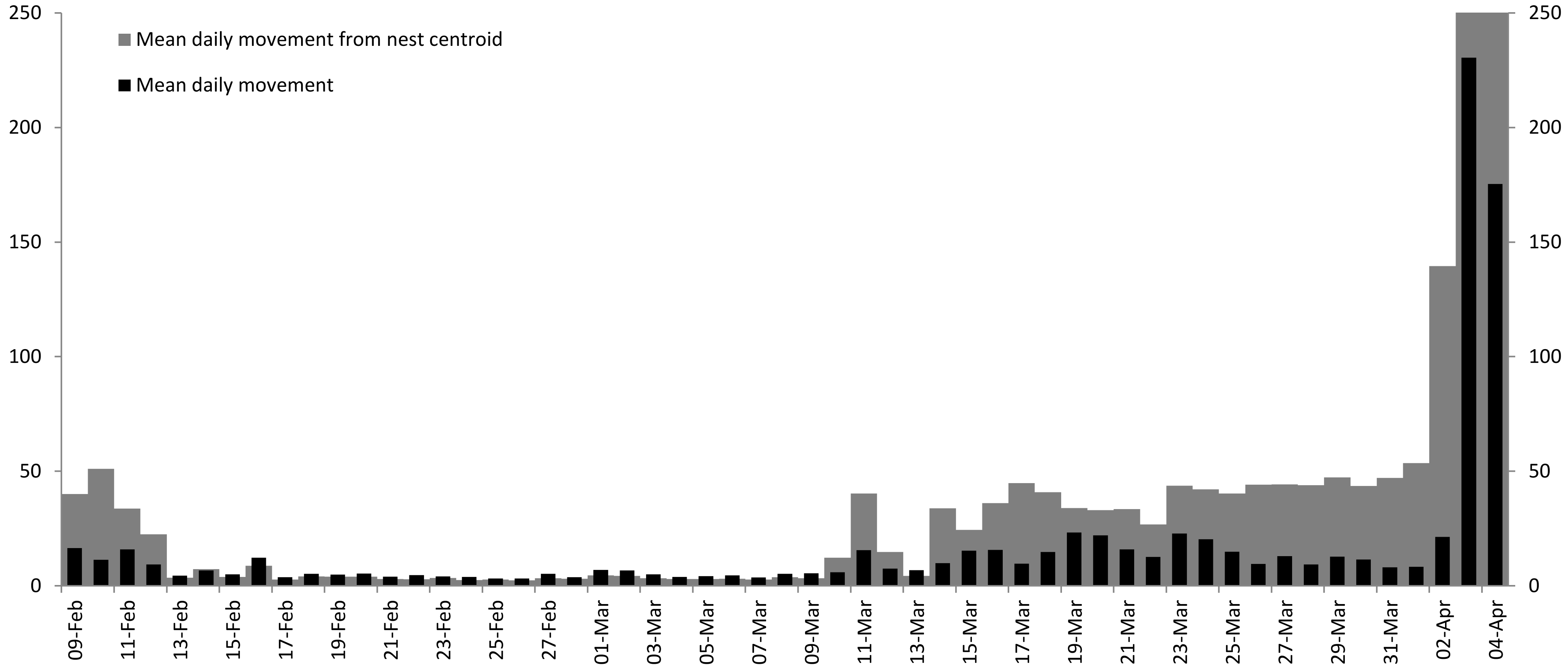


Figure 6 – Mean daily movements (black) and mean movements from the nest (grey) of Female 125 during the nesting period.

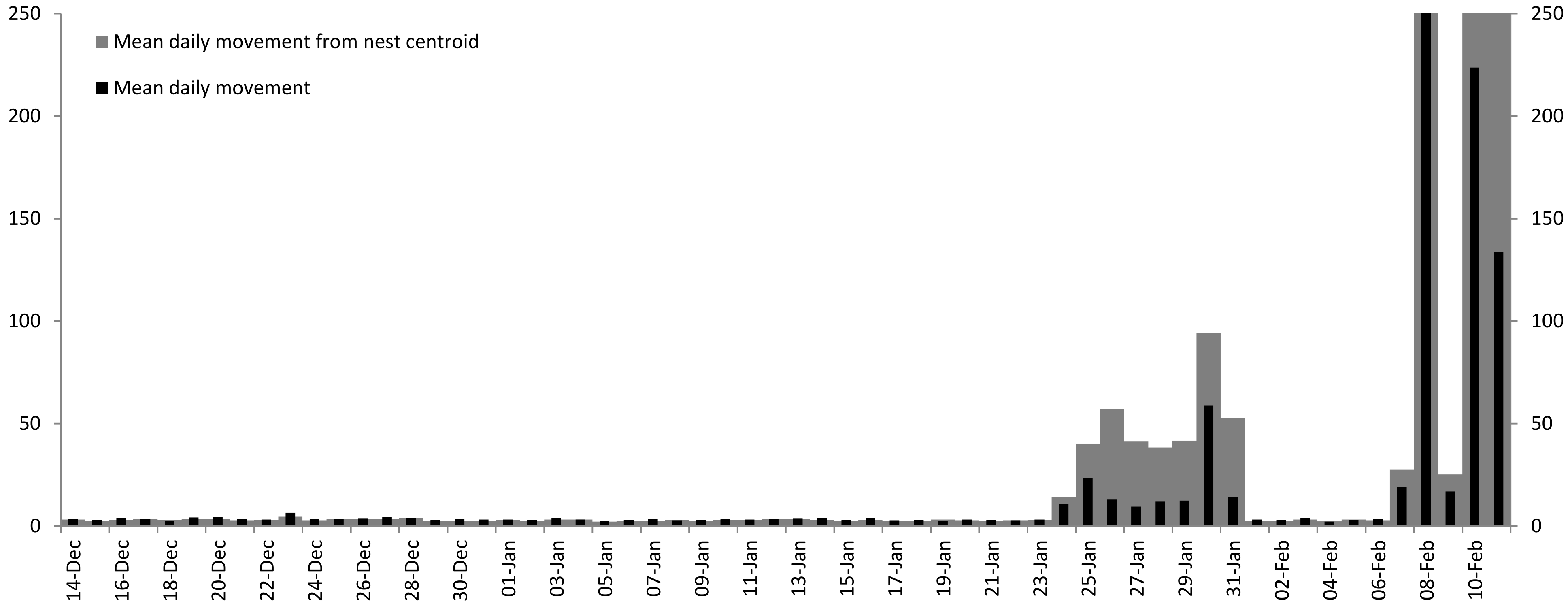


Figure 7 – Mean daily movements (black) and mean movements from the nest (grey) of Female 449 during the 2010/11 nest season.

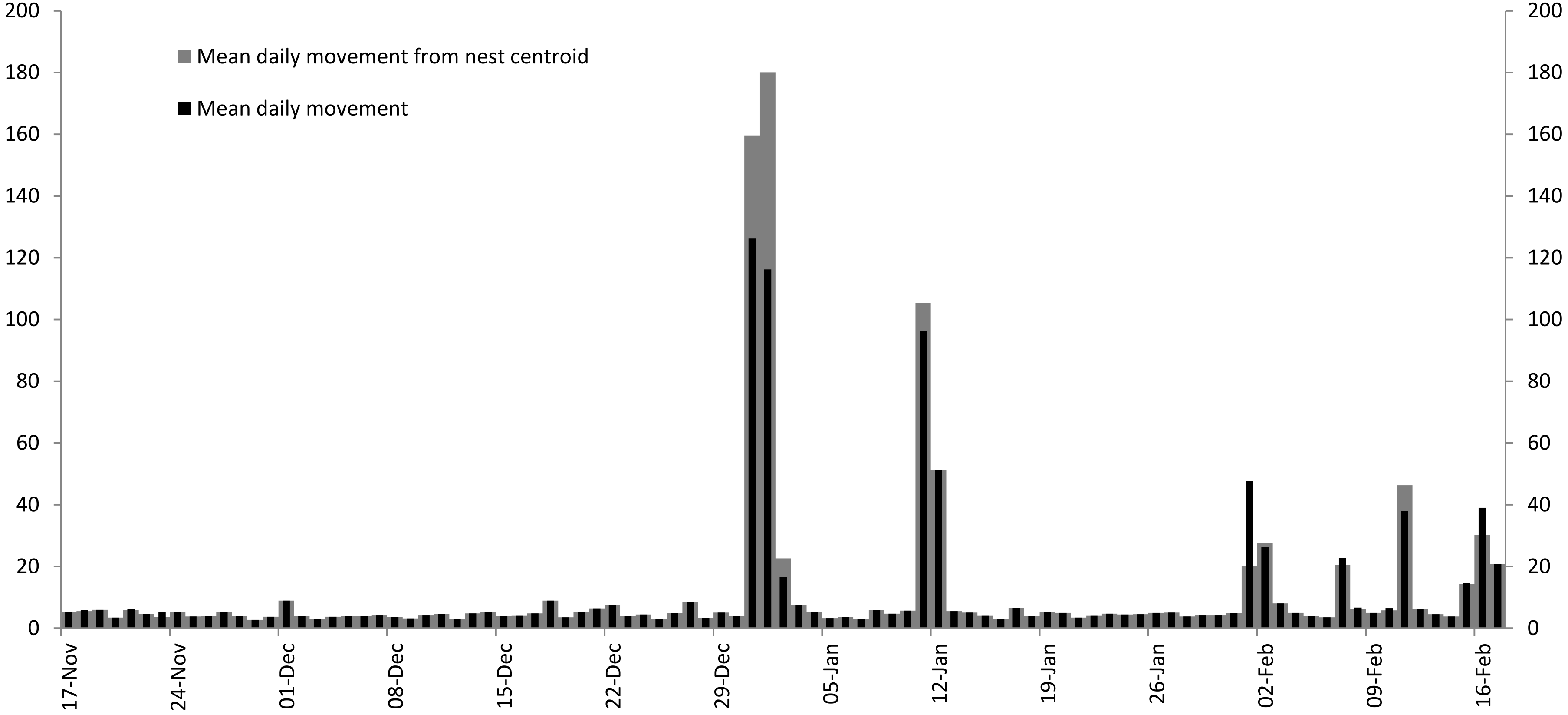


Figure 8 – Mean daily movements (black) and mean movements from the nest (grey) of Female 515 during the nesting period.

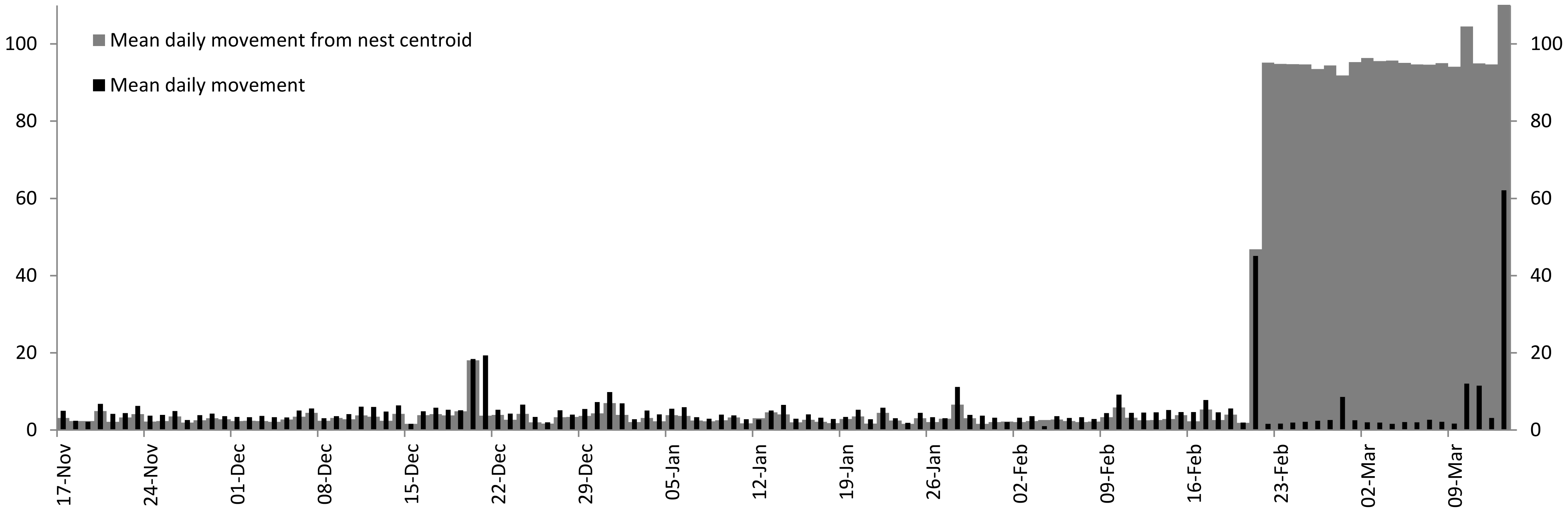
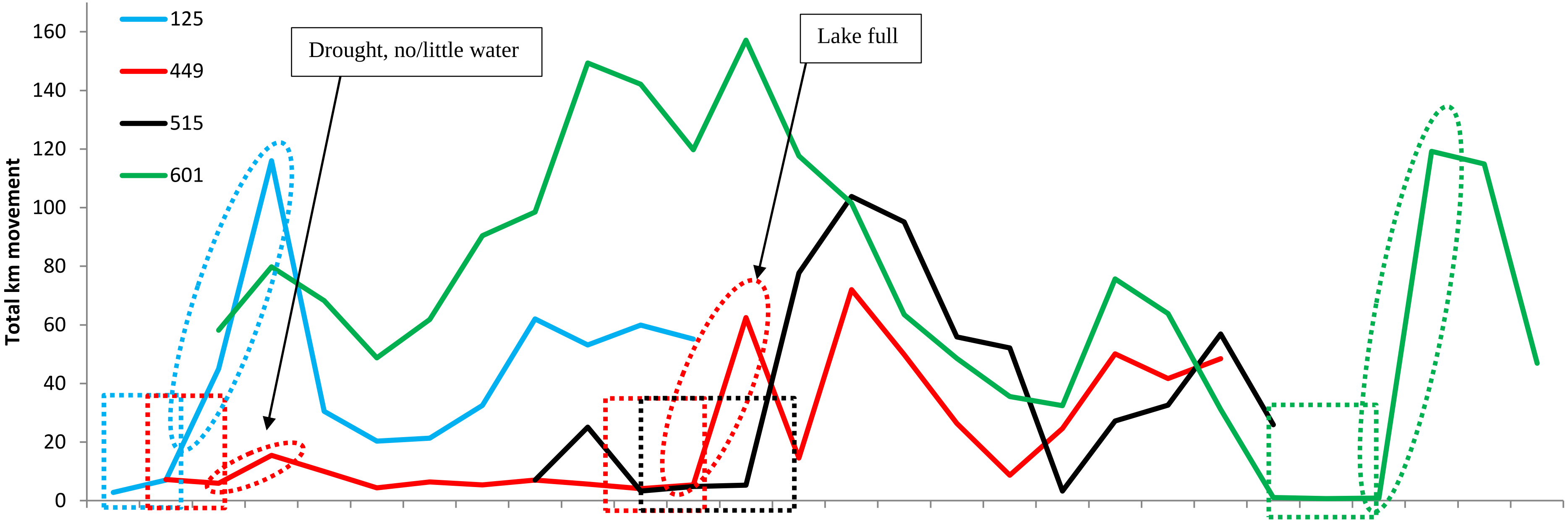


Figure 9 – Mean daily movements (black) and mean movements from the nest (grey) of Female 601 during the nesting period. Subsequent to liberating her hatchlings on 21 Feb., she moved to an ephemeral pan, ~90 m away from the nest.



