EUROPEAN JOURNAL OF ECOLOGY

EJE 2017, 3(2): 67-76, doi: 10.1515/eje-2017-0015

Population surveys of Nile crocodiles (*Crocodylus niloticus*) in the Murchison Falls National Park, Victoria Nile, Uganda

Mathias Behangana[1], Wilber Lukwago [2], Daniele Dendi[3,4], Luca Luiselli[3,4,*], David Ochanda[5]

[1] National Biodiversity Data Bank (NBDB), Department of Environmental Management, Makerere University, P.O. Box 7062, Kampala, Uganda

[2] School of Forestry, Environment and Geographical Sciences, Department of Forestry, Biodiversity and Tourism, Makerere University P.O. Box 7062 Kampala, Uganda

[3] IDECC - Institute for Development, Ecology, Cooperation and Conservation, via G. Tomasi di Lampedusa 33, I-00144 Rome, Italy
*Corresponding author, E-mail:l.luiselli@ideccngo.org

[4] Department of Applied and Environmental Biology, Rivers State University of Science and Technology, P.M.B. 5080, Port Harcourt (Rivers State), Nigeria

[5] Total E & P Uganda, Department of Environment and Social Affairs, P.O. Box 34867, Kampala, Uganda

ABSTRACT

1. A 12-month-long survey (April 2013 to March 2014) for Nile crocodiles (Crocodylus niloticus) was conducted along a section of the Victoria Nile/Ramsar site of Murchison Falls National Park, in order to update the historic information on crocodile populations in the area, locating nesting areas, determining seasonality patterns and habitat use, and assess the current abundance and the population size trends since the 1960s. The methods employed included visual encounter surveys, transect counts and opportunistic methods, by using boats.
2. In general, there were diurnal and seasonal fluctuations in the number of crocodile sightings. The crocodile sightings peaked between the months of June and August, with the highest mean number of sightings encountered on any single day being 67 (in July 2013), and the second peak was between January and March with the highest mean of 118 recorded in January 2014. The second peak also coincided with the crocodile breeding season. This clearly shows that the distribution of the sub-population sampled followed a climatic regime.
3. Crocodiles were observed most frequently in water (37%). Grassy banks, islands, river mouths and sandy banks constituted about 47% of the habitats utilised by the crocodile population. Although basking was the most frequent type of activity performed by crocodiles (50%) over the entire survey period, their key activities varied significantly from month to month. Nesting was very visible during the last quarter of the year and the first quarter of the New Year.
4. There was a clear decline of the abundance of crocodiles in this population between 1960s and nowadays. This declining trend was obvious also taking into account the various survey methodologies employed over the decades.

KEYWORDS

Crocodiles; East Africa; natural history; management; conservation

INTRODUCTION

With a wide distribution in the eastern, central and southern Africa (Hekkala et al. 2011), the Nile crocodile (*Crocodylus niloticus*) has been intensively studied in terms of its population ecology (e.g., Cott 1961; Modha 1967; Hutton 1987; Kofron 1989; Wallace & Leslie 2008), with aspects of its conservation biology also being investigated in different regions of the continent (e.g., Bishop et al. 2009; Ashton 2010). In particular, the field studies on Nile crocodiles in Uganda have a long tradition, which started during the colonial age and continued after the country's independence, for instance Pitman (1952), Cott (1961, 1968, 1969), Parker (1969), Parker & Watson (1970), Baguma (1996) and Thorbjarnarson & Shirley (2009b, 2011). Some Nile crocodile populations have been among the most intensively surveyed reptile populations in the whole of Africa, thus achieving the role of study models for crocodilian biology research. The crocodile population inhabiting the section of the Victoria Nile between the delta and the Murchison Falls National Park (MFNP, Uganda) is one of such 'historically prominent' populations (Cott 1968; Thorbjarnarson & Shirley 2009a).

Despite its high conservation value, a number of development activities are currently being undertaken within the MFNP and surrounding landscape under the auspices of the Government of Uganda, including for instance oil and gas exploration, hydropower dams, railways and roads construction. In recent years, an overall declining trend of the MFNP crocodile population has been suspected by environmentalists and zoologists (M. Behangana, unpublished), possibly due to a plethora of causes including habitat disturbance and overhunting (also for the crocodile ranching initiatives). Thus, it has been widely thought by competent authorities that the status and population ecology of the MFNP crocodiles would need a reassessment (Plumptre et al. 2015).

European Journal of Ecology

This paper presents the results of a survey commissioned by Total E&P Uganda and was undertaken over a period of 12 months, in order to determine the population status, phenology, natural history and distribution of the crocodiles in the MFNP, with a focus on population size variations over time, habitat use, and seasonal distributions of crocodiles. In this regard, it should be mentioned that the Ugandan crocodile population inhabiting the stretch of the Victoria Nile below Murchison Falls has been subjected to commercial crocodile rancher (Uganda Crocs, Ltd) since 1991.

This survey provides the only data on the Nile crocodile sub-population obtained over a 12-month period for the Victoria Nile, Uganda. The specific objectives of the survey were to: undertake a comprehensive survey and determine key habitats utilised by the Nile crocodile in the survey area; (ii) assess the abundance and distribution of the Nile crocodile in these habitats and in relation to seasonal changes; (iii) assess activity patterns of the Nile crocodile such as breeding activity (through locating nesting areas and determining seasonality of breeding); (iv) determine the long-term abundance trends of the studied crocodile population throughout the decades.

