N-mixture models provide informative crocodile (*Crocodylus moreletii*) abundance estimates in dynamic environments

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Estimates of animal abundance provide essential information for population ecological studies. However, the recording of individuals in the field can be challenging, and accurate estimates require analytical techniques which account for imperfect detection. Here, we quantify local abundances and overall population size of Morelet's crocodile (*Crocodylus moreletii*) in the region of Calakmul (Campeche, Mexico), comparing traditional approaches for crocodilians (Minimum Population Size – MPS; King's Visible Fraction Method – VFM) with binomial N-mixture models based on Poisson, zero-inflated Poisson (ZIP) and negative binomial (NB) distributions. A total of 256 nocturnal spotlight surveys were conducted across 50 representative locations (hydrologically highly dynamic aquatic sites locally known as aguadas) over a period of five years (2015-2019). Population size estimates through MPS and VFM revealed a median of 0.4 (min – max: 0 – 67; Q1 – Q3: 0 – 3) and 0.95 (0 – 159; 0 – 8) non-hatchling *C. moreletii* for each aguada, respectively. The ZIP based N-mixture model structure shown overall superior confidence over Poisson and NB, and revealed a median of 5 ± 2 individuals (min = 0; max = 116 ± 15; Q1 = 0.9 ± 0.6; Q3 = 23 ± 4) jointly with high detectabilities in drying aguadas with low and intermediate vegetation cover. Extrapolating these inferences across all waterbodies in the study area yielded in an estimated ~12,000 *C. moreletii* present, demonstrating that Calakmul is an important global stronghold for this species. Because covariates enable insights into population responses to local environmental conditions, we confirm that N-mixture models applied to spotlight count data result in particularly insightful estimates of crocodilian detection and abundance.

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Abstract

Estimates of animal abundance provide essential information for population ecological studies. However, the recording of individuals in the field can be challenging, and accurate estimates require analytical techniques which account for imperfect detection. Here, we quantify local abundances and overall population size of Morelet's crocodile (*Crocodylus moreletii*) in the region of Calakmul (Campeche, Mexico), comparing traditional approaches for crocodilians (Minimum Population Size – MPS; King's Visible Fraction Method – VFM) with binomial *N*-mixture models based on Poisson, zero-inflated Poisson (ZIP) and negative binomial (NB) distributions. A total of 256 nocturnal spotlight surveys were conducted across 50 representative locations (hydrologically highly dynamic aquatic sites locally known as aguadas) over a period of five years (2015-2019). Population size estimates through MPS and VFM revealed a median of 0.4 (min – max: 0 – 67; Q1 – Q3: 0 – 3) and 0.95 (0 – 159; 0 – 8) non-hatchling *C. moreletii* for each aguada, respectively. The ZIP based *N*-mixture model shown overall superior confidence over Poisson and NB, and revealed a median of 5 ± 2 individuals (min = 0; max = 116 ± 15; Q1 = 0.9 ± 0.6; Q3 = 23 ± 4) jointly with high detectabilities in drying aguadas with low and intermediate vegetation cover. Extrapolating these inferences across all waterbodies in the study area yielded in an estimated ~12,000 *C. moreletii* present, demonstrating that Calakmul is an important global stronghold for this species. Because covariates enable insights into population responses to local environmental conditions, we confirm that *N*-mixture models applied to spotlight count data result in particularly insightful estimates of crocodilian detection and abundance.

Introduction

Measures of abundance and population size are key to understand the ecology and natural history of wild animals, and form a main basis for the implementation of conservation management plans. However, due to elusive behaviours and logistic constraints, researchers are often unable to record all individual animals in a given location. Because detectability also interacts with for example local environmental conditions, precise abundance estimates based on census data alone are generally difficult to obtain (e.g. Mazerolle et al., 2007; Sutherland, 2006).

An emerging approach to estimate population sizes from repeated standard count surveys is represented by N-mixture models, which jointly quantify a measure of abundance (λ) with the probability of detecting an individual (p) (Denes, Silveira & Beissinger, 2015; Kéry & Royle, 2016; Royle, 2004; Zipkin et al., 2014). Binomial N-mixture models, for example, treat λ as a random independent variable generated from a statistical distribution to estimate p (Kéry, Royle & Schmid, 2005; Royle, 2004). N-mixture models are particularly promising for wildlife studies because they have the potential to reveal estimates which are comparable to those obtained by more labour-intense (and often more invasive) capture-mark-recapture approaches, and because explanatory variables that may influence λ and p can be investigated in a straightforward way using generalized linear models (GLMs; Courtois et al., 2016; Ficetola et al., 2018; Priol et al., 2014). N-mixture models have already been applied to a wide range of wildlife species (e.g. Belant et al., 2016; Hunter, Nibbelink & Cooper, 2017; Kéry, 2018; Kidwai et al., 2019; Manica et al., 2019; Romano et al., 2017; Ward et al., 2017), but are still considered as an emerging framework with ongoing extensions to original parameterizations (Barker et al., 2018; Bötsch, Jenni & Kéry, 2019; Denes, Silveira & Beissinger, 2015; Kéry & Royle, 2016).

Despite their large size, crocodilians are an example taxonomic group for which imperfect detection during surveys is common (e.g. Balaguera-Reina et al., 2018; Da Silveira, Magnusson & Thorbjarnarson, 2008; Hutton & Woolhouse, 1989). Historically, crocodilian population size estimations outside the capture-recapture framework have largely been based on spotlight surveys to reveal minimal counts, or accounting for visible fractions (Balaguera-Reina et al., 2018; Bayliss, 1987; King, Espinal & Cerrato, 1990). Although not yet widely used, N-mixture models have already been explored to investigate the influence of covariates on both local

87   abundance and crocodile detection (Fujisaki et al., 2011; Gardner et al., 2016; Lyet et al., 2016;

88   Mazzotti et al., 2019; Naveda-Rodriguez, Utreras & Zapata-Ríos, 2020; Waddle et al., 2015), but

89   detailed comparisons with more traditional methods particularly in hydrologically dynamic

90   habitats are as yet lacking.

