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Original Research Article

Estimating population status and site occupancy of saltwater crocodiles *Crocodylus porosus* in the Ayeyarwady delta, Myanmar: Inferences from spatial modeling techniques

Kay Zin Than [a, b, e], Colin T. Strine [f], Tuanjit Sritongchuay [a, d], Zaw Zaw [b, g], Alice C. Hughes [a, c, d, *]

[a] *Landscape Ecology Group, Centre for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan Province, 666303, PR China*
[b] *International College, University of Chinese Academy of Sciences, Beijing, 100049, PR China*
[c] *Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw, 05282, Myanmar*
[d] *Center of Conservation Biology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla, 666303, China*
[e] *Watershed Management Division, Forest Department, Ministry of Natural Resources and Environmental Conservation, Nay Pyi Taw, 15011, Myanmar*
[f] *School of Biology, Institute of Science, Suranaree University of Technology, 111 University Avenue, Muang, Nakhon Ratchasima, 30000, Thailand*
[g] *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan Province, 666303, PR China*

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A B S T R A C T

Saltwater crocodiles *Crocodylus porosus* are listed as critically endangered in Myanmar because they are limited to Meinmahlakyun Wildlife Sanctuary (MKWS) in the Ayeyarwady delta region. Little contemporary data exists on their distribution and population size which hinders effective conservation and management. We conducted standardized spotlight surveys and camera trap surveys along the rivers inside MKWS, and two nearby reserved forests. We used Hierarchical N-mixture models, Spatial Count models, and the relative abundance index to estimate site use by and population sizes of saltwater crocodiles in the Ayeyarwady delta. To address biases in detectability, we used maximum-likelihood and Bayesian approaches (1) to assess occupancy (site use) and population parameters of saltwater crocodiles, and (2) to assay abiotic and anthropogenic factors affecting it. Saltwater crocodiles were more likely to be abundant and occupy in the waterways inside MKWS than the reserved forests, and in the narrow and low salinity waterways than the wide and high salinity ones. Abundance of saltwater crocodiles was lower in areas with the human settlements than in areas with no settlement. Creeks within MKWS had moderate salinity and no human settlement and therefore it can be regared as the last remaining optimal saltwater crocodile habitat of the Ayeyarwady Delta. We estimated the saltwater crocodile population sizes in MKWS were 75 ± 9.92 individuals as absolute spotlight index, 58 ± 8.02 individuals as the maximum likelihood estimate of the N-mixture models and 68 ± 10.00 individuals as the Bayesian estimate of the spatial count models. Current population estimates of saltwater crocodiles are lower than the previously reported population size in 1999, and the declining population is now restricted to MKWS. We suggest developing buffer zones in the reserved forests around the wildlife sanctuary

* Corresponding author. Landscape Ecology Group, Centre for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan Province, 666303, PR China.
E-mail address: ach_conservation2@hotmail.com (A.C. Hughes).

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to increase habitat areas for saltwater crocodiles and to improve the outlook for long-term saltwater crocodile survival in Myanmar.

1. Introduction

There are 24 described species of crocodilian including crocodiles, alligators, caimans, and gharials, and all are semi-aquatic apex predators living in the world's tropics and warm temperate regions (Grigg and Kirshner, 2015). Of the 24 species of crocodilian, 30% are critically endangered according to the International Union for Conservation of Nature (IUCN) Red List 2020. Moreover, tropical regions contain the greatest proportion of threatened and data-deficient reptile species, and 75% of species within the Crocodylidae are threatened as a consequence of overexploitation and habitat loss (Böhm et al., 2013). The estuarine or saltwater crocodile, *Crocodylus porosus Schneider 1801*, is the largest in size (Britton et al., 2012) and most widely distributed crocodilian, ranging from southern India and Sri Lanka, across Southeast Asia, east through the Philippines to Palau Islands and down through Indonesia, the Solomon Islands and Papua New Guinea to northern Australia. Saltwater crocodiles are ecosystem architects through predation, nutrient cycling, and shaping the vegetation community in the coastal and wetland environments that they inhabit (Mazzotti et al., 2009; Hanson et al., 2015; Somaweera et al., 2019·Somaweera et al., 2020).

Although saltwater crocodiles are widely distributed, they are listed in CITES Appendix I except in Australia, Papua New Guinea and Indonesia because of over-exploitation and habitat loss elsewhere. The species was deemed to be at risk of extinction due to excessive wild harvest, illegal international trade and, commercial skin hunting across much of its range since in the early 1940s. The populations in Northern Australia and the Solomon Islands have now recovered following the protective measures in the 1970s and 1990s. (Webb et al., 2010; Fukuda et al., 2011; van der Ploeg et al., 2019). The rapid increase of the saltwater crocodile population in the Solomon Islands and Timor-Leste in the 1990s and 2000s had a resultant increase in crocodile attacks on humans—thus the species has substantial potential for human-wildlife conflict (Brackhane et al., 2018, 2019; van der Ploeg et al., 2019). With a healthy population in Australia and nearby islands, but generally "poorer" status elsewhere, the species was listed as Least Concern (LC) in the IUCN Red List (1996), despite many local populations' trends remaining unknown. Habitat loss due to landuse conversion continues to be a major problem in much of its range (Das and Jana, 2018), the species may be extinct in the wild in Thailand, Cambodia, and Vietnam (Webb et al., 2010). Despite rapid land use conversion to support growing industry and development (Hughes, 2017), little conservation on *C. porosus* has occurred in Southeast Asia.

In Myanmar, *C. porosus* is a protected reptile species under the Protection of Biodiversity and Natural Areas Law (Rao et al., 2013). The occurrence of saltwater crocodiles had been recorded in the coastal areas of Rakhine, Mon, Ayeyarwady and Tanintharyi regions of Myanmar (Thorbjarnarson et al., 1999, 2006; Platt et al., 2012, 2014; 2016). Saltwater crocodiles were extirpated in Lampi Marine National Park (LNMP) by 2000 as a result of illegal exploitation and harvesting for domestic consumption (Platt et al., 2015). Based on crocodile attack records and interview surveys, there may be a few individuals persisting on other islands in the Myeik Archipelago and the Tanintharyi mainland which may have conservation value but further research is needed to confirm the presence of such populations (Platt et al., 2012, 2014; 2015).

