Estimating demographics of the Nile crocodile (*Crocodylus niloticus* Laurenti) in the panhandle region of the Okavango Delta, Botswana

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Abstract

The population status of the Nile crocodile (*Crocodylus niloticus* Laurenti) in the panhandle region of the Okavango Delta, Botswana, was assessed using mark–recapture and spotlight survey techniques following a decline because of commercial utilization. A total of 1717 individuals, ranging from 136 to 2780 mm in Snout Vent Length, were captured over a 4-year period. Eighty-one per cent of young juveniles encountered were successfully captured, representing 59.3% of total captures and 75% of recaptures. A Bayesian technique was used to estimate the number of young juveniles, and these estimates were then extrapolated for the other size classes. Survival and recapture analyses highlighted individual size-dependent increases in wariness and survival. The total annual population was estimated to be $2570 \pm 151.06$ individuals, with an adult population of 649.2 individuals, including 364 females. We suggest that the harvest of breeding animals for commercial purposes should be halted until population recovery in this region is established.

Key words: Nile crocodile, Okavango Delta, population ecology

Introduction

The effective conservation and management of world crocodilians often involves a range of management interventions (for example, strict protection to harvesting), depending on the status of the species, their habitats and the national context within which crocodilians and people interact. The ability to quantify the relative and/or absolute abundance of a population, and population structure in terms of juveniles versus adults, is fundamental to management.

Throughout their range in Africa, widespread crocodile eradication programs were implemented in the 1930s and continued into the 1960s with the added incentive of selling hides (Cott, 1961; Parker & Watson, 1970). This slaughter abated when international trade came under control of the Convention on International Trade in Endangered Species of Wild Fauna and Flora in 1975. Today, Nile crocodiles are on Appendix II in Botswana.
Ethiopia, Kenya, Malawi, Mozambique, South Africa, Tanzania, Zambia and Zimbabwe (CITES, 2007). In the other 33 range states, they are listed as CITES Appendix I. The main factors reducing Nile crocodile populations have been unsustainable hunting for skins, meat and pest control, and both habitat loss and pollution (Cott, 1961; Abercrombie, 1978; Thorbjarnarson, 1992). The Crocodile Specialist Group of the IUCN has recommended different management strategies to sustain different national populations of Nile crocodiles, depending on their current status (Thorbjarnarson, 1992).

The Nile crocodile population in the Okavango Delta has undergone three periods of human-induced decline over the last century. In 1957, the Department of Wildlife and National Parks (DWNP) allowed a quota of 2000 animals per year for the hide-trade, to each of two concessionaries. Between 1957 and 1969, although 40,000–50,000 crocodiles were thought to have been killed/traded (Taylor, 1973; Pooley, 1982), c. 80,000 crocodiles may actually have been removed because some estimates indicate that only 50% of crocodiles shot were recovered (Taylor, 1973).

In 1973, the DWNP set a quota of 500 animals per year for the Botswana Game Industries to resume hide-hunting (Graham, Simbotwe & Hutton, 1992). This quota was filled in 1973, but only 440 crocodiles were shot in 1974 and the venture was thus regarded as uneconomic and disbanded (Taylor, 1973). After a decade of no exploitation, crocodile farmers removed 1053 live adults for captive breeding and 14,000 eggs from the system in the period 1983–1988 for commercial use in ranching operations. According to an aerial nesting survey conducted by DWNP in 1987, this led to an estimated 50% reduction in the breeding population (10,000 individuals) (Simbotwe & Matlhare, 1987). Subsequently, from 2004 to 2006, a local crocodile farm harvested 2000 eggs per year. In addition to this, disturbance by boat motors (Mbaiwa, 2002), fires and destruction of nests and eggs by fishermen (Shacks, 2006), habitat loss, crocodile/human conflict (Thomas, 2006) and pollution are contributing to the crocodiles decline in the Okavango.

A good understanding of population dynamics and status is required where harvesting strategies seek the maximum sustained yield (Tucker, 1995; Bradshaw et al., 2006). The aim of this study was to estimate population abundance using capture–mark–recapture and spotlight survey techniques and to model survival and recapture rates to assess the overall status of the Nile crocodile population in the panhandle region of the Okavango Delta.