91   The Morelet's crocodile (*Crocodylus moreletii*) is a medium-to-large crocodile species occurring

92   in Atlantic lowlands surrounding the Gulf of Mexico (Belize, Guatemala and Mexico; Sigler &

93   Gallegos, 2017). Our knowledge on the population ecology and status of *C. moreletii* has

94   markedly increased over the last decades, and a standard international survey program to monitor

95   its wild populations was developed in 2010 (Sánchez-Herrera et al., 2011). However, only

96   rudimentary information about this species is available for the southern region of the Yucatan

97   Peninsula, an area which is characterized by very dynamic hydrological regimes and which

98   harbours parts of the largest remaining expanse of tropical forest in Mesoamerica (Carr III, 1999;

99   Vester et al., 2007). In the present study, we estimate both local abundances as well as the total

100 population size of *C. moreletii* in this region, using a set of binomial *N*-mixture modelling

101 approaches for comparison with more traditionally used methods. Because *C. moreletii* locally

102 inhabits particularly unstable and heterogeneous waterbodies, the study area provides an

103 excellent opportunity to probe the versatility of *N*-mixture models under highly variable levels of

104 detectabilities.

105

Materials & Methods

106

Study area and data collection

107

108 Calakmul Biosphere Reserve (CBR) is located within the southern portion of the Yucatan

109 Peninsula in Campeche, México (18°21.921′ N, 089°53.220′ W; Fig. 1), and together with the

110 adjacent state reserves Balam-Ku and Balam-Kin encompasses more than 1.2 million hectares of

111 protected forest for which *C. moreletii* represents one of the main flagship species. CBR is part

112 of the Selva Maya, which was home to the ancient Mayan civilization and covers 10.6 million

113 hectares of forest across Mexico, Guatemala and Belize (Vester et al., 2007). Precipitation

114 gradually increases from 900 mm annually in the north to 1,400 mm in the south, with significant

115 effects on local forest structure and tree species composition (Martínez & Galindo-Leal, 2002;

116   Vester et al., 2007). The majority of the reserve is composed of tropical semi-deciduous forest

117   with a canopy ranging from 15 to 40 m in height, with the northern parts containing deciduous

118   forest with canopy heights of 8 to 20 m (Chowdhury, 2006). The geological characteristics of the

119   CBR result in rapid rainwater belowground runoff, and non-permanent as well as semi-

120   permanent small to medium-sized waterbodies, locally known as aguadas, represent the only

121   source of water during the dry season (Barão-Nóbrega, 2019; García-Gil, Palacio-Prieto & Ortiz-

122   Pérez, 2002; Reyna-Hurtado et al., 2010). The distribution, prevalence and morphology of

123   aguadas across Calakmul is strongly influenced by annual precipitation cycles, resulting in high

124   levels of seasonal and yearly variation in their general structure (hydric coverage, vegetation

125   communities and cover; Barão-Nóbrega, 2019; García-Gil, Palacio-Prieto & Ortiz-Pérez, 2002;

126   Márdero et al., 2019).

127   Candidate aguadas for *C. moreletii* surveys were identified using existing information (García-

128   Gil, 2000), *Google Earth Pro* (Gorelick et al., 2017), and local knowledge by environmental

129   authorities (*Comisión Nacional de Áreas Naturales Protegidas* - CONANP and *Pronatura*

130   *Península Yucatán*), local guides and community representatives to define a total of 50 survey

131   locations spread across the CBR and its surroundings. While accessibility by vehicles as well as

132   landowner permissions were a prerequisite for field surveys, information on the presence or

133   absence of *C. moreletii* was largely unavailable for survey site selection. Exhaustive nocturnal

134   spotlight counts were performed in July (wet season) 2017 and in March (dry season) as well as

135   July 2018-2019 for all 50 waterbodies whenever possible, supplemented with additional surveys

136   for a subset of 20 waterbodies in July 2015 and 2016. Water levels for each aguada were

137   classified into Dry, Drying, Stable, or Full, and vegetation cover was defined as Low, Medium or

138   High (for details see Barão-Nóbrega, 2019; Fig. S1). Avoiding days of full moon, high winds

139   and heavy rain, surveys were conducted by systematically traveling along the perimeter of the

140   waterbody on foot or by paddling along the shoreline aboard a 3.5 meters aluminium boat.

141   Individual *C. moreletii* were located by their eyeshine reflection (Sánchez-Herrera et al., 2011).

142   If the waterbody was empty, the number of detected crocodiles was assumed zero. Crocodile

143   hatchlings (TL < 30 cm) have high mortality rates (Grigg & Kirshner, 2015) and were excluded

144   from the count data (Balaguera-Reina et al., 2018). Research permits for fieldwork activities in

145   CBR were issued annually by Mexico's Secretariat of Environment and Natural Resources

146   (SEMARNAT; SGPA/DGVS/03030/17; SGPA/DGVS/005403/18) and National Commission of

147   Natural Protected Areas (CONANP; D-RBC-118/2017; D-RBC-030/2018; D-RBC-087/2019).

148   **Abundance estimation**

149   As abundance estimation methods which are in common use for many crocodilians including *C.*

150   *moreletii* (Cedeño-Vázquez, Ross & Calme, 2006; Tellez et al., 2017), we used a Minimum

151   Population Size (MPS) approach as well as the King's Visible Fraction Method (VFM). MPS

152   quantifies the number of recorded individuals per spatial unit to obtain baseline data (Sánchez-

153   Herrera et al., 2011). VFM makes use of repeated counts per site, estimating the percentage of

154   the total population observed during a single count (the visible fraction) as $vf = \frac{\bar{x}}{1.05(2\sigma + \bar{x})}$,

155   where σ is the standard deviation and $\bar{x}$ is the mean number of crocodiles counted (Balaguera-

156   Reina et al., 2018; King, Espinal & Cerrato, 1990). Local absolute abundances (n) at given

157   waterbodies can therefore be expressed as $n = \frac{RA}{vf}$, with RA being the observed local relative

158   abundance.