The confirmed population of saltwater crocodiles (*C. porosus*) is limited to Meinmahlakyun Wildlife Sanctuary (hereafter MKWS) and nearby reserved forests (hereafter RFs) in the Ayeyarwady delta (Thorbjarnarson et al., 2006). Scattered crocodiles reports from other areas in Myanmar exist in the form of anecdotal records such as attacks (i.e. the Myeik Archipelago and coast of southern Myanmar) (Platt et al., 2012, 2014) but despite repeated surveys, crocodiles have not been confirmed as present outside our study region. It is also the flagship species of the MKWS which is the last remaining mangrove forest and intertidal mudflat in the Ayeyarwady delta. Given the few scattered individuals in Tanintharyi and Rakhine regions (Thorbjarnarson et al., 2006; Platt et al., 2014), the protected habitats in MKWS are of the utmost importance for the continued survival of saltwater crocodiles in Myanmar and thus maintaining genetic diversity for the entire species.

Historically, Myanmar had the largest overall forest cover of any country in Southeast Asia (Leimgruber et al., 2005). Myanmar experienced a 62.6% loss of mangroves between 1975 and 2014 with a rate of 0.18% per year which is four times faster than the global average mangrove loss in 2012 (Richard and Friess, 2016). Rapid decline and deterioration of mangroves, especially in the Ayeyarwady delta began in 1990 due to conversion to rice fields for agriculture, settlement encroachment into the RFs as a result of population growth, overexploitation and illegal tree felling (Webb et al., 2014). Habitat loss due to the clearance of mangrove forests in Pyindayae (hereafter PYD) and Kadonkani (hereafter KDK) RFs near MKWS to boost agricultural productivity may be one of the greatest threats to remaining Ayeyarwady delta's saltwater crocodile population (Thorbjarnarson et al., 2000; Webb et al., 2014). Rapid habitat loss in the Ayeyarwady delta and frequently reported human-crocodile conflict in local media emphasizes that there is an urgent need for proper management of saltwater crocodiles in Myanmar (Zinn, 2019).

Saltwater crocodiles inhabit in wetlands, coastal waterways, shorelines, mangrove-fringed tidal flats, tidal creeks, and they disperse inland via freshwater rivers, creeks, and swamps (Magnusson et al., 1980; Read et al., 2005; Semeniuk et al., 2011). Mangroves are also good habitats for saltwater crocodiles providing abundant food and protective cover for juveniles from adults which may otherwise eat them (Brazaitis et al., 2009). There can be considerable variation in the suitability of various microhabitat features for crocodiles even within the same geographic region, for example in Australia these may include mangrove fringed salt flats and tidal creeks, densely mangrove-inhabited delta, rocky coast and shores, narrow mangrove-inhabited ravines all of which show varying population abundance (Fukuda et al., 2008; Semeniuk et al., 2011). Environmental and anthropogenic factors (i.e. temperature, vegetation structure, elevation, precipitation, salinity, land use composition, prey availability, human population density and human settlements) can influence saltwater crocodile habitat use (Fukuda et al., 2008; Rich et al., 2016; Mazzotti et al., 2019). Studies from Sri Lanka and Sundarbans of Bangladesh found that salinity and proximity to human settlements impacted on activity and population density of saltwater crocodiles (Gramentz, 2008; Aziz and Islam, 2018). Understanding landscape features which the species avoid or depend helps managers and conservationists to elucidate the biological underpinnings for the habitat use patterns of the species (Manly et al., 2002).

The Ayeyarwady delta forms an estuary between the freshwater discharged by rivers originating from the Ayeyarwady river and the influx of saline water from the Bay of Bengal. As a result, the water salinity varies spatially with the volume of freshwater coming from the upstream rivers and intermittent tidal of the Bay of Bengal. Therefore, assessing habitat features such as salinity, and level of protection (i.e. reserved forest or wildlife sanctuary) and the presence of human disturbance which could influence saltwater crocodile distribution may provide critical insights into their regional-spatial ecology in the Ayeyarwady delta (Read et al., 2004).

Spotlight surveys for crocodiles conducted by MKWS have been ongoing since 1999 but the surveys have been haphazard and thus the results cannot be used in reliable population estimates—particularly for population trends. Annual MKWS spotlight count data (Fig. 1) showed stable numbers in adult and sub-adult crocodiles detection trends but large annual fluctuations in numbers of detected juveniles. Fluctuation in detected juveniles between the years may result from the season when the surveys were conducted. Most surveys occurred in the breeding season (especially late months of a year) when juvenile crocodiles were abundant. As the repeated surveys were not conducted to calculate sighting fractions to consider imperfect detection and did not standardize or quantify effort, annual spotlight counts of MKWS do not represent population sizes. It is well reported that uncorrected census techniques such as spotlight counts are not useful estimators of absolute abundance and hence approaches to standardize counts must be applied such as standardizing of surveys techniques under identical conditions, measuring the environmental variables and deriving the correction factor (sighting fraction) to correct the detectability bias (Hutton and Woolhouse, 1989). Many authors have developed methods for visibility bias in spotlight surveys and made corrections to population estimates (Messel et al., 1981; King et al., 1990). Still, robust population estimates are difficult and costly when individuals cannot be reliably recognised or the species is elusive (Skalski, 1994).

Over the last decade, developments in field survey techniques have caused a shift from labour-intensive—often invasive—field surveys towards non-invasive remote sensing devices, such as camera traps which limit the time needed in the field (e.g. Shannon et al., 2014; Burton et al., 2015). In parallel with technological innovations, the standard of analysis has also progressed (e.g. relative density, capture-recapture models) to more appropriate statistical techniques, such as "N-mixture models, Spatial Count models" (Chandler and Royle, 2013; Balaguera–Reina et al., 2018; Burgar et al., 2018; Kidwai et al., 2019) which can be used to estimate density even when individuals are unmarked. Historically, the distribution and abundance of crocodiles have been estimated by using spotlight counts as indices of relative abundance for long-term crocodile monitoring programs (Bayliss et al., 1986; Bayliss, 1987; Hutton and Woolhouse, 1989; Thorbjarnarson et al., 2000; Read et al., 2005; Fukuda et al., 2008; Jet et al., 2011). However, when no estimate is made for visibility bias, the spotlight relative abundance index represents the minimum number of animals in the stable population (Hutton and Woolhouse, 1989). Many factors can influence the number of crocodiles seen during counts i.e. a state (presence or absence) process determining species occurrence or abundance at each site and a detection process that yields observations conditional on the state process (Fiske and Chandler, 2011). Thus, the use of more robust statistical approaches considering the biological (e.g. home-range

