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Using a binomial mixture model and aerial counts for an accurate estimate of Nile crocodile abundance and population size in the Kunene River, Namibia

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The Nile crocodile, *Crocodylus niloticus,* is found throughout sub-Saharan Africa, including Namibia, Botswana and Angola. The species was transferred from CITES Appendix I to Appendix II in 2004, although it is recognized as peripherally endangered in Namibia due to diminishing habitat availability primarily from human encroachment. In 2013, a species management plan was approved in Namibia to assess the management of the Namibian Nile crocodile populations. During 2012, an aerial survey was conducted to provide an estimate of Nile crocodile population numbers. A recently developed *N*-mixture model for estimation of abundance and spatial variation was used. Detection probability correlated to animal size and environmental covariates. Our data also suggest that small crocodiles are easier to detect during the spring. The abundance for different size classes was influenced by river complexity (vegetation, depth, channels) and the distribution of human settlements. An estimated 806 individuals were counted along the 352 km Namibian portion of the Kunene River system with a conservative estimate of 562 crocodiles regardless of size. The parameter estimates generated by the analysis suggested that the class-structured model can produce reliable estimates of total abundance and of local abundance for this section in the Kunene River system.

Key words: aerial survey, census, conservation, *Crocodylus niloticus*, Kunene River, management, *N*-mixture model, population abundance.

INTRODUCTION

The Nile crocodile, *Crocodylus niloticus,* is found throughout sub-Saharan Africa, including Angola, Botswana and Namibia (Aust, 2009; Fergusson, 2010; Leslie, Lovely & Pittman, 2011) and is classified under Least Concern on the IUCN RED List of threatened species (IUCN, 2014). In 2004, Namibian authorities transferred the species from CITES Appendix I to Appendix II (CITES, 2004). This reclassification was partly prompted by the diminishing of habitat caused by human encroachment (United States Fish and Wildlife Service, 1999; Griffin, 2003; Mendelsohn, Jarvis, Roberts, C. & Robertson, 2003). This resulted in competition between man and crocodile for both food and space. Human contact with crocodiles is more likely in the presence of livestock, such as cattle (*Bos taurus*). The Nile crocodile undergoes an ontogenetic shift from fish to small mammals in the upper end of the juvenile size class (SVL   40cm). Evidence for this is based on stomach content (Wallace & Leslie, 2008) and scute isotope levels (Radloff, Hobson & Leslie, 2012). Crocodiles undergo a second ontogenetic shift when they exceed 119 cm SVL (Radloff *et al.*, 2012) from eating fish and small mammals towards preying on larger terrestrial mammals (Cott, 1961). Since local inhabitants keep large herds of goats (*Capra aegagrus hircus*) and cattle, which are considered as a sign of wealth (Comaroff & Comaroff, 1990)

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there is an increased chance of interaction with crocodiles, because these animals forage along the banks of the Kunene River (Irving & Ward, 1999).

Crocodylus niloticus is recognized as a protected game species in Namibia under the Nature Conservation Ordinance No. 4 of 1975 and only allows licenced trophy hunting. The quota for Namibia is assessed by the Ministry of Environment and Tourism (Ordinance No. 4, 1975), with the current quota set at a total of 25 adult crocodiles per year, which was determined on 14 April 2014 (CITES, 2014). CITES Appendix II allows the trade of no more than 1600 skins of Nile crocodiles from Namibia originating from both trophy hunting and ranched specimens (Act No 9, 2008; CITES, 2014). Crocodilians also play an important role in the ecosystem (Mazzotti *et al.,* 2009) and they have been found to be economically beneficial towards tourism (Llewellyne, 2007). A Namibian species management plan drafted in 2012 was approved in 2013 (Species Management Plan, 2012) and focuses on the economic utilization of crocodiles in a sustainable way, while protecting the species at the same time.

Census data for Nile crocodiles in Namibia are limited to the eastern Namibian river systems, namely the Okavango, Kwando, Mamili, Linyanti/Chobe and Zambezi Rivers (Brown, Stander, Meyer-Rust & Mayes, 2005; Chase, 2009). Reports of human/crocodile conflict by B.M. Siyanga (pers. comm.), a ranger for the Ministry of Environment and Tourism in Opuwo, stated that from January 2010 to March 2011 an estimated 44 domestic animal deaths and one human death occurred in the Kunene River system. Human/crocodile conflict reports such as these only provide information on the number of livestock or individual human deaths and do not give an accurate estimation on the number of crocodiles found at the incident site or within the river system. The fact that the Kunene River is situated in an isolated area makes population estimation even more of a challenge. Establishing a crocodile management plan requires several parameters to be considered such as conservation and population control (Bayliss, 1987).

Spotlight surveys by boat have been the most commonly used survey method to estimate crocodilian abundance in river systems (Letnic & Connors, 2006). Spotlight surveys are usually only conducted on a portion of the whole river and presented as a population index (Bayliss, 1987; Wallace, Leslie & Wallace, 2011). These surveys are dependent on a number of environmental and physical factors, namely access to large parts of the river, observer skill, boat speed (Cherkiss, Mazotti & Rice, 2006), water level, water temperature, time of day and crocodile behaviour (Hutton & Woolhouse, 1989). For the Kunene River, an aerial survey was considered the most viable option, as large areas of the river are inaccessible by car or boat. Aerial surveys have shown lower detection rates compared to boat surveys in Crocodylia (Woodward, Hines, Abercrombie & Nichols, 1996; Stirrat, Lawson, Freeland & Morton, 2001), but by using helicopters, greater manoeuvrability, controlled speeds, wider fields of view and photographic data can be obtained. This could lessen bias for submerged animals or dense vegetation areas effecting observer visibility (Bayliss, 1987; Pollock & Kendall, 1987; Bourquin, 2007).

In this study, an aerial survey was conducted to provide a population estimate for Nile crocodiles in the Namibian portion of the Kunene River to implement a crocodile management plan for the country. One of the primary objectives of this study was to estimate the distribution and abundance of the Nile crocodile across the study domain in Namibia and understand patterns of variation in relation to environmental and anthropogenic factors. Detectability of individual animals is highly variable and nearly always <1; and imperfect detection must be accounted for to reliably estimate population sizes and trends (Royle & Dorazio 2008). Due to expected heterogeneity in both local abundance and local detection probability (due to environmental or sampling covariates), we considered the *N*-mixture model as the most appropriate model as it can simultaneously estimate abundance and effective detection probability of animals. The state process of the *N*-mixture model describes ecological mechanisms that generate spatial and temporal patterns in abundance, while the observation model accounts for the imperfect nature of counting individuals due to temporary immersion and false absences. The model also assumes sampling in a closed system, regarding mortality, recruitment immigration and emigration (Royle, 2004).