1. STUDY AREA AND METHODS

1.1. Study Area

The field surveys were conducted along the Victoria Nile between the bottom of the falls and the Nile delta. The Victoria Nile River covers a distance of about 45 km from the bottom of the Murchison falls to the opening of the river into Lake Albert (36 N 318720 250713). Crocodile surveys were conducted between below the falls (36 N 352677 251538) and the beginning of the delta (36 N 324927 247556); the stretch of the river surveyed covering approximately 31 km. This area coincides with the Ramsar area. From the most downstream point of sampling, the river is relatively wider and deeper and interspersed with papyrus dominated islands that are continuous with the delta area. The banks are mostly dominated by extensive mats of *Vossia* grass, sometimes mixed with papyrus and *Leersia* grass on either bank. Further upstream near the Nile Safari Lodge, the large papyrus dominated islands end and the river is dotted with smaller islands with different vegetation composition thereafter until one passes Nyamusika cliff. Both river banks are dominated by either woody vegetation or grassy vegetation, with stream estuaries, mostly dry and sandy. The river becomes relatively narrower (about 100-200 m wide) and faster with strong movement of the current and rapids over rocky outcrops as one sails towards the falls. Big islands are located in areas that are shallow because there are high levels of soil and sand deposition.

1.2. Protocol

The field study was carried out between 6th April 2013 and 20th March 2014. The overall field effort by date of survey is reported in Table 1. In each field day, surveys began in the morning as early as 0700 hours (earliest) and ended in the afternoon (1700 hours) latest using a boat(s). All surveys were conducted by three persons, and started from the same spot (Paraa) moving either downstream or upstream in alternating days during the survey periods. The observers would keep an open eye on the banks and the waters in close proximity to the banks. Pairs of binoculars were used to aid the observers see crocodiles from a distance before they fled into water from the banks or submerged as the boat(s) approached. On encountering an individual, its size (length in metres) would be estimated, the bearing and its closest distance from the boat

Table 1. Summary of the crocodile survey periods and actual number of days spent in the field to observe the crocodiles

Activity	Dates	Total No. of Field days	Actual No. of days of survey
Reconnaissance	21 – 23 March 2013	3	2
Survey Trip 1	06 April – 13 April 2013	7	6
Survey Trip 2	27 April – 10 May 2013	14	12
Survey Trip 3	29 June – 9 July 2013	11	9
Survey Trip 4	30 July – 9 August 2013	11	7
Survey Trip 5	08 – 18 August 2013	11	9
Survey Trip 6	08 – 16 September 2014	10	8
Survey Trip 7	14 – 23 October 2014	10	6
Survey Trip 8	09 – 18 November 2014	10	4
Survey Trip 9	08 – 14 December 2013	7	5
Survey Trip 10	07 – 16 January 2014	9	8
Survey Trip 11	08 – 17 February 2014	9	8
Survey Trip 12	14 – 19 March 2014	6	4
	Total	118	88

were initially measured using a range finder but later, the bearing was read-off from a hand-held compass, while the distance was estimated by naked eye and its GPS location taken using a Garmin model GPSmap 60Cx.

Visual Encounter Surveys (VES) were conducted by the researchers, sailing along transects in the entire section of the river-course, visually searching for crocodiles and other herpetofauna. The number and sizes of crocodiles encountered were recorded and their locations geo-referenced. The habitats in which the crocodiles were encountered were also documented. VES method is recognized as useful to document the presence or absence of herpetofauna and is effective in most habitats and for most species that tend to breed in lentic habitats (Heyer et al. 1994). In addition, VES generates encounter rates of species in their habitats.

The following variables were recorded: abundance; (ii) habitat types; (iii) individual crocodile activity; (iv) crocodile size estimates; (v) distance of the sighted crocodile from boat at a bearing read from the compass; and (vi) weather conditions at the beginning and end of the survey

i) Abundance: this refers to the number of individuals sighted.

ii) Habitat classification: the habitat in which each individual was sighted was recorded. Since crocodiles are primarily nocturnal, spending nights in water and during the days they mostly bask in sun and stay cool in shade or water when necessary, we counted crocodiles in the various habitat types after the animals came ashore in the morning to bask in order to get more accurate counts (Huchzermeyer 2003). The following key habitat types were recorded:

a) Banks with woody vegetation

These were sections of the river that were covered with a significant proportion of shrubs and trees compared to grasses. The most dominant woody vegetation was *Acacia kirkii, Acacia sp. Harrisonia abyssinica, Sesbania sp., Albizia sp., Ficus sp.* and *Kigeria sp*.

b) River mouth (estuaries)

Here we are referring to the river mouth openings of the tributaries into the main river Nile. The river mouths of tributaries tended to attract all sizes of crocodiles (from juvenile to large). Most of them were sand beds during dry season and over flooded during wet season. Thus, compared to the 'sandy banks' described below, this habitat type was characterized by being ephemeral, thus being available during the dry season peaks.

c) Rocks

These comprised large boulders distributed along the edges of the river found mostly after the 'crocodile bar' (see below for a description) and below the falls.

d) Grassy banks

Grassy banks were dominated by grass (representing at least 80% of the vegetation), which varied in height. Most open banks were covered by grasses dominated by *Hyperrhenia* sp., *Panicum* sp., *Imperata cylindica, Cyperus* sp. and *Chloris* sp. All these grasses usually burned during dry seasons leaving a few remnants. The wetter parts (i.e., along the banks of the Nile) however retained their vegetation un-burnt throughout the whole year. The 'crocodile bar' was a special type of grassy bank where the highest congregations of crocodiles were recorded. It was a relatively raised ground between the main river and a lagoon closer to the land and found just below the Murchison Falls. It had open short grasses, for basking and a dense canopied tree that provided crocodiles with reliable shade.