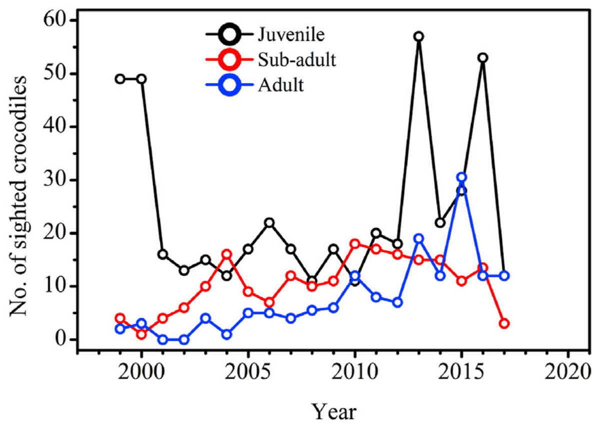

Fig. 1. Numbers of sighted crocodiles during spotlight surveys in MKWS with estimated size classes ("juveniles" < 120 cm, ≥ 120 cm "sub-adults" ≤ 200 cm, "adults" > 200 cm) from 1999 to 2017. (Source: unpublished data from Meinmahlakyun park warden office).

sizes) and ecological requirements (e.g. habitat situation) of the species enables more precise and reliable estimates of population and population structure.

Based on the study of Thorbjarnarson et al. (2000), we expected that saltwater crocodiles would still occupy the adjacent RFs to MKWS but their occupancy and abundance are higher in MKWS because of the high mangrove cover inside the MKWS compared to RFs. Here we aim to (1) estimate proportion of areas occupied (PAO) by saltwater crocodiles across the sampling sites, (2) assess the regional environmental and anthropogenic covariates influencing on the occurrence and abundance of crocodiles, and (3) provide site-specific population sizes of saltwater crocodiles in the Ayeyarwady delta, and (4) evaluate the current population size estimates of MKWS which were observed by different approaches with the previously reported population size.

2. Materials and methods

2.1. Study area

The study was conducted in MKWS in the Ayeyarwady delta as it is the last area in Myanmar where a small population of saltwater crocodiles inhabits. The Ayeyarwady delta is the southernmost part of the Ayeyarwady region of Myanmar where the Ayeyarwady River diverges into the Bay of Bengal and the Andaman Sea. The climate in Myanmar is defined by three seasons, the rainy season from mid-May to October, the winter season from November to February, and the summer season from March to mid-May (Lwin, 2000; Qian and Lee, 2000). The climate in the Ayeyarwady delta is mainly influenced by the tropical southwest monsoon and rainfall always commences during the hot humid months (May to October) (Besset et al., 2017). The total area of the Ayeyarwady region is approximately 155,795 km^2.

In the Ayeyarwady delta, 29 mangrove species have been recorded and the dominant mangrove species include *Avicennia alba*, *Sonneratia caseolaris* and *Heritiera fomes* (Oo, 2002). MKWS covers 137 km^2, and is the last remaining protected mangrove forested island in the Ayeyarwady delta (Webb et al., 2014). Pyindayae (PYD) and Kadonkani (KDK) RFs are located on the east and west sides of this sanctuary. According to the National Biodiversity Strategies and Action plan of 2015, MKWS hosts a wide range of fauna species including 12 mammals, 27 reptiles and 148 bird species, etc. According to the 2014 Myanmar census report, the delta region is densely populated with 6.1 million human inhabitants whose dominant livelihoods include rice cultivation in alluvial soil, fishing, and cultivating oil-palm plantations.

2.2. Sampling design and field surveys

The sampling area extended from 15°51′N to 16°5′N and 95°7′E to 95°28′E to cover all the wetland areas of MKWS and the two adjacent KDK and PYD RFs. The study area was plotted into 3’ × 3’ (minute) gridded plots. We used the “sample” function in R (version 3.4.3) to select random sampling plots (Fig. 2). Thirty sampling plots were established with a total extent of approximately 36 km^2. When random sampling plots fell into the agricultural land or residential areas, we shifted the generated point to the nearest plot which had rivers inside.

We applied Conroy et al. (2008) and Pacifici et al. (2016) two-phase adaptive sampling which is designed to focus on occupancy surveys over a wide area of interest in the first season (phase I during February to May) and abundance surveys within areas of high predicted occupancy in the second season (phase II during September to February) (Appendix A: Table A.1). To account for the fact that crocodiles go undetected at sites (Fiske and Chandler, 2011), we used hierarchical N-mixture models which have been widely used in other taxa particularly mammalian wildlife studies (MacKenzie et al., 2002; Fiske and Chandler, 2011; Shannon et al., 2014; Rich et al., 2016; Penjor et al., 2018; Kidwai et al., 2019). We follow a hierarchical modelling approach (MacKenzie et al., 2002, 2003), to derive abundance from detection/non-detection and repeated count models using spatial and temporal replications (Royle and Nichols, 2003; Royle, 2004). This unified framework for analysis allows us to model detection probability and occupancy. In metapopulation design hierarchical N-mixture models, the regional population is the aggregation of subpopulations and the counts are of individuals that are independent but not uniquely identified (Fiske and Chandler, 2011). In metapopulation design single-season occupancy modelling, the population is assumed to have no immigration or emigration during the survey i.e. the survey period should be short enough to be in line with this assumption. To meet the closure assumption, we conducted field activities in two short survey periods (at most 5 months long) within a year across two seasons: February to May for winter/summer season and October to February for late rainy/summer season to cover the three seasonal gradients of Myanmar (Fig. A.1 for monthly rainfall of Bogalae township). Four repeated surveys were made within each selected sampling site which took four days per site assuming that repeated visits to a site were independent.