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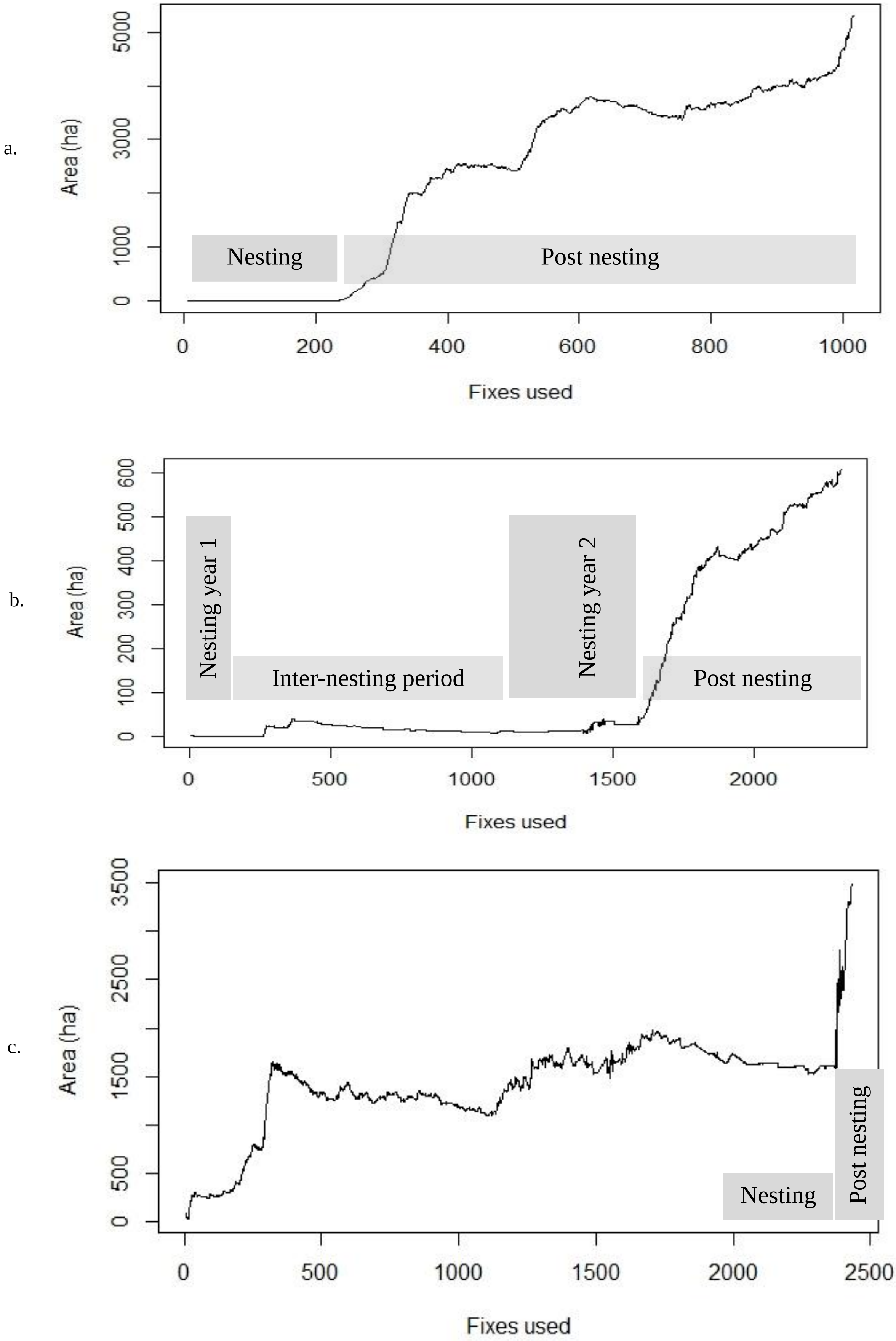

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Caption for Tables

Table 1 – Descriptive statistics for nesting females at the Lake St Lucia estuarine system

Tables

Table 1 – Descriptive statistics for nesting females at the Lake St Lucia estuarine system

Crocodile	447	449	125	449	515	601	Mean ± S.E.
Size (cm)	277	285	289	285	304	293	291.20 ± 3.53
Nesting season	2009/10	2009/10	2009/10	2010/11	2010/11	2012/13	-
No of days nesting	-	12	51	59	92	116	66.00 ± 17.8
No of GPS-observations during nesting	-	257	1079	1405	1088	690	903.8 ± 197.5
Duty cycle per 24 hours	24	24	24	24	12	6	-
Total home range (ha)	-	1.50	0.15	2.42	0.19	0.02	0.85 ± 0.47
Core-use area (ha)	-	0.64	0.03	1.73	0.06	0.02	0.49 ± 0.33
Number of sites used	-	2	2	1	1	1	1.4 ± 0.3
Activity level (%)	-	16.4	8.3	6.8	8.7	0.6	8.1 ± 2.5
Activity level: Post nesting (%)	-	7.2	44.4	48.6	61.9	77.1	47.9 ± 11.7
MDM: Pre-nesting (m)	-	-	-	-	1208	2795	2002 ± 793
MDM: Nesting period (m)	-	378	194	327	131	28	212 ± 64
MDM: Post-nesting period (m)	-	240	1716	1324	3648	3954	2176 ± 708
Nest-site fidelity: % Observations < 25 m from nest: total	-	36.6	91.4	89.9	96.6	99.7	82.8 ± 11.7
Nest-site fidelity: % Observations < 25 m from nest: day	-	15.3	90.7	87.5	97.6	99.7	78.1 ± 15.9
Nest-site fidelity: % Observations < 25 m from nest: night	-	56.4	92.1	92.5	95.7	99.7	87.3 ± 7.8

CHAPTER 7

Maternal care and predation of Nile Crocodile (*Crocodylus niloticus*) nests at the Lake St Lucia estuarine system, South Africa

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ABSTRACT

The Lake St Lucia system hosts the largest Nile Crocodile (*Crocodylus niloticus*) estuarine population within the species' range and the largest recorded Nile Crocodile nesting population in South Africa. Despite a long-term monitoring programme, minimal information is available for the St Lucia population on nest predation, nest abandonment, and maternal care. In this study we investigated nesting biology using remote camera traps over four years. We captured 4305 photographs (daylight captures = 90.1 %, nocturnal = 9.9 %) of 19 nest-guarding females. On average, females settled back on a nest 1.9 days after the cameras were initially set. Of 19 monitored nests, seven (36.8 %) were raided by egg predators, at an average of 12.1 ± 6.2 days subsequent to camera placement. All females returned to their nests following the first predation event, and on average returned three times between predator raids before nest abandonment. Nesting raids lasted 5.9 ± 1.6 days on average, with 18.8 ± 4.0 photographed robbing's per nest recorded.

Water Monitors (*Varanus niloticus*) were the initial predator at five nests, of which three were completely robbed at the outset and the remaining two nests predated during female hatchling liberation. Water Monitors were also recorded as the secondary predator at three additional nests, initially opened by Marsh Mongoose (*Atilax paludinosus*). Marsh Mongoose was the secondary predator at one nest opened by Water Monitor.

Five females were captured on camera liberating their hatchlings from the nest. A detailed sequence of 214 photographs of a mother excavating and transporting hatchling crocodiles revealed 13 separate excursions between nest and water over 32 h and 29 min (periods at nest = 25.6 ± 2 min ; periods away = 45.6 ± 7.1 min). This behaviour, after months of continual nest attendance and defence, reveals an exceedingly high level of maternal care for the Nile Crocodile.

Camera trap data allowed unique identification of seven females (36.8 %) based on dermal patterns and nine females (47.4 %) based on other unique morphological features. Three females (15.8 %) were unidentified.

During daylight females were seldom photographed on top of the nest, except during cool/cloudy weather or rain, preferring instead to motionlessly guard the nest in nearby shade. During late afternoon or early evening females moved back onto nests and remained there during night. Females always defended nests aggressively against non-human intruders. We present motion sensitive camera trapping as an effective, non-invasive method with great potential for further crocodile nesting behaviour research.

Keywords: Nile Crocodile, nesting biology, nest predation, nest liberation, nest guarding, camera traps, remote monitoring, animal identification.

INTRODUCTION

The Lake St Lucia estuarine system contains the largest Nile Crocodile population in a single waterbody in South Africa, estimated at 1005 ± 137 adult and sub-adult crocodiles (Chapter 2). It is also the largest estuarine population within its range, and largest recorded nesting population in the country (Combrink et al. 2013), with 76.2 ± 6.4 nests (range: 29-141) recorded from 1982 to 2013 (Chapter 5). The Nile Crocodile has a well-defined breeding season at the Lake St Lucia estuarine system, with oviposition during November to December and hatching from January to March (Pooley 1982, Leslie 1997).

A historically recent factor affecting female reproductive frequency at Lake St Lucia is prolonged droughts and its effect on food availability (Leslie 1997). Nesting effort, abundance, distribution, and embryo survival are furthermore determined by disturbance near nesting areas (Pooley 1969, Fawcett 1987a, Leslie 1997), intentional killing of females (Pooley 1969, Leslie 1997, Combrink and Robertson 2013), and natural nest predation (Pooley 1969, Fawcett 1987b, Leslie 1997). Pooley (1969) recorded a 33.8 % predation rate by Water Monitor and Marsh Mongoose at a communal nesting area at St Lucia in 1968 (n = 65), while in Ndumo Game Reserve (NGR), where nests were less concentrated, nest predation was rarely above 20 %. More recently, Calverley (2013) recorded higher predation levels at NGR for observed nests, with 86 % for 2009/10 (n = 7) and 66 % for 2010/11 (n = 9). Champion (2011) found 27.8 % nest predation at Pongolapoort Dam. Modha (1967) recorded 3.3 % Water Monitor predation (n = 152) at Lake Turkana, while Cott (1961) found in Uganda and northern Zimbabwe 55.1 % (n = 350) of nests destroyed by Water Monitor, Baboon and Hyaena.

Cott (1961) and Pooley (1969) observed nest guarding by brooding females on or nearby nests during the day and night for the entire incubation period. Nest excavation by the attending female is crucial, and failing to liberate the hatchlings will result in complete nest mortality (Graham 1968, Pooley 1969, Hutton 1984, Combrink and J Warner pers. obs.). Pooley (1969) recorded female assistance with nest opening for all wild nests examined in Zululand. In addition to opening the nest, a mother may mechanically assist hatchling emergence through a pressurised rolling movement of the egg between her tongue and palate, with hatchling transportation to water then occurring via buccal pouch (Pooley 1969).

Despite these observations, very little is known about Nile Crocodile nest-guarding behaviour, nest excavation, hatchling liberation, and modes of nest predation. Our aim in this study was to employ camera traps (Ogden 1978, Hunt and Ogden 1991, Somaweera et al. 2011, Somaweera and Shine 2012) at known nest-sites to remotely record data on visual aspects of crocodile nesting biology, and to determine any direct effects of the cameras themselves on nest success. Additionally, we hypothesized that remote camera trapping could assist in uniquely identifying nesting females for future nest monitoring efforts.

METHODS

Study area

The Lake St Lucia estuarine system is situated in northeastern KwaZulu-Natal province, South Africa. At ~67 km in length with an average width of 6 km when filled to capacity, it is the largest estuarine system in Africa (Cowan 1997). Lake St Lucia is a shallow system, shaped by dynamic environmental and ecological processes at various spatial and temporal scales (Taylor 2006). See Chapter 1 for a more detailed description of the study area.

Camera traps

Bushnell digital Trophy camera traps were positioned at Nile Crocodile nest-sites during the 2009/2010 to 2012/13 nesting seasons. These cameras are triggered by movement, detected by a highly sensitive passive infra-red motion sensor. Photograph size was set to 3 megapixels, with cameras recording three photographs in rapid succession at a triggering interval of 5 minutes (reduced to 1 minute near the end of the incubation period). A two gigabyte secure digital (SD) memory card was used for storing photographs, the PIR sensitivity was set at high, and all photographs were recorded with a date and time stamp. Cameras were mounted on small, steel reinforcing bar poles and positioned 1.5 m to 9 m from the nest, 0.3 m to 1.5 m above the ground. Camera setup time at each nest was < 20 min. The manual download frequencies of memory cards was nest-site specific, with open windy sites requiring more frequent downloads due to moving vegetation.. Results are presented as mean ± standard error (S.E.).

Female identification

Nesting females were uniquely identified using a coding system developed by R. Taylor (pers. comm.) for captive crocodiles, which we adapted for field application. Unique identification was based on the predominant colouration (B = black or Y = yellow) of 18 (or less) pre-selected dermal scutes, and can be applied to both sides of the animal (pattern differs on each side). We used the first three vertical scutes of the first six single caudal verticils, subsequent to where the double caudal verticils converge with the single caudal verticils. A numerical value 0-7 is derived from the unique dermal sequence (i.e. YYY = 0, BYY = 1, YBY = 2, BBY = 3, YYB = 4, BYB = 5, YBB = 6, and BBB = 7), and a total value is acquired through summation. The result is a six numbered code, unique to each side of the individual crocodile (Fig. 1).

Nest guarding, predation, and excavation

Photographs that recorded both the nest and nest guarding behaviour of the female were analysed to detect presence/absence of the female on the specific nest-site. We also analysed photographic sequences indicating intra- or interspecies aggressive behaviour.

RESULTS

Camera traps

Best results were obtained with cameras positioned 1-4 m from the nest. Cameras placed too close to the nest provided good data on nest attendance, but the field of view was too restricted to extensively record female guarding behaviour. Consequently, we shifted our monitoring tactic from 1 camera per nest to 2-3 cameras per nest set at different angles, heights, and distances. Due to equipment costs, this reduced the overall number of monitored nests, but allowed for more comprehensive documentation at selected sites.

Using 26 cameras, we obtained 4305 photographs (daylight captures = 90.1 %, nocturnal = 9.9 %) from 19 nests with attending females over the 2009/2010 to 2012/2013 nesting seasons. On average, females settled back at the nesting area 1.9 ± 0.3 days after the camera deployment. The mean number of crocodile photographs per nest was 215.1 ± 59.5 (range: 6-1005). Cameras positioned > 4 m from the nest were not triggered by movement of the female, but were attributed to moving vegetation or other animals. At night the detection zone between camera and crocodile had to be < 2 m to capture movement on the nest. In total, 59.5 % of photographs taken at night were due to female movement, with the remainder triggered by other animals (Fig. 2).

Female identification

We identified seven females (36.8 %) based on dermal patterns and nine females (47.4 %) based on unique features such as missing caudal scutes or highly distinguishable dorsal patterns. Three females (15.8 %) in the study were not identified due to photo quality, limited number of photo captures, or physical obstruction at the nest-site. On two occasions cameras confirmed the use of a specific nest-site by different females during different years.

Nest predation

Of 19 nests, seven (36.8 %) were robbed by egg predators, on average 12.1 ± 6.2 days (range: 1-53d) subsequent to camera deployment. Two nests were predated within 24 hours of camera placement. At one of these nests the female had returned, but predation occurred nonetheless at 13:45 the following day. In this instance, an unknown number of eggs were removed by a Water Monitor, but the mother liberated the remaining hatchlings (Fig. 3a – Fig. 3d).

Six incubating nests were predated at three locations (Dead Tree Bay, eSingeni, Mphathe Stream), with all females settling back on the nest following the first robbing event. Mothers returned to their nests on average three times (± 0.8; range: 1-6) between nest robbing's before abandonment. The average duration of a predation raid (first to last egg removed) was 5.9 ± 1.6 days (range: 1-12d) while on average 18.8 ± 4 robbing's per raid were recorded (range: 8-35). Water Monitor and Marsh Mongoose both predated three nests each, but on four occasions Water Monitor secondarily predated nests opened by Marsh Mongoose (Fig. 4a – Fig. 4c).

We recorded one incident of a female permanently abandoning her nest following a flooding event, with the exception of one return visit to the site on 12 March 2012 for 10 minutes (Fig. 5a, photo 1). On 18 March at 5:45 a Marsh Mongoose dug into the nest over a 90 minute period (Fig. 5a, photo 2-4). Small scattered egg shells indicated the scavenging of one egg (Fig. 5a, photo 4 and 5b, photo 1), and between 27 - 30 March a Water Monitor completed the nest raid (Fig. 5b, photo 2-4).

Although a number of confirmed egg predators of Nile Crocodile nests in other localities such as Common Warthog (*Phacochoerus africanus*), Bushpig (*Potamochoerus larvatus),* Leopard (*Panthera pardus*), Honey Badger (*Mellivora capensis*), Cape Porcupine (*Hystrix africaeaustralis*) occur at Lake St Lucia, only Water Monitor (*Varanus niloticus*) and Marsh Mongoose (*Atilax paludinosus*) were recorded raiding nests during this study. All nests opened by Marsh Mongoose were subsequently raided by Water Monitors.

Hatchling liberation

We recorded five events of females liberating their hatchlings. The mean excavation time was 12.9 ± 5.2 hours and on average, the female made 6.4 ± 1.8 trips between the nest and the nursery area. See Figs 6 a-c for a particular liberation event at the Nkazana Stream. In total this female made 13 excursions to the nest over 32 hours and 29 minutes. Her mean time at the nest was 25.6 min ± 2.02, range 19-41 min. The mean time between nest excursions at the nursery area was 45.6 min ± 7.10, range 14-88 min. Her final visit to the nest was the shortest, 7 minutes and the duration at the nursery site subsequent to her second last nest visit was the longest, 14 hours 37 minutes. The last visit to the nest (7 min.) and second last visit to the nursery area were excluded from the derived mean (25.6 min).

Nest guarding behaviour

During daylight, all females guarded their nests from the shade of nearby vegetation, although camera traps could not always verify the exact position of each guarding female. However, we were able to determine that the respective daylight guarding positions for seven females continually within camera sensor range remained unchanged during the incubation period. On average 14.5 % ± 4.9 of photos (n = 276) recorded females lying on nests (n = 7), while 85.5 % ± 4.5 of photos (n = 2321) recorded females in close attendance (~2-8 m). Despite infrared function, trap cameras were seldom activated at night (2.0 % of all photographs) due to high inactivity levels of females at nests. However, 46.4 % ± 8.2 of our photographs that recorded females lying directly on nests were captured at night, confirming high nocturnal fidelity to nests. Cameras positioned < 1.5 m from nest from 2011-2013 (n = 4) confirmed females move from the guarding position in close proximity to the nest onto the actual nest itself during the late afternoon, and then reverse this process in the early morning hours. For one nest we could accurately determine the mean time the female would move onto to the nest (18:29 ± 26.74 min, n = 39) and then depart (06:07 ± 19.35 min, n = 15).