e) Sandy banks

Sandy banks were stretches of river that touched water. These banks were bare, with no vegetation and covered by sand either as deposition from rivers or natural. This habitat category included only non-ephemeral sandy banks that were located along the Nyamusika cliff. Most sandy banks occurred just off the river mouths, representing a depositional zone. Their area however varied remarkably with season, being higher during the dry season than during the wet season. Despite sandy banks fluctuating in size (length and width) with season, their positions were stable throughout the whole year. They were more abundant as one moved upstream, especially on the northern bank in locations where the land gently sloped towards the water.

f) Islands

These were relatively extensive terrestrial-features found within the river and covered with dense grassy vegetation including *Cyperus* spp. and ephemeral sandy depositions.

g) Reeds

These were habitats dominated by *Vossia* and *Phragmites* grasses.

h) Muddy banks

These were the shallow banks of the river that regularly experienced over flooding. They were most times occupied by hippos and most of them were ephemeral.

i) Water

This was the main habitat; water in River Nile flows constantly and its volume is greatly influenced by season.

j) Papyrus

Habitats dominated by *Cyperus papyrus,* described as Papyrus habitats and found dominating the islands and most depositional river banks downstream, especially towards the delta area. They are important habitats for crocodile ecology, more so than other riverine habitats as feeding grounds for hatchlings and juveniles, while hiding from predators.

iii) Activity

The following activities engaged in by the crocodile population were investigated:

a) Basking: when a crocodile was observed in thermo-regulation under the sun.

b) Hiding: when a crocodile was seen camouflaged, hidden away from stronger rivals or ambushing in well vegetated sites.

c) Feeding: when a crocodile was observed while eating a given prey.

d) Nesting: when a female crocodile was observed while sitting on or next to their nests.

e) Fighting: when two or more animals were observed while being involved in territorial combats.

f) Resting: when a crocodile was seen motionless under shade, mostly along the river banks. Compared to the category 'hiding', 'resting' was attributed when the crocodile was in the open, whereas there was always a considerable degree of camouflaging when 'hiding'.

g) Fleeing: when a crocodile ran into water from the river banks; it was normally a mechanism of running away from a potential threat on either land or in distant waters.

h) Scouting: was the hunting behaviour of crocodiles while in water. They can either swim or float submerged under water with only their snouts out. Crocodiles also do scouting when looking out for potential danger from other animals such as human beings and hippos. They were, for example, seen scouting for the survey boat as it approached their nesting sites.

iv) Crocodile sizes: The estimated size of each crocodile sighted was ranked into three: big (> 4 m), medium (2–3.9 m), and small (< 2 m).

v) Perpendicular distance of the sighted crocodile from the boat: This was the distance of the sighted crocodile group or individual from the boat at a bearing read from the compass. At the beginning of the surveys, the distance was determined using a range finder. By the end of the second survey, the rangefinders either became faulty and or had no battery replacements (not available in Uganda). We then resorted to estimating the distance using the boat size. The large boat was about 10 metres long. We would then estimate about how many boats would fit into the distance to the position of the crocodile sighted. The perpendicular distance of each sighted crocodile from the boat trail was recorded. This ranged from zero distance (i.e., if very close to the boat) to about a kilometre, that is, as far as we could sight a crocodile with certainty. Beyond 1 km, the activity the crocodile(s) would be undertaking was not certain, and as such, only the number(s) of individual(s) sighted was recorded.

vi) Weather: The general weather conditions (rainy, sunny, cool, hot) of the previous evening and of the counting day (morning and afternoon) were assessed as well as the river water conditions (calm, ripples or with waves). The previous evening's weather conditions could influence the crocodile sightings in several ways: for example, if it rained very heavily the previous evening, the crocodiles might move upstream the tributaries and the rain pools elsewhere within the park, thus resulting in fewer sighting along the main course of the river the next day. It was also easier to sight crocodiles, especially in water, when the river was calm — that is — when there were no waves and ripples.

Opportunistic observations were also made outside the time of sampling along the stretch of the river surveyed. This *ad hoc* approach enabled the documentation of crocodiles outside the survey area to be made and a basic list to be compiled of other reptile species encountered.

In order to evaluate the long-term population trends of crocodiles, we collated literature data with present surveys, and considered in all cases only the highest number of different individuals clearly seen during a given field day. This procedure was necessary to avoid data pseudo-replication due to the same animals being seen multiple times during the surveys (for instance, in different field days).

1.3. Statistical analysis

The data collected was recorded into a field datasheet on a daily basis, and subsequently transferred into an excel sheet for data-basing before analysis. Variables that were not normally distributed were log-transformed prior to the application any parametric statistical test. Contingency χ^2 tests were used for comparisons between different frequencies. Correlations between field effort (per day and within each field trip, expressed in hours) and observed number of crocodile individuals were performed by using the Pearson's correlation coefficient. PASW statistical software (version 18.0) was used for the analyses, with all tests being two-tailed and alpha set at 5%.

2. RESULTS

2.1. Abundance and seasonality of crocodiles during the present survey

Crocodile roosts were widespread throughout the study area, but their concentration was clearly higher upstream (particularly on the northern bank) than downstream (Figure 1). A total of 6,336 sightings were made for the entire section of the river sampled during the study period (Table 2). The highest number of sightings recorded ever on a single day was 218 in January 2014. Overall, there was no significant correlation between the (log) mean number of individuals per day and the field effort (expressed as the (log) number of days in each field trip) (r = -0.31, n = 12, P = 0.324). However, in each trip, the (log) total number of sightings was significantly correlated with the (log) field effort (r = 0.703, n = 12, P < 0.05), thus showing that, within each trip, the more the days one spends in the field, the more animals are sighted.