During phase I, we conducted spotlight surveys by boat. The phase I survey lasted three and a half months including 120 total working days from February to May 2018. Night-time spotlight survey has a high detection success rate as eyeshine of saltwater crocodiles at night enables efficient sampling (Magnusson, 1980; Bayliss, 1987; Fukuda et al., 2013). Spotlight surveys are suitable for tidal regions and used during the ebb tide when the crocodiles can be seen and counted more easily (Bayliss, 1987; Fukuda et al., 2013). In the delta area, understanding daily tidal inundation is important to determine the lowest water level to enable the spotlight survey to occur at the minimum volume of water. The duration of each rising (flood tide) and falling (ebb tide) lasts 6 h. Therefore, two peaks for ebb tide and flood tide occur per day and the time of each peak is late 1-h day after day. Therefore, the ebb tide time which reaches the lowest water level changes daily. We began counting crocodiles when the tide reached its’ lowest level so the riverbank was visible and the initial survey time at each site was

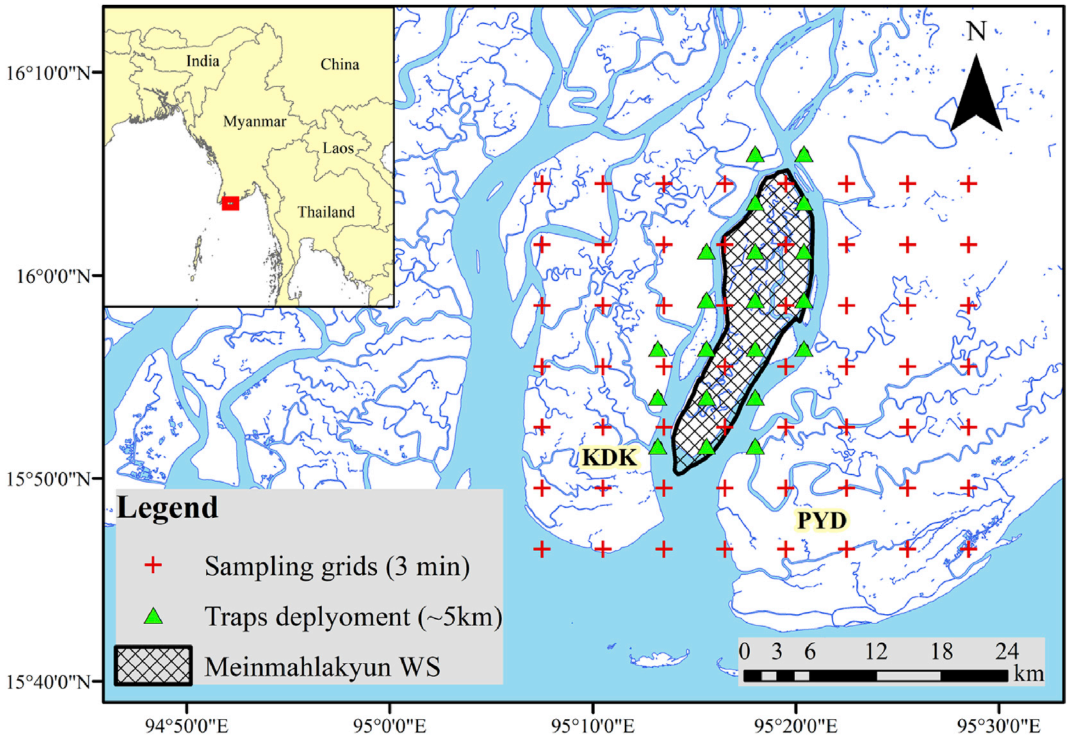

Fig. 2. The study area encompassed MKWS and two reserved forests (KDK RF and PYD RF) in the Ayeyarwady delta (Myanmar). Sampling plots were selected randomly each within 3 min × 3 min grid cell. Spotlight surveys were conducted in randomly selected sampling plots (phase I) and images were collected from 20 camera traps (phase II).

recorded. The 10-V(Volts) spotlights with beams of 50,000 to 200,000 candlepower were used to reduce glare in sightings. A global positioning system (GPS) with WGS84 as a reference coordinate system was used to record each unique location of detected crocodiles in decimal degrees. A single observer observed and the locations of detected crocodiles were reported at 3m GPS accuracy. Although the observer was the same individual on all surveys, we sought consensus from the Meinmahlakyun sanctuary's staff in estimating the size of the detected crocodiles. The detected crocodiles' sizes were estimated and each individual classified as juveniles (<120 cm), sub-adults (≥120 cm and ≤200 cm), adults (>200 cm) and eyeshine only (EO) for submerged individuals (Bayliss, 1987; Thorbjarnarson et al., 2000). To reduce uncertainty in estimating crocodile sizes, we turned off the boat's engine as soon as we sighted the crocodiles and approached as close as possible to the detected crocodiles to record the size. Detected crocodiles that we could not estimate the size of during surveys were listed as eyeshine only (EO) crocodiles and analysed as a separate category in the population size estimation. The surveys were carried out independently in different sampling waterways with equal survey effort — 4 visits to each waterway.

During daylight hours, we measured the environmental parameters along the waterways when the tide reached its' lowest level to maintain the standardization of survey protocols. In this study, we did not use elevation and climate variables (i.e. temperature and precipitation) because the study catchment shows little variation in elevation (approximately 3 m above sea-level) or climate. Although there was no former assessment of the environmental variables affecting the distribution and abundance of saltwater crocodiles in the Ayeyarwady delta, adapting the environmental variables used in the other studies, for example, the studies of Fukuda et al. (2008), Mazzotti et al. (2019), at very different spatial scales and resolutions would not be appropriate at a local scale. Therefore, we conducted the preliminary survey in the Ayeyarwady delta to ensure the environmental variables which were used in this study represent the on-ground ecologically important variables to the presence of saltwater crocodiles in the Ayeyarwady delta region. Based on the preliminary survey and literature, the following variables which were believed to have a potential contribution for abundance and occupancy of the species at the scale of this study were selected and measured at every 500 m along surveyed waterways; (1) depth (2) width (3) salinity (4) mangrove/vegetation cover (5) human disturbance levels (factors, included undisturbed, slightly disturbed, moderately disturbed, and heavily disturbed) (6) site (as a factor, characterizing MKWS and RFs) (Appendix B).

In phase II, as we tried to calculate density estimates within a high predicted occupancy area, we deployed camera traps instead of spotlight surveys. By placing the camera traps at the distances which are smaller than the daily movement distance of the species, we can infer the activity centres of the species. Intuitively, individuals with activity centres close to a trap are more likely to be detected than individuals whose activity centres are further away from a trap. Different approaches for example camera-traps, track plates, sound recordings are used to obtain spatially correlated detection data of the wildlife (Royle and Chandler, 2013). Camera-traps are widely used to monitor and assess wildlife abundance, behaviour, and distribution for large-scale biodiversity conservation (Burton et al., 2015). Although crocodiles are primarily aquatic, they typically require access to a terrestrial environment, such as mudflats and water-edges for nesting, foraging for terrestrial prey (Adame et al., 2018) and thermoregulatory purposes (Mohd-Azlan et al., 2016). We deployed 30 commercially available passive infrared Bestguarder SG-880V cameras for 140 days from September 20, 2018 to 10th February 2019. Camera traps were placed systematically at ~5.5 km away from each other—the spacing was approximately equal to male crocodile daily movement distance (4.0 ± 5.4 km per day) reported by Kay (2005) (Fig. 2). Cameras were attached to the trees lining the riverbank at a height that could not be inundated. The cameras faced the mudflat (potential basking sites) and waterways and the average distance of the camera and target mudflat was set to 4.5 m. Cameras were triggered by heat and motion in front of the camera sensors and had no delay between the detection events.