Materials and methods

Study site

This study was undertaken in 300 km of permanent channels within the northern Okavango system, known as the ‘panhandle’ region, in Botswana. The panhandle and the upper part of the Delta forms a permanent swamp with Papyrus and Phragmites spp. as the dominant vegetation types and the Delta’s southern parts forming seasonal floodplains. Annual rains begin in October and continue through February with water flow augmented by rainfall from the Angolan catchments. Warm/hot conditions prevail during most of the year (Mendelsohn & El Obeid, 2004). The Delta is a closed system where all recruitment into the crocodile population occurs through breeding and 99% of breeding occurs in the panhandle (Graham, Simbotwe & Hutton, 1992).

Capture–mark–recapture (CMR)

A continuous CMR programme was conducted from January 2002 to December 2006. Crocodiles were located at night along predetermined nonoverlapping transects using a boat and spotlight and captured by hand or noose. Animals were sampled with replacement (Underhill, 1990), and each animal was permanently marked by scute-clipping. Larger crocodiles (>1400 mm Snout Vent Length (SVL)) were fitted with numbered, coloured plastic tags. All crocodiles were assigned to size classes based on SVL (Bourquin, 2008). A global positioning system position was recorded at the site of capture, and water and air temperatures were recorded at intervals throughout each survey period. Crocodiles were sexed by visual inspection of the cliteropenis (Leslie, 1997). Subadult and adult crocodiles were used to determine the sex ratio of breeding animals (breeders or imminent breeders), while smaller crocodiles were excluded from the calculation because of higher mortality rates (Webb & Manolis, 1993).

Size class distribution

The lengths of all crocodiles encountered, but not captured, between June 2004 and October 2006 were estimated to determine size class distribution. When croc-
odiles submerged before obtaining a reliable size estimate, they were recorded as ‘eyes only’. If captured, a number of morphometric measurements were taken including total length (TL), SVL, neck and tail-base circumference and various head measurements. Size classes (SVL) were defined as: hatchlings < 169 mm (0–1 years old), young juveniles 169–389 mm (1–4 years old), juveniles 390–663 mm, subadults 664–1158 mm, adults > 1158 mm (Bourquin, 2008).

Data analysis

Although sampling took place continuously throughout the panhandle, data were separated into northern and southern panhandle datasets. Crocodiles in the northern panhandle region were exposed to higher levels of human-induced disturbance than in the south (Shacks, 2006) and as early as 1973, a north/south separation was evident within the population (Taylor, 1973). We assumed that crocodiles in the northern panhandle region would be more wary of people, thus violating the assumptions of the CMR models because of differing capture probabilities between the two regions. We used size as an indicator of age because of our lack of data on size/age relationships and determined the minimum size of adults from data collected by Detoeuf-Boulade (2006).

Survival and recapture estimates

The software program MARK version 3.2 (White & Burnham, 1999) was used to determine the most parsimonious Cormack–Jolly–Seber (Cormack, 1964; Jolly, 1965; Seber, 1965) model to fit the capture–mark–recapture data, for the estimation of survival and recapture probability. The latter were constrained to be linear functions of body length (SVL) by forcing MARK to estimate survival and recapture probabilities after imposing a specific set of linear constraints, in this case SVL, on the structure of the underlying model. Models follow the notation in Lebreton et al. (1992).

Survival and recapture parameters for the models were estimated using maximum likelihood approaches (Cooch & White, 2005), and models were evaluated using likelihood-based approaches. Models were ranked based on Akaike’s information criterion, a second-order correction for small sample sizes (AICc) (Akaike, 1973). AICc ranking was also used to test for sources of variation in the selected models. Where models were nested, likelihood ratio tests (LRT) were used to compare models (Cooch & White, 2005). All SVL measurements were z-transformed, and survival and recapture probabilities were calculated (Pollock, Hines & Nichols, 1984).

Population estimates

We utilized a Bayesian approach (Du Feu, Hounsome & Spence, 1983; Underhill & Fraser, 1989; Underhill, 1990) to estimate the annual population size of young juveniles, as they were generally not wary and had the highest capture and recapture rates. Demographic closure was assumed (see also Kay, 2004) for this size class. The abundance of larger crocodiles was then extrapolated based on size class distribution data from all crocodiles that were encountered. The northern panhandle recaptures were low, resulting in unacceptably high upper and lower confidence limits, allowing for a 2002 population estimate only.

Results

General

A total of 1717 individuals were captured (January 2002–December 2006) ranging in size from 136 to 2780 mm SVL. Overall, 148 (8.6%) hatchlings, 1018 (59.3%) young juveniles, 311 (18.1%) juveniles, 177 (10.3%) subadults and 63 (3.7%) adults were captured. A total of 224 crocodiles were recaptured once, 44 twice, seven were recaptured three times and one was recaptured five times. A total of 75.0% of recaptures were young juveniles (Fig. 1), and 81.0% of all the young juveniles encountered were captured.