A plot of the animals combined over the entire period of survey (Figure 2) shows a bi-peaked monthly pattern, significantly different from an equal activity intensity across months

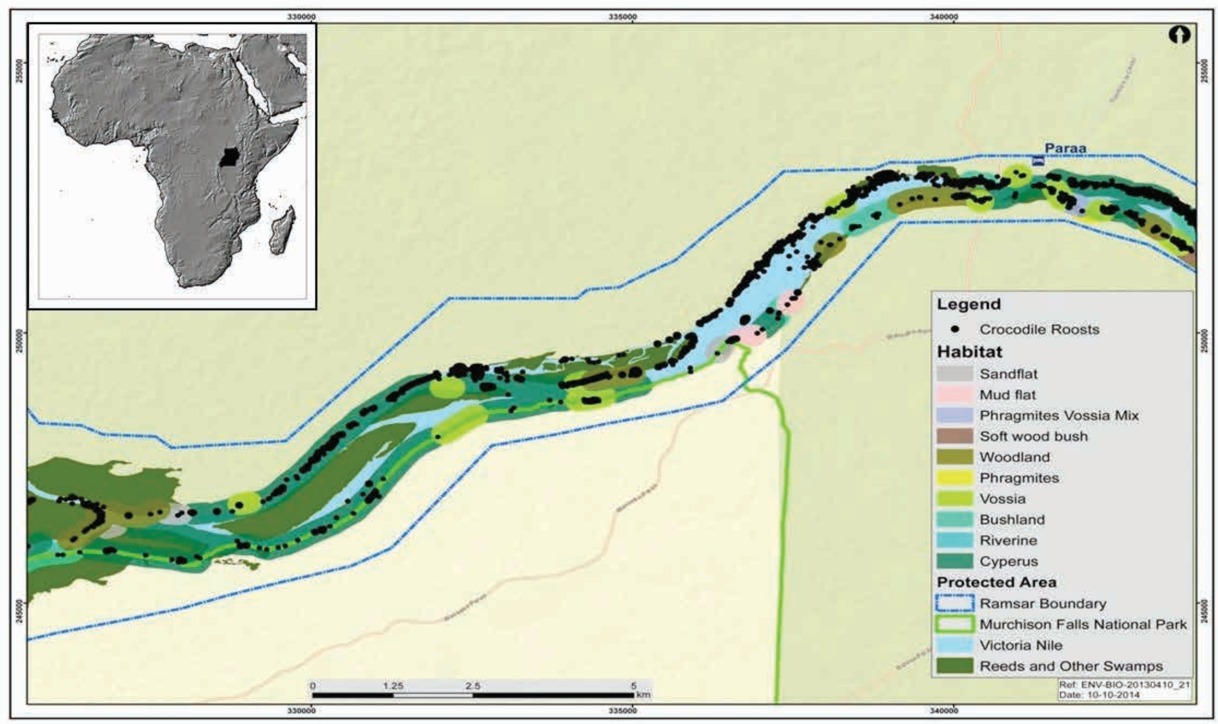

Figure 1. Map of the study area, showing the Nile river stretch that was surveyed during the field works, and the major habitat types available to crocodiles. The exact location of each crocodile sighting is also shown. Note that most crocodile sightings occurred in the northern bank of the river course.

Table 2. Number of crocodile sightings recorded per survey regime

Trip Number	Month of the year	Number of days	Total No. of Individuals	Mean No. of Individuals per day
1	April 2013	11	689	63
2	May 2013	12	685	57
3	June 2013	9	438	49
4	July 2013	7	467	67
5	August 2013	9	588	65
6	September 2013	8	458	57
7	October 2013	6	304	51
8	November 2013	4	269	67
9	December 2013	5	321	64
10	January 2014	8	942	118
11	February 2014	8	721	90
12	March 2014	4	454	114

(observed-versus-expected χ^2, df = 11, P < 0.01), with a lower peak in July–August and a higher peak between January and March.

2.2. Long-term variation in the apparent abundance of the MFNP crocodile population

The crocodile counts between the Paraa and Murchison Falls, 1967—2014, are given in Table 3. Pooling together all the survey methods, it appeared that the Nile crocodile population declined significantly (69% population decline) over time (P < 0.01; Figure 3). More interestingly, even considering the distinct survey methods separately, the decline was apparent. Using boats, the number of crocodile sightings declined from 420 in 1968 to 218 in 2013—2014 (Table 3). However, the highest number of sightings (218) recorded on a single day in January 2014 was the same number as Kaija-Baguma recorded in 1994/1995 – about 20 years ago. Using only aircraft counts, the apparent decline was even more significant: from about 700 in the late 1960s to less than 100 in 1990s (Table 3).

2.3. Habitat Use

During this survey, the crocodiles exhibited a clearly uneven habitat use (χ^2 with df = 9, P < 0.01). The most utilised habitats during daytime were water and grassy banks (37% respectively), followed by islands (8%), river mouths (7%), and sandy banks (6%) (Figure 4).

2.4. Crocodile Sizes

The body size was not estimated in 39% of the sighted crocodiles, because these individuals were either sighted from too far (> 200m) or almost totally submerged in water. Large adults were 21% of the surveyed population, medium sized animals accounted for 20%, while the small sized individuals represented 20% of the population.