Aggressive defence by guarding females in response to non-human intruders at nest-sites was frequently captured on camera. Camera position often precluded the identity of the intruder, but females showed aggression toward egg predators, most frequently Water Monitors. Figure 7 shows a typical aggressive response towards an intruder. Previous disturbance caused the female to move from her usual shaded guarding position (indicated by white arrowhead, photo 1) to a more protective position on top of her nest (photo 1, perforated oval). When she sensed the intruder’s presence, probably through audible or olfactory cues, she lifted her head (Fig. 7, photo 2) to obtain visual cues. This prompted a rapid movement response and she positioned herself toward the intruder (Fig. 7, photo 3), and then left the nest to inspect the threat (Fig. 7, photo 4).

We recorded two types of threat response behaviours from guarding females (Fig. 8); aggressive chasing/charging in response to Water Monitor predation (Fig. 8, photo 1 and 2), and threatening mouth gaping in response to nest disturbance (Fig. 8, photo 3 and 4). A single incident of intraspecific aggression was recorded when a larger crocodile (likely a male) entered a nesting area behind the guarding female. The female quickly moved forward onto the nest. Six hours later the larger individual was observed walking ~4 m from the nest, which resulted in a sudden aggressive response by the female in which she turned 180° to challenge the intruder, successfully scaring the crocodile away from the nest.

DISCUSSION

Camera traps

Camera traps in our study were an effective, minimally-invasive method to remotely observe female behaviour and maternal care at the nest, nest predation, and the hatching process. Because females at St Lucia guard their sun-exposed nests from nearby vegetation, we recommend a minimum of two cameras per site to monitor the nest itself and the immediate surrounding area. Cameras should be placed > 1 m from the nest, but not further than 4 m. Females, on average, settled back on their nest < 2 days after setting the cameras, and on average predation occurred > 12 days after the cameras were set. This suggests that predation events were not linked to researcher or camera presence at the nest, despite the fact different females demonstrated varying levels of initial camera wariness.

Female identification

Camera traps positioned close to nests effectively helped us uniquely identify most nest-guarding females. Re-use of nesting areas is well documented at St Lucia (Pooley 1969) and other Nile Crocodile populations (Hutton 1984, Kofron 1989, Hartley 1990, Calverley 2013), but the identity of a particular female at a specific nest-site is generally not known. With camera trapping, we were able to confirm use of the same nest-site by different females. During this study we also observed specific site re-use by the same female during 2010 and 2012 (Chapter 5).

Suitable habitat for crocodile nesting (see Chapter 5) is abundant at Lake St Lucia, yet nesting is mainly restricted to particular areas along the Mphathe Stream and Eastern Shores. Data from this camera trapping study confirms females annually return to nest at the exact locations of previously successful nests, based possibly on memory and/or map and compass senses. Home range data from this study show Nile Crocodiles demonstrably exhibit site fidelity and homing ability, and it may be the case that females return to the same nest-sites year after year simply because they know those sites have been successful – the “if it’s not broken, don’t fix it” approach. However, other explanations are possible, including natal philopatry (e.g. sea turtles) or some other form of breeding site philopatry.

Nest predation

The frequencies and mechanistic processes by which specific predators attack nests and consume crocodile eggs are sparsely understood, yet the identification of predator threats and predation rates to nests are critical for understanding recruitment into crocodile populations, and ultimately should inform crocodile conservation efforts (Somaweera et al. 2011).

Pooley (1969) mentioned Water Monitor as the main egg predator in Zululand. Trap camera data from this study supports this, and shows a higher frequency of Water Monitor predatory activity at crocodile nests compared to Marsh Mongoose. Our data also support Pooley’s (1969) observations that Marsh Mongoose remove only one or two eggs, and in doing so, expose the nest to Water Monitor predation. This study shows Nile Crocodile nest predation is usually not a “binge” event, but can occur over periods of days or even weeks, and can involve multiple species. Females in our study returned to partially predated nests until a critical threshold of egg depletion was reached and the nest was abandoned.

Interestingly, both Water Monitor and Marsh Mongoose were also photographed at the end of the nesting season at abandoned nests. While they located the correct position of the nest through olfactory cues, they did not excavate the eggs. We dug up these eggs (post-incubation period) and confirmed they were non-viable, suggesting that some predators are able to distinguish between viable and non-viable eggs without excavating the nest.

Hatchling liberation

Some degree of parental care is provided by most, if not all crocodilian species, and nest opening and transportation of hatchings to the nursery area seems to be typical female behaviour (Somaweera and Shine 2012). Nest opening and egg removal by female Nile Crocodiles was previously documented by Pooley (1969), and Graham (1968) believed this action by female crocodiles is more important to hatchling survival than any other function during incubation. However, this study is the first to our knowledge to extensively document the behavioural mechanisms associated with nest excavation and hatchling transportation in the wild (Figs. 3 and 6).

The nest liberation sequences we observed showed intentional maternal care, with females using both their mouths and feet to initially open the nest and then to carefully deepen and enlarge the nest cavity. Hatchlings and eggs were then collected in the female's mouth and embryos liberated from their eggshells when necessary by applying pressure between the tongue and palate. All hatchings were then moved by means of buccal transport to the aquatic nursery area.

Nest guarding behaviour

The critical task of nest excavation notwithstanding, active nest-guarding for ~90 days by females while ceasing to feed (Cott 1961) is a level of maternal care unequalled in any other reptilian order. Females in our study showed a clear pattern of lying directly on nests at night and defending them from shaded guarding positions during day. Mothers always defended their nests aggressively against non-human intruders and predatory threats. We observed novel nesting defence behaviours such as mouth gaping (usually toward large intruders) and charging (directed toward smaller predators). Additionally remote biotelemetry data revealed mean female nest-site fidelity at Lake St Lucia is 82.8 % ± 11.70 with maximum of 99.7 % (Chapter 4); much higher than other studies (Joanen and McNease 1970).

CONCLUSIONS

Our camera trapping study of Nile Crocodile nesting biology at the Lake St Lucia estuarine system yielded important and novel insights into crocodile maternal care, nest predation, and egg predator - crocodile interaction. Female Nile Crocodiles are diligent mothers throughout all stages of the nesting process, and will willingly and repeatedly defend their nests. Egg predators however, particularly Water Monitor and Marsh Mongoose, can be equally motivated and patient, making multiple raids on individual nests over prolonged time periods. Camera trapping is an effective, non-invasive approach to gathering information at crocodile nest-sites and yields a rich data return for minimal field labour. Comparative studies on other species and populations will further the collective knowledge of this critical crocodilian life-history phase.

In light of our findings, we also suggest crocodiles are good subjects for exploring the origins and biological mechanisms of maternal care and breeding site fidelity; life history traits that are uncommon in other ectotherms. Far from primitive, this study adds to a growing body of literature that shows crocodiles are biologically and ecologically complex animals with capable – even caring – parental behaviour.

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Caption for Figures

Figure 1. Code allocation based on dermal pattern of St Lucia Nile Crocodiles.

Figure 2. Mammal species that triggered camera traps at Nile Crocodile nests at the Lake St Lucia estuarine system. Leopard, Warthog, Honey Badger, Bushpig and Porcupine have been documented to predate Nile Crocodile eggs in other populations (Pooley 1982). The Marsh Mongoose is a major egg predator at St Lucia.

Figure 3a. Water Monitor predation (photo 1-3) at Mphathe Stream, followed by the female settling back on the nest (photo 4).

Figure 3b. Female liberation at Mphathe Stream. Photo 1 and 2 indicate the use of her front leg to open the nest and enlarge the nest cavity, in photo 3 and 4 she is collecting hatchlings with her mouth, moving them to her buccal pouch.

Figure 3c. Photo 1 and 2 show the female continuing to use her mouth to collect hatchlings from the nest cavity and photo 3 and 4 indicate the re-position of hatchings to her buccal pouch by flicking her head and neck upwards.

Figure 3d. Female picked up an egg with her mouth (photo 1). Photo 2 indicates how she used her hind leg and photo 3 her front leg to enlarge the nest cavity. In photo 4 she reaches deep in the nest cavity with her mouth, possible to excavate more soil or/and collect hatchlings.

Figure 4a. Nest guarding female at Nkazana Stream (photo 1). Photo 2 shows a Water Monitor on the nest and photo 3 two Water Thick-knees in the shade while in photo 4 the Water Monitor appears to their right (in white oval) and they respond with apparent threat display.

Figure 4b. Apparent threat display from two Water Thick-knees directed at a Water Monitor, its head visible inside the black oval (photo 1). Female lying over the nest at night with visible caudal tags, see black circle (photo 2). Photo 3 and 4 indicates scraping movements of the hind legs as she stared to open the nest.

Figure 4c. Water Monitor moving away from the nest with a crocodile egg in its mouth (photo 1). Three Water Monitors can be seen in photo 2, one on the nest to the left of the Water Thick-knees, and two in the shaded foreground.

Figure 5 (a). Marsh Mongoose predation at the Mphathe Stream. 5(b). Photo 1 indicate crocodile egg fragments after a Marsh Mongoose opened a crocodile nest (Fig. 4a). Photo 2-4 recorded subsequent predation of the same nest by Water Monitors.

Figure 6a. Nest liberation of at the Nkazana Stream. Photo 1 shows a portion of the nest-site after heavy rain. Photo 1-2 indicate the female leaving the water, and starting to open the nest, possibly responding to hatchling vocalisation. Photo 4 record her coming back to the nest, possibly after releasing the first few hatchlings in the stream.

Figure 6b. The female continues to liberate hatchlings from the nest. Photo 2-3 indicate her picking up a hatchling, while photo 3 seemingly indicate how she liberate a hatchling from the egg by pressing the egg between her palate and tongue.

Figure 6c. Photo 1 shows the extended buccal pouch of the female as she is moving back to the water. Photo 2-3 indicate her using both front legs to open and enlarge the nest cavity.

Figure 7. Nile Crocodile threat display directed towards a non-human intruder on a nest adjacent to the Nkazana Stream

Figure 8. Nile Crocodile nest defence at the Lake St Lucia estuarine system

Figures

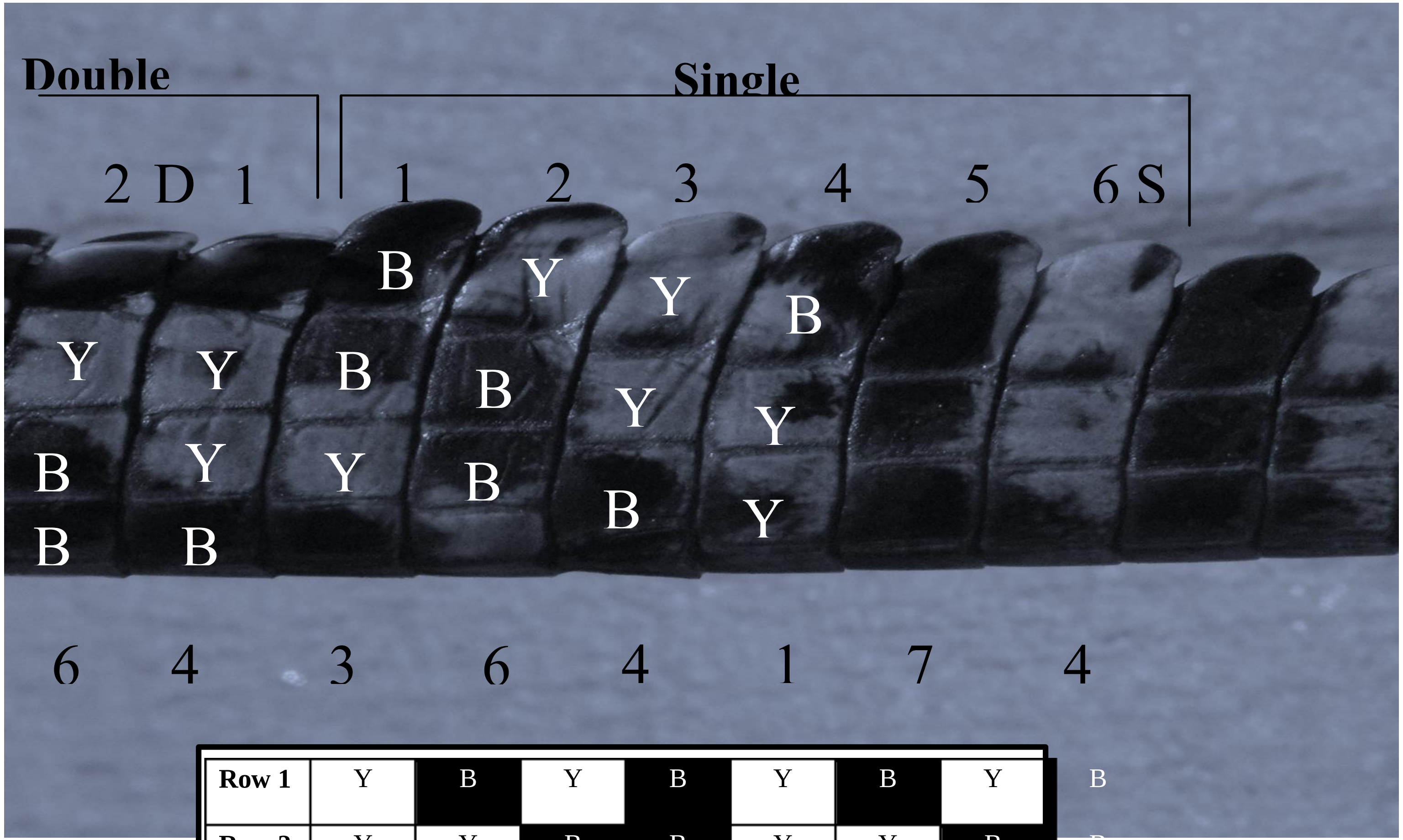

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Figure 1. Code allocation based on dermal pattern of St Lucia Nile Crocodiles

Leopard (*Panthera pardus*) Hippopotamus (*Hippopotamus amphibius*) Aardvark (*Orycteropus afer*) Bushbuck (*Tragelaphus scriptus*)

Common Warthog (*Phacochoerus africanus*) Red Duiker (*Cephalophus natalensis*) Honey Badger (*Mellivora capensis*) Bushpig (*Potamochoerus larvatus)*

Cape Porcupine (*Hystrix africaeaustralis*) Waterbuck (*Kobus ellipsiprymnus*) Greater Kudu (*Tragelaphus strepsiceros*) Marsh Mongoose (*Atilax paludinosus*)

Figure 2. Mammal species recorded by camera traps at Nile Crocodile nests at the Lake St Lucia estuarine system. Leopard, Warthog, Honey Badger, Bushpig and Porcupine have been documented to predate Nile Crocodile eggs in other populations (Pooley 1982). The Marsh Mongoose is a major egg predator at St Lucia.

Photo 1

Photo 2

Photo 3

Photo 4

Figure 3a. Nest predation by Water Monitor at the Mphathe Stream (photo 1-3). The female arrive at the nest after dark, subsequent to the initial raid (photo 4).

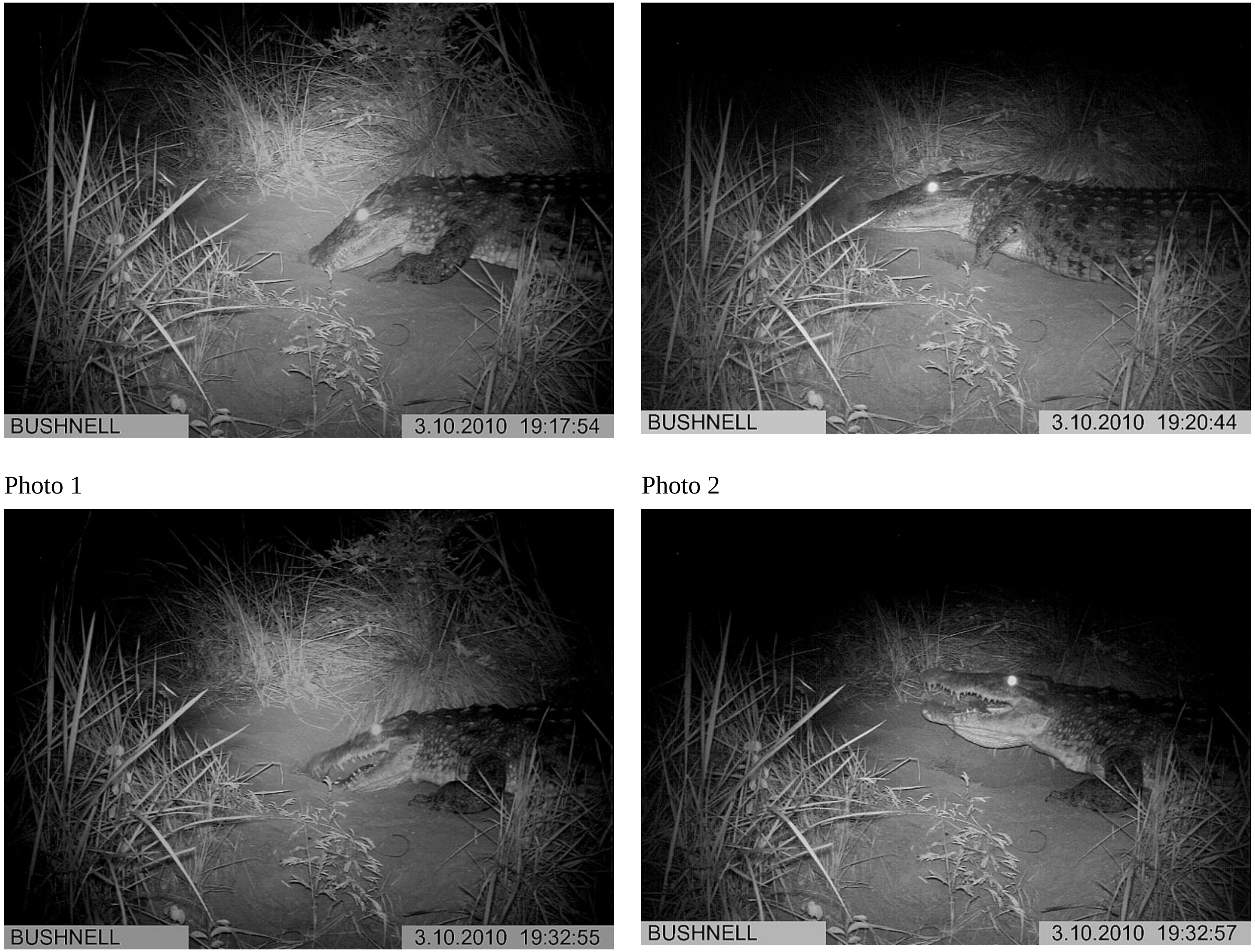

Photo 1

Photo 2

Photo 3

Photo 4

Figure 3b. By 19:17 she started liberating hatchlings from the nest with her front foot (photo 1 and 2). She then collects the hatchlings with her mouth, moving them to her buccal pouch (photo 3 and 4).