159   Aside of these traditionally applied methods, we also used binomial *N*-mixture models and

160   explored three alternative statistical distributions: Poisson, Negative Binomial (NB), and Zero-

161   Inflated Poisson (ZIP). Poisson distributions are generally applied to describe relative density,

162   but have a variance which is equal to its mean and therefore do not conform well to under- or

163   over-dispersed data (Denes, Silveira & Beissinger, 2015). Both Poisson and NB distributions

164   tend to perform poorly in the presence of a significant number of true zeros in the dataset (Joseph

165   et al., 2009; Wenger & Freeman, 2008), whereas the ZIP distribution is generally able to better

166   accommodate both true and false zeros (Denes, Silveira & Beissinger, 2015). Both ZIP and NB

167   distributions allow for over-dispersion (Kéry & Royle, 2016; Mazzotti et al., 2019). All *N*-

168   mixture models were fitted to the dataset using the *pcount()* function in the unmarked package in

169   R (Fiske & Chandler, 2011; R Development Core Team, 2019), using RStudio version 1.1.456

170   (RStudio Team, 2016). At first, we allowed λ to vary as a linear function of year to investigate

171   the general assumption of population closure and presence of any temporal trend in the dataset.

172   As no significant difference in abundance values was observed between years ($F = 1.7$; $p =$

173   0.151; Fig. S2), we then assumed that λ remained overall constant with respect to survey year

174   within survey locations in the final models. Waterbody perimeter (in metres) was used as a

175   covariate for λ, in addition to a geographic specifier to account for possible spatial differences in

176   abundance within Calakmul. Waterbody hydric state (Dry, Drying, Stable, Full) and vegetation

177   cover (Low, Medium, High) were used as covariates of p. Waterbody perimeter was scaled and

178   centred by subtracting the mean from each value, divided by the standard deviation (Kéry &

179   Royle, 2016). We discarded models that failed to converge, and used Akaike's Information

180   Criterion (AIC, Akaike, 1974) to identify the best models from each N-mixture approach. The

181   *predict*() function in unmarked was used to generate plots of estimated relationships with

182   predictors for each covariate. Parametric bootstrapping (1000 simulations) was conducted using

183   the *parboot*() function (Fiske & Chandler, 2011), to calculate p-values from sums of squares

184   (SSE), Pearson's Chi-square and Freeman-Tukey fit statistics that quantified the fit of models to

185   the dataset. A dispersion parameter (ĉ) was calculated as the ratio of the observed fit statistic to

186   the mean of the simulated distribution (Kéry & Royle, 2016). As caution is often advised when

187   using NB, even when it is greatly favoured by AIC, particularly when this distribution produces

188   substantially higher estimates than Poisson and ZIP distributions (Kéry, 2018; Kéry & Royle,

189   2016), we've further investigated which model structure would provide most overall confidence

190   in crocodile abundance estimations by running a residual diagnostic analysis using the

191   *plot.Nmix.resi*() function available in the *AHMbook* package for R (Kéry & Royle, 2016).

192   To assess the total number of *C. moreletii* present in the study area ($\hat{N}$), we extracted the total

193   number of semi-temporary and permanent aguadas in the study area (CBR and surroundings)

194   from an existing GIS-based dataset (García-Gil, 2000), and calculated their perimeters using

195   QGIS Desktop software version 3.0.2 (QGIS Development Team, 2019). $\hat{N}$ was assessed

196   through four local abundance estimators (n^{MPS}, n^{VFM}, N-mixture NB and N-mixture ZIP). For n

197   ^{MPS} and n^{VFM}, the relationship between local *C. moreletii* abundance and the perimeter of each

198   surveyed waterbody was determined through a GLM and extrapolated to all waterbodies. Total

199   population sizes based on MPS and VFM were also calculated by solely multiplying average

200   local abundance estimations with the total number of waterbodies.

201

202   **Results**

203   A total of 256 surveys were conducted between 2015 and 2019 (20 surveys in July of both 2015

204   and 2016, 42 surveys in July 2017, 47 and 48 surveys in March and July 2018, as well as 50 and

205   47 surveys in March and July 2019), yielding a total of 1,105 *C. moreletii* records (Total

206   waterbody perimeter = 24,980 metres; Total survey distance covered = 127,897 m). *Crocodylus*

207   *moreletii* was detected at least once in 32 of the 50 surveyed sites (64%). Counts per spotlight

208   survey ranged between zero and 89 (median = 0; Q1 = 0; Q3 = 2) and relative abundance per

209   waterbody (mean number of individuals counted) averaged between 0 and 67 (median = 0.4; Q1

210   = 0; Q3 = 3). Across sites, vf varied between 0.16 and 0.95 (mean ± SD = 0.48 ± 0.24), with the

211   resulting local population size estimates (n^{VFM}) ranging from 0 to 159 individuals (median =

212   0.95; Q1 = 0; Q3 = 8).