3. Data analysis

3.1. Occupancy

We quantified saltwater crocodiles' site occupancy, environmental and anthropogenic factors affecting occupancy with single-season occupancy models in both maximum-likelihood and Bayesian frameworks, which accounts for imperfect detection of crocodiles during the surveys (MacKenzie et al., 2002). We used the data collected from the repeated spotlight surveys to meet the assumptions of single-season occupancy analyses. The main assumptions in single-season occupancy analysis include (1) closure i.e. the population is assumed to be demographically closed during the course of surveys, (2) site independence i.e. species detection at a site is assumed to be independent of detections at the other sites (Fiske and Chandler, 2011), (3) no-false positives i.e. the species is correctly identified and if in doubt detections must not be counted, and (4) constant probability of occupancy and detection assumption i.e. the default psi(.) p(.) model which assumes that probability of occupancy and probability of detection are the same for all sites during the surveys or probability of occupancy and detectability is explained by site and observation level covariates. We used environmental parameters collected at the 500 m intervals along the waterways as site-level covariates which might affect saltwater crocodile occupancy. Nearest neighbour, inverse distance weighting, and spline interpolation methods were used to interpolate the collected environmental parameters for the entire study site (Kinoshita et al., 2016). The best interpolated model was chosen using RMSE (root mean square errors) with the null model. Survey time likely influences the detection process and thus it was used as observational level covariate affecting detection probability.

We adopted maximum-likelihood (MLE) and Bayesian (Bayes) frameworks for inference of the occupancy and detection estimates. We ran a single-season site occupancy model from detection and non-detection data using the "unmarked" package (Fiske and Chandler, 2011) for maximum-likelihood estimates and "wiqid" package (Meredith, 2016) for Bayesian estimates in R (version 3.4.3). All continuous covariates were standardized to obtain a mean of zero before the analysis. Two-stage modelling was used where the models with observational covariates on detection probability p were run first while keeping the probability of occupancy ψ constant. Then we evaluated whether detectability was influenced by environmental covariates with both Bayesian and multivariate maximum likelihood occupancy models.

For maximum-likelihood occupancy models, R package "AICmodavg" was used to compare Akaike Information Criterion (AICc) of all possible models with covariates and the goodness-of-fit tests were performed using chi-squared (Fiske and Chandler, 2011) and Freeman-Tukey (Sillet et al., 2012) tests with 200 bootstraps using the R package "unmarked" (Fiske and Chandler, 2011). For Bayesian occupancy models, Markov chains Monte-Carlo (MCMC) with 30,000 iterations were used of which 1000 were discarded as burn-in and checked the values of Rhat ($\widehat{R}$) validate whether or not the models reached convergence. If all MCMC chains converge similarly, the variance between the chains is approximately equal to the average variance within chains and the estimated $\widehat{R}$ will be close to 1. The effective sample size (neff) was also reported to assay the approximate number of independent draws in the models (Muth et al., 2018). Uninformative uniform (flat) priors on the probabilities of occupancy and detection were used because there was no published occupancy study of saltwater crocodiles of the Ayeyarwady delta to provide prior information. Moreover, the flat priors are considered as the reference priors so that parametric inference is primarily driven by the data, rather than the prior (Northrup and Gerber, 2018). The mean values with 95% highest density interval (HDI) of the MCMC samples were used to report the posterior probabilities. The Watanabe-Akaike information criterion WAIC (Watanabe, 2010) was used for the selection of Bayesian occupancy models with environmental covariates. WAIC has been shown to perform better than traditional information-criterion based model selection methods such as DIC (deviance information criterion) in Bayesian models (Luo, 2019).

3.2. Population sizes

The population size was estimated using spotlight index (relative abundance estimates which were used formerly), N-mixture models (maximum-likelihood estimates), and a Spatial Count (SC model i.e. Bayesian estimates) by addressing environmental factors, and home-range size of saltwater crocodiles which can influence the detectability during surveys. In this study, metapopulation design N-mixture models (Royle and Nichols, 2003; Royle, 2004) were used to determine the maximum-likelihood estimates of abundance from spatially replicated count data accounting for imperfect detection. To obtain Bayesian estimates, we applied the Spatial Count (SC) model (Chandler and Royle, 2013) to the camera trap data through integrating an informative prior—home-range sizes of saltwater crocodiles accounting for the distance-related heterogeneity in encounter rates. The Spatial count (SC) model is the extension of spatial capture-recapture (SCR) models for those animals which are not uniquely identifiable or for which identification may be prohibitively costly or invasive. It has been applied for a variety of data sources such as avian point count data and marked or unmarked data from camera traps etc. (Royle, 2004; Royle and Young, 2008; Royle et al., 2009; Chandler and Royle, 2013; Burgar et al., 2018). In contrast to N-mixture models, the movement of individuals among the sampling locations is assumed to occur in the SC model and the counts are not considered as the independent individuals associated with each site.

We used "occuPcount" function in the "unmarked" R package to get the maximum-likelihood estimates of site-specific abundance and to identify the significant environmental parameters affecting it. Functions (ranef) and (bup) in the "unmarked" R package were used to report the empirical unbiased abundance estimates (λ) of different size-classed saltwater crocodiles from the posterior maximum-likelihood distribution. N-mixture models with covariates affecting abundance were assessed by comparing (AICc) values. The goodness- of- fit tests in the "unmarked" package were performed with 200 bootstraps (Fiske and Chandler, 2011) in R (version 3.4.3).