Photo 1

Photo 2

Photo 3

Photo 4

Figure 3c. The female reaches deep into the nest cavity to collect hatchlings (photo 1 and 2). Occasionally she would re-position hatchlings in her buccal pouch by flicking her head and neck upwards (photo 3 and 4).

Photo 1

Photo 2

Photo 3

Photo 4

Figure 3d. The female returned to the nest 08:33 the next day and picked up an egg with her mouth (photo 1). She used her hind foot for excavation (photo 2) as well as her front foot and mouth to dig into and enlarge the nest cavity, excavating soil and collecting hatchlings (photo 3 and 4). The last photo of the female on the nest was recorded at 9:31, after which she abandoned the nest.

Photo 1

Photo 2

Photo 3

Photo 4

Figure 4a. The female settled on the Nkazana Stream nest 66 minutes after the camera was set (photo 1) and remained on the nest for the rest of the day and night. She left the nest the next morning by 07:42 and by 09:22 a Water Monitor was recorded at the nest digging (photo 2) which was repeated at 12:52 (photo 3). Using the shade resulted in a defensive display (photo 4) from a pair of Water Thick-knees (*Burhinus vermiculatus*) apparently nesting very close to the female's nest.

Photo 1

Photo 2

Photo 3

Photo 4

Figure 4b. At 14:58 a Water Monitor approached the nest again, resulting in defensive display behaviour from the *B. vermiculatus* (photo 1). At 15:18 the female returned to the nest, left the nest by 16:31 and returned by 18:29. At 21:56 she started making digging movement with her hind legs, while moving backwards and forwards over the nesting site (photo 2) which continued to 01:59. From 6:40 to 8:33 she continued to excavate the sand on the nest-site, also moving up and down the nest (photo 3 and 4). Threat display from two *B. vermiculatus* towards the Water Monitor, its head visible inside the black oval (photo 1).

Photo 1

Photo 2

Figure 4c. Nine minutes later (10:23), a Water Monitor arrived at the nest and robbed an egg (photo 1). From 10:32 to 10:55, 30 photos of at least two individual Water Monitors were taken either in or < 2 m of the opened nest. The female arrived back on the nest at 11:25, for four minutes, possibly checking for more hatchlings, and left. Sixteen minutes later a Water Monitor was back at the nest. Between 11:47 and 15:46, 149 photos of at least three individual Water Monitors (photo 2) were recorded at or < 2 m of the open nest. By this time all eggs/hatchlings were possibly either removed by the female or predated, and the majority of the photos indicated the monitors moving in and out of the opened nest and general movement around the nest and resting in the shade. At 15:57 the female visited the nest for < 5 minutes and the last nest visit by the female was 21:13.

Photo 1

Photo 2

Photo 3

Photo 4

Figure 5a. Marsh Mongoose predation at the Mphathe Stream

Photo 1

Photo 2

Photo 3

Photo 4

Figure 5b. Photo 1 indicate crocodile egg fragments after a Marsh Mongoose opened a crocodile nest (Fig. 4a). Photo 2-4 recorded subsequent predation of the same nest by Water Monitor.

Photo 1

Photo 2

Photo 3

Photo 4

Figure 6a. Nest liberation of at the Nkazana Stream. The female did not settle back on the nest but apparently continued nest guarding from the pool in front of the nest. On 18 February 01:28 the female started to open the nest (photo 2), likely in response to hatchling vocalisations and continued at 02:15 (photo 3). The next morning at 07:54 she was back at the nest (photo 4) and continued to liberate hatchlings. Photo 1 shows a portion of the nest-site after heavy rain. Photo 1-2 indicate the female leaving the water, and starting to open the nest, possibly responding to hatchling vocalisation. Photo 4 record her coming back to the nest, possibly after releasing the first few hatchlings in the stream.

Photo 1

Photo 2

Photo 3

Photo 4

Figure 6b. Some of the hatchlings had not emerged from their eggs and she collected them in her mouth (photo 2 and 3). She used her tongue to press the egg against her palate, subsequently cracking the eggshell and escape of the hatchling (photo 4). The female continues to liberate hatchlings from the nest. Photo 2-3 indicate her picking up a hatchling, while photo 3 seemingly indicate how she liberate a hatchling from the egg by pressing the egg between her palate and tongue.

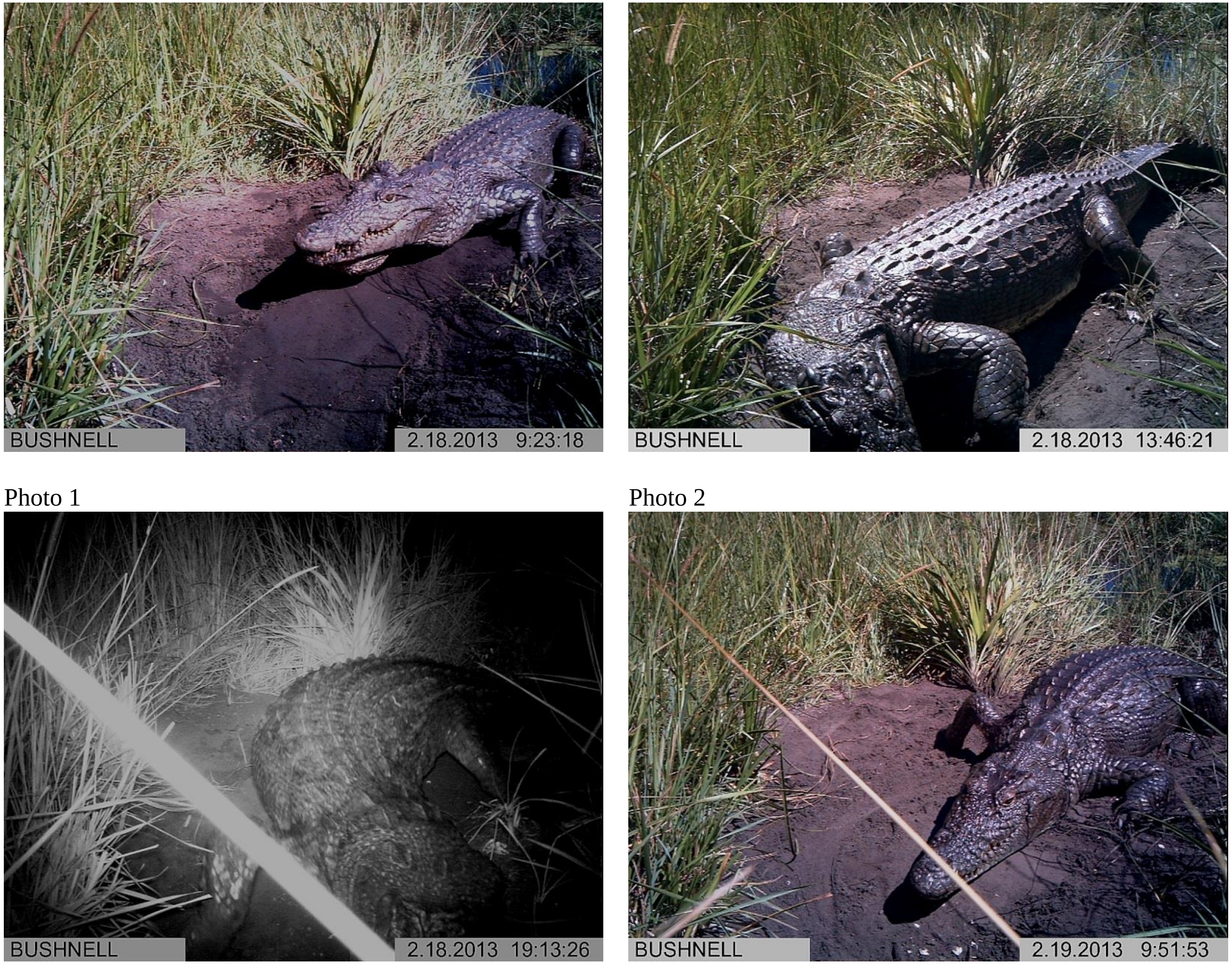

Photo 1

Photo 2

Photo 3

Photo 4

Figure 6c. After each visit to the nest the female returned to the water with distended buccal pouch (photo 1) and once back at the nest continued to enlarge the nest cavity, often using her front legs for digging (photo 2). She continued to liberate hatchings up to 19:13 that evening (photo 3) and came out the next morning for the last time (photo 4). We recorded a total of 214 photos of the female at the nest. Photo 1 shows the extended buccal pouch of the female as she is moving back to the water. Photo 2-3 indicate her using both front legs to open and enlarge the nest cavity.

Photo 1

Photo 2

Photo 3

Photo 4

Figure 7. Nile Crocodile threat display directed towards a non-human intruder on a nest adjacent to the Nkazana Stream

Photo 1. White arrow is indicating the direction of the stream and the oval fresh excavation marks on the next.

Photo 2. White arrow is indicating the direction of the stream and the oval a predated eggshell.

Photo 3. White arrow is indicating the shaded position of the female and the black oval the nest.

Photo 4. White arrow is indicating the direction the female is laying on the nest, which is indicated by the oval.

Figure 8. Nile Crocodile nest defence at the Lake St Lucia estuarine system

CHAPTER 8

Homing behaviour and movements of a translocated Nile Crocodile (*Crocodylus niloticus*) in the Lake St Lucia estuarine system, South Africa

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ABSTRACT

Homing behaviour and site fidelity have been documented for six crocodilian species, but not for Nile Crocodiles (*Crocodylus niloticus*). Globally, Nile Crocodiles are responsible for more human deaths than any other crocodilian, and human-crocodile conflict is currently a major conservation and human health concern in several African countries. In management attempts to mitigate human-crocodile conflict, a number of African conservation agencies relocate “problem”, “nuisance” or “damage-causing” crocodiles away from conflict sites, usually to remote areas or sparsely populated by humans. However, the efficacy of this practice is unknown, primarily because whether Nile Crocodiles are prone to navigate back to the conflict site, is unknown.

Consequently, we investigated homing behaviour and specific movements of a translocated Nile Crocodile in the Lake St Lucia estuarine system, South Africa. An adult female (2.7 m) was monitored pre- and post-translocation using a GPS (Global Positioning System)-satellite transmitter. It was captured on 1 May 2012 with a known home range (from previous telemetry data) in the Mphathe Stream and translocated on the same day ~50 km north (straight line distance) into False Bay. Following release the individual moved a total distance of 178.3 km over 136 days (daily average = 1311 ± 207 m), compared to 60.4 km (daily average = 444 ± 32 m) for the identical time period the previous year. Homing movement was not continuous, and was characterised by periods of extensive and directed mobility followed by prolonged periods of inactivity associated with freshwater or low salinity habitats.

The translocated crocodile displayed remarkable navigational abilities, even though this required negotiating complex habitat challenges including extensive areas of the lake that were either hypersaline or completely dry, resulting in frequent and extensive overland movements. On 14 September 2012, the individual returned to the same freshwater pool where it was captured 136 days previous. This is the first study to confirm homing behaviour of the Nile Crocodile, and supports growing evidence that crocodilians and other ectothermic taxa possess complex navigational abilities. Habitat heterogeneity is likely the primary influencing factor on the route and duration of crocodile homing forays.

Keywords: Nile Crocodile, telemetry, translocation, movement, homing behaviour, navigation, human-wildlife conflict

INTRODUCTION

Human-crocodilian conflict is a growing concern across many countries, involving a number of species (Kofron 2004, Mazzotti et al. 2007, Aust et al. 2009, Lamarque et al. 2009, Dunham et al. 2010, Fergusson 2010, Fukuda et al. 2011, Wallace et al. 2011). Because crocodile attacks on humans are often unobserved by third parties, the cause and mechanism of a fatal incident frequently remains idiopathic. However, the overarching causal factor for conflict is always humans attempting to partition a shared aquatic resource with resident crocodiles. This scenario can either be historic, or relatively recent due to expanding human populations or where effective protection policies have resulted in increasing crocodilian populations (Guillette et al. 1997, Letnic and Connors 2006, Mazzotti et al. 2007, Aust et al. 2009, Hamlin et al. 2011). Consequently certain conservation agencies have adopted policies where, in some instances, "problem" or "damage-causing" crocodilians are relocated (Child 1987, Loveridge 1996, Kofron 2004, Taylor et al. 2006, Domínguez-Lazo 2008, Hamlin et al. 2011). At the same time, other agencies consider this practice impractical due to manpower limitations (Hines and Woodward 1980) or the tendency of relocated crocodiles to return to the capture location (Webb et al. 1983, Webb et al. 1987, Walsh and Whitehead 1993, Leach et al. 2009).

Homing in animals is a mechanistic navigational process that includes both determination of position in relation to a target (map sense), and access to a reliable compass to maintain orientation toward the target, i.e. compass sense (Gould 1998). For crocodiles, it has been suggested that execution of the map sense occurs by sensors in the brain detecting magnetic cues that change predictably through space (Morgan 2009). The compass sense of crocodiles has not been explored, but similar to other large ectotherms, it is possibly achieved through the use of olfactory, celestial, magnetic or polarized light cues, or some combination thereof, (Pittman et al. 2014).

Homing behaviour has been documented in six crocodilian species to date: American Alligator (*Alligator mississippiensis*), Spectacled Caiman (*Caiman crocodilus*), American Crocodile (*C. acutus*), Morelet's Crocodile (*C. moreletii*), Estuarine Crocodile (*C. porosus*) and the Australian Freshwater Crocodile (*C. johnstoni*) (Chabreck 1965, Hines et al. 1968, Gorzula 1978, Webb and Messel 1978, Hines and Woodward 1980, Murphy 1981, Webb et al. 1983, Rodda 1984, Woolard et al. 2004, Read et al. 2007, Domínguez-Lazo 2008), with one study on American Alligator supports the hypothesis that homeward paths are based on true navigational ability (Rodda 1984). Not all translocated crocodilians documented in the literature exhibited homing behaviour (Chabreck 1965, Hocutt et al. 1992, Kofron 2004, Domínguez-Lazo 2008).

Most data on crocodilian homing behaviour has been gathered by uniquely marking the animal at the site of release and then recapturing the same individual at the original capture site. However, mark-recapture studies on translocated crocodilians provide no information regarding the route taken by the returning individual, or the temporal profile of the journey (Read et al. 2007). VHF telemetry has been used in some homing studies (Rodda 1984, Kay 2004) but is constrained by researcher accessibility to remote locations, cryptic nature of the study animal, and the sensitivity of monitored individuals to researcher presence. Conversely, satellite tracking allows for continuous data collection from a remote location without human interference (Read et al. 2007). Read *et al.* (2007) used Argos-satellite tracking to document the spatial and temporal journeys of three translocated Estuarine Crocodiles, which circumnavigated the Cape York Peninsula in Australia while homing back to their initial capture localities.

Notwithstanding incomplete reporting of attacks, Nile Crocodiles are responsible for more human fatalities than any other crocodilian due to the reliance of numerous local people on the same waterways inhabited by crocodiles, and the species’ wide distribution throughout Africa (Guillette et al. 1997, Aust et al. 2009). In certain African localities human-crocodile conflict is a major problem, and management of this issue is a key focus for wildlife and community development programs in various countries (Aust et al. 2009, Lamarque et al. 2009, Fergusson 2010).

St Lucia village, situated at the southernmost tip of the Lake St Lucia estuarine system, is a popular eco-tourism destination with water-based activities that include guided kayaking and fishing in the lake and estuary. Seven tour-boats provide daily excursions on the estuary, where large pods of hippopotamus (*Hippopotamus amphibius*) and basking Nile Crocodiles are popular with domestic and international visitors. Synchronously, many local inhabitants are reliant on the natural resources that local rivers and streams flowing into the lake provide, significantly heightening the possibility for conflict between humans and crocodiles.