213   Considering all possible combinations of covariates, twelve *N*-mixture models were generated

214   for each distribution (Poisson, ZIP and NB). Overall, NB distributions yielded the lowest AIC

215   values across all parameter combinations, although Poisson and ZIP models achieved a better

216   agreement between both observed and expected data as well as between residuals and fitted

217   values (Table 1, Fig. 2). The models which accounted for waterbody location and perimeter on λ

218   as well as the cumulative effects between co-variates on p exhibited the lowest AIC values

219   amongst all possible *N*-mixture combinations (Table 1). Median abundance estimates for NB,

220   ZIP and Poisson were 10 ± 9 (min–max = 0 – 308 ± 264; Q1 = 1 ± 1; Q3 = 31 ± 16), 5 ± 2 (min–

221   max = 0 – 116 ± 15; Q1 = 0.9 ± 0.6; Q3 = 23 ± 4) and 6 ± 3 (min–max = 0 – 123 ± 13; Q1 = 0.9

222   ± 0.6; Q3 = 26 ± 4) individuals per waterbody, respectively. Taken together, we considered that

223   *N*-mixture ZIP provided superior model confidence over the Poisson and NB models, as

224   particularly the latter showed poor residual diagnostic performance and yielded unrealistically

225   high abundance estimates with wide-ranging confidence intervals, in comparison to the other two

226   (Fig. 3, Fig. S3). Based on the *N*-mixture ZIP model, the highest probabilities of detection (p =

227   0.70) were observed in Drying waterbodies with Low to Moderate vegetation cover, whereas low

228   detectability was associated with High vegetation cover ($p < 0.25$, Fig. 4, Fig. S4). Bootstrap p-

229   values for the best-fit *N*-mixture ZIP model based on SSE, Freeman-Tukey, and Chi-square

230   statistics were 0.14, 0.01 and 0.20 (Fig. S4), respectively, at evidence for over-dispersion (ĉ =

231   2.70).

232   The relationships between waterbody perimeter and local abundance estimates (n^{MPS}, n^{VFM}, N-

233   mixture NB and N-mixture ZIP) were used to provide an estimate for the total number of non-

234   hatchling *C. moreletii* in the study area (Table 2). Analyses of the GIS-based dataset revealed a

235   total of 1,663 aguadas, which had a median perimeter of 139 (min = 40 m; max = 3639 m; Q1 =

236   98 m; Q3 = 207 m; Fig. 5). Based on these numbers, MPS$^{\text{GLM}}$ defined a minimum *C. moreletii*

237   population size of 4,273 non-hatchling individuals, which is considerably lower than the values

238   obtained by approaches which take detectability into account (Table 2). The N-mixture ZIP

239   model revealed a total population size of 11,681 crocodiles, which was slightly below the value

240   obtained by VFM$^{\text{GLM}}$ (12,177 crocodiles). The highest population size estimate of 15,184

241   individuals was produced by VFM without taking waterbody perimeter into account.

242   **Discussion**

243   Allowing for the separate estimation of abundance and detection probabilities from replicated

244   counts of unmarked individuals (e.g. Kéry & Royle, 2016; Zipkin et al., 2014), N-mixture

245   models have in recent years become applied to taxa ranging from mosquitoes to megafaunal

246   mammals (Kidwai et al., 2019; Manica et al., 2019). In the present study, we applied a set of

247   such models to multi-year and multi-site data for the Morelet's crocodile *C. moreletii* in southern

248   Yucatan, where it inhabits particularly dynamic waterbodies and serves as an important flagship

249   species for a large expanse of protected forest. We reveal that Calakmul represents a global *C.*

250   *moreletii* stronghold and show that N-mixture models offer a flexible approach for abundance

251   estimates when ecological conditions cause wide variations in detectability.

252   Count data are often used as a proxy for true abundance, but require the implicit assumption that

253   the relationship between observed counts and actual population sizes remains constant (e.g.

254   Kéry, Royle & Schmid, 2005). For crocodilians, count data may indeed serve as abundance

255   surrogates to capture population temporal and spatial trends related with for example habitat

256   structure or human induced changes to the environment, but only when conditions during

257   multiple surveys allow for the recording of similar proportions of individuals (Bayliss, 1987;

258   Platt & Thorbjarnarson, 2000). As this was likely not the case in our study, we assumed that

259   local crocodile abundances remained overall constant and did not allow λ to vary with respect to

260   survey year, water level and vegetation cover, due to the more evident effect on these variables

261   on the observational process rather than on local abundance (Fig. 4). In Calakmul, decreasing

262   water availability caused by disruptions in the timing and intensity of precipitation resulted in

263   marked shifts in water level and vegetation cover of aguadas across the study period (Barão-

264   Nóbrega, 2019; Márdero et al., 2019; Reyna-Hurtado et al., 2019). Under such conditions, the

265   observer's ability to detect individuals will widely vary both temporally as well as spatially,

266   requiring the effects of environmental conditions to be taken into account for obtaining accurate

267   estimates (see also Fujisaki et al., 2011).

268   Given that the majority of *C. moreletii* habitat across its range is represented by rivers and lakes

269   where spotlight searches are conducted over larger areas than in the case of our more confined

270   aguadas (Cedeño-Vázquez, Ross & Calme, 2006; Sánchez-Herrera et al., 2011; Tellez et al.,

271   2017), we argue that our surveys provide particularly accurate information. The non-linear rise in

272   abundances with increasing size of aguadas for the MPS, VFM and *N*-mixture ZIP curves is

273   likely linked to larger waterbodies representing more hydrologically stable environments,

274   therefore supporting higher relative numbers of reproductive individuals. Small to medium sized

275   aguadas are generally more prone to desiccation (Barão-Nóbrega, 2019), and are often inhabited

276   by only 1-2 adult *C. moreletii* which might not locally reproduce. It also needs to be born in

277   mind that the relationship between waterbody surface and volume with perimeter, while

278   depending on the overall shape, is non-linear in general. Given that detection rates are not

279   accounted for, the low abundance values for the MPS approach are not surprising. The VFM and

280   the *N*-mixture ZIP model, on the other hand, consider detectability and reveal remarkably

281   converging abundances for waterbodies below 1200 metres in perimeter, a size class which

282   accounts for 98% of aguadas in the study area (Barão-Nóbrega, 2019; García-Gil, Palacio-Prieto

283   & Ortiz-Pérez, 2002). The lower abundance estimates as predicted by the *N*-mixture ZIP model

284   for larger sites, where relative variation around mean counts for repeated surveys are low,

285   suggests that this model generally assumes higher detectabilities under such scenarios; that

286   surface area is related to encounter rates for crocodilians has been previously documented (e.g.