2.5. Activity patterns

Overall, the commonest activity undertaken by most individuals overtime was basking (50%), mostly with open mouths facing the sun's direction (Figure 5). Since the survey was mostly done from morning to afternoon, this observation is in conformity with crocodile behaviour: crocodiles come ashore to bask in the morning sun and then take to shade or water when it gets too hot (Huchzermeyer 2003). The next commonest activity was scouting (41%), while resting took 4% of the crocodiles' time. Nesting took only 2% of the crocodiles' time, while fighting, feeding and hiding less than 1% each.

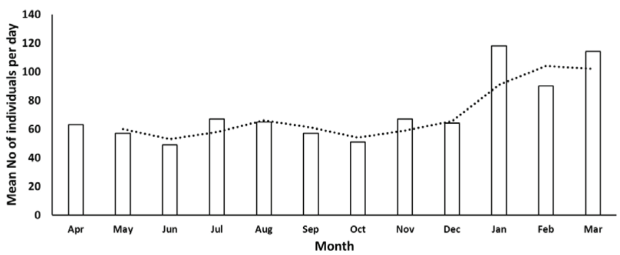

Figure 2. Monthly variation of the mean number of crocodiles observed in each day of survey at MFNP, over the 12-month period of survey. Dotted line would indicate the tendency line (mean between two adjacent periods)

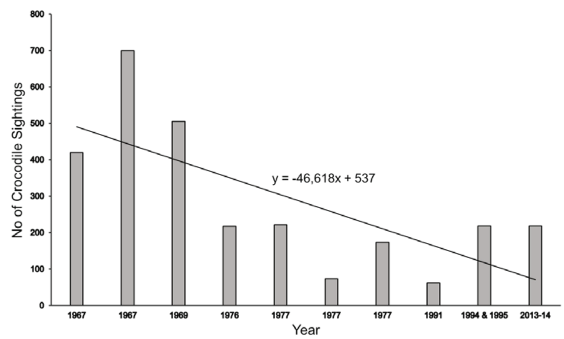

Figure 3. Crocodile population decline at MFNP, from the late 1960s through 2014

Table 3. Crocodile counts between Paraa and Murchison Falls, 1967–2014

Date	Year	Made by	Method	Total	Source
	1967	Fisheries Dept.	Boat	420	Cott, 1968
	1967	Parker	Aircraft	700	Cott, 1969
	1969	Parker and Watson	Aircraft	505*	Parker & Watson 1970
Sept	1976	Edroma	Aircraft	217	U.I.E Reports
March	1977	Edroma	Aircraft	221	U.I.E Reports
July–Sept	1977	Edroma	Aircraft	73	U.I.E Reports
Dec	1977	Edroma	Aircraft	173	U.I.E Reports
	1991	Hutton	Aircraft	61*	Hutton, 1991
	1994 & 1995	Kaija-Baguma	Boat	218*	UWA Report
	2013/14	Behangana et al.	Boat	218**	This paper

*Note: *counts from the foot of Murchison Falls to the Delta*
***highest count on a single day along the survey route*

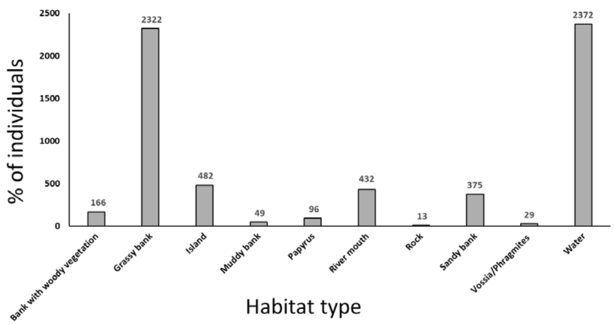

Figure 4. Percent distribution of the number of crocodile sightings across the key habitats, during the study period. Sample sizes are inserted above each bar.

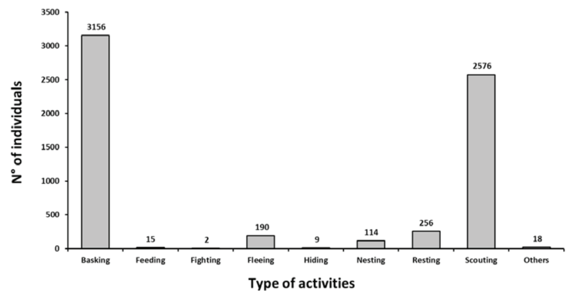

Figure 5. Overall number of observed crocodiles displaying the various types of activity during the whole study period