The first recorded Nile Crocodile attack in the Lake St Lucia system occurred in 1854 (Struthers 1991), and between 1950 - 2014, 12 fatal and 6 non-fatal attacks were recorded on local inhabitants and tourists in the lake and mouths of streams/rivers where they flow in (Pooley 2013). Ezemvelo KwaZulu-Natal Wildlife, the provincial conservation agency, has adopted a policy for the species (3.4 of 1997) which stipulates for the “capture and relocation of a problem crocodile elsewhere” following “conflict with legitimate human interests” (Taylor et al. 2006). However, few records exist of “damage-causing” Nile Crocodiles captured and released elsewhere in Lake St Lucia. Most notably, in February - March 1976, six adults near Charters Creek jetty were captured that had presumably lost their fear of humans due to suspected localised fish cleaning activities of tourists. The individuals were marked via scute removal and relocated to the Nyalazi River. On 6 January 1984 a 3.9 m crocodile was also caught at Charters Creek jetty and released the following day at Sengwana (Pooley 1976; Pooley. pers. comm.; see Fig. 1 for all lake localities referenced in text). More recently, a crocodile implicated in an attack on a local person in the Mzinene River was captured and released north of Fani’s Island (Dickson, pers. comm.). However, these relocated animals were not visibly marked, and no information is available to confirm whether any individual returned to its capture location.

Despite the prevalence of human-crocodile conflict in Africa and the local management practice of “damage-causing” crocodile relocation (Taylor et al. 2006), homing behaviour remains undescribed for wild Nile Crocodiles in Africa. However, preliminary evidence of homing behaviour in captive bred Nile Crocodiles in the Okavango Delta and Lake St Lucia (Shacks, pers. comm.; Combrink & Warner, unpublished data) suggests this behaviour may be prevalent in wild individuals.

The aims of our study were 1.) to capture an adult Nile Crocodile fitted previously with a GPS-satellite transmitter and thereby having a known home range, 2.) relocate the animal a considerable distance outside of its known range, 3.) record detailed movements and precise spatial orientation in the weeks or months following release, and 4.) document any observed homing behaviour.

METHODS

Study area

Located in KwaZulu-Natal, South Africa, the Lake St Lucia estuarine system is ~67 km in length, including the ~27 km long Narrows channel south of the lake body which connects the system to the Indian Ocean. It is 6 km in width when filled to capacity, and the largest estuarine system in Africa (Cowan 1997). Lake St Lucia is characteristically shallow, with an average depth of 0.98 m and maximum depth of 2 m (Hutchison 1974). At capacity, the main lake basin is ~23 000 ha in size and connects to False Bay (~7000 ha) in the west via an area known as Hell’s Gate (Fig. 1). When the estuary mouth is open lake salinities range from 35 psu at the mouth to completely fresh at inflowing rivers and streams, and the system supports an anadromous fish species assemblage important to Nile Crocodile diet (Whitfield 1980).

Four streams enter the lake with intermittent flows due to water extraction and extensive afforestation and agriculture in their associated catchments (Fig. 1). When rivers stop flowing during drought periods, salt is concentrated through evaporation, and water in the system reaches the highest salinities in northern areas furthermost from the estuary mouth. Under such conditions salt concentrations can become excessively hypersaline (Taylor 2006). The study area is described in further detail in Chapter 1.

Capture and translocation

On 1 May 2012 we captured an adult female Nile Crocodile (no. 514, total length = 270 cm, snout-vent length = 139 cm, mass = 73.2 kg) with a baited snare-trap array activated the previous evening in the freshwater Mphathe Stream (Fig. 1), ~7 km upstream from where the stream mouth connects to the Narrows. Female 514 was previously captured ~2 km downstream on 23 October 2010 and fitted with a GPS-satellite transmitter (African Wildlife Tracking, Pretoria), as described in Appendix 5. Consequently, it had a known home range. We translocated Female 514 to False Bay Park (a straight-line distance of ~50 km from the capture location) via road and released her at Lister's Point (Fig. 1) later the same day, approximately 10 h after capture.

GPS-satellite transmitter

The GPS-satellite transmitter (length = 120 mm, width = 69 mm, height = 56 mm) consisted of four D-cell batteries with a Taoglas passive GPS patch antenna. The unit was attached to the nuchal plate of the individual with stainless wire and monofilament nylon traced transversally through three hollow tubes 10 mm from the base. Following attachment, the unit was further set to the nuchal plate with a cold-curing dental acrylic mould. The composite transmitter unit and materials weighed 1160 g (1.6 % of individual body mass). The duty cycle was set to record a GPS-fix (point locality) every hour during directed movements, but during prolonged periods of inactivity the duty cycle interval was remotely decreased to 4 h transmissions. Data from the unit was uploaded to a server at the same frequency as the duty cycle. Downloaded data were projected in ArcView 9.3.1 (ESRI, Redlands, USA) in WGS 84 and LO 33 format.

Displacement between successive GPS points x_1y_1 and x_2y_2 were calculated using the following equation: 1000 x (6371.1 x ((2 x asin (sqrt ((sin((radians(y_1) - radians(y_2))/2)^2) + cos (radians (y_1)) x cos (radians(y_2)) x (sin((radians(x_1) –radians (x_2))/2)^2)))))). The mean ± standard error is reported.

RESULTS

Pre-translocation movements

Subsequent to initial capture on 23 October 2010, the individual had movements characterised by six distinctive periods. For the first 47 days she utilised a small section of stream near the initial capture site. On 10 December 2010 she moved downstream to the Narrows and then back again, covering a total distance of ~13 km over 12 days. Back in the Mphathe Stream she continued to move upstream for ~6 km to a relative deep pool created by a low-water bridge with concrete weir. From 29 December 2010 - 21 July 2011 she moved within a 5 km area upstream of the weir, spending the majority of that time period in a section of forested stream ~l.5 km above the weir. On 21 July 2011 during the winter courtship and breeding season, she moved downstream below the weir, possibly in search of mate(s), as crocodile densities were much higher below the weir (Combrink, unpublished aerial survey data). She returned 6 August 2011 after moving a total distance of ~6 km, and stayed within an area ~150 m above the weir until re-capture for translocation on 1 May 2012 (Figs. 1).

Post-translocation movements

Days 1 - 28

Initial orientation upon release at Lister Point took approximately 24 h, after which the individual moved in a southerly direction along the western shoreline of Ndhlozi Peninsula and through Hell’s Gate, entering the main lake (Fig. 1). Once in the main lake body, she turned around and moved to the southwestern shoreline of False Bay and continued in a southerly bearing, terminating at the dry southern section of False Bay, possibly due to extremely dry conditions, the crocodile turned around and moved northward along the western shoreline of Ndhlozi Peninsula, re-entering Hell’s Gate and navigating toward the 9.2 ha freshwater Ndhlozi Pan. At this stage the individual had travelled ~50 km since translocation and release three days prior, at a mean speed of ~569 m h^{-1} in predominately hypersaline conditions (~45 psu). The translocated Nile Crocodile showed fidelity to Ndhlozi Pan for the next 24 days, moving within the pan at a rate of ~430 m day^{-1} (Figs. 1, 2).

Days 29 - 85

On 29 May the crocodile exited Ndhlozi Pan eastward through Hell’s Gate, navigated south, and walked across Lane Island. Crossing Tewati Bay, she abandoned the dry lakebed and walked onto the eastern shoreline. Continuing overland with discontinuous movements in a southerly direction for ~7 km over the following 25 days, the individual utilised a number of wetland refugia created by shoreline seepage (Combrink and Warner, pers. obs.) until finally entering Dead Tree Bay. From here she moved southwesterly for 4.3 km, terminating movement again at the dry lakebed. Moving north-eastward, she settled in freshwater seepage pools on the eastern shoreline of Dead Tree Bay and stayed here for nine days (Figs. 1, 2).

Days 86 - 132

From Dead Tree Bay the crocodile moved overland 2.7 km south to Mamba Stream, a ~400 m narrow freshwater seepage stream that drains into a small shoreline pool. It stayed here for 13 days before again moving overland ~3.6 km to Catalina Bay, where she remained for 47 days. On 8 September the individual relocated south from Catalina Bay into Makakatana Bay (Figs. 1, 2). At the time there was a substantial flow from Makakatana Bay into Catalina Bay because of heavy rains and a full Mfolozi River pushing water into the estuary, up the Narrows and into the two respective Bays (Combrink, pers. obs.).

Days 133 - 136

Once on the southern shoreline of Makakatana Bay, the translocated Nile Crocodile made small-scale directional movements until finally entering Potters Channel, and continued to move southerly down the Eastern Fork of the Narrows. Around 23h00 on 10 September 2012, the individual moved back into the Mphathe Stream and slowly meandered back to the original pool where she was captured 136 days previous, arriving on 14 September 2012 (Figs. 1, 2).

Temporal and movement profile

Although the straight-line distance between release and capture sites was 50.4 km, the translocated Nile Crocodile travelled 178.3 km back to the capture location over 136 days (mean daily distance = 1311 ± 207 m^{-1} day). It's journey back was not continuous, but rather characterized by three movement patterns (P_1, P_2 and P_3) as illustrated in Figure 2. The first pattern (P_1) consisted of strong directional movements (534 m h^{-1}, 185 m h^{-1}, 203 m $h^{-1}$and 179 m h^{-1}) of short duration (2 - 4 days) over extensive distances through unfavourable habitats (e.g. hypersaline waters or dry lakebed). These movements were immediately followed by long periods (i.e. 2 - 3 weeks) of low mobility (18 m h^{-1}, 11 m h^{-1} and 11 m h^{-1}) in freshwater habitats.

The second pattern (P_2, Fig. 2) was delineated by the crocodile's average movement behaviour at Catalina Bay. P_2 consisted of a high frequency of non-directional movements (51 m h^{-1}) between basking sites on the shoreline and two freshwater seepage areas. Salinities at these freshwater habitats were ~10 psu, significantly lower compared to shallow and hypersaline water remaining in Tewati Bay and Dead tree Bay.

The final pattern (P_3) was marked by a high directional movement rate (average = 196 m h^{-1}) through favourable habitat (5 psu and freshwater), with the individual stopping only at basking sites (Fig. 1, 2).

Habitat use during homing movements

During its 136 day navigation back to the site of capture, the translocated crocodile spent more than 50 % of the time in freshwater and approximately a third of the time in low salinity (< 11 psu) areas (namely, Catalina Bay). Although 37 % of the traversed return route was comprised of hypersaline habitats, only 8 % of the total time was spent occupied in these areas (Fig. 3).

Overland locomotion

The translocated Nile Crocodile was challenged with numerous dry areas between the release site in False Bay and the capture location. Seven overland excursions ranging from 670 m to 7360 m were recorded (Table 1). Walking speed ranged from 92 m h^{-1} to 224 m h^{-1} with a mean walking speed of 131 ± 17 m h^{-1}.

The translocated individual appeared reluctant to venture overland unless adequate cover was available. For example, on 28 June 2012 while moving south from Dead Tree Bay the animal reached a point where the lake was completely dry. Instead of crossing the exposed lake bed, it turned around and moved back to the eastern shoreline of Dead Tree Bay. Almost a month later (24 July 2012) after collective additional movements of 22 km, the crocodile entered Catalina Bay, 2 km due east of where it would have walked from the north if it had undertaken the relatively short 4 km overland venture previously.

Comparison of movements: pre-and post-translocation

Differences in movement rates for the translocated Nile Crocodile during the 136 days of the homing experiment (hereafter homing) were compared with the identical time period the previous year while resident to its home range (hereafter pre-translocation; Table 2, Fig. 4). During the 136 days of homing, total movement, mean, median and maximum daily movements were 178.3 km, 1311 ± 207 m, 435 m and 17.4 km, respectively, compared to 60.3 km, 444 ± 33 m, 349 m and 2.5 km during pre-translocation (Table 2). Only one notable movement event occurred during pre-translocation; a 2.6 km journey downstream from the core-use area and back (21 July - 4 August 2011, Fig. 4). Mobility was significantly higher during homing (Wilcoxon Matched Pair Test, $Z = 3.193$, $p = 0.001$; Fig. 5).

Daily distance mobility patterns during pre-translocation and homing were considerably different (Fig. 6). During pre-translocation, her daily distances were proportionally shorter (0 - 500 m and 500 m - 1 km) while during homing more longer movement (1- 2 km and > 2 km) were made. For instance, 1 % of daily movements were > 2 km during pre-translocation, compared with 19.9 % while homing (Fig. 6).

Despite a shared temporal diel movement pattern between homing and pre-translocation activity, distances moved during homing were considerably greater for all six temporal periods (Fig. 7). The translocated female was more mobile than the mean for all other females in the study over the same time period (n = 5), except for the 18h00-22h00 period. The general mobility pattern for the translocated female was characterised by increased movement during the early morning (06h00-10h00), followed by decreased movement during peak basking time during winter (10h00-14h00). Movement increased again during the afternoon (14h00-18h00) and continued to increase into early evening (18h00-22h00), decreasing during late evening/early morning (22h00-02h00) and continuing to decrease marginally from 02h00-06h00 (Fig. 7).

Post-translocation movements

Following the translocated crocodile's return to the capture site, she continued to use the ~5 km section of the Mphathe upstream from the weir, consistent with the individual's previously documented home range. She never moved below the weir up to the point of transmitter failure (Jan. 2014), indicating continued strong site fidelity to this part of the stream.

DISCUSSION

Our use of satellite tracking was successful in documenting movement path structure indicative of homing behaviour in a translocated wild female Nile Crocodile. In particular, temporal profiles of space use throughout a wide geographic range clearly showed directional movements back to the original home range. The individual displayed remarkable navigational abilities despite having to negotiate complex habitat and geographic challenges, including extensive areas of hypersaline and dry lake. This is the first study of a crocodilian where comprehensive home range use and movement data were available prior to translocation, and the 136 day detailed homing navigation is the longest and most detailed to be published for any crocodilian species to date. It is also the first application of satellite telemetry to a female crocodilian.

Evidence of homing behaviour with captive bred Nile Crocodiles has been reported in the Okavango Delta in Botswana (Shacks, pers. comm.) and at Lake St Lucia. On 19 March 2009 we released a uniquely marked adult male Nile Crocodile of unknown age born at the St Lucia Crocodile Centre into Catalina Bay, approximately 25 km away. The individual moved south into the Narrows where it was recaptured once and resighted on three separate occasions. Remarkably, on 21 November 2011 (977 days after its release) the crocodile returned to the enclosure where it had been kept at the Centre (Combrink, Warner & M. Robertson, unpublished data). Incidents such as this, along with other anecdotal and published accounts, lead us to confidently infer the spatial pattern we observed in our translocated telemetered female is representative of true homing ability, and not random movement back to the site of capture.

Our study and that of Read *et al.* (2007) suggest that there is a variable orientation period subsequent to the release of translocated crocodiles into areas disjunct from their original home ranges. This phase is marked by random directional movements of varying distances, often in the opposite direction of an individual’s home range. In our study, the orientation period appeared to last approximately 24 hours, while Read *et al.* (2007) reported apparent random movements around the release site lasting 10 - 108 days for three male Estuarine Crocodiles. Factors influencing the duration of the orientation period likely include animal stress, physiological condition, structure of the habitat matrix, distance from the capture site, and individual homing ability.

The spatial data we obtained from the translocated crocodile clearly illustrate how habitat heterogeneity at the landscape scale influences movement behaviour during the homing process. The availability of freshwater is an important habitat requirement for Nile Crocodiles, primarily for rehydration after prolonged periods in hypersaline waters, as well as for providing cover and feeding opportunities. Freshwater pans, pools and seepage areas may also help to buffer air temperatures that can approach 5 °C during winter.

Habitat requirements (e.g. freshwater) and an aversion to overland travel likely explain the somewhat circuitous route that was observed in our study and in that of Read et al. (2007). Circuitous long-distance travel composed of orientated movements toward a goal is unique amongst translocated animals with homing ability (Pittman et al. 2014). We suggest that in addition to the ability of homing to accurately navigate, individuals also possess the capacity to select movement strategies en-route that optimise suitable habitat use, even if this increases overall route distance and duration.

This is the first study to confirm homing behaviour in a wild Nile Crocodile and it supports a growing body of evidence (Chabreck 1965, Gorzula 1978, Hines and Woodward 1980, Webb et al. 1983, Rodda 1984, Messel and Vorlicek 1986, Webb et al. 1987, Walsh and Whitehead 1993, Tucker et al. 1997, Kay 2004, Woolard et al. 2004, Read et al. 2007) that crocodilians have navigational abilities. Our findings have direct and obvious implications for the management of this potentially dangerous apex predator in the St Lucia estuarine system. If Nile Crocodiles cannot be separated by extensive distance and contiguous unsuitable habitat from its capture location, other options must be considered. It remains unclear what distances crocodiles will move overland between water bodies but given adequate cover and opportunities for hydration, such distances are likely considerable.

Researchers in Mexico recently experimented with magnets by taping them to a crocodile's head at the capture site for the duration of the journey to the release site, and a good proportion of these experimental individuals did not return home (Domínguez-Lazo 2008). This implies that a magnetic compass internal navigation system constitutes at least part of the homing component for some crocodilian species (Campbell et al. 2010). Given the high rate of human-crocodile conflict in Africa, the spatial ecology of homing Nile Crocodiles, and the homing mechanism itself, are fertile grounds for further research.