MATERIALS AND METHODS

Study area

The Kunene River is a freshwater perennial system and is fed from natural springs in the Bie

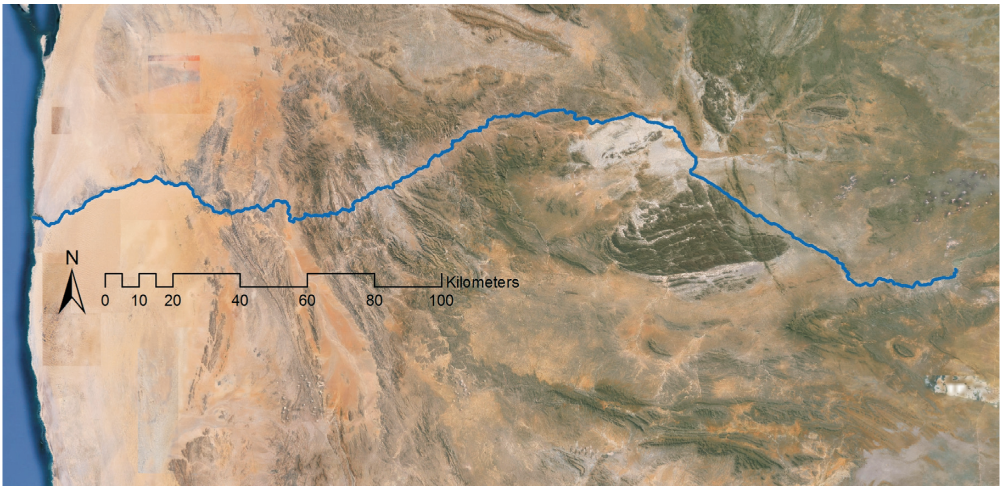

Fig. 1. Namibian portion of the Kunene River surveyed during the study. The river was manually drawn on Google earth to better fit the true river course.

Highlands in Angola (Irving & Ward, 1999) and by an annual summer rainfall from October to March, which ranges from 50 mm in the Namib Desert, to 1500 mm in the highlands of Angola (Hay, Van Zyl, Van der bank, Ferreira & Steyn, 1997). There is a high level of endemic fauna and flora in the central and Eastern Kunene, namely: trumpet thorn (*Cataphractes alexandri),* gum myrrh (*Commiphora* spp.) (Irving & Ward, 1999), black-faced impala (*Aepyceros melampus petersi*) and Hartmann's mountain zebra (*Equus zebra hartmannae*) (Kunene River Awareness Kit, 2014). Several communal conservancies are situated in the Kunene area with some bordering on the Kunene River, namely Marienfluss, Uunolonkadhi-Ruacana and the Kunene conservancy (NACSO, 2009). The Skeleton Coast National Park is situated on the northwestern Namibian shore, through which the Kunene River flows; the region consists of desert vegetation with no local inhabitants. The estimated human population of the Kunene province was 88 300 in 2011 and approximately 18 000 (20.4%) of these individuals live in the Epupa constituency bordering the Kunene River (Namibian Census, 2011).

The Kunene River system covers a total area of 110 200 km^2, consisting of an upper and middle, situated in Angola. The lower Kunene (14 900 km^2, 13.3%) considered for the aerial survey, forms the border between Namibia and Angola and covers 352 km from the river mouth (0 km, latitude –17.249515 and longitude 11.752746) to Ruacana Falls (352 km, altitude 775 metres above sea level, latitude –17.403902 and longitude 14.216841) (Fig. 1). However, the delta of the Kunene river (~5 km), which has a completely different environment from the rest of the river system (much larger, with brackish water) was excluded from the statistical analysis below. The aerial survey was conducted under a Ministry of Environment and Tourism Division Support System (DSS) approved work activity permit (Permit number: 2003/2015).

Survey design and effort

The Kunene River area surveyed in 2012 was separated into two parts, namely: east and west. The helicopter (Bell Jet Ranger B206 and a Bell Long Ranger B206L) had a pilot, two to three observers (two permanent experienced observers and a third interchangeable less experienced observer) and a data recorder and was flown 24–27 feet above ground level at 110–130 km/h. The western part of the river was surveyed from the 24 to 28 April 2012 (early dry season) and the eastern part from the 9 to 12 August 2012 (late dry season). Only a segment of each river part could be covered within a single day and flights were flown during the late morning or early afternoon, since the majority of crocodiles would be basking on the banks during these times. The river segments were covered in 10 sessions (referred to as S##) surveyed as shown in Fig. 2.

For the statistical analyses, every session (S01–10) was considered to be a different sampling occasion. The river was divided into segments of equal length, with every segment being considered an independent sampling unit (referred to as a site in the rest of the paper). At the site level, one

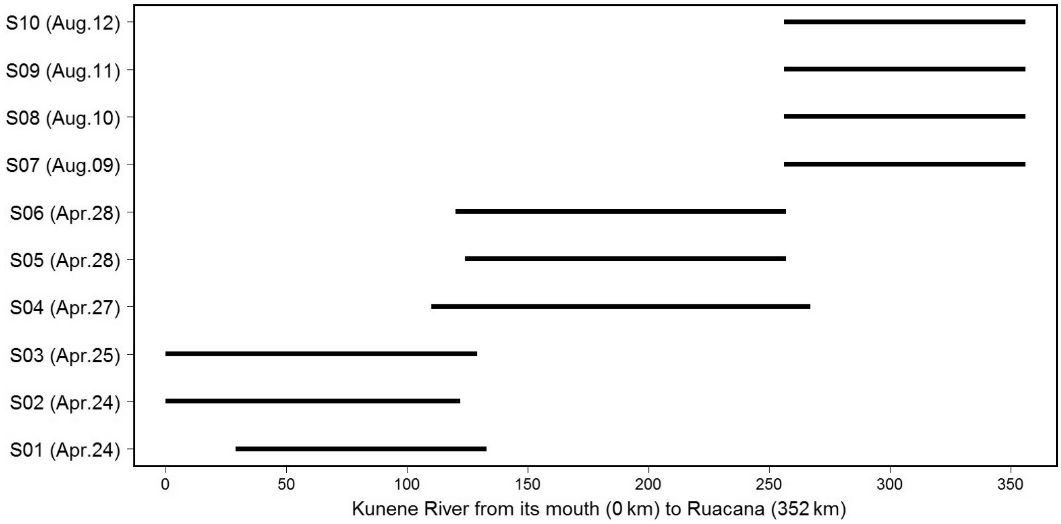

Fig. 2. Helicopter survey design. Each bold dark line represents a flight over a portion of the Kunene River. The *x*-axis shows the distance to the mouth of the river and the *y*-axis indicates the survey ID and the date at which it was conducted.

aerial sampling occasion consisted of one flight over the river segment. Since segments are adjacent, crocodiles could freely move in and out of the segments during the repeated surveys, especially those on the tail end of a segment. As a result, local abundance at a segment might vary between surveys due to possible disequilibrium between animal entries and exits. This would violate the population closure assumption required for the statistical analysis (Williams, Nichols & Conroy, 2002) and could therefore bias estimates of abundance at the site level and an estimate of total population size. Population closure is a common and recurrent issue while dealing with repeated surveys. In our study we have addressed this issue in two ways. We first reduced the time between consecutives surveys to one day and we chose a segment length long enough so that most animals would likely stay in the same segment of the river from one day to the next. We used crocodile GPS tracking data to get an idea of daily movement pattern of our species in Namibia to help us deciding upon the most appropriate length for the river segment. As no GPS tracking data were available for the Kunene River crocodiles, we used Okavango River crocodile movement data ($n = 5$ individuals – 2 males and 3 females), collected by the Ministry of Environment and Tourism, on five adults from August 2011 to April 2013, assuming that animal movement patterns were not too different in the two river systems (African Wildlife Tracking SAT collars, Iridium system). The GPS data indicated that 50% of those movements were shorter than 639 metres, 75% shorter than 1236 metres, and 95% shorter than 3034 metres over a 24-hour period, with one crocodile seldom moving further than 8 km (Fig. 3). These data confirmed that a significant proportion of animals located within the first one kilometre tails of a segment were likely to move out between two consecutive surveys. Given that information, and because we were interested in relationship between the characteristics of the river system (see covariates below) and the local abundance of crocodiles, we thought that 8-km was a good compromise between a fine scale description of the river characteristics and limit the variation in local abundance of crocodiles caused by animal movements between sites. The possible biases on abundance estimates and further recommendation will be discussed hereinafter.