Model selection and testing

No gender-specific differences in survival or recapture rates for young juveniles were evident; therefore, males and females were combined for the analyses. The most parsimonious model, according to the AICc values, was the model Phi(SVL)p(SVL) (Table 1). The models making up the selected suite were subjected to a LRT to test for significant differences between them. The model in which both survival and recapture probabilities were constrained [Phi(SVL)p(SVL)] or where either parameter was constrained [Phi(SVL)p(.); Phi(.p(SVL))] and were significantly different from other less constrained models, suggesting that the AICc ranking of this model was valid (Table 2).
Estimating survival and recapture probabilities

It is common for large crocodilians to be more wary than small ones (Webb & Messel, 1979; Ron, Vallejo & Asanza, 1998), resulting in heterogeneous capture probability, and it is also common for age-specific survival rates to increase with increasing size (Kay, 2004). In this study, the expected trends of increasing wariness and survival with increasing size were confirmed using the Cormack–Jolly–Seber model. Both survival and recapture rates were

![Graph showing percentage of young juveniles recaptured from 2002 to 2006 in the study area. The figures above columns represent the percentage of total annual recaptures of young juveniles. Striped columns represent the southern panhandle data, while clear columns represent the northern panhandle data.](image)

**Figure 1** The proportion of young juveniles as recaptures from 2002 to 2006 in the study area. The figures above columns represent the percentage of total annual recaptures of young juveniles. Striped columns represent the southern panhandle data, while clear columns represent the northern panhandle data.

**Table 1** The selected models ranked according to Akaike’s information criterion (AIC), with the most parsimonious model, as ranked by the AICc (the corrected AIC), listed in order from most parsimonious to least parsimonious.

<table>
<thead>
<tr>
<th>Cormack–Jolly–Seber model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>AICc weight</th>
<th>Model likelihood</th>
<th>No parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phi(SVL)p(SVL)</td>
<td>518.358</td>
<td>0</td>
<td>0.79002</td>
<td>1</td>
<td>4</td>
<td>510.314</td>
</tr>
<tr>
<td>Phi(SVL)p(.)</td>
<td>522.346</td>
<td>3.99</td>
<td>0.10752</td>
<td>0.1361</td>
<td>3</td>
<td>516.32</td>
</tr>
<tr>
<td>Phi(SVL)p(t)</td>
<td>522.346</td>
<td>3.99</td>
<td>0.10752</td>
<td>0.1361</td>
<td>3</td>
<td>516.32</td>
</tr>
<tr>
<td>Phi(.)p(.)</td>
<td>524.728</td>
<td>6.37</td>
<td>0.03268</td>
<td>0.0414</td>
<td>2</td>
<td>520.715</td>
</tr>
<tr>
<td>Phi(.)p(t)</td>
<td>529.827</td>
<td>11.47</td>
<td>0.00255</td>
<td>0.0032</td>
<td>6</td>
<td>517.736</td>
</tr>
</tbody>
</table>

**Table 2** The Maximum-likelihood ratio test results for the selected models in this study. Only the model in which both survival or recapture probabilities were constrained [both survival and recapture probabilities constrained by time or size – Snout Vent Length (SVL)] by SVL [Phi(SVL)p(SVL)] was marginally significantly different from the unconstrained model.

<table>
<thead>
<tr>
<th>Reduced model</th>
<th>General model</th>
<th>Chi-square ($\chi^2$)</th>
<th>Degrees of freedom</th>
<th>Probability (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phi(.)p(SVL)</td>
<td>Phi(SVL)p(SVL)</td>
<td>5.808</td>
<td>1</td>
<td>0.016</td>
</tr>
<tr>
<td>Phi(SVL)p(.)</td>
<td>Phi(SVL)p(SVL)</td>
<td>6.006</td>
<td>1</td>
<td>0.0143</td>
</tr>
<tr>
<td>Phi(.)p(.)</td>
<td>Phi(SVL)p(SVL)</td>
<td>10.401</td>
<td>2</td>
<td>0.0055*</td>
</tr>
<tr>
<td>Phi(.)p(SVL)</td>
<td>Phi(SVL)p(t)</td>
<td>2.902</td>
<td>2</td>
<td>0.2343</td>
</tr>
<tr>
<td>Phi(.)p(.)</td>
<td>Phi(.)p(SVL)</td>
<td>4.592</td>
<td>1</td>
<td>0.0321</td>
</tr>
<tr>
<td>Phi(SVL)p(.)</td>
<td>Phi(.)p(t)</td>
<td>3.1</td>
<td>2</td>
<td>0.2123</td>
</tr>
<tr>
<td>Phi(.)p(.)</td>
<td>Phi(SVL)p(.)</td>
<td>4.395</td>
<td>1</td>
<td>0.0361</td>
</tr>
<tr>
<td>Phi(.)p(.)</td>
<td>Phi(SVL)p(t)</td>
<td>7.495</td>
<td>3</td>
<td>0.0577</td>
</tr>
<tr>
<td>Phi(.)p(.)</td>
<td>Phi(t)p(t)</td>
<td>2.979</td>
<td>4</td>
<td>0.5613</td>
</tr>
</tbody>
</table>