The "rjags" package was used for the SC model which provides Bayesian density estimates with 95% BCI (Bayesian Credible Interval) and addresses spatial autocorrelation among sampling sites by integrating the home-range sizes of the species as informative priors. In the SC model, N individuals are located within a State-space (S) which is an observation window during the survey. Theoretically, S may be defined by geographic boundaries, encompasses all traps, and should be large enough so that individuals' encounter rates are negligible if their home-range centres are at the edges of the boundary. Each individual has an activity centre (s_i) within S and we modelled the individual encounter rate as a function of Euclidean distance between s_i and the location of trap j. Hence the baseline encounter probability of individual i becomes $\lambda_0 = 0$ where its activity centre and trap location are at the same location. The Bayesian analysis of the SC model includes the data augmentation process by setting latent encounter individual N to augmented population size M (Liu and Wu, 1999). Camera trap spacing of 5.5 km which is approximately equal to the daily movement distance of male crocodiles (Kay, 2005), was used and a buffer of 2 km was reserved to the outermost camera coordinates comprising a state space (S) of 517.45 km^2. For the uninformative models, we specified the prior with a uniform distribution between 0 and 1000. For the informative models, we considered different home-range sizes of saltwater crocodiles reported by Brien et al. (2008). We used 13.5 ha, which is the average home-range estimate of saltwater crocodiles as a vague or flat prior. Male and female saltwater crocodiles' home-range estimates of 26.19 ha and 4.64 ha were used as the two informative priors. We used a gamma distribution to specify priors following Chandler and Royle (2013) (Appendix C). The data augmentation value was set to 300 and λ_0 and ψ priors were set with a uniform distribution between 0 and 10 and beta distribution having shape and scale set to 1. We executed 50,000 Markov chain Monte Carlo (MCMC) iterations, a burn-in of 10,000, with a thinning rate of 1 and checked the values of Rhat and neff to validate whether or not the models reached convergence.

Lastly, we calculated the population size of saltwater crocodiles by using the spotlight relative abundance index allowing comparison with earlier population estimates of saltwater crocodiles in the Ayeyarwady delta. To standardize data, we used the first spotlight survey records from each site to calculate spotlight abundance indices. In line with the previous studies of Thorbjarnarson et al. (2000) and Caughley (1980), the sampling waterways were categorized into three groups: Meinmahlakyun wildlife sanctuary (MKWS), Pyindayae reserved forest (PYD), and Kadonkani reserved forest (KDK) depending on the sites that they were located inside the study area. The total distances (kilometres) of waterway surveyed under the three site categories were calculated to estimate the mean encounter rate of saltwater crocodiles. To obtain the absolute population size from the mean encounter rates per kilometre surveyed rivers, sighting fraction p was calculated based on the four replicated surveys (King et al., 1990).

$$p = \frac{m}{(2s + m)^{1.05}}$$

Where m = mean survey value and s = standard deviation. Population size (N) at the sites with size class structure (adult, sub-adult, and juvenile) was estimated by the formula of Messel et al. (1981).

$$N = \frac{m}{p} \pm \frac{[1.96(s)]^{\frac{1}{2}}}{p}$$

4. Results

4.1. Crocodile detections

A total of 141 crocodile detections occurred during the repeated spotlight surveys inside 30 random sample plots in 2018. The size class structure was skewed towards the juveniles (65%, n = 141). The camera trap dataset consisted of 20 sites working for 130 days from 1st October 2018 to 10th February 2019. Ten of the 30 camera traps were either stolen or broken during the study period. Twenty camera traps were successfully deployed in and around MKWS (the area of high predicted occupancy probability) during phase II (Fig. 3). There were 16 independent crocodile detection events recorded on camera traps across the 20 sites for the final 130 sampling days.

4.2. Occupancy or site use

Saltwater crocodiles were detected in 9 of the 30 sampling plots with a naïve occupancy estimate of 0.3 (i.e. occupancy before accounting for detection probability). The probability of detection was influenced by survey time (the time of the day when the spotlight survey was initiated) (Appendix D: Table D.1). In both maximum-likelihood and Bayesian occupancy models, detection probability was negatively associated with the survey time $\widehat{\beta}_{\mathrm{MLE}}$ $(\widehat{SE}) = -1.74$ (1.068) and $\widehat{\beta}_{\mathrm{Bayes}}$ $(\widehat{SD}) = -0.348$ (0.191). Therefore, spotlight surveys conducted early morning (1 a.m.–5 a.m.) had higher detection probabilities than those conducted in late-night (7 p.m.–12 p.m.). The model with the variables of width, salinity, and site (factor) had the highest support from the likelihood-based and Bayesian analyses (Table D.2). The empirical unbiased best maximum-likelihood estimate of the proportion of area (sites) occupied (PAO) is 11 ± 3 (95% CI). The goodness of fit test (Sillett et al., 2012) of the most parameterized multivariate likelihood-based occupancy model showed no evidence of over-dispersion ($\widehat{c} = 1.0487$, freemanTukey = 16.2, p = 0.148) (Fig. D.1) and the Bayesian-based model reached convergence showing the evidence of fit to the data (Fig. D.2). Saltwater crocodile occupancy was negatively associated with the width, salinity of the rivers, and the reserved forest area (MKWS was the reference category) in both likelihood-based and Bayesian analysis (Table 1). The range of average salinity of the sampling rivers inside the study area ranges between 7 and 22 ppt (parts per thousand) (Appendix H). We found that saltwater crocodiles were more likely to occupy in the waterways with low salinity areas compared to the areas with high salinity. Moreover, if the site was randomly selected, the probability of saltwater crocodiles occupying the protected area (MKWS) would be $\widehat{\psi}_{\mathrm{PA(MLE)}} = 0.93$ (0.102 SE) and outside of the protected area (two reserved forests) would be $\widehat{\psi}_{\mathrm{NAPA(MLE)}} = 0.2006$ (0.092 SE). We predicted higher occupancy probability of saltwater crocodiles in MKWS because of the lower salinity and smaller width of rivers than those in the RFs (Fig. 3). As for the Bayesian analysis, a higher posterior occupancy probability was reported for the intercept-only model compared to the Maximum-likelihood model ($\psi_{\mathrm{Bayes}} = 0.445 \pm 0.088$ SD; $\psi_{\mathrm{MLE}} = 0.433 \pm 0.091$ SE). There was strong evidence to suggest that saltwater crocodile occupancy was negatively associated with salinity and reserved forest site as the 95% CRIs did not overlap zero (Table 1).