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Caption for Figures

Figure 1. The Lake St Lucia estuarine system and homing route indicated by GPS-satellite observations for a wild Nile Crocodile. The map indicates capture and release sites as well.

Figure 2. Temporal and movement profile of the translocated crocodile from day 1 to 136, indicating daily movements, salinities and rate of movements in m^{-1} per hour. It also indicates names of areas where she frequented for a relative long period.

Figure 3. Habitat use based on GPS-observations for the translocated crocodile during her homing route.

Figure 4. Temporal and movement profile of Crocodile 514 from 1 May – 14 September 2011 (black line) and 2012 (grey line), to indicate the relative difference between her daily movements in her home range (black line) and homing experiment (grey line) during the 136 days.

Figure 5. Median daily movements during the homing experiment (434.63 m) differed significantly compared with the exact same period (2 May – 14 Sep) one year earlier (348.91 m). Even more noteworthy is the variation in the daily range (i.e. min. and max.) between the two periods.

Figure 6. Daily movements per distance category for Crocodile 514 from 1 May – 14 September 2011.

Figure 7. Mean movements per time period for the translocated crocodile indicating pre-translocation (home range, 1 May – 14 Sep. 2011), translocation (1 May – 14 Sep. 2012, homing experiment), and six other females during winter.

Figures

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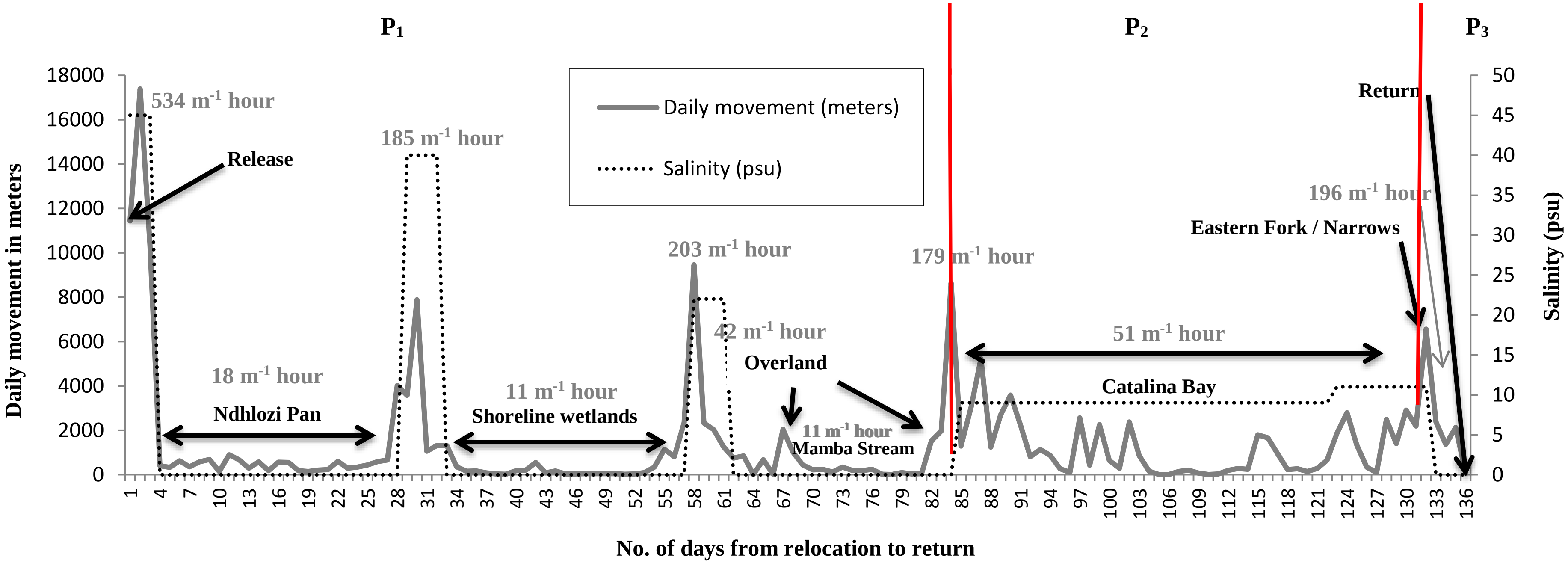

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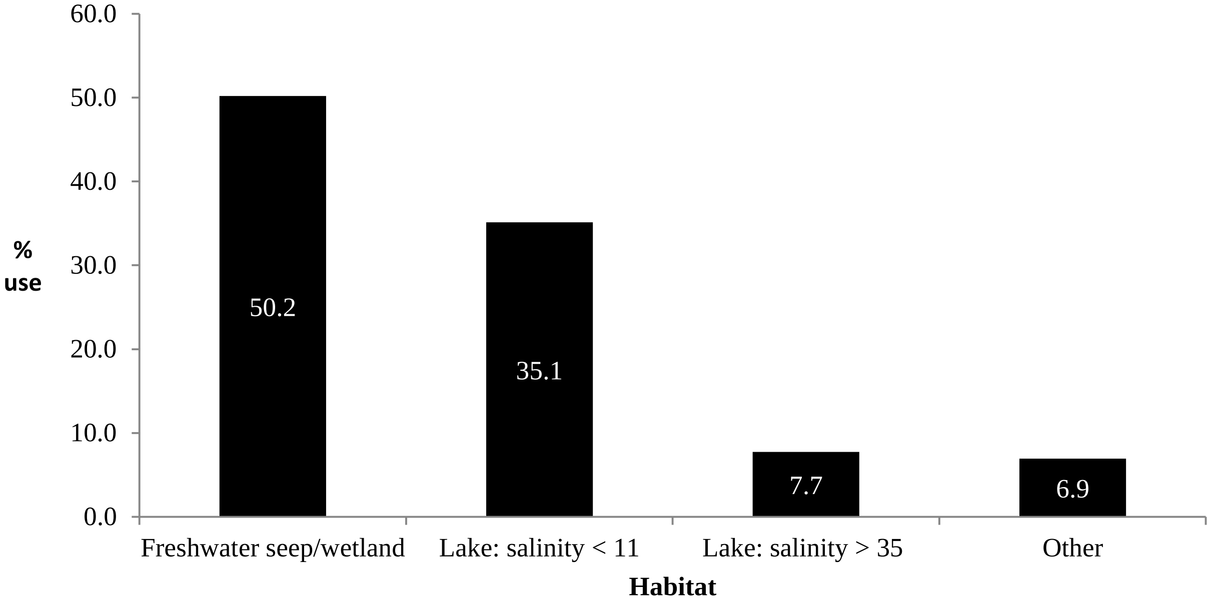

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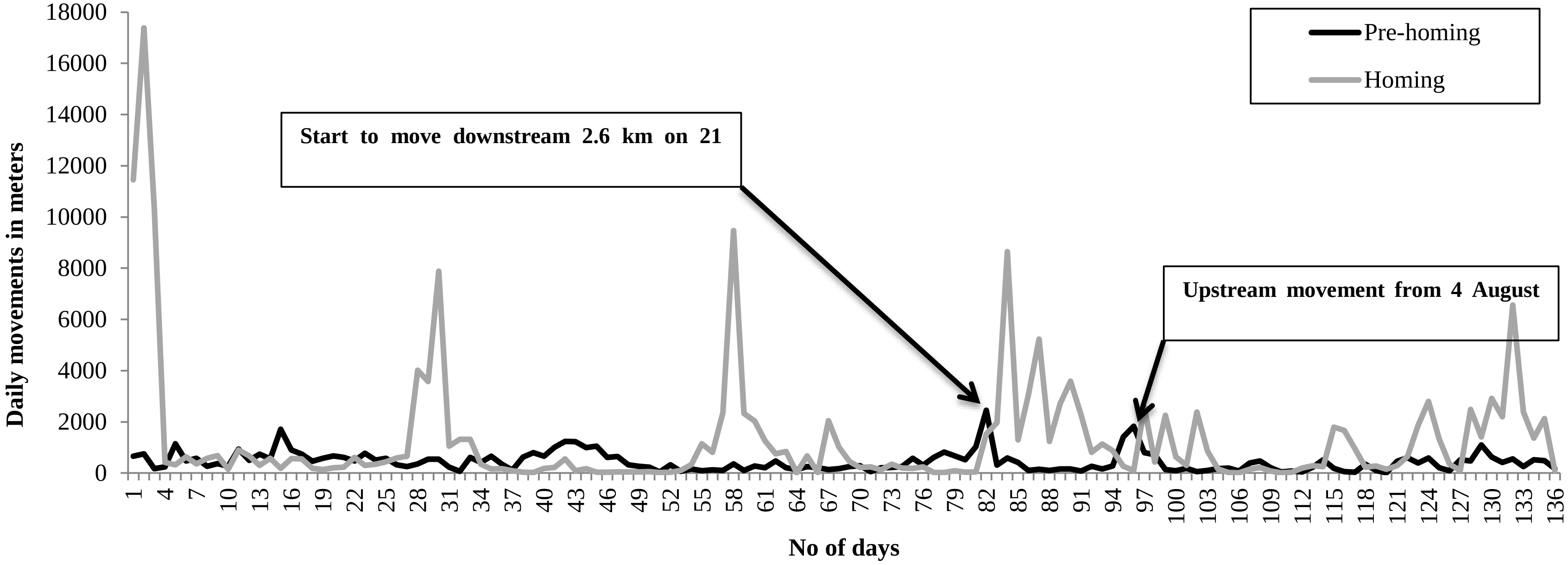

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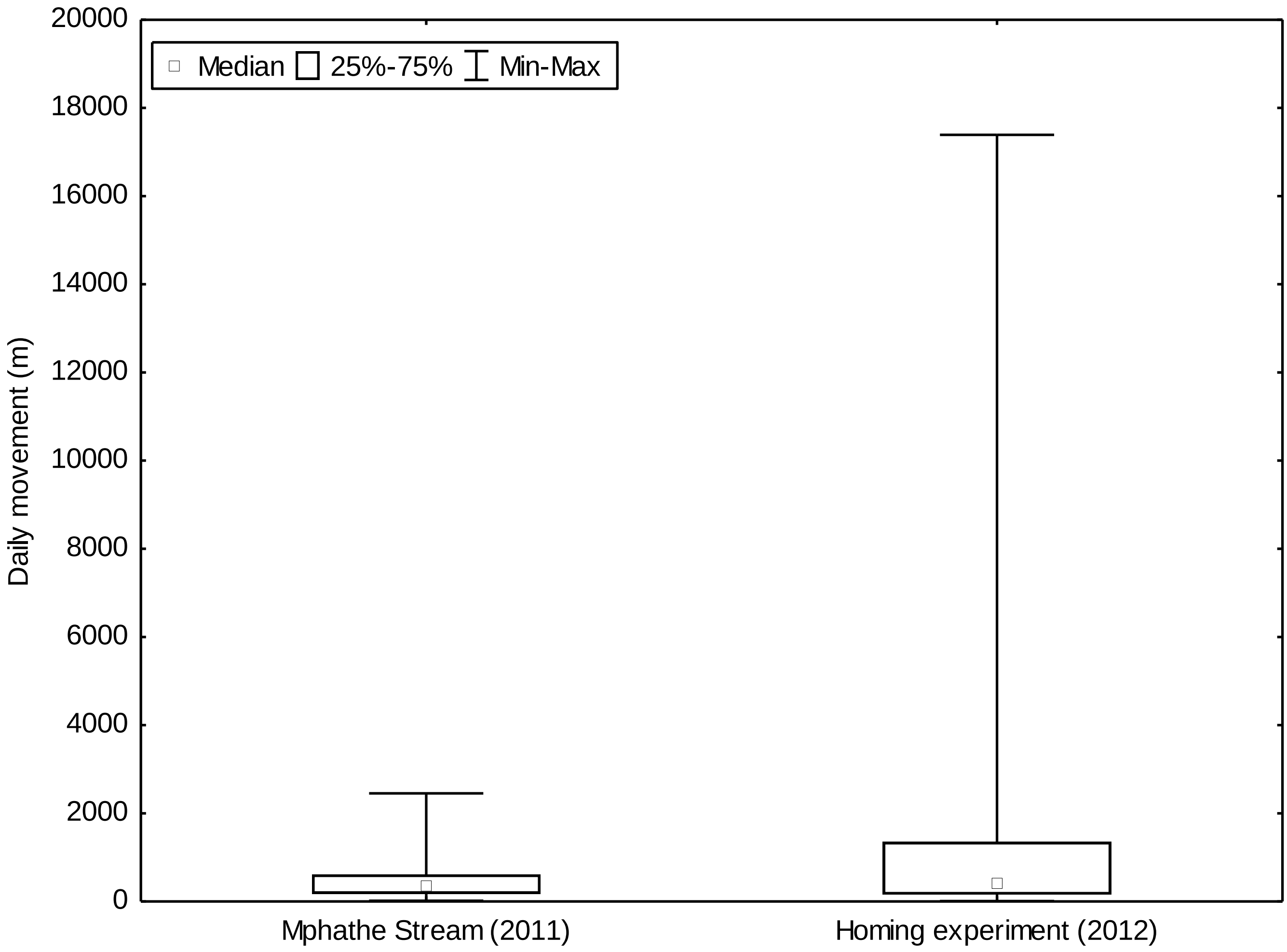

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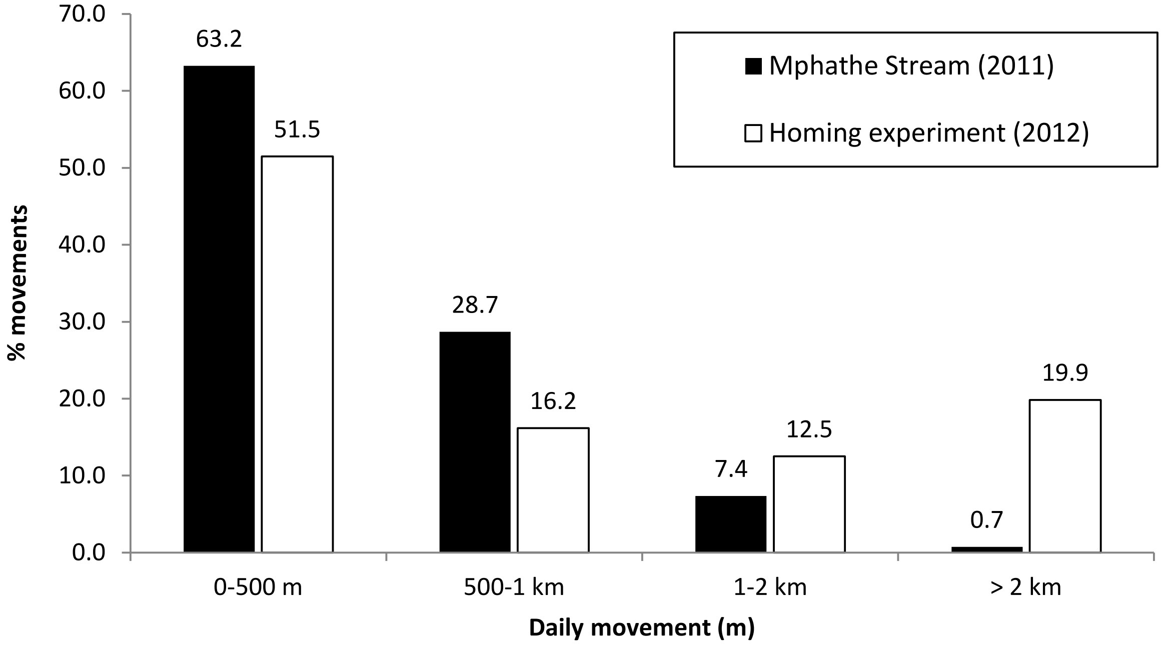