287   Da Silveira, Magnusson & Thorbjarnarson, 2008; Fujisaki et al., 2011).

288   *N*-mixture models yield unbiased estimates of abundance and detectability in simulated datasets

289   of closed populations (Kéry & Royle, 2016; Royle, 2004), but benchmarks to assess the

290   performance of *N*-mixture models from field data are difficult to obtain (Kéry, Royle & Schmid,

291   2005). A particular feature of our dataset is a wide range of count values across sites, with zero

292   detections being a common occurrence (no *C. moreletii* were recorded for about 40% of aguadas,

293   and approximately 60% of all surveys yielded in no counts). This likely led to the limited fit of

294   our data to assumptions of specific distributions, which is a common problem in count data

295   (Kéry & Royle, 2016; Lee & Nelder, 2000; Ver Hoef & Boveng, 2007). Estimates of local

296   abundances in Drying aguadas were also possibly slightly biased downward, as such situations

297   can lead to temporary emigration or hiding behaviour in dens and burrows within or in the

298   vicinity of waterbodies (Barão-Nóbrega et al., 2016; Platt, 2000). That the geographic specifier

299   significantly improved the performance of our models however also suggests a high degree of

300   philopatry, supporting the assumption of closed populations; low levels of dispersal are also

301   evidenced by genetic data on the relatedness structure within and between aguadas (Barão-

302   Nóbrega et al., unpublished). A particular strength of the *N*-mixture models was their ability to

303   directly relate detectability with ecological parameters. While our findings confirm existing

304   studies on the general nature of such relationships (Bayliss et al., 1986; Cherkiss, Mazzotti &

305   Rice, 2006; Da Silveira, Magnusson & Thorbjarnarson, 2008; Fujisaki et al., 2011; Montague,

306   1983; Wood et al., 1985), they enabled an accurate quantification for the estimation and

307   interpretation of *C. moreletii* abundances specifically for our study setting.

308   The comparison between the three binomial *N*-mixture models suggested that the ZIP

309   distribution provided best confidence overall. The NB model overall exhibited lower AIC values,

310   but performed poorly during the residual diagnostic analysis and revealed excessively large

311   confidence intervals which are likely linked to model unidentifiability (the "good fit/bad

312   prediction dilemma"; see Dennis, Morgan & Ridout, 2015; Joseph et al., 2009; Kéry, 2018; Kéry

313   & Royle, 2016 for detailed discussion on this topic). It also resulted in abundance estimates

314   which appeared unrealistically high, linked to low projected detection probabilities related to

315   water level and vegetation cover (see also Mazzotti et al., 2019 for a similar finding on the

316   closely related *Crocodylus acutus*). Hierarchical modelling of abundance from unmarked

317   individuals using *N*-mixture models will remain a rich ground for both theoretical and applied

318   investigations also in the future (Bötsch, Jenni & Kéry, 2019; Kéry, 2018; Kéry & Royle, 2016).

319   Extrapolating our abundance data across Calakmul requires that the surveyed aguadas are

320   unbiased representatives for the entire area. While a randomization process for site selection was

321   not possible due to logistic constraints (landowner permission and site accessibility), we did not

322   take previous information on the presence or absence of *C. moreletii* into account, and based our

323   inferences on a large sample size of sites. Comparing our overall population sizes derived for

324   Calakmul with country-wide estimates for *C. moreletii* numbers (largely based on the MPS

325   approach, the total population size in Mexico has been estimated at 78,157 – 104,815

326   individuals; Álvarez, 2005; Rivera-Téllez et al., 2017), reveals that our study area represents a

327   significant stronghold for the study species. The importance of Calakmul for *C. moreletii* is

328   further reinforced by the finding that it still harbours genetically pure individuals, whereas

329   genetic pollution through increased hybridization with the American crocodile *C. acutus* is

330   common across other parts of its range (Barão-Nóbrega et al., unpublished; Pacheco-Sierra et al.,

331   2018).

Conclusions

333   Long-term monitoring data using landscape-level systematic surveys provide useful information

334   to describe spatial and temporal patterns of relative density in crocodilians (Fujisaki et al., 2011;

335   Waddle et al., 2015). This study constitutes the first population size estimates for the south-

336   central region of the Yucatan Peninsula, and reveals a healthy population of *C. moreletii*, likely

337   involving multiple active reproduction areas across the region. Because covariates enable

338   insights into population responses to local environmental conditions, we confirm that *N*-mixture

339   models applied to spotlight count data result in particularly insightful estimates of crocodilian

340   detection and abundance. Future studies could expand the existing field surveys and *N*-mixture

341   models to investigate whether further factors such as annual precipitation, water quality,

342   surrounding forest structure, human activity and reproductive activities account for local

343   presence and abundance. On a larger scale, we also recommend the use of *N*-mixture approaches

344   to analyse existing and future *C. moreletii* spotlight count data collected across its range

345   (Álvarez, 2005; Rivera-Téllez et al., 2017; Sánchez-Herrera et al., 2011), to provide more

346   accurate baseline information for future conservation management plans at species level.