The 352 km of river was divided into 43 consecutive, non-overlapping 8-km segments, each segment being considered as an independent site unit. The statistical method used to analyse the data required that all sites were surveyed at least once and a subsample of the sites were to be surveyed several times. In the study, all sites were surveyed: two sites surveyed twice, 21 sites three times, 19 sites four times, and one site six times.

Data recording survey

Data were logged as follows: each observation of a crocodile was recorded with its corresponding

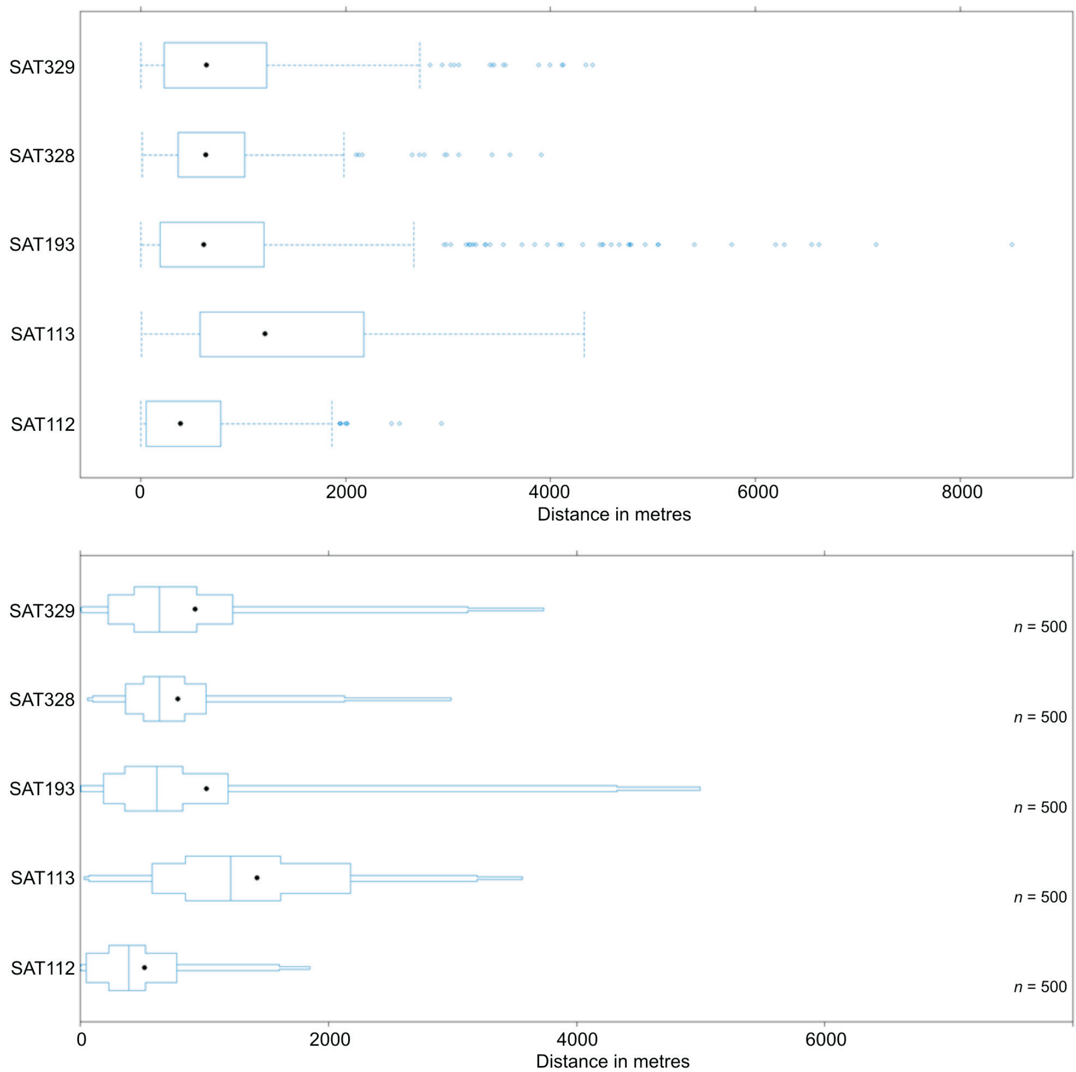

Fig. 3. Average movement (in metres) recorded over a 24-hour period for five adult crocodiles in the Kunene and Okavango river systems. Area of the boxes is proportional to the frequency of the distance recorded. Data show that 50% of those movements were shorter than 639 metres, 75% shorter than 1236 metres, and 95% shorter than 3034 metres.

geographic coordinates (latitude and longitude), time of sighting and size class. The size class of crocodiles was based on its estimated length (Class 1 = 1–2 m, Class 2 = 2.1–3 m, Class 3 = 3.1–4 m and Class 4 = >4.1 m). The length of each crocodile was estimated visually. The same observers were used throughout the counting, which kept the bias introduced by estimation consistent. This makes it more challenging to compare size class data using previous and future census events, but this was the best method available at the time. Figure 4 indicates the distribution of all observations along the river. Every observation was assigned to the nearest *site* using ArcGIS software (ESRI, 2008). Hence the number of crocodiles observed at *site i* on session *j* in size class *g*, is noted as n_{ijg}. Appendix 1 in the online supplement shows an example of the data recorded on *site* #71. For this *site* $n_{71.Occ8.G2} = 2$.