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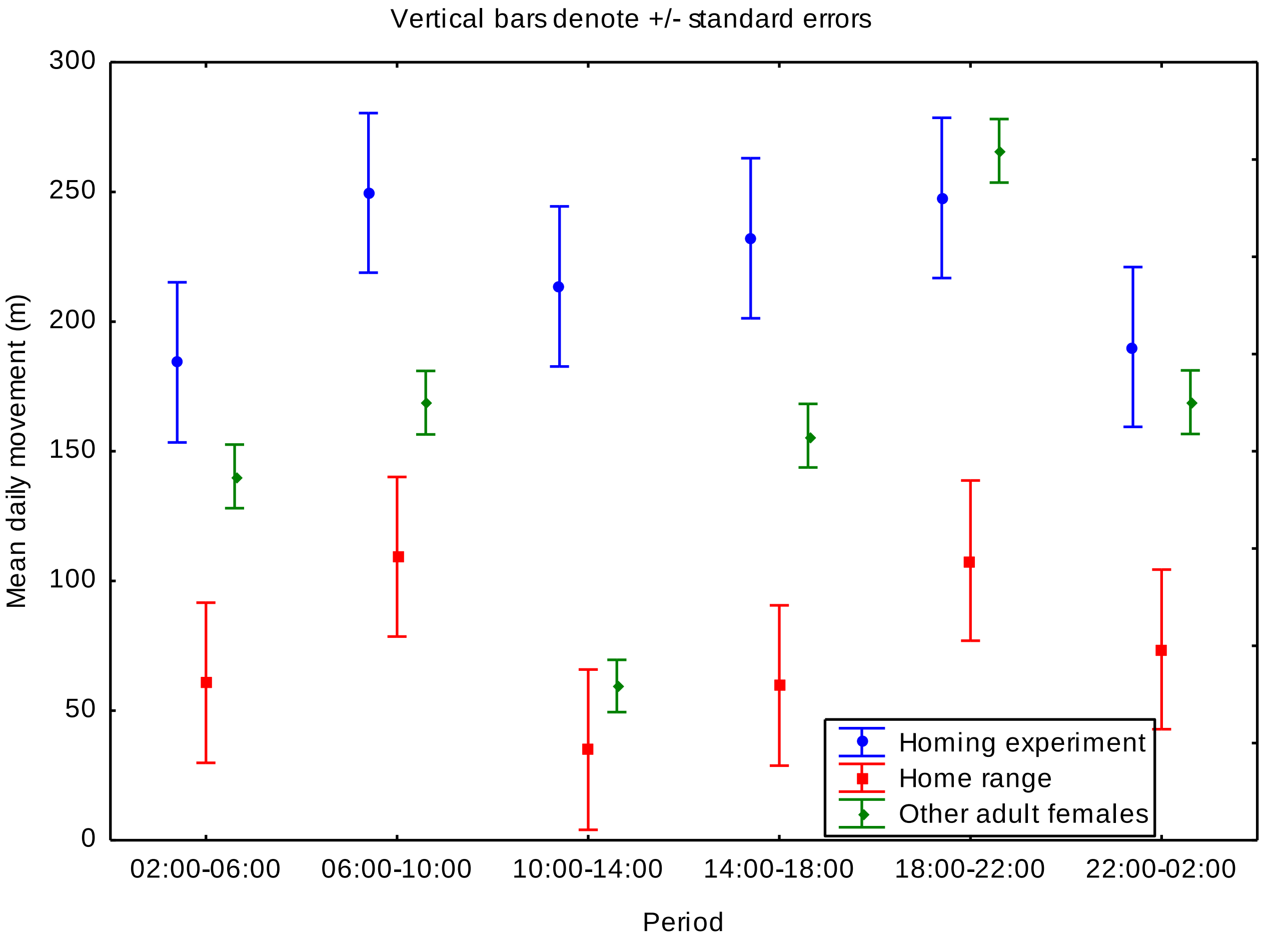

Figure 7. Mean movements per time period for the translocated crocodile indicating pre-translocation (home range, 1 May – 14 Sep. 2011), translocation (1 May – 14 Sep. 2012, homing experiment), and six other females during winter.

Caption for Tables

Table 1. Overland movements of the relocated crocodile during its homing journey.

Table 2. Comparison of pre- and post-translocation movements for the relocated crocodile.

Tables

Table 1. Overland movements of the relocated crocodile during its homing journey.

Overland section	**walked (m)**	**speed (m h^{-1})**
Hell's Gate - Ndhlozi Pan	673	224
Lane Island	734	92
Eastern Shoreline	7358	112
Dead Tree Bay - Mamba Stream	3035	143
Mamba Stream to Catalina Bay	3588	131
Catalina Bay attempt 1 (return)	1048	117
Catalina Bay attempt 2 (return)	1583	101

Table 2. Comparison of pre- and post-translocation movements for the relocated crocodile.

	Mphathe Stream home range	**Homing experiment**
	1 May - 14 Sep. 2011	**1 May - 14 Sep. 2012**
Total movement (m)	60380	178295
Mean daily movement ± S.E. (m)	444 ± 33	1311 ± 207
Median daily movement (m)	349	435
Minimum daily movement (m)	15	10
Maximum daily movement (m)	2452	17389

CHAPTER 9

Conclusions

The status and future of viable wild Nile Crocodile populations in South Africa remains uncertain, despite national protection of the species and a substantial proportion of its extant range under formal conservation.

Within the last decade a number of studies highlighted declines in local Nile Crocodile populations (Ashton 2010, Botha 2010, Combrink et al. 2011, Ferreira and Pienaar 2011, Calverley and Downs 2014, Marais 2014) as well as the biological extirpation of at least one population (Botha et al. 2011).

There is a clear need to formulate a national conservation strategy for the species (Combrink et al. 2011) underpinned by improved biological and ecological understanding, with consideration for the social and cultural aspects of local people that share resources with crocodiles.

The aim of this thesis was an attempt to provide some insight into the biology, ecology and behaviour of wild Nile Crocodiles, in order to better manage and conserve local populations.

The Lake St Lucia estuarine system provided fertile grounds for our study. It is the largest estuarine system in Africa, hosting the largest Nile Crocodile population within a single waterbody in South Africa, estimated at 1005 ± 137 sub-adult and adult crocodiles. Furthermore it is the largest recorded nesting population in the country. It is provincially, nationally and regionally valuable from a scientific perspective, being the only viable estuarine population in the country, and situated at the southern extremity of the species' range.

The St Lucia estuarine system is an extremely dynamic system (Whitfield 2013) and our study period (2009 - 2013) included a particularly severe drought period (2002 - 2011) with the estuary being separated from the ocean for almost a decade. While this provided us with a unique opportunity to record aspects of crocodile biology, ecology and behaviour and their resilience to perturbations during this period, our findings should be interpreted against this background. However, not all study animals were affected equally and numerous aspects of their life history were possibly very typical of an estuarine population, where variation, e.g. salinity fluctuations, may be considered normal.

A number of questions deserve further investigation:

- The geographical positioning of the St Lucia system results in longer and cooler winters compared to more northern Nile Crocodile populations, and this might have a profound, yet unconfirmed influence on the life history and dynamics of the St Lucia population, i.e. through slower growth rates that affect population dynamics.
- Determination of the age-size structure through standard skeletochronology methodologies (Hutton 1986, Tucker 1997).
- Elevated lead (Pb) levels have been confirmed in some crocodile tissues tested from St Lucia (Warner et al. in prep.). Lance et al. (2006) documented lead shot causes chronic health problems such as reproductive failure in captive American Alligators. Investigate the extent of fishing sinker ingestion in Nile Crocodiles at St Lucia as well as the likely impact on reproduction (Combrink et al. 2013).
- Examine the spatial and temporal use and importance of Nile Crocodile burrows, as well as spatial properties and temporal thermal ranges of burrows. Crocodile burrowing behaviour should be investigated by recording temperature ranges inside

the terminal burrow cavity, quantify the spatial dimensions using LADAR technology and determine use through controlled infrared videography (Combrink et al. 2013).

- Determine dispersal dynamics and hatchling mortality at a selected number of natal areas.
- Investigate multiple paternity of Nile Crocodiles at nesting areas to quantify the level of promiscuity and test the hypothesis that dominant males control paternity in specific areas, such as stream systems.

Despite a long and proud research legacy on Nile Crocodiles at Lake St Lucia, numerous biological and ecological questions remain unanswered. Nile Crocodile research is always a logistically challenging and time-consuming endeavour, often dangerous due to the ever presence of hippopotamus, especially at Lake St Lucia. However, few research projects are as rewarding, both in terms of data collecting and personal satisfaction. It is my hope that many of the remaining questions will be answered in future studies, allowing for an improved understanding and ultimately management of this charismatic and iconic keystone species, associated with the estuarine lake, wetlands, streams and rivers of the St Lucia system.

APPENDIX 1. ROUTE FLOWN DURING AERIAL SURVEYS

Nile Crocodiles are counted annually in June at Lake St Lucia, mostly with a four-seater fixed-wing. We have also used other types of aircraft, including Microlight, two-seater fixed-wing aircraft and a double motorised paraglider to count Nile Crocodiles and their nests (Fig. 1). The surveys commenced over the "intake works" site on the Mfolozi River and the aircraft followed the river to Maphelane, then the Msunduzi River for 5 km in a southerly direction (Fig. 2). From the St Lucia estuary mouth the count continued over the Backchannels, Link Canal, wetlands west of St Lucia beach, following the Narrows northwards, surveying a single shoreline bank at a time to the Mphathe Stream. The Mphathe Stream was surveyed to the low-water bridge. From the confluence in the Narrows the survey continued northwards including the Western Fork, Eastern Fork as well as Brodies Crossing, eSingeni wetland and Potters Channel. From Catalina Bay we surveyed the shoreline perimeter of the main lake in an anti-clockwise direction, Nkazana Stream, Lake Bhangazi and back to Catalina Bay. Then continued north along the northern shoreline of Catalina Bay, Mamba Stream, Dead Tree Bay, Fani's Island, Tewati Bay, Lane Island, Selly's, Mkhuze River mouth, False Bay, Hluhluwe River, Ndhlozi Pan and back along the Western Shoreline where the count ended at Makakatana Bay (Fig. 2).

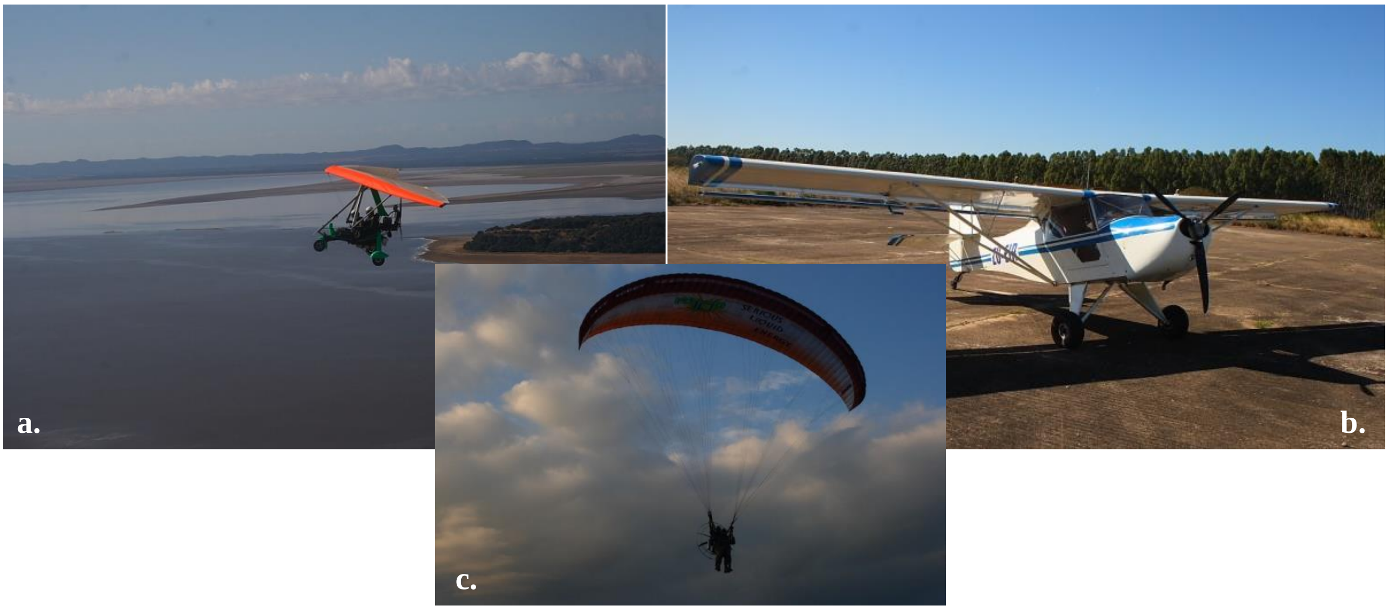

Figure 1. Microlight (a.), fixed-wing airplane (b.) and paraglider (c.) were used to count Nile Crocodiles at Lake St Lucia.

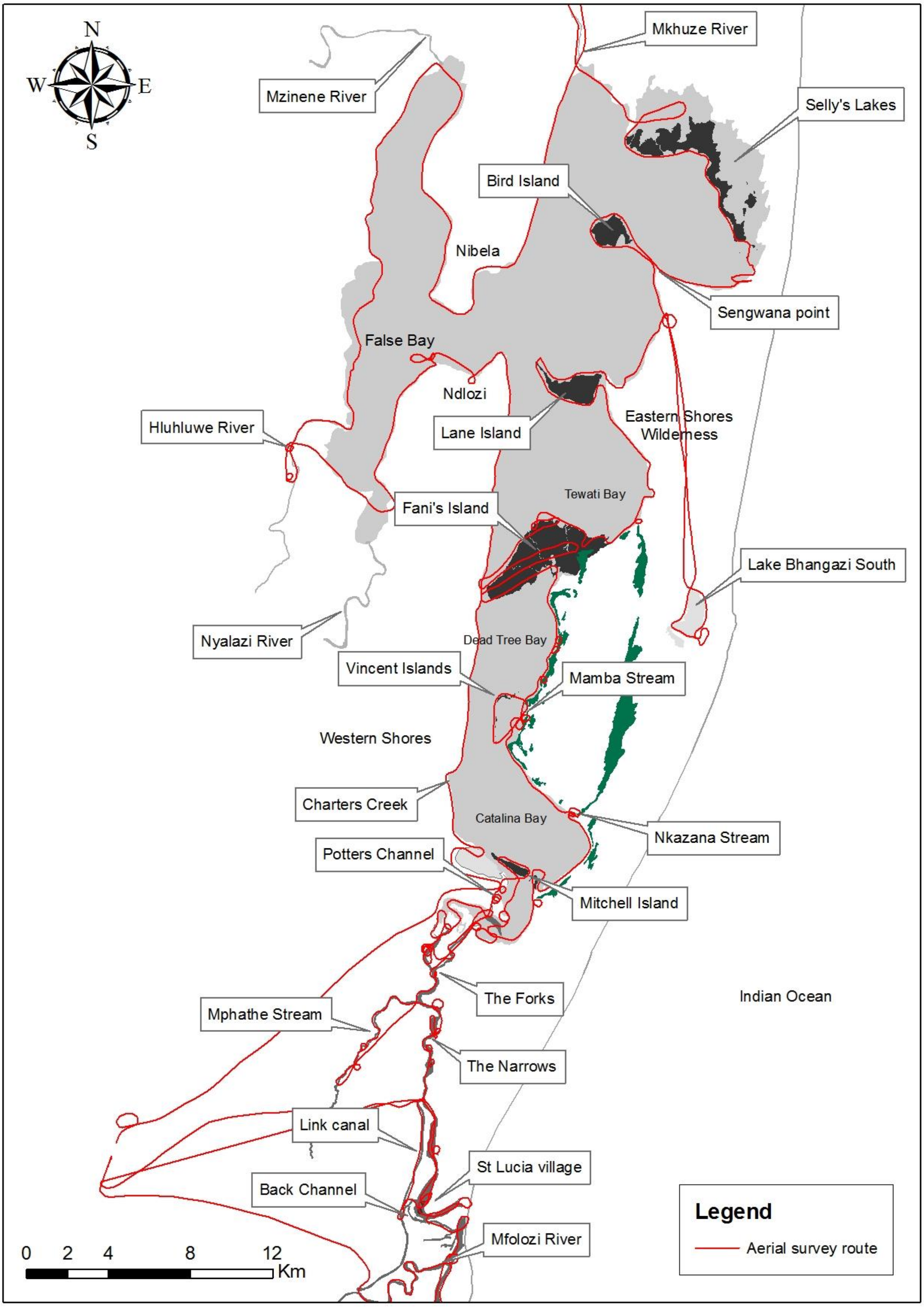

Figure 2. Aerial survey route for counting Nile Crocodiles at the Lake St Lucia estuarine system

APPENDIX 2. CAPTURE METHODS

We used a combination of capture techniques to maximise success under diverse habitat conditions. The preferred capture technique was noosing, i.e. securing a self-locking cable around the head of the crocodile. The cable was attached to a climbing carabiner, secured to a rope and tied to a 4 m pole (Fig. 1). As soon as the noose was secured over the head, the noose was closed and the crocodile was effectively attached to the rope. The effectiveness of this method was inversely related to the wariness of crocodiles and it was often used from a boat at night combined with a spotlight. This method was used during the day if crocodiles were encountered in small, shallow streams, shoreline pools with good visibility or parts of the lake where water depth was < 50 cm, often near the shoreline (Fig 1.). Noosing was the preferred method of securing a crocodile during active capture and was also employed as the final stage of restraint when other active capture techniques were required.

In deeper channels and open waterbodies, we used a small detachable harpoon head (Webb and Messel 1977) connected to 80 m kevlar rope and secured to a buoy (Fig. 2). The harpoon head consisted of two or three short (2 cm) sharpened steel tips each with a barb inserted in a brass rod. The harpoon head was secured to the end of a 4 m pole and forced through the skin of the crocodile, along the side or the neck area devoid of osteoderms. As soon as the barb pierced through the skin the pole would detached from the head of the harpoon and the harpoon head would be connected to the rope and buoy. The steel tips were secured on the base of the harpoon head, which prevented penetration > 2 cm. Harpooning was always used from a boat at night in combination with a spotlight.

In narrow shallow streams and shoreline pools with zero visibility we used an 8/0 barbless weighted treble hook, attached to 80 m kevlar rope (Lowers, pers. comm., Fig. 3). The success of this method depended on the accuracy of throwing the treble hook over the crocodile, with often only the head visible above the water surface or completely submerged.