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577

Abundance estimation models of *Crocodylus moreletii* in Calakmul using three different *N*-mixture model approaches (Poisson, Negative Binomial - NB and Zero Inflated Poisson - ZIP).

Models were fitted with different combinations of waterbody perimeter as covariate of abundance (λ) and vegetation cover (Low, Moderate, High) and water level (Dry, Drying, Stable, Full) as categorical co-variables of detection (*p*). The models highlighted in bold exhibited the lowest AIC values amongst all possible N-mixture combinations.

1 **Table 1.** Abundance estimation models of *Crocodylus moreletii* abundance in Calakmul using

2 three different *N*-mixture model approaches (Poisson, Negative Binomial - NB and Zero Inflated

3 Poisson - ZIP), with different combinations of waterbody perimeter as covariate of abundance (λ)

4 and vegetation cover (Low, Moderate, High) and water level (Dry, Drying, Stable, Full) as

5 categorical co-variables of detection (*p*). The models highlighted in bold exhibited the lowest AIC

6 values amongst all possible N-mixture combinations.

Covariates	Model	AIC	LogLike	Parameters	AIC weight
p (.), λ (.)	NB	920	457		< 0.01
	ZIP	1960	977	2	< 0.01
	Poisson	2399	1197		< 0.01
p (.), λ (perimeter)	NB	913	452.5		< 0.01
	ZIP	1440	716.3	3	< 0.01
	Poisson	1775	884.7		< 0.01
p (vegetation), λ (.)	NB	798	394.3		< 0.01
	ZIP	1521	755.7	4	< 0.01
	Poisson	1888	940.3		< 0.01
p (vegetation), λ (perimeter)	NB	794	391.4		< 0.01
	ZIP	1171	579.6	5	< 0.01
	Poisson	1430	710.2		< 0.01
p (waterlevel), λ (.)	NB	650	319.2		< 0.01
	ZIP	1273	630.6	5	< 0.01
	Poisson	1636	813.2		< 0.01
p (waterlevel), λ (perimeter)	NB	643	314.7		< 0.01
	ZIP	963	47.7	6	< 0.01
	Poisson	1195	591.8		< 0.01
p (waterlevel+vegetation), λ (.)	NB	643	313.5		< 0.01
	ZIP	1152	568.1	7	< 0.01
	Poisson	1472	729.4		< 0.01
p (waterlevel+vegetation), λ (perimeter)	NB	638	310.1		< 0.01
	ZIP	894	438.3	8	< 0.01
	Poisson	1103	543.9		< 0.01
p (waterlevel*vegetation), λ (.)	NB	626	299.0		0.37
	ZIP	1141	438.3	13	< 0.01
	Poisson	1459	716.7		<0.01
p (waterlevel*vegetation), λ (perimeter)	NB	630	297.5		0.45
	ZIP	878	424.5	15	< 0.01
	Poisson	1083	528.0		< 0.01
***p* (waterlevel+vegetation), λ (perimeter+region)**	**NB**	**626**	**248.3**		**0.27**
	ZIP	**740**	**403.7**	**26**	**< 0.01**
	Poisson	**748**	**493.0**		**< 0.01**

Estimates of total population size of *Crocodylus moreletii* occurring in the region of Calakmul based on five different estimation approaches.

MPS – crocodile count data alone (without considering detection probability); VFM – King's visible fraction method; MPS^{GLM} – Generalized linear model considering the relation between MPS and waterbody perimeter; VFM^{GLM} – Generalized linear model considering the relation between VFM and waterbody perimeter; ZIP – Zero Inflated Poisson N-mixture approach.

1 **Table 2.** Estimates of total population size of *Crocodylus moreletii* occurring in the region of

2 Calakmul based on five different estimation approaches. MPS – crocodile count data alone

3 (without considering detection probability); VFM – King's visible fraction method; MPS^{GLM} –

4 Generalized linear model considering the relation between MPS and waterbody perimeter;

5 VFM^{GLM} – Generalized linear model considering the relation between VFM and waterbody

6 perimeter; ZIP – Zero Inflated Poisson *N*-mixture approach.

Approach	Total population size
MPS	9,941 (6,651 – 13,230)
VFM	15,184 (14,014 – 16,355)
MPS^{GLM}	4,273 (4,112 – 4,440)
VFM^{GLM}	12,177 (11,543 – 12,846)
N-Mixture ZIP	11,681 (2,010 – 19,653)