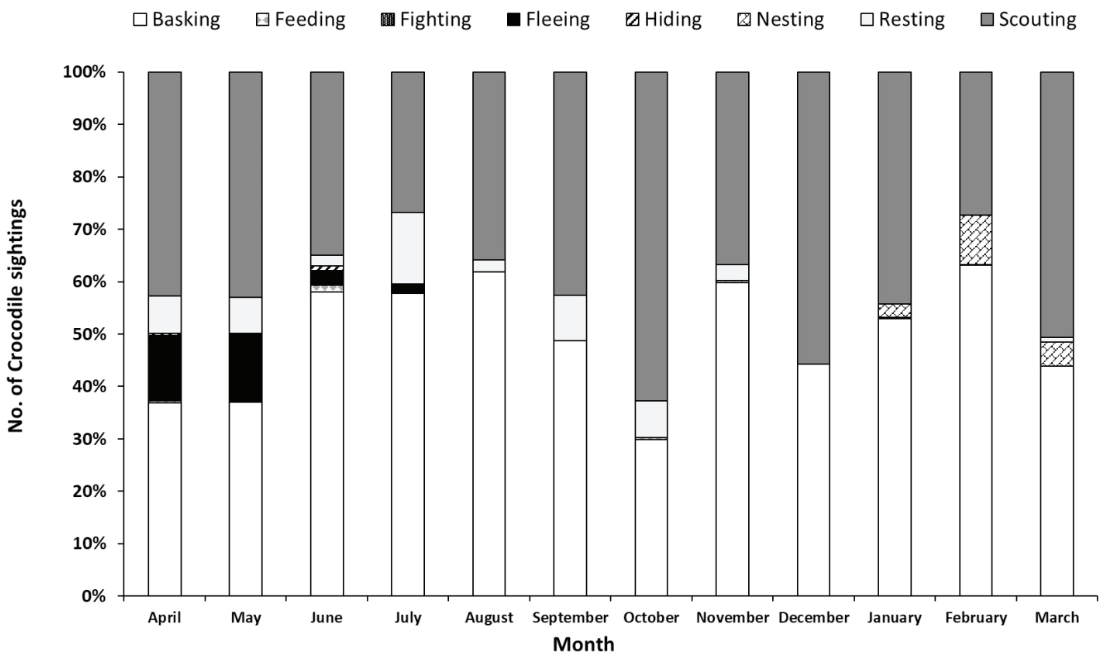

Figure 6. Key activities (expressed as monthly % of observed individuals) undertaken by the crocodiles over the 12-month survey period

The key activities varied significantly from month to month ($P < 0.001$ at χ^2 test, Figure 6). Whereas scouting and basking were the major activities in every other trip, resting and fleeing fluctuated considerably with some months having no records of these activities. Feeding was recorded in only six of the sampling trips. Nesting was visible during the last quarter of the survey with 25 nests recorded for January, 68 nests for February and 21 nests in March 2014. During the month of March 2014, hatchlings were recorded in grassy waters close to the nesting sites and the number of active nests with big crocodiles sitting over the nests had started to go down, while the number of juveniles was increasing.

3. DISCUSSION

Overall, our study highlighted that the crocodile sightings showed variations following the seasons during the year of survey. Indeed, the sightings were at their highest during the dry seasons (i.e., between June–August and January–March), being instead relatively low during the wet seasons (i.e., between April–June and August–November). This pattern was apparently related to the local bimodal rainfall regime. More specifically, there were both month-to-month and season-to-season variations in the mean number of individuals per day, with highest coefficient of variation during the dry season months. The high population densities during the last and first quarters of the year corresponded with the breeding seasons of the Nile crocodile. This time also corresponded with the end of the second wet season of the year and the beginning of the dry season.

Generally, in the last quarter of the year, the peak of crocodile sightings was due to the mating individuals pairing up in large numbers for mating before dispersing to breed (Behangana et al. unpublished observations). The sighting peak in the first quarter of the year was due to the many hatchlings that were added to the population, and that were easily observed during our field surveys. On the other hand, the low crocodile numbers along the River Nile during the rainy seasons were due to the river filling up and flooding the commonly used crocodile habitats, resulting in fewer crocodiles being sighted. Thus, the high sighting numbers during the last and first quarters of the year corresponded with the breeding seasons of the Nile crocodile in the study area. In this regard, it should be mentioned that activity peaks in correspondence with breeding events were frequently observed in reptiles (e.g., Bonnet et al. 1999; Filippi & Luiselli 2007).

Comparison between the results of the present survey with the available literature from the same crocodile population showed that the MFNP crocodiles have been declining considerably since the 1960s. Indeed, apparently the crocodiles reached their highest densities in the late 1960s, despite the different surveying methods employed in various surveys (for instance, aircraft versus boat) may have considerably affected the outcomes. The population appeared to have declined, along with much of the other wildlife, during the turbulent 1970s and 1980s (Lamprey et al. 2000). The crocodile population decline was apparent even considering the methods of surveys separately, and there was no evidence that the population had grown in the recent years, although the decline seemed to have in part stabilized during the last two decades. An obstacle to the re-growth of the population size of MFNP crocodiles may be that the site had been the source of eggs collected by a commercial crocodile rancher (Uganda Crocs, Ltd) since 1991. According to Thorbjarnarson & Shirley (2009a), a total of 32,686 crocodile eggs were collected from the nests in MFNP between 1991 and 2009. Up to our surveys, the collection exercise was reported to be still going on (unconfirmed reports). Thus, an updated monitoring of the egg collections by the commercial crocodile ranchers would be necessary to establish whether this activity was still sustainable, given the reduced population size of the MFNP crocodiles compared to some decades ago.

Unsurprisingly, the crocodiles showed an uneven preference for some habitat types (e.g., Laurent & Kingsbury 2003), as was also typically observed in Afrotropical reptiles (e.g., Muhigwa 1998; Eniang et al. 2015) including crocodiles (e.g., Cott 1961; Magnusson 1985; Luiselli et al. 2012). Outside the water habitat, grassy banks, islands, river mouths and sandy banks constituted about 47% of the habitats utilised by crocodiles, thus showing that these habitats were very important and should be appropriately preserved if we are to appropriately protect the crocodile population. River banks with short grass and sandy banks, where the crocodiles come out of water easily to bask, were therefore preferred as opposed to banks in deeper waters. The waters next to these banks were also shallower and therefore warm up easily such that a crocodile can easily stay firmly on solid substrate while being partly covered by water. There were also more crocodile roosts on the northern bank than the southern bank. This was because the northern bank is generally east-facing and therefore preferred by the crocodiles in the morning. There is also more diversity of habitats on the northern bank than the southern bank.