The rope was quickly retrieved, setting the barbless hook in the epidermal scale of the animal. This method was effective where crocodiles were too far out to reach with the noosing pole. As soon as the animal was brought within reach, the self-locking noose was placed over its head.

In wide open waterbodies, small weighted barbless treble hooks (3/0 or 4/0) were used from a boat with a fishing rod and reel (Cherkiss et al. 2004). The treble hook was cast over the crocodile and by rapidly retrieving the line one of the hooks could become embedded into the epidermal scale of the animal (Fig. 4a). This method was used where water depth was not exceeding two meters, as a hooked animal will often sit at the bottom. In shallow water the crocodile was probed with the noose pole to break the water's surface which allows the noose to be placed around the animals head. Considering all available methods, this technique was the least successful, especially with adults.

In vegetated shallow habitats with high hippopotamus densities, where boating was impossible, crocodiles were captured with baited traps (Fig. 4b). Due to manpower limitations, we refrained from using heavy cage traps but employed a minimalistic approach setting baited wire spring, or pulley traps. Traps were activated late afternoon and check at first light. Nesting females were captured at or near their nest-sites and moved away from the immediate vicinity of the nest for transmitter attachment.

The presence of hippopotamus in densely vegetated juvenile habitat, rendered catching excursions impossible, and this size class together with sub-adults, was underrepresented. Capture methods were all in line with the guiding principles as summarised in the South African National Parks' Standard Operating Procedure for the monitoring, capture and sampling of Nile Crocodiles (Combrink et al. 2012). Refer to Table 1 for a listing of capture methods for the different size classes captured at St Lucia during the study.

Capture techniques

Figure 1. Nile Crocodile capture using noose and pole in different habitats: shallow lake (a, b), shoreline pool (c.), stream (d.) and burrow (e.).

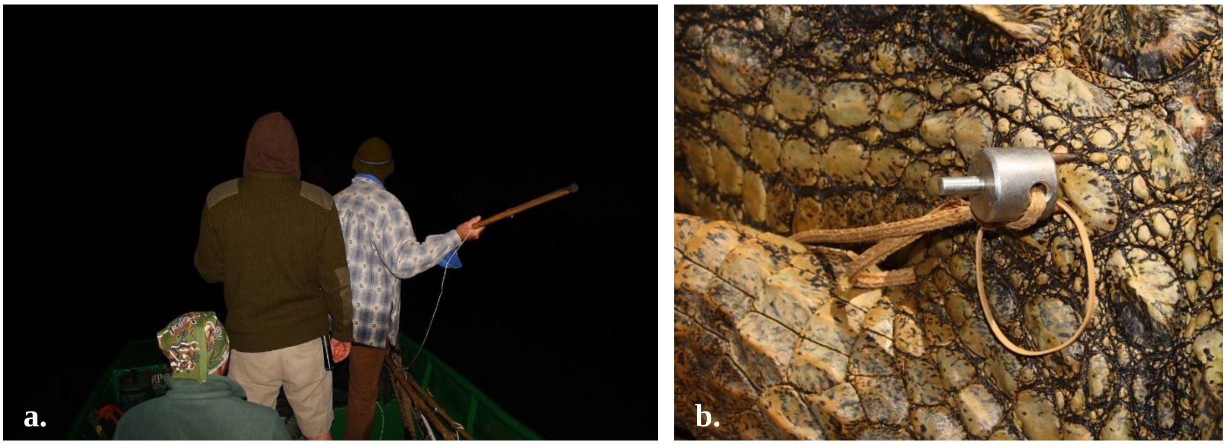

Figure 2. Boat based captures using a harpoon (a.), and one barb of the harpoon head through the skin.

Figure 3. Capture throwing larger weighted treble hook and kevlar rope (a.) and subsequently the noose (b.).

Figure 4. Boat based captures using a rod and reel with small treble hook (a) and trapping in the Mphathe Stream (b).

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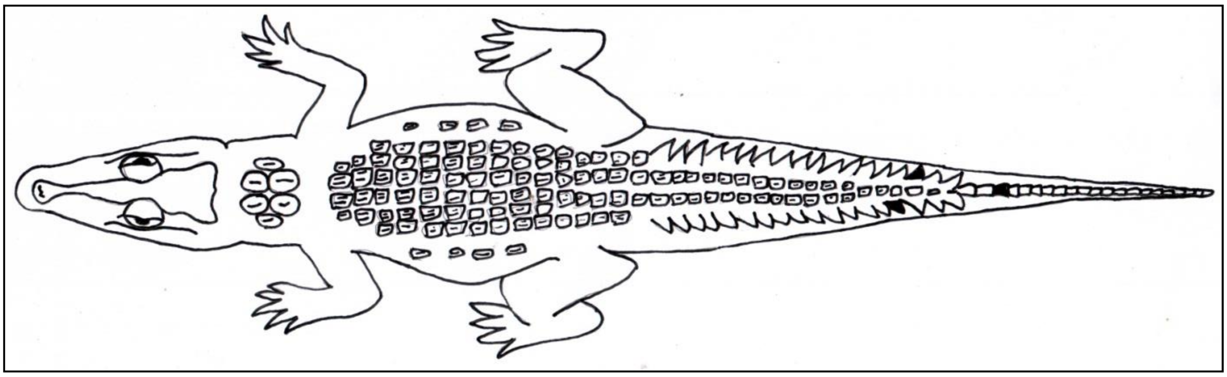
Table 1. Capture methods per size class for Nile Crocodiles in the St Lucia Estuarine system

Capture method	**Size class**	**Crocs caught**	**% per size class**	**% of total #**	**Land ***	**Boat ***	**Trap ***
Large treble hook from boat	Adult	4	3.88	2.99			
Large treble hook from land	Adult	16	15.53	11.94			
Noose from land	Adult	57	55.34	42.54			
Small treble hook from boat	Adult	12	11.65	8.96			
Small treble hook from land	Adult	1	0.97	0.75			
Trap	Adult	13	12.62	9.70			
Adult total		**103**	**100.00**	**76.87**	**71.84**	**15.53**	**12.62**
Harpoon	Sub-adult	1	7.14	0.75			
Hand capture from land	Sub-adult	1	7.14	0.75			
Large treble hook from land	Sub-adult	2	14.29	1.49			
Noose from boat	Sub-adult	4	28.57	2.99			
Noose from land	Sub-adult	4	28.57	2.99			
Small treble hook from boat	Sub-adult	2	14.29	1.49			
Sub-adult total		**14**	**100.00**	**10.45**	**50.00**	**50.00**	
Hand capture from boat	Juvenile	11	64.71	8.21			
Hand capture from land	Juvenile	2	11.76	1.49			
Harpoon	Juvenile	1	5.88	0.75			
Noose from boat	Juvenile	1	5.88	0.75			
Small treble hook from boat	Juvenile	2	11.76	1.49			
Juvenile total		**17**	**100.00**	**12.69**	**11.76**	**88.24**	
Hand capture from boat	Hatchling	21	10.99				
Hand capture from land	Hatchling	170	89.01				
Hatchling total		191	**100.00**				
TOTAL		**325**					
Total excluding hatchlings (#)		134					

APPENDIX 3. MARKING CROCODILES

All captured Nile Crocodiles were uniquely marked by clipping the caudal verticils with a sharp knife using a numbering system based on the Australian Queensland Parks and Wildlife Service Kay (2004), see below.



Example of Crocodile number 322. Scute removal sequence: Left Horizontal Scute 4, Right Horizontal Scute 3 and Vertical Scute 3. Note that the three reference scutes (Vertical 1, Left Horizontal 1 and Right Horizontal 1, were never removed.

Crocodile number 129. Scute removal sequence (white circles indicate removed scutes): left horizontal scute no. 2, right horizontal scute no. 3 and vertical scute no. 10. The reference scutes were not removed.

APPENDIX 4. MARKING CROCODILES WITH TAGS

Colored flexible plastic tags (TAGEM, Ramsay Engineering), 36 x 58 mm, were secured to adult and sub-adult crocodiles in order to estimate the population through mark re-sight analysis. Three or four tags were attached to both sides of the tail, usually the first three or four single caudal verticils, using five colours in total. This resulted in a unique colour sequence and identification code for each crocodile. It was possible to recorded and identify at a distance of 100 m with a field spotting scope (Bausch & Lomb 20 - 60 x 80 mm). Tags were attached by drilling a hole through the respective scute to position a 20 mm stainless steel washer at the closed end of a 50 mm stainless steel bolt, which was pushed through the neck/eye of the tag. Each tag and bolt was pushed through the scute and on the opposite side the procedure was repeated in reverse order, adding another tag of the same colour, a washer and a 10 mm stainless steel nylock nut, securing the bolt.

Crocodile number 129 showing coloured tags (orange, green, green) for re-sight analysis.

APPENDIX 5. TRANSMITTER ATTACHMENT

We attached 21 GPS-satellite transmitters (African Wildlife Tracking) to 19 Nile Crocodiles in the Lake St Lucia estuarine system. The first five transmitters consist of three D cell batteries (SAFT LSH 20 Lithium, 3.6 V) powering the Taoglas passive GPS patch antenna while two C cell batteries (SAFT LS 26500 Lithium, 3.6 V) supplied power to the VHF component. However, to increase battery longevity the rest of the transmitters consisted of four D (GPS) and one C (VHF) cell batteries. The batteries and other components were set within a dental acrylic mould with three hollow tubes running transversely 10 mm from the base of the transmitter. Transmitter dimensions were as follows: length 143 mm, width 75 mm, height 67 mm in front sloping to 44 mm at the back. Transmitters weighed ~ 880 g, but including dental acrylic and nylon, the total weight of the unit was ~1240 g, which equates to 0.36 – 4.88 % of the 19 crocodiles' body weight. The duty cycles was set to record GPS point localities in Greenwich Mean Time (GMT) every one, two and four hours. Transmitters were set to download data, once daily via the GSM network to a remote server from where data were downloaded through a website. If a crocodile was not in the GSM network, data were stored on the unit and whenever the animal entered coverage, data was transmitted to the server. The Lake St Lucia estuarine system was well covered with the GSM network and data were received for 20 of the 21 transmitters.

Successfully attaching transmitters to crocodilians for extended periods (e.g. to record seasonal data) is a fundamental challenges of crocodile field studies (Strauss et al. 2008) and most telemetry studies on Nile Crocodiles have reported transmitter loss within the first few months (Leslie 1997, Swanepoel 1999, Botha 2005, Bourquin 2007, Calverley 2010, Champion 2011). We used a recently developed method (Brien et al. 2010) of attaching transmitters to the Estuarine Crocodile with some modifications.

Subsequent to capture, the nuchal rosette area of the crocodile was disinfected with povidone-iodine (Betadine) and injected with 20 ml Lignocaine (4 x 5 ml), a local anaesthetic. A sharpened stainless steel rod (355 mm in length and 3 mm in diameter, with a 2 mm hole drilled 25 mm posteriorly) were forced through the skin, 10 mm on the posterior side of the rosette and in line with the two left nucal scutes. The rod was guided subcutaneously with the aid of pliers under the osteoderms of the rosette, to the anterior side, where it was forced through the skin, 10 mm on the posterior side of the rosette. An 800 mm orthopaedic stainless steel wire (2 mm) was fed through the posterior hole in the rod and folded back onto the rod. The stainless steel rod was then drawn with the aid of pliers completely through the skin until the double stainless steel wire, now protruding on both sides of the nuchal rosette, were equal in length, approximately 150 mm depending on the size of the crocodile (Fig. 1a). One of the strands of wire was cut 5 mm from the posterior hole in the rod and the rod was removed. The rod was cleaned with absolute alcohol and a 400 mm single strand of nylon (100 kg breaking strain) was fed 100 mm through the posterior hole in the rod. The rod was then guided subcutaneously, following the stainless steel wire to the anterior side, where it was guided through the existing hole in the skin. The rod was then drawn with the aid of pliers completely through the skin until the nylon, now protruding on both sides of the nuchal rosette, were equal in length, approximately 150 mm. The exact procedure was now repeated for the two right nuchal scutes, until four wires and two strands of nylon was protruding both posteriorly and anteriorly from the nuchal rosette (Fig. 1a). The transmitter was positioned on the nuchal rosette with the aerial posterior. The subcutaneous wires and nylon were threaded through tubes along the bottom of the transmitter and the attachment loops were tightened and locked with crimped aluminium (Fig. 1b). Clear Vertex cold-curing dental acrylic (260 g) was mixed with Vertex cold-curing liquid (152 ml) and as soon as the mixture was clay-like, the four openings where wire and nylon was protruding through the skin, were covered. Additional acrylic was then used to complete a mould around the transmitter, maximising the surface area of contact between the rosette and the mould. Even though the acrylic used was cold-curing, due to considerable heat generated the transmitter and acrylic mould were cooled with cold water in the final stages of setting (Fig. 1c).

Prior to employing this technique in the field on a wild Nile Crocodile, we fitted a non-functional transmitter with similar specifications to an adult Nile Crocodile at the St Lucia Crocodile Centre under the supervision of Dr Dave Cooper, Ezemvelo Veterinarian. Approval for the research was obtained from the University of KwaZulu-Natal, Animal Ethics Research Committee, reference number: 014/12/Animal.

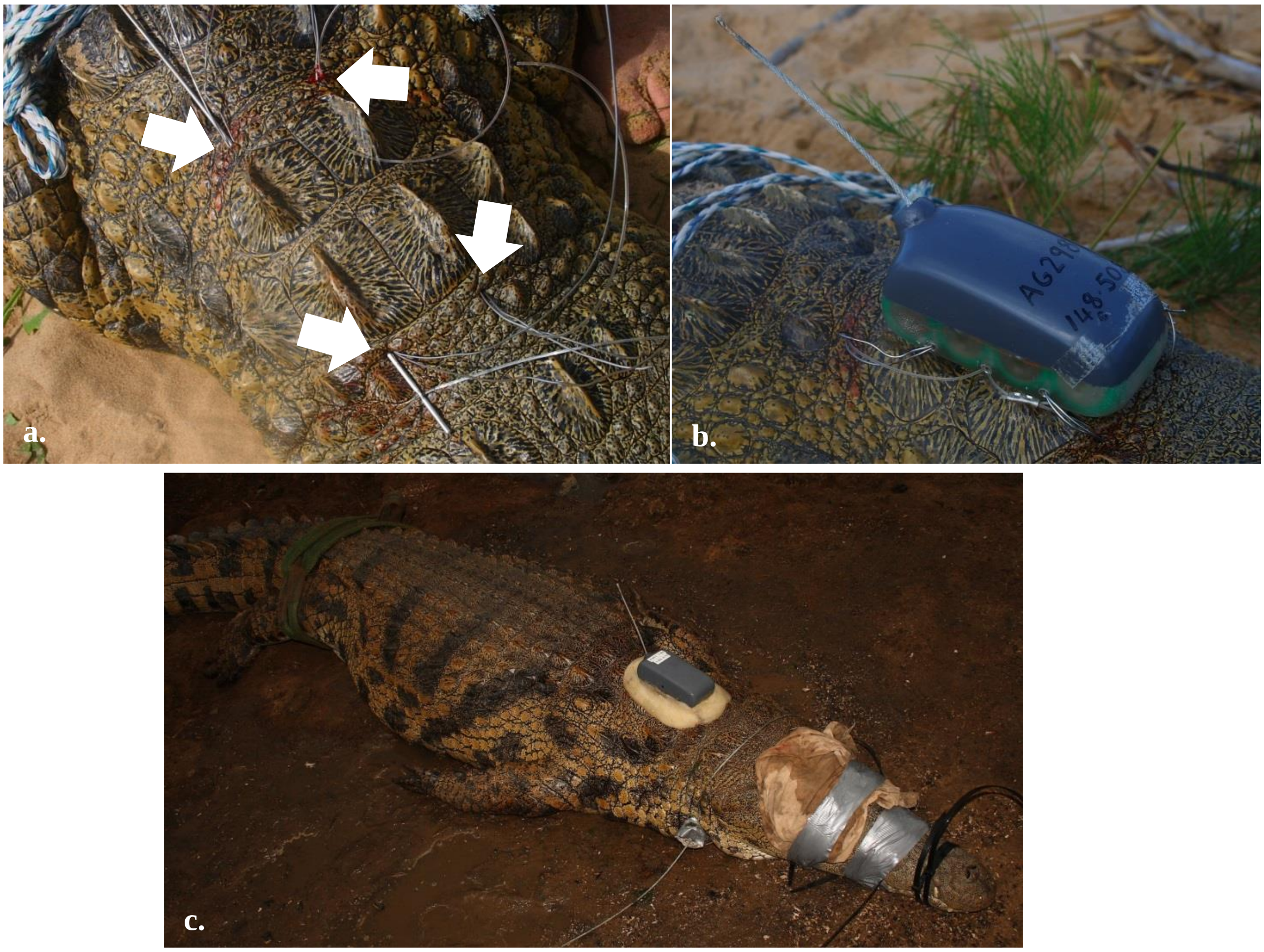


Figure 1. Transmitter attachment procedure, (a.) illustrate the subcutaneously rod, stainless steel wires and four localities where Lignocaine was administered, (b) the crimped transmitter before dental acrylic, and (c.) the crocodile prior to release.

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