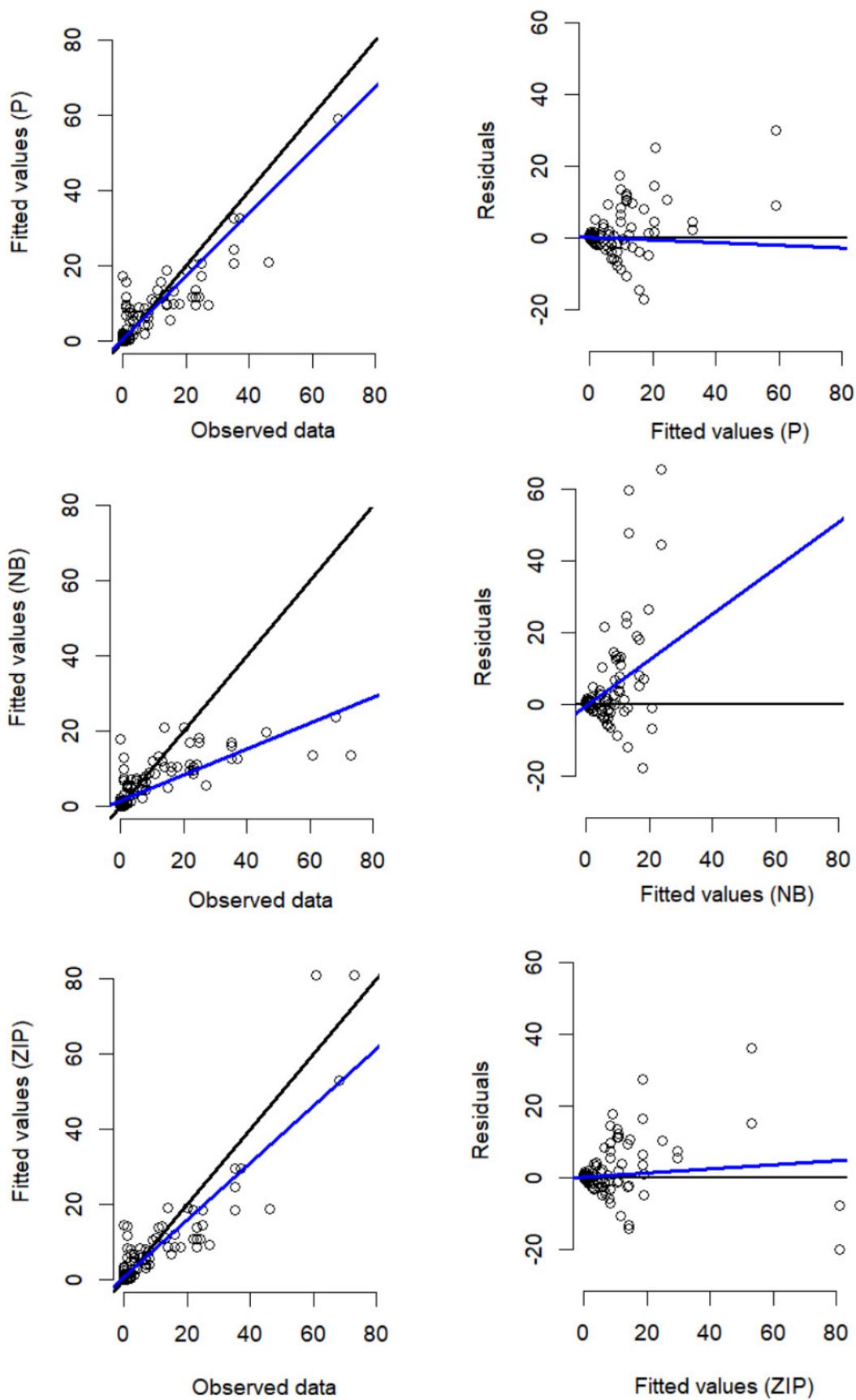
Figure 1

Location of the Calakmul Biosphere Reserve (CBR) in southern-central region of the Yucatan Peninsula (Mexico).

The area delimited inside the inner lines within the grey and dark grey areas (CBR) represent, respectively, the politically established buffer and core zones of the biosphere reserve. White squares represent *C. moreletii* survey locations.

Figure 2

Residual diagnostics for the three *N*-mixture models fitted to the *C. moreletii* spotlight count dataset.

Left hand side figures represent Poisson, NB and ZIP *N*-mixture fitted values vs observed crocodile counts, where the black line shows a 1:1 relationship and the blue line is the linear regression line of best fit. Right hand side figures represent residuals vs fitted values (black line denotes a zero residual and the blue line is the linear regression line).

low2000["