*P < 0.05.
significantly affected by the size of the crocodiles, with smaller animals experiencing higher mortality despite a higher rate of being recaptured (Fig. 2).

**Population estimate**

The size class distribution data included 188 night shifts during which 2687 crocodiles were encountered. Of these, 1001 (37.2%) were successfully captured, and 452 (16.8%) were recorded as ‘eyes only’. Young juveniles (n = 772) constituted one-third of the size-estimated or measured crocodiles (n = 2235), while adult crocodiles made up 28.7% (n = 642) of them.

Estimates for population size were obtained separately for each year and for the northern and southern young juvenile populations. Data were too sparse to estimate the northern panhandle young juvenile population from 2003 to 2006, and the southern young juvenile population in 2002. The annual average population estimate of young juveniles (≤ age 4) for the southern section of the panhandle was 539 ± 146, and the 2002 estimate for the northern panhandle was 305 (95% CI = 251–373) individuals (Table 3). The total number of young juveniles estimated at any given time for the entire panhandle was 857 individuals; therefore, c. 25% would be the annual number of new recruits into the population. The total annual Nile crocodile population was estimated at 2570 ± 151 individuals after extrapolating from the size class distribution data. The harmonic mean of the number of adults estimated annually (2003–2006) was 649 individuals (for full survey data sets refer to http://www.unep-wcmc.org).

### Table 3 Young juvenile population estimates calculated using the Bayesian method. Data were separated into northern and southern panhandle data sets as per Fig. 1

<table>
<thead>
<tr>
<th>Year</th>
<th>Recapture rate</th>
<th>Population estimate</th>
<th>Lower limit</th>
<th>Upper limit</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Southern panhandle</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2002&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td>No estimate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.16</td>
<td>477.8</td>
<td>345</td>
<td>668</td>
</tr>
<tr>
<td>2004</td>
<td>0.1</td>
<td>471.5</td>
<td>301</td>
<td>746</td>
</tr>
<tr>
<td>2005</td>
<td>0.09</td>
<td>756.9</td>
<td>542</td>
<td>1063</td>
</tr>
<tr>
<td>2006</td>
<td>0.05</td>
<td>448</td>
<td>287</td>
<td>709</td>
</tr>
<tr>
<td><strong>Northern panhandle</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2002</td>
<td>0.25</td>
<td>304.5</td>
<td>251</td>
<td>173</td>
</tr>
<tr>
<td>2003&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>No estimate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>No estimate</td>
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<tr>
<td>2005&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>No estimate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>No estimate</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>No recaptures.
<sup>b</sup>Recapture data too sparse to estimate yearling population.

### Sex ratios

Sex ratios revealed a significant male bias for young juveniles and juveniles (61.8%, P < 0.05 Chi-squared test, n = 849 and 61.2%, P < 0.05, n = 313, males, respectively), with a nonsignificant female bias for the subadult (P = 0.21, n = 186) and adult (P = 0.82, n = 77) size classes (45.2% and 44.7% males, respectively). The sex ratio for captured subadults and adults (combined) revealed a female-biased ratio (44% male: 56% female, P < 0.05).