As expected, crocodiles are primarily nocturnal animals spending nights in water and during the days they mostly bask in sun and stay cool in shade or water when necessary (Cott 1961). This was corroborated by the data collected during the survey with 37% of the time being spent in water during the day when the surveys were conducted, while 63% of the time was spent in other terrestrial habitats. Depending on weather and season, there was a considerable variation in the type of activities performed by crocodiles.

In MFNP, 41% of the sighted crocodiles were either big adults or medium sized adults, thus possibly implying that the breeding population was still relatively healthy. However, no such data are available for historical surveys, thus impeding us to assess whether the body size distribution of the local crocodile population has changed over the years. We suggest that the monitoring of the body size distribution of MFNP crocodiles should be continued in order to detect eventual temporal changes.

Our surveys had however some limitations. To begin with, evening and night-time spotlight surveys to search for crocodiles and their nests were not conducted. Yet this is one of the standard methods for estimating crocodile population size. Night surveys were not performed because permit to work at night was not granted due to safety concerns. Second, there was no opportunity to catch and measure the sizes of crocodiles. As such, size estimates were assigned to the individual crocodiles and the reproductive condition of the various crocodiles could not be precisely assessed. Third, only boats were used during these surveys. Their noise could have caused some crocodiles to flee before being sighted. Fourth, there were interferences from tourists. In some occasions, these tourists would scare away the crocodiles before being sighted by the survey team.

3.1. Conservation considerations

MFNP crocodile population was subject to: (i) tourism-linked disturbance and (ii) the risks coming from the exploration aquatic seismic activities.

Concerning threat (i), crocodiles fled whenever the survey boat approached. We had to use binocular to sight some of the crocodiles before they fled into water. Crocodiles have also been fleeing from other boats including the tourist boats (our unpublished observations). With increase in tourist traffic along the river, this threat will also increase. This will probably disrupt crocodile activities including breeding.

Concerning threat (ii), the immediate potential impact to crocodiles was the seismic survey activity across the Nile, which is however now completed and thus not a threat anymore. Seismic surveys involve the use of high energy, low frequency noise sources operated in the water column to probe below the bed. Almost all routinely used seismic sources involve the rapid release of compressed air from an air gun, towed behind the boat, to produce a pulse that is directed downward towards the bed, to be reflected upwards again by the density or velocity discontinuities within the underlying rock strata (Payne et al. 2008). The potential impacts of seismic activity are also not spatially homogenous (Hovem et al. 2012). The pulses initiated by aquatic seismic are broad band (most energy being concentrated in the 10 – 200 Hertz (Hz) frequency range, with lower energy levels in the 200 – 1000 Hz range). The airguns are fired repeatedly as the vessel traverses an area of interest. In a typical survey, the sound levels from the airgun array are in the range of 200 – 250 dBrms re 1uPa at 1m. Typically, the boat traversed the Nile at a speed of approximately 1 km/hour, emitting a bubble period of 58 / 101.5 ms directed down through the water column. Although the disturbance effects of seismic activities on crocodile activity can be predicted, however, we did not collect any quantitative data on the eventual effects that such seismic explorations would have on the local crocodile population. In addition, future oil development work, in and around the Nile, that have the potential to impact crocodile behaviour and population status will include the construction of a ferry crossing. Careful monitoring of the crocodile population should therefore be continued by competent agencies also in view of these ongoing anthropogenic pressures and disturbances.

ACKNOWLEDGEMENTS

This work was funded by TOTAL E&P Uganda BV, supported by National Biodiversity Data Bank and Geo-Taxon Consult Ltd under a service contract to survey crocodiles in the Victoria Nile, Ramsar Site area of Murchison Fall National Park. We acknowledge the field assistance of Ms Dorcas Atuhaire and Ronald Asiimwe. We thank the Uganda Council of Science and Technology for granting us the Research Permit and Uganda Wildlife Authority for the field support and providing us with permit to conduct research in Murchison Falls National Park. Finally, we are greatly indebted to the Government of Uganda, specifically the Petroleum Authority of Uganda for approving this study, that was designated to allow proper mitigation measures to be put in place during oil and gas exploration activities. Dr Laurent Chirio (Paris, France) and one anonymous referee critically reviewed and improved the submitted draft.

REFERENCES

Ashton, P.J. (2010) The demise of the Nile crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in South Africa: The case of the Olifants River. Aquatic Conservation: Marine and Freshwater Ecosystems, 20, 489–493.

Baguma, R.K. (1996) Some ecological aspects of the Nile crocodile (*Crocodylus niloticus*) in Murchison Falls National Park, Uganda. Master's Degree Programme Progress Report 11/96 to UWA, March 1996.

Behangana, M. (2014) Surveying crocodiles in the Victoria Nile/Ramsar Site of Murchison Falls National Park. Reference: pr. 10001203. Geo-Taxon Consult Ltd., Kampala, Uganda, pp. 67.

Bishop, J.M., Leslie, A.J., Bourquin, S.L. & O'Ryan, C. (2009) Reduced effective population size in an overexploited population of the Nile crocodile (*Crocodylus niloticus*). Biological Conservation, 142, 2335–2341.

Bonnet, X., Naulleau, G. & Shine, R. (1999) The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation, 89, 39–50.

Cott, H.B. (1961) Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and northern Rhodesia, Transactions of the Zoological Society of London, 29, 211–358

Cott, H.B. (1968) The Status of the Nile crocodile below Murchison Falls. Report to the Uganda National Parks, Kampala, Uganda. 9 pp.

Cott, H.B. (1969) Further observations on the status and biology of the Nile crocodile below Murchison Falls. Report to Uganda National Parks. Report to the Uganda National Parks, Kampala, Uganda. 12 pp.