Site and sampling covariates

In the analyses, the first flight over a segment of the river was considered to be an exploratory flight (S01, S04 and S07). When the same portion of a

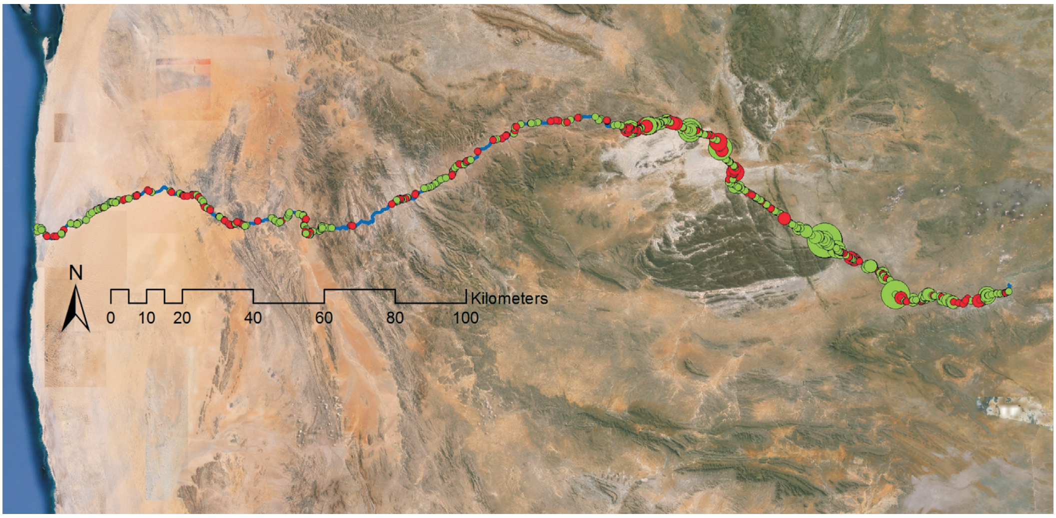

Fig. 4. Observations of Nile crocodiles on the Kunene River during the 2012 aerial survey. Green dots indicate animals between 1 and 3 metres in length, red dots indicate animals greater than 3 metres. The size of the circle is proportional to the number of individuals observed at the location.

river was flown over in a single day, S01; S02 and S05; S06, we modelled separately for each flight path. This was to account for any possible disturbance caused by the first flight, which would have made the crocodiles less detectable during the second flight. S07 and S08 were flown on different days. A subset of six predictor variables was chosen which were believed to be a potential contribution to the driving forces for abundance of species at the scale of this study (Jablonicky, 2013). Crocodiles larger than 3 metres will be expected to show a preference for river width and shore steepness that would facilitate the capture of prey when they need to cross the river (Jarman, 1972; Aust, 2009). Crocodiles less than 3 metres long are expected to correlate to the number of channels, because they tend to seek shelter on islands and possible nesting sites (Aust, 2009). Another factor influencing the density of crocodiles is the proximity of human settlements. The predictor variables for the Kunene River aerial survey were derived from physical characteristics of the Kunene River explained every km. Making use of high-resolution satellite imagery, available on Google Earth, a 30 metre resolution digital elevation model based on ASTER satellite imagery and data from the Namibian Atlas (Mendelsohn *et al.,* 2003). This fine description of the river was therefore averaged along the 8-km segment (*site* unit) to build the set of *site* covariates to be used in the statistical analysis. To limit the co-linearity within factors, we used a principal components analysis and selected a subset of non-co-linear variables. The selected predictors and their respective sources are shown in Table 1.

In addition, we also considered four independent sampling covariates that could affect the probability of detecting crocodiles at a *site*. We first considered two factors related to the intensity of a survey effort: 1) is described by length of the helicopter GPS track log divided by number of channels and 2) describes the number of observers in the aircraft (Tables 2 and 3). We expected the probability to detect crocodiles to be positively correlated with either or both the length of the flight and the number of observers. All flights had two observers, except for flights S09 and S10 which had three observers aboard, in an attempt to increase the probability of detection of animals. Factors three and four were discovery and return flights, respectively (Tables 2 and 3).

Description of the model

Recently developed *N*-mixture models allow for the estimation of abundance and spatial variation in abundance from count data alone for closed (Royle, 2004) and open (Dail & Madsen, 2011) populations. *N*-mixture models are a class of state-space models in which the 'true' state of the system (abundance) is observed imperfectly. The 'true' abundance here '*is the (unobserved) abundance* […] *of individuals on the spatial sample unit*' (Royle & Dorazio, 2008) or can be defined as well as the abundance corrected for imperfect detec-

Table 1. Description of the environmental factors used as covariates in the statistical analysis. See also Appendix 2, Figs I, II, III and IV, in the online supplement.

Factor name	Description of the factor	Source	Data type and unit
width	River width. Measured manually at every kilometre on Google earth and corresponds to the length of the perpendicular section of the river from one shore to the other after ground areas are excluded.	Google earth	Continuous, metre
shore	Shore steepness. Assessed visually every kilometre using Google earth pro software 3D imagery and Play tour mode to fly along the Kunene River. Proxy for the accessibility to the river by large prey species.	Google earth	Categorical, index between 0 and 5, 0 corresponding to a flat shore.
channel	Index of river complexity. The number of channels was assessed visually at every 1-kilometre segment on Google earth software. Proxy for basking and nesting site availability.	Google earth	1, 2, 3, 4, and 5+ channels.
dis.V	Distance to the nearest village. Measured at every 1-kilometre segment using ArcGIS software. Proxy for environmental disturbance and hunting pressure.	Atlas of Namibia	Continuous, kilometre
den.H	Index of human population density. Assessed on an 8 × 10 km strip centred on the river course using ArcGIS software. Proxy for environmental disturbance and hunting pressure.	Atlas of Namibia	Continuous, inhabitants per square kilometre

tion (Kéry, 2010). Unlike classical state-space models used in ecology (*e.g.* De Valpine & Hastings, 2002, Staples, Taper & Dennis, 2004), *N*-mixture models do not make unrealistic assumptions about the Gaussian process and sampling errors and instead assume that abundance is a discrete random variable (Buckland, Newman, Thomas & Koesters, 2004). Similarly, *N*-mixture models attribute observation error to a specific phenomenon, such as the inability to detect all individuals that are available during sampling and are referred to as imperfect detection. The *N*-mixture model for a closed population (Royle, 2004) was considered, as surveys were only conducted in a single year. Animals ranging in size class from 1.0–3.0 m (referred to as Group 1)

Table 2. Summary of the *N*-mixture analysis for crocodiles in group 1 (crocodile size from 1.0–3.0 m). The table shows the Bayesian posterior mean, standard deviation and 95% credibility interval for each parameter included in the model as described in the text. Rhat < 1.05 indicates that the chains have converged.

Parameter		Mean	S.D.	2.50%	97.50%	Rhat
α	Origin	2.227	0.187	1.863	2.595	1.001
α_1	River width	0.033	0.131	–0.227	0.284	1.001
α_2	Shore steepness	–0.048	0.123	–0.284	0.195	1.001
α_3	Channels	0.363	0.184	–0.002	0.726	1.001
α_4	Distance to village	–0.299	0.176	–0.652	0.040	1.001
α_{44}	Distance to village (quadratic)	0.041	0.093	–0.140	0.227	1.001
α_5	Density human population	–0.310	0.154	–0.610	–0.010	1.002
α_{55}	Density human population (quadratic)	0.155	0.099	–0.035	0.356	1.001
β	Origin	–0.678	0.284	–1.241	–0.128	1.002
β_1	Flight length	–0.477	0.173	–0.820	–0.147	1.001
β_2	Discovery	–1.107	0.278	–1.662	–0.585	1.001
β_3	Return	–0.990	0.333	–1.668	–0.354	1.001
β_4	No. of observers	1.444	0.378	0.749	2.217	1.001
sd.p	Random effect	0.964	0.138	0.710	1.251	1.001

Table 3. Summary of the *N*-mixture analysis for crocodiles in group 2 (>3 metres in size). The table shows the Bayesian posterior mean, standard deviation and 95% credibility interval for each parameter included in the model as described in the text. Rhat < 1.05 indicates that the chains have converged.