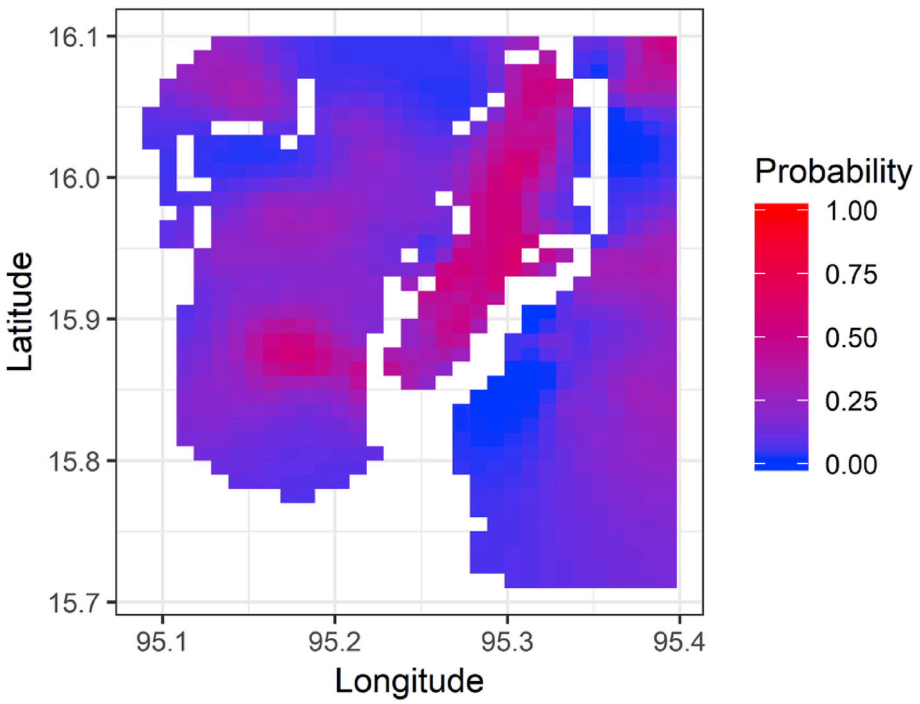

Fig. 3. Predicted probability of occurrence based on the spotlight count data of saltwater crocodiles across sampling sites (logistic transformation of linear estimates in 500 m × 500 m gird cell): Predictions were made on the basis of significant site and observation covariates (see Table 4).

Table 1
Beta summary of best fitted single season occupancy models with detectability of saltwater crocodiles in Ayeyarwady delta, Myanmar.

#	Covariates	Maximum-likelihood (*logit scale*)				Bayesian (*Probit scale*)			
		Mean	SE	95% CI_a		Mean	SD	95% BCI_b	
Ψ	Intercept	20.936	11.036	−0.693	42.565	0.8	0.477	−0.131	1.728
	Width	−3.563	2.182	−7.840	0.714	−0.463	0.345	−1.143	0.202
	salinity	−0.951	0.527	−1.984	0.081	−1.029	0.423	−1.865	−0.216
	Site R	−18.743	0.433	−18.743	0.433	−1.456	0.567	−2.574	−0.350
p	Intercept	1.78	0.756	0.298	3.260	0.351	0.191	−0.012	0.736
	Time	−1.74	1.068	−3.830	0.359	−0.329	0.185	−0.695	0.030

Best fitted site covariates: river width (width), river salinity (salinity), mangrove vegetation cover (mangro_cov) and factor characterizing MKWS (site M) or RFs (site R) where M is the reference category. Observation covariates tested: survey time of a day (time). $_a$Confidence interval. $_b$Bayesian credible interval.

4.3. *Population size*

4.3.1. *Maximum-likelihood estimates*

Population size estimates varied between maximum-likelihood λ_{MLE} N-mixture models and Bayesian estimates D_{Bayes} Spatial Count (SC) models. The maximum-likelihood abundance estimate of saltwater crocodiles with no identification of size classes across the study area λ_{MLE} was 58.10 (8.02 SE) (Table 2). The bootstrap Chi-square p-values for the null models with no environmental covariates were 0.512 for juveniles, 0.557 for sub-adults, 0.562 for adults, and 0.507 for total (a combination of total counts without identifying size-classes) respectively, suggesting that our models provided an adequate fit to the data. The values of $\hat{c}$ (ratio of observed/expected) were 0.99 and 0.96 in total population size model and juvenile size-class models indicating no evidence of over-dispersion. But the adult size-class and sub-adult class model have $\hat{c}$ values of less than 0.5 indicating less variation in the observed data than predicted by the model. We estimated that 22 adult crocodiles and 26 sub-adult crocodiles were present in the Ayeyarwady delta (Fig. 4a). Among the three size classes, juveniles had the highest detection probability of 0.423 (0.051 SE) followed by sub-adults of 0.203 (0.092 SE) and adults had the lowest probability of 0.103 (0.109 SE) (Table 2).

N-mixture abundance models were run without covariates on detection probability as the survey time had no significant effect on detectability (Appendix E: Table E.1). Site-specific abundance was influenced by the width, depth, mangrove cover, human disturbance levels and site factors (Table 3). Width and depth of the rivers, mangrove trees cover and also the heavy presence of human disturbance had negative effects on the abundance of saltwater crocodiles in the Ayeyarwady delta region (Table 3).

4.3.2. *Bayesian estimates*

The estimates with uninformative and vague priors were between 0.185 and 0.141 crocodiles per kilometre square with 95% BCI ranging from 0.004 to 0.503 crocodiles per kilometre square (Table 4). In contrast, the density estimates were influenced by the informative priors ranging from 0.458 (0.224–0.576, 95% BCI) of crocodiles per kilometre square for the male home-range prior to 0.494 (0.311–0.578, 95% BCI) for the female home-range prior (Table 4 and Fig. 4b). The posterior Bayes abundance estimates without informative priors have wide credible intervals (BCI) implying that further information is needed to get a more precise estimate. Male and female priors gave the posterior estimates with narrower credible intervals (BCI) than uninformative flat priors. The 95% credible interval of female prior SC model gave the narrowest interval and hence density produced by female prior SC model D_{Bayes} 0.494 km^2 was likely the most robust estimate of saltwater crocodile density.

The prior σ on λ_0 (encounter probability) influenced the estimates of λ_0 indicating that the SC model with uninformative priors produced the smallest λ_0 estimates which were 0.027 and 0.042, respectively (Table 4). Conversely, the σ (spatial scale parameter) estimates from the SC models with informative priors σ were consistently low from 0.132 (0.085–0.197, 95% BCI) to 0.090 (0.060–0.127, 95% BCI) compared to the SC models with uninformative the prior σ (Table 4).