### Discussion

**Population estimate**

With crocodiles, different size classes differ in both life histories and behaviour (Hutton, 1984) and as such, the assumption of equal survivorship and recapture probability were violated to some degree (Bayliss et al., 1986). This violation was, however, minimized by selecting the young juvenile size class for application of the model. Bayliss et al. (1986) found that recapture rates peaked between 900 mm TL (c. 475 mm SVL) and 1200 mm TL (c. 635 mm SVL), a range corresponding to the juvenile size class in this study. In the case of the ‘no mortality’ assumption, violation would lead to an over-estimation of the population if no more than 50% of the captured crocodiles were recaptures. However, mortality had little
effect on the estimates if marked and unmarked individuals had an equal probability of mortality, and this was assumed (Gibbons, 1968; Jennings, David & Portier, 1991). The effects of mortality on the model were minimized by dividing the data set into annual northern and southern panhandle data sets. Hutton & Woolhouse (1989) estimated crocodile population size using a modified Peterson estimate, using only those animals seen subsequent to the recapture session in the estimate; thus, mortality and loss of marks uniquely identifying the individuals could be ignored. This was not feasible in the Okavango study as only using animals known to be alive at the time of recapture would have restricted the data set to the point where population estimates would have been unrealistic. Violating the ‘equal catchability’ assumption would, however, be more problematic. If animals exhibited a ‘trap response’, this would be difficult to quantify without recapturing many more animals for a third time (Underhill & Fraser, 1989), and so population estimates would not be valid. Additionally, the larger size classes could not be used as it was assumed that these were the more wary animals, emigration and immigration (demographic closure) could not be assumed in subadult (Hutton, 1989) and hatchling (S.L. Bourquin, Personal Observation) animals as these are traditionally the size classes that disperse.

The proportion of crocodiles in each size class differed slightly when compared to those from other regions of Africa (Gibbons, 1968; Parker & Watson, 1970; Hutton & Woolhouse, 1989; Games, 1990). While the proportion of young crocodiles (≤663 mm SVL) was higher than those in other studies, they occurred in lower densities. The proportion of adults and subadults was lower than in other studies (Gibbons, 1968; Parker & Watson, 1970; Hutton & Woolhouse, 1989; Games, 1990). Bishop et al. (2009) suggested that the longevity and delayed sexual maturity of Nile crocodiles may have acted to buffer the expected effects of hide-hunting and the removal of breeders for farming purposes in the panhandle (i.e. reduced heterozygosity).

The survivorship/recapture model

When using the most restrained model, Phi(.)p(.), the only model that differed significantly from the best-fit model, all individuals are assumed to be the same and there is no time variation in the model. This was clearly not the case. While it may have been feasible to fix time variation to a constant, individual crocodiles differed in both survival and recapture probability (Webb & Smith, 1987), and this difference was highly correlated with the size of the individual. Larger animals have increased survival probabilities, are less likely to be captured and are highly unlikely to be recaptured (Webb & Manolis, 1993).

In addition to the large confidence intervals surrounding the slope for the survival parameter (Fig. 3), this slope represents data collected over 4 years and so the cumulative survival rate for the smaller size classes is low. Recruitment and survivorship are subject to a range of influences and are not constant over time, so the data reflects a ‘snap-shot’ of the panhandle population and serves as a basis for future monitoring.

Sex ratio

Hutton (1987) found the Lake Ngezi crocodile population significantly skewed towards females. This included all size classes, and there was no evidence of mortality, dispersal- or migration-affecting sex ratio. Mortality was restricted to animals <120 cm TL and was not gender specific, and dispersal and migration were negligible. The Okavango crocodile population had a higher proportion of subadult and adult males than the Ngezi population. The adult and subadult crocodile population in St. Lucia (South Africa) was again female-biased with only 38.1% males (Leslie, 1997), possibly because of gender-specific mortality from male–male competition. Hutton (1987) theorized that females would predominate amongst successful embryos.
with the narrow temperature range in which males developed responsible for this bias.

**Conclusion**

The panhandle crocodile population is an exploited population because of commercial ventures. As such, there are few adult animals remaining (Cott, 1961; Webb & Messel, 1978; Bourquin, 2008) but their progeny exhibit high survival, giving a bimodal size distribution between large adults and young juveniles. Whether this number is sufficient to rebuild the adult population to the levels that could support the historical harvest described by Taylor (1973) is far from clear. However, being ‘exploited’ does not necessarily mean ‘depleted’, and therefore sound management practices are required. We suggest that the harvesting of breeding animals for commercial purposes is halted until population recovery, and stability is attained.

**Acknowledgements**

We thank the Okavango Crocodile Research Group for all their efforts in this undertaking. Prof Daan Nel is thanked for his statistical advice and Dr Res Altwegg is thanked for assisting with the population modelling. The Government of Botswana provided the necessary research permit. This work was supported by a grant to Dr A.J. Leslie from the National Research Foundation (South Africa), and the work was supported by a grant to Dr A.J. Leslie from the National Research Foundation (South Africa), and the Earthwatch Institute, (U.S.A.).

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(Manuscript accepted 11 July 2011)

doi: 10.1111/j.1365-2028.2011.01285.x