Parameter		Mean	S.D.	2.50%	97.50%	Rhat
α	Origin	1.669	0.188	1.290	2.037	1.001
α_1	River width	0.491	0.153	0.190	0.802	1.001
α_2	Shore	–0.157	0.124	–0.402	0.079	1.002
α_3	Channels	–0.246	0.255	–0.743	0.256	1.002
α_4	Distance to village	0.225	0.200	–0.171	0.618	1.001
α_{44}	Distance to village (quadratic)	–0.256	0.110	–0.475	–0.041	1.001
α_5	Density human population	–0.051	0.174	–0.388	0.286	1.001
α_{55}	Density human population (quadratic)	0.110	0.107	–0.100	0.311	1.001
β	Origin	0.302	0.299	–0.283	0.873	1.001
β_1	Flight length	0.132	0.269	–0.403	0.643	1.001
β_2	Discovery	–0.387	0.323	–1.045	0.228	1.001
β_3	Return	–0.514	0.410	–1.335	0.283	1.001
β_4	No. of observers	0.628	0.362	–0.043	1.403	1.001
sd.p	Random effect	0.964	0.138	0.710	1.251	1.001

and animals larger than three metres (referred to as Group 2) were modelled separately. We used the respective frequencies of every group to estimate the total number of animals in each size class. A model accounting for covariate effects on abundance, both covariate effects and extra Poisson dispersion (extra heterogeneity) was used for detection probability. However, the introduction of random effects into linear predictors can be seen as an over dispersion correction and it increases the uncertainty in the estimates. The total population size and its credibility interval over the 352 km river was computed directly in JAGS, by summing the segment-level abundance estimates (see Appendix 3 in the online supplement).

The hierarchical model is described below (refer to Table 1 for complete description of covariates' abbreviations).

Level 1

The realized abundance of animals for size group *g* at *site i* is:

$N_{i,g} \sim \text{Poisson}\ (\lambda_{i,g})$

GLM for level 1:

The mean $\lambda_{i,g}$ abundance at *site i* for group *g* is described by the following relation

$$\log(\lambda_{i,g}) = \alpha_g + \alpha_{1,g}{*}\text{width}_i + \alpha_{2,g}{*}\text{shore}_i + \alpha_{3,g}{*}\text{channel}_i + \alpha_{4,g}{*}\text{dis.V}_i + \alpha_{44,g}{*}\text{dis.V}_i^2 + \alpha_{5,g}{*}\text{den.H}_i + \alpha_{55,g}{*}\text{den.H}_i^2$$

Level 2

The observed count for group g at *site* i and on survey j is:

$c_{i,j,g} \mid N_{i,g} \sim \text{Binomial}\ (N_{i,g}, P_{i,j,g})$

GLM for level 2:

The detection probability at a *site* i for group g and survey j is described by the following relation

$$\text{Logit}(P_{i,j,g}) = \beta_g + \beta_{1,g}{*}\text{flight}_{i,j} + \beta_{2,g}{*}\text{discov}_{i,j} + \beta_{3,g}{*}\text{return}_{i,j} + \beta_{4,g}{*}\ \text{observ}_{i,j} + \text{rand}_{i,j,g}$$

Level 2b (random survey effect):

$\text{rand}_{i,j,g} \sim \text{Normal}\ (0,\sigma)$

A Bayesian approach to estimate the model parameters was used as this provides a computationally tractable method to integrate across unobserved states and quantifies the uncertainty of the estimates. A Bayesian analysis requires specification of prior distributions for parameters. We assumed vague priors in all analyses presented in this paper. We ran three MCMC (Gelman *et al.*, 2004) of the model, each for 2 200 000 iterations after a burn-in of 200 000 and thinned by 2000. We implemented our analyses with the program R (R Core Team, 2012) using the software program JAGS (Plummer, 2003) to use Markov Chain Monte Carlo (MCMC) to approximate posterior distributions for each of the parameters. The model code for the analysis can be found in Appendix 3 in the online supplement.

RESULTS

Model fit and performance

Visual inspection of the MCMC and Rhat values, all smaller than 1.05, indicated that all parameters have mixed properly and converged (Gelman & Rubin 1992) (Tables 2 and 3). In addition, the comparison of the discrepancy between the observed and the simulated data (Fig. 5) shows that they correlated, suggesting that the model is adequate for the data set. This is supported by a Bayesian posterior predictive *p*-value of 0.52. This *p*-value quantifies the discrepancies between the data and the model, and a *p*-value near 0 or 1 indicates a lack of fit of the model (Gelman *et al.*, 2004). The parameter estimates generated by the analysis have demonstrated that the class-structured model can produce precise estimates of total abundance and reliable estimates of local abundance for the Kunene River population of crocodiles as shown in Fig. 6.

Mean detection probability and total population size

Mean detection probability was significantly higher for group 2 (mean: 0.55, 95% CI: 0.454–0.626) than for group 1 (mean: 0.35, 95% CI: 0.273–0.418) and the difference can be considered significant as the CIs of the two estimates do not overlap. Along the 352 km stretch of the Kunene, the total population of crocodiles was estimated at 806 individuals (95% CI: 674–1015) (Table 4). For the different size-classes the model estimated 239 (189–320), 340 (268–455), 149 (131–180), and 78 (68–94) individuals for class 1, 2, 3 and 4, respectively (Table 4). These values are to be compared with the direct count population estimate which is given by the sum of the maximum number of individuals observed at every *site* on a single sampling occasion. In this survey, the direct count estimates in each size class, from the smallest to the largest, were 154, 199, 131 and 78 individuals with a total of 562 crocodiles of all sizes.

Covariate effects on detection probability and local abundance

Covariate effects on both detection and local abundance were considered significant when the credibility interval did not contain the zero value. The covariates that were tested in the model showed very different responses between the two groups. None of the covariates had a significant effect on the detection probability of crocodiles from Group 2, while all were significant for detection probability of Group 1. The estimates and credibility intervals of the parameters are shown in