Eniang, E.A., Akani, G.C., Vignoli, L., Luiselli, L. & Petrozzi, F. (2015) Size-related habitat selection of a population of Nile monitors (*Varanus niloticus*) from western Nigeria. African Journal of Ecology, 53, 246–248.

Filippi, E. & Luiselli, L. (2007) Non-random seasonal variation in the structure of a Mediterranean snake community. Web Ecology, 7, 40–46.

Hekkala, E., Shirley, M.H., Amato, G., Austin, J.D., Charter, S., Thorbjarnarson, J., Vliet, K.A., Houck, M.L., DeSalle, R. & Blum, M.J. (2011) An ancient icon reveals new mysteries: mummy DNA resurrects a cryptic species within the Nile crocodile. Molecular Ecology, 20, 4199–4215.

Heyer, W.R., Donnely, M.A., Mc Diarmid, R.W., Hayek L.C. & Foster M.S. (Eds.) (1994) Measuring and Monitoring Biological Diversity: Standard Methods for Reptiles and Amphibians. Smithsonian Institution Press, Washington.

Hovem, J.M., Tronstad, T.V., Karlsen, H.E. & Lokkeborg, S. (2012) Modeling Propagation of Seismic Airgun Sounds and the Effects on Fish Behavior. IEEE Journal of Oceanic Engineering, 37, 576–588.

Huchzermeyer, F.W. (2003) Crocodiles: biology, husbandry and disease. CAB International, Wallingford.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. Ecological Monographs, 54, 187–211.

Hutton, J.M. (1987) Growth and feeding ecology of the Nile crocodile *Crocodylus niloticus* at Ngezi, Zimbabwe. Journal of Animal Ecology, 1987, 25–38.

Hutton, J.M. (1991) Crocodiles and their management in the Murchison Falls National Park of Uganda. Agriconsulting/Uganda Institute of Ecology, Kampala, Uganda.

Kofron, C.P. (1989) Nesting ecology of the Nile crocodile (*Crocodylus niloticus*). African Journal of Ecology, 27, 335–341.

Krebs, C.J. (1966) Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs, 36, 239–273.

Krebs, C.J. (1999) Ecological Methodology, 2nd ed. Harper and Row Publ., New York, N.Y.

Lamprey R.H., Michelmore, F., Buhanga, F., Okecha, E., Omoding, J., Egunyu, J., Mukwaya, F.G., Behangana, M., Mafumbo, J. & Tiyoy, L. (2000) Protected Area Systems Plan for Uganda, Vol. 4 Uganda Wildlife Authority, Kampala.

Laurent, E.J. & Kingsbury, B.A. (2003) Habitat separation among three species of water snakes in Northwestern Kentucky. Journal of Herpetology, 37, 229–235.

Luiselli, L., Akani, G.C., Ebere, N., Angelici, F.M., Amori, G. & Politano, E. (2012) Macro-habitat preferences by the African manatee and crocodiles – ecological and conservation implications. Web Ecology, 12, 39–48.

Magnusson, W.E. (1985) Habitat selection, parasites and injuries in Amazonian Crocodilians. Amazoniana, 9, 193–204.

Modha, M.L. (1967) The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. African Journal of Ecology, 5, 74–95.

Muhigwa, J.B. (1998) Diel activity and biotope choices of the Nile Monitor Lizard in western Kenya. African Journal of Ecology, 36, 271–275.

Parker, I.S.C. (1969) Crocodile Distribution and Status in the Major Waters of Western and Central Uganda. African Journal of Ecology, 8, 85–103.

Parker, I.S.C. & Watson, R.M. (1970) Crocodile Distribution and Status in the Major Waters of Western and Central Uganda in 1969. East African Wildlife Journal, S, 85–103.

Payne, J.F., C. Andrews & Fancey, L. (2008) Potential effects of seismic energy on fish and shellfish: an update since 2003. Can. Sci. Advis. Sec. Res. Doc.2008/060, Ottawa, Canada.

Pitman, C.R.S. (1952) Pigmy crocodiles in Uganda. The Uganda Journal 16(2), 119–124.

Plumptre, A.J., Ayebare, S., Mugabe, H., Kirunda, B., Kityo, R., Waswa, S., Matovu, B., Sebuliba, S., Behangana, M., Sekisambu, R., Mulondo, P., Mudumba, T., Nsubuga, M., Isoke, S., Prinsloo, S. & Nangendo, G. (2015) Biodiversity surveys of Murchison Falls Protected Area. Wildlife Conservation Society, Kampala, Uganda, pp. 26.

Thorbjarnarson, J. & Shirley, M.H. (2009a) Observations on Nile Crocodiles (*Crocodylus niloticus*) and their Management in Murchison Falls National Park. A Report to the Wildlife Conservation Society and the Uganda Wildlife Authority, Kampala, Uganda.

Thorbjarnarson, J. & Shirley, M.H. (2009b) Population Assessment of the Nile Crocodile (*Crocodylus niloticus*) in Kidepo Valley National Park, northern Uganda. A Report to the Wildlife Conservation Society and the Uganda Wildlife Authority, Kampala, Uganda.

Thorbjarnarson, J. & Shirley, M.H. (2011) Evaluation of the populations of Nile Crocodile (*Crocodylus niloticus*) and Congo Dwarf Crocodile (*Osteolaemus osborni*) in Queen Elizabeth and Lake Mburo National Parks, Uganda. Wildlife Conservation Society, Kampala.

Wallace, K.M., & Leslie, A.J. (2008) Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. Journal of Herpetology, 42, 361–368.