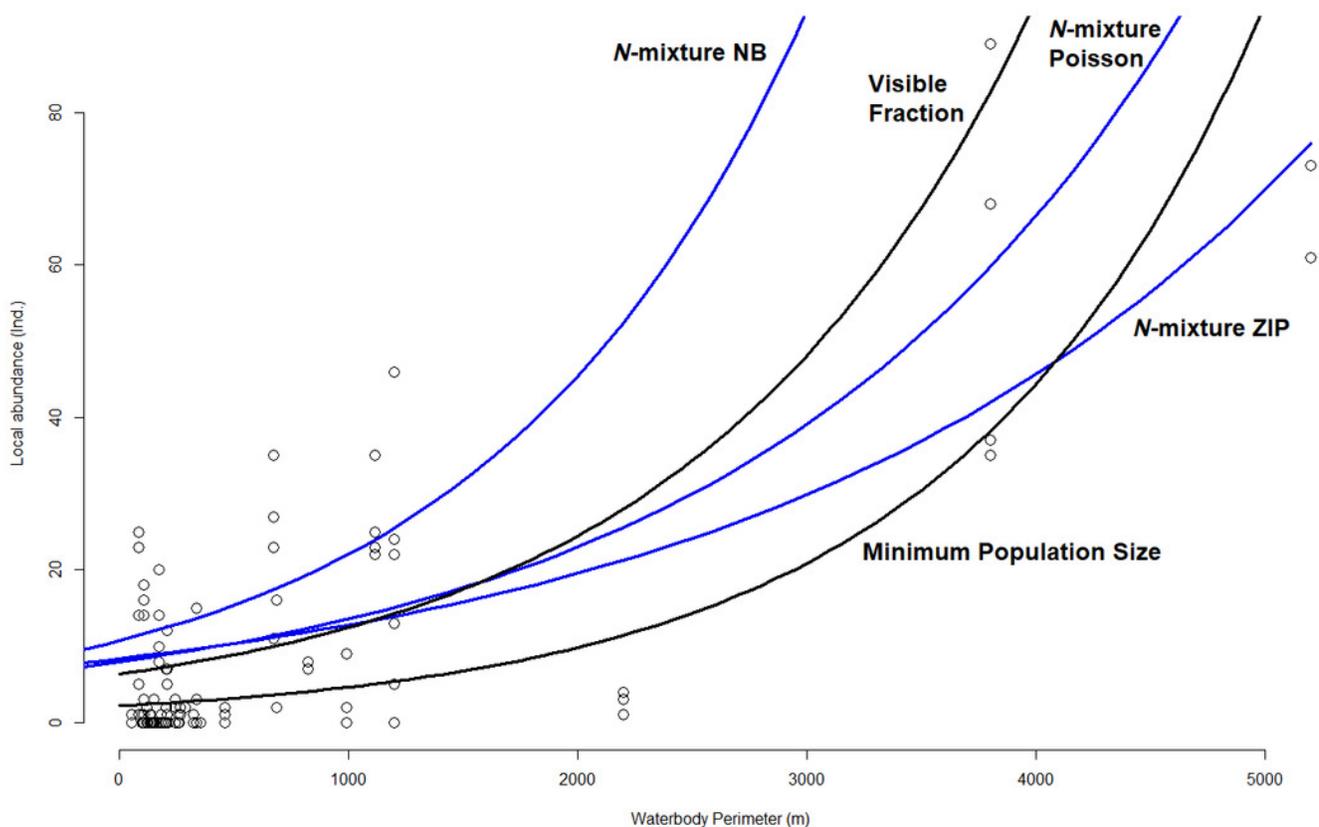



Figure 4

Crocodylus moreletii detection probability estimations in function of water level and vegetation cover inside the waterbody calculated through Zero Inflated Poisson *N*-mixture modelling.

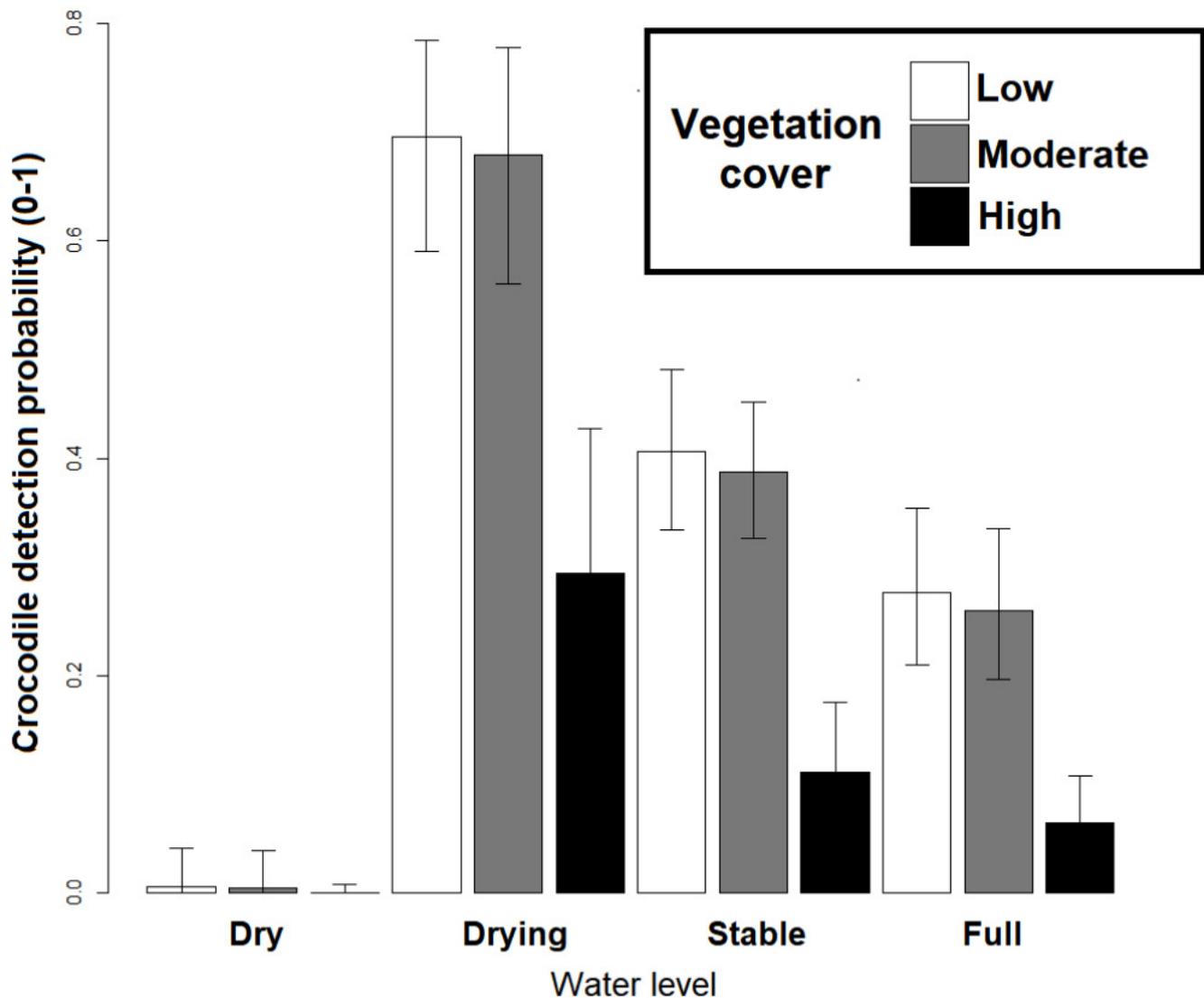



Figure 5

Perimeter distribution of the 1663 semi-temporary and permanent waterbodies across the region of Calakmul (Campeche, Mexico).

Data extracted from a GIS hydrological dataset published for this region (García-Gil, 2000).

Dashed lines represent the median (red) and mean (blue) waterbody perimeter values.