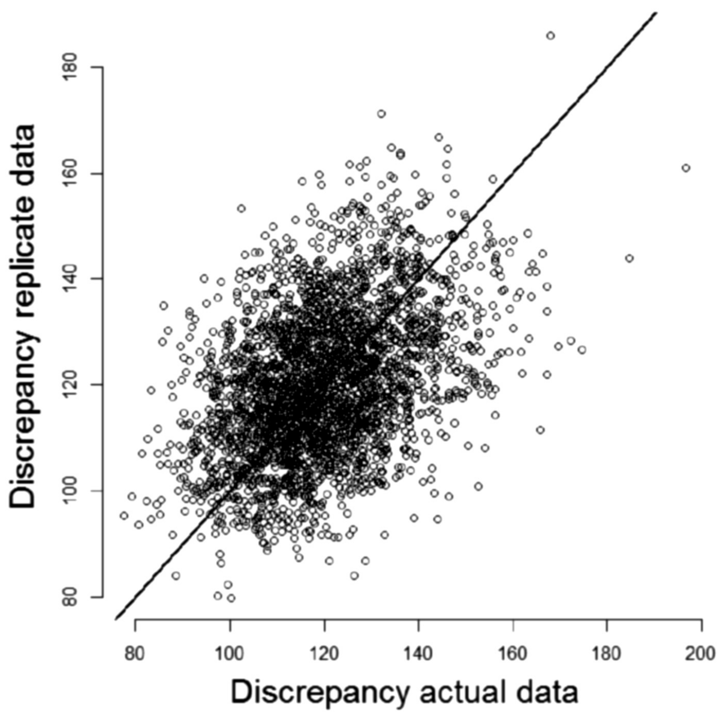

Fig. 5. Posterior predictive check of model fit by a scatter plot of the discrepancy measure for replicate (simulated) *versus* actual (observed) data in a *N*-mixture model. The Bayesian *p*-value is the proportion of points above the 1:1 line.

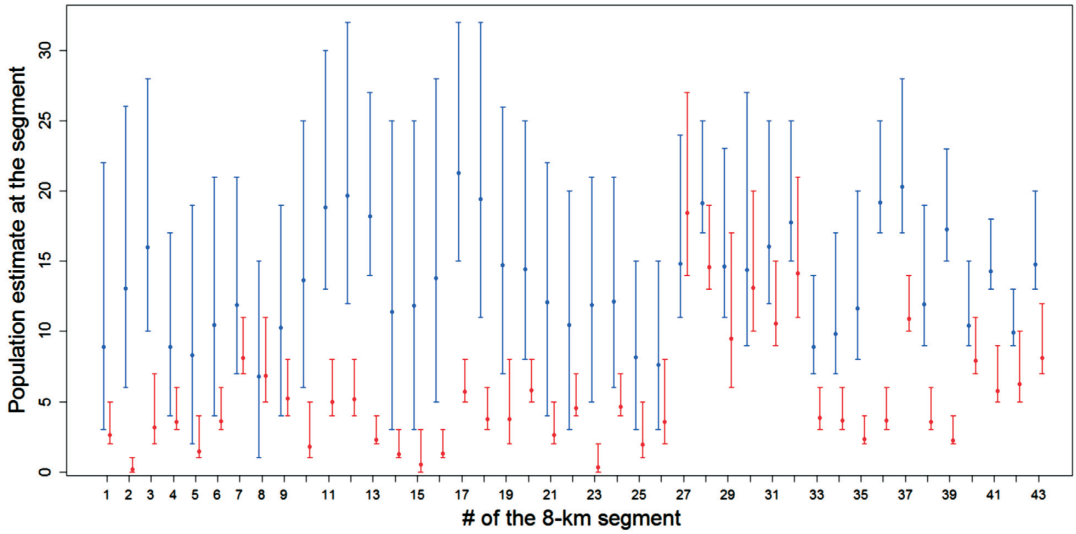

Fig. 6. Estimates of local abundance of crocodile at every 8-km segments along the Kunene River, with segment #1 corresponding to the River mouth and segment #43 to Ruacana dam. Filled circles indicate the estimate and the bar correspond to the 95% Bayesian credibility interval. Blue corresponds to the 1 to 3 metres size class, and red, to the 3+ metres size class.

Table 4. Total population size and number of crocodiles in each size-class.

	Mean	S.D.	Bayesian Credibility Interval 95%	
			Low	High
No. of crocodiles [1–2 m]	238.98	35.12	189	320
No. of crocodiles [2.1–3 m]	340.26	50.00	268	455
No. of crocodiles [3.1–4 m]	149.01	12.65	131	180
No. of crocodiles [4.1+ m]	78.12	6.63	68	94
Total no. of crocodiles	806.36	91.03	674	1015

Tables 2 and 3. Results indicated that the length of the flight path for the discovery and return flight mode had a negative effect on detection probability, while the number of observers participating in the aerial survey had a positive effect on the probability of detecting a crocodile at a *site*. The variance for the random effect σ was estimated at 0.964 (0.710–1.251 95% CI), which represents the part of the variance in the detection probability that is not explained by the covariates. Local abundance of crocodiles was highly variable among *sites* for both groups (Fig. 6), and usually higher for Group 1. The upper part of the river (segment #27 – #32) had a much higher density of crocodiles from Group 2 than the rest of the river, while there was no such clear pattern for Group 1 crocodiles. It is also worth noting that the precision of the estimate is much higher for Group 2. Local abundance ranged from 8.30 (2–19 95% CI) individuals on segment #5 to 21.28 (15–32 95% CI) on segment #17 for Group 1, and from 0.17 (0–1 95% CI) on segment #2 to 18.46 (14–27 95% CI) on segment #27 for Group 2. The results in Tables 2 and 3 also show that the local abundance for the two different size classes is explained by different covariates namely, channels and flight length.

DISCUSSION

The survey conducted along the Kunene river system provided valuable insight into the abundance and distribution of the Nile crocodile. Furthermore, the accuracy of the *N*-mixture model was evaluated to provide an indication of accuracy within the study and the possibility of using the model for future studies.

Total abundance

Along the Kunene River, Nile crocodiles were estimated at a direct count abundance of 562 total individuals (1.60 crocodiles per km). With final population abundance estimated at a total of 806 individuals after considering observer and environmental bias (2.29 crocodiles per km). An estimate of 2.29 crocodiles per km can be considered plentiful compared to other African river populations (Bourquin, 2007). This could be the result of limited poaching in the area in the past and very few tribal settlements situated on the river. Ignoring detection probabilities of crocodilians clearly leads to an underestimate of the population size, in particular for animals less than 3 metres in length (Fujisaki *et al.,* 2011). The underestimation for the direct count abundance could be the result of inexperienced observers, crocodile submergence and/or the distance from the area/transects being surveyed (Bayliss 1987; Hutton & Woolhouse 1989; Jablonicky, 2013). Similar underestimations were seen in the studies of Shirley *et al*. (2012) and Jablonicky (2013).

Local abundance and covariates effects

Estimates of local abundance of crocodiles along the Kunene River are highly variable for both groups (Fig. 6) specifically for Group 1. In the Materials and Methods we suggested that movements of animals between sites have most likely happened over the duration of our study. These movements might have caused variation in local abundance at some segments unless the numbers of animals leaving those segments were equal to the numbers of animals entering. Unfortunately, our data do not allow us to quantify the magnitude of these changes and it is therefore difficult to know how much this has biased the estimates of abundance and total population size. We have also suggested that the easiest way to reduce this bias is to increase the length of the river segment used as a site unit or reduce the time between two consecutive surveys. On one hand, if a segment is much longer than the distance travelled by the animals between two surveys, one could assume that only animals on the tail end are likely to move from one segment to another. On the other hand, the shorter the time between consecutive surveys the shorter the expected distance travelled by the animals and therefore the lesser proportion of animals is expected to move between sites. The use of a longer river segment would probably reduce this bias but it is not completely satisfactory as we would also lose the ability to use river covariates to explain and predict the local abundance of crocodiles and this would also reduce the precision of the estimates. A more appealing solution would be to reduce the time between two surveys. We have shown during this study that it was possible to survey a 100 kilometre stretch twice in a single day with a short break in between surveys. GPS tracking data indicated that 50% of those movements were shorter than 100 metres, 75% were shorter than 383 metres, and 95% were shorter than 1194 metres over a 6-hour period. These data corroborate the idea that a survey design based on two surveys per day, with a one hour break in between, could be a viable approach for a more accurate estimate of local abundance and total population size of crocodiles in the Kunene River.

Detection probability is higher for larger sized crocodiles (>3 m in length) when compared to smaller crocodiles (<3 m in length). This was also observed in the study of Fujisaki *et al*. (2011) for *Alligator mississippiensis*. Local abundance of crocodiles from Groups 1 and 2 in this study were influenced by the number of channels and human settlements. Abundance of Group 1 animals seems primarily correlated to the number of channels (Table 2 & Fig. 7a) which is indicative of the complexity of the river system. Channel shape effect seems logical, as the islands that separate the channels are ideal for crocodile nesting (Leslie & Spotila, 2001; Aust, 2009). Vegetation and water depth in these areas further provide more shelter for animals of small to medium size (Group 1). This was corroborated in a study by Hutton (1989) who showed that Nile crocodiles smaller than 2.2 metres were restricted to nesting areas in the Ngezi River, with larger crocodiles occupying the lake system. The abundance of Group 1 crocodiles was found to be the greatest nearest human settlements (monotonous negative trend; see Table 2 and Fig. 7b) and where human density was slightly higher (positive quadratic effect; see Table 2 and Fig. 7c). However, the uncertainty around the effects of human density is high. There was a possible impact from human population density and distance to the nearest settlement, but the confidence level was low and would thus require more data for confirmation. This could be the result of combining two size classes and each size class responding differently to each of these factors. Splitting the group into two subgroups was not possible in the analysis and would require a larger dataset to be explored thoroughly.

It is interesting to observe a gradual increase in

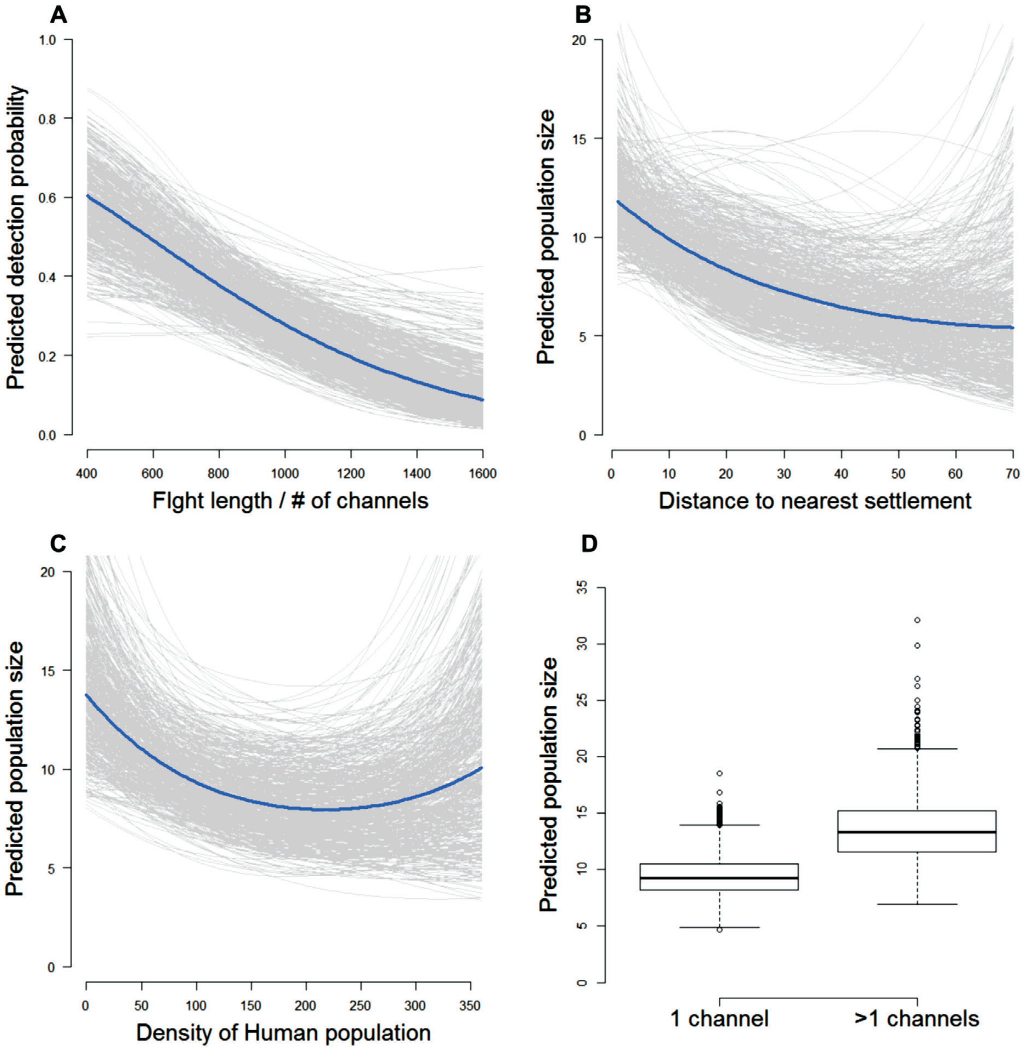

Fig. 7. Predictions of the covariate relationships that account for estimation uncertainty, 1–3 metre crocodile class. **A**, Relationship between covariate and the detection probability. **B**, **C** and **D**, relationship between the site covariates and the predicted abundance. The blue line shows the posterior mean, and grey lines show the relationships based on a random sample of size 500 to visualize estimation uncertainty.

Group 2 abundance (Fig. 8a) from 0 to 20 km from a human settlement followed by a gradual decline as the distance increases. The abundances can be negatively affected due to the physical presence of people, habitat disturbances and hunting pressures (Musambachime, 1987; McGregor, 2005) which can explain the lower abundance nearer the settlement. The higher abundance at the 20 km range might suggest that the crocodiles prefer that area, because it is far enough from a settlement for them to avoid humans, but close enough to a potential food source such as roaming cattle or goats. The main environmental driving force for Group 2 animals has been shown to be river width (monotonic positive trend; see Table 3 and Fig. 8b), indicating that crocodiles 3 metres and above show preference for exploiting larger bodies of water, corresponding to previous studies for larger crocodilians (for *e.g.* Aust, 2009). Group 2 crocodile abundance was also found to decrease with steepness of the bank (negative monotonous trend; see, Table 3 and Fig. 8c). This effect may be related to the availability of large prey mammals in these areas which prefer accessing and crossing the river at low to mild steepness of the bank (Jarman, 1972).

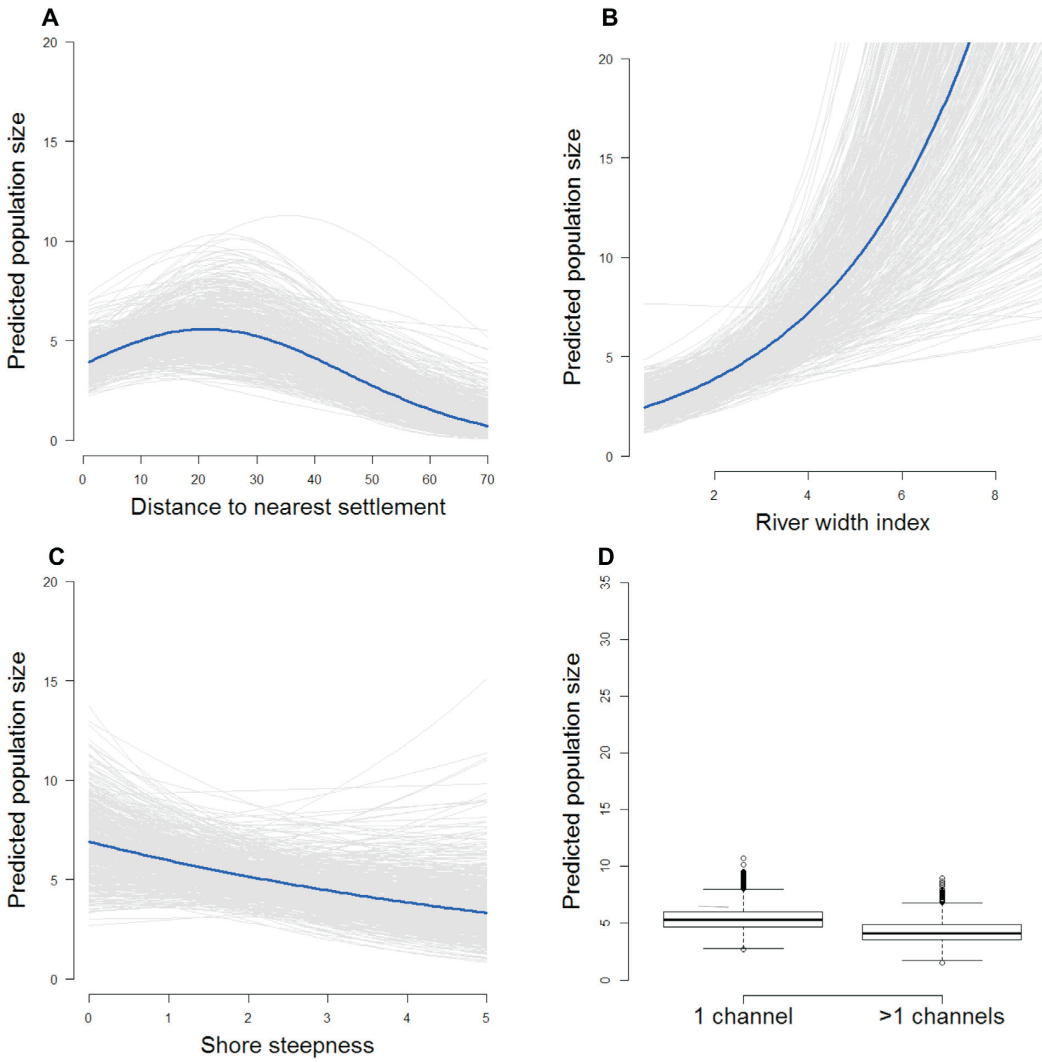

Fig. 8. Predictions of the covariate relationships that account for estimation uncertainty, 3+ metres crocodile class. **A**, **B**, **C** and **D**, relationship between the site covariates and the abundance. The blue line shows the posterior mean, and grey lines show the relationships based on a random sample of size 500 to visualize estimation uncertainty.

Detection probability

The advantage of using an *N*-mixture model here is that it provides estimates of population size at the river segment level that are corrected for possible bias in the detection probability of animals. In our model, this detection probability of crocodiles is segment, survey and group specific, $P_{i,j,g}$. A random effect was added to account for extra dispersion (*e.g.* seasonal effect) not caused by any of the covariates that were tested.

As expected, the model showed that the detection of crocodiles is imperfect and animal size dependent. The probability of detection was slightly higher during the first flight when compared to the return flight. This could be the result of observer effectiveness and fatigue. During aerial surveys it is impossible to change observer's mid-flight or on 30 min intervals as during boat survey studies (Bourquin, 2007). The loud noise from the helicopter also results in animals seeking shelter during the return flight. It would be recommended to have a 2 hour break before the return flight around midday rather than a 30 min break midday to refuel the helicopter as during this survey. The 2 hour break will alleviate observer fatigue and reduce animal disturbance for the *sites* counted. Surprisingly, the detection probability of crocodiles from Group 1 decreased proportionally with the length of the flight per river segment (sampling effort per segment of river), while it was expected to increase (Fig. 3d). The observed increase in flight length is primarily due to extra flight loops conducted when the course of the river was more complex due to numerous channels, swampy areas and more dense vegetation. These riverine areas offer more shelter and decrease the detection of small crocodiles when compared to more open portions of the river, having a negative effect on flight length. Crocodiles are able to hide under the shrubs and in the swampy areas to reduce chances of mortality (Woodward *et al.* 1987). Group 2 has shown not to be affected by the covariates as they are easier to detect and not covariate dependant. Detection probability in our case is clearly imperfect and correlates to animal size and environmental covariates. Therefore this parameter should not be ignored and needs to be modelled accordingly to obtain unbiased estimates of population size.

Although seasonal effect was not included as a covariate in our analysis, our data suggest that small crocodiles are easier to detect during the spring. Indeed, the average detection probabilities for Group 1 were 0.22 in autumn and 0.51 in spring, while for Group 2, the difference was much smaller with average detection probabilities of 0.50 in autumn and 0.59 in the spring.

CONCLUSION

The parameter estimates generated by our analysis have demonstrated that a class-structured model can produce precise, unbiased estimates of total abundance and reliable estimates of local abundance for this population of crocodiles. This study represents a good benchmark for the monitoring of the Namibian crocodile populations in the future. The recent development of open population models based on animal counts (Dail & Medsen, 2011; Zipkin *et al.,* 2014), as conducted in our study, indicated sufficient information to monitor the trend of a population over time and perhaps estimate other demographic parameters required to effectively manage a population in the future. The abundance of Nile crocodiles in the Kunene River was estimated at 806 individuals after considering observer and environmental bias (2.29 crocodiles per km) and is considered healthy in comparison to other African river crocodile populations (Bourquin, 2007). Our data set will assist with the eventual implementation of the crocodile species management plan, but will also require updated aerial surveys of the Okavango, Kwando, Linyanti, Chobe and Zambezi River systems. The efficient integration of abundance data, the assessment of genetic diversity and structure, data on dietary habits and information on nesting sites will greatly increase the effectiveness of the National crocodile species management plan.

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