4.3.3. *Spotlight abundance index*

During the repeated counts, 87% of crocodiles were detected along the sampling waterways inside MKWS (Table 5). However, these spotlight indices are biased by repeated counts and only the first spotlight surveys were used to estimates the crocodile encounter rates in MKWS, KDK and PYD. The overall encounter rate of saltwater crocodiles including adults, sub-adults, juveniles, and eye-shine only individuals in MKWS was 0.64/km (Table 6). The absolute population sizes (N) of each size class were different in MKWS, KDK, and PYD depending on the numbers of detected crocodiles within their size classes. Therefore, based on the calculated sighting fractions, population sizes (N) in the study area were 109, 54, 38 for juvenile, sub-adult, and adult crocodiles respectively (Appendix F: Table F.1). The highest population size estimate of 74.666 ± 9.92 (SE) was found in MKWS which was followed by 24.725 ± 3.83 (SE) in KDK, and the lowest estimate of 7.404 ± 6.52 (SE) was found in PYD (Fig. 4c). The juvenile population size estimate was calculated only for MKWS as no crocodile was sighted during the initial spotlight surveys inside the two RFs. An adult population size estimate of 26.453 ± 4.05 (SE) was calculated for KDK

Table 2
Latent parameter summaries of N-mixture site specific abundance models with size-classes of saltwater crocodiles sampled in the Ayeyarwady delta from March, 2018 to June, 2018. Parameter values are estimated from the null models without covariates with 95% Confidence interval (CI).

Maximum-likelihood estimates																
#	Total				Adult				Sub-adult				Juvenile			
	Mean	SE	95% CI_a		Mean	SE	95% CI_a		Mean	SE	95% CI_a		Mean	SE	95% CI_a	
Ψ[a]	0.856	0.039	0.780	0.856	0.519	0.363	−0.193	1.230	0.577	0.165	0.254	0.990	0.840	0.048	0.747	0.933
λ_i[b]	1.940	0.267	1.477	1.94	0.731	0.754	0.097	5.518	0.861	0.390	0.354	2.092	1.832	0.297	1.333	2.519
λ[c]	58.10	8.020	44.32	76.16	21.93	22.62	2.90	165.5	25.82	11.70	10.63	62.76	54.96	8.93	39.98	75.76
p[d]	0.607	0.041	0.523	0.607	0.103	0.109	0.011	0.535	0.203	0.092	0.077	0.437	0.423	0.051	0.328	0.524

[a] Occupancy of saltwater crocodiles (integrating heterogeneity in detection probability p).
[b] Abundance per sample unit.
[c] Average abundance across the sampling sites.
[d] Detection probability. $_a$Confidence interval.

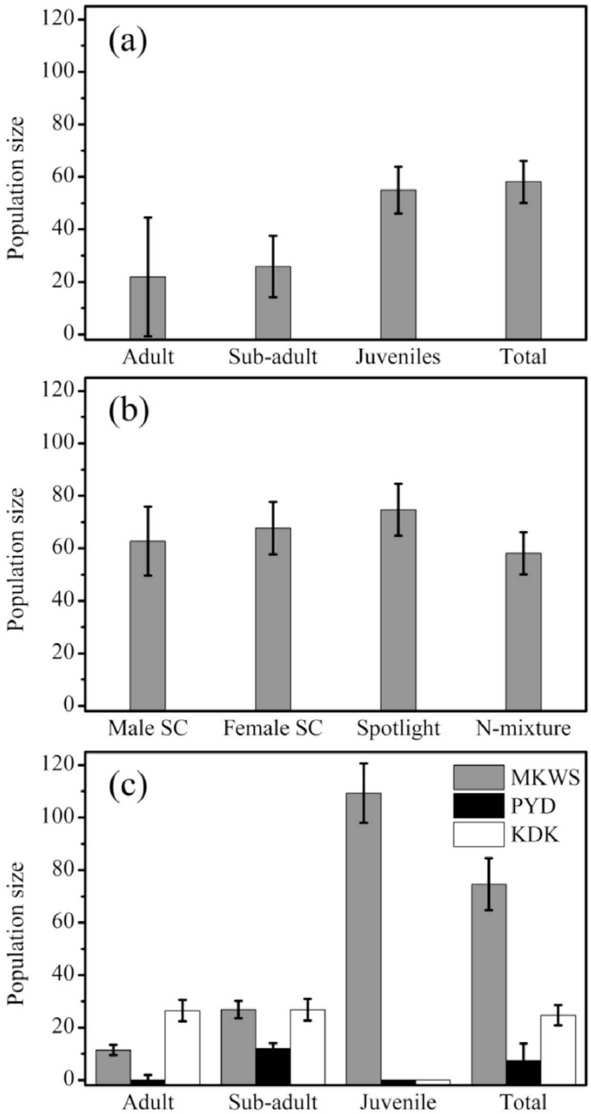

Fig. 4. Population size estimates of saltwater crocodiles by models. (a) Empirical Bayes estimates of λ abundance across all the sampling sites (Mode ± 95% Confidence intervals of N-mixture null models from aggregated counts data), (b) Population size estimates in MKWS by Spatial Count model with informative priors, N-mixture model without covariates, and Spotlight relative abundance index (estimates ± 95% Bayesian credible interval and confidence interval), (c) Spotlight relative abundance estimates of saltwater crocodiles in the study area. MKWS, Meinmahlakyun wildlife sanctuary; PYD, Pyindayae reserved forest; KDK, Kadonkani reserved forest.

Table 3
Beta summaries of best fitted N-mixture model of abundance and detectability of saltwater crocodiles in the Ayeyarwady delta, Myanmar.

N-mixture models	Parameters estimated		Maximum-likelihood (logit scale)			
		Covariates	Mean	SE	95% CI$_a$	
Best fitted model (aggregate counts data)	Λ	Intercept	2.837	0.410	2.033	0.975
		Width	−0.807	0.265	−1.327	−0.287
		Depth	−0.169	0.089	−0.343	0.005
		Mangrove_cov	−0.130	0.139	−0.402	0.142
		Site R	−3.550	0.8	−5.118	−1.982
		hu_distubHc	−9.112	114.902	−234.316	216.091
		hu_distubOc	−0.942	0.914	−2.733	0.850
		hu_distubSc	2.498	0.848	0.836	4.161
	P	Intercept	−0.169	0.288	−0.732	0.395

Site covariates tested: river width (width), river depth (depth), mangrove cover (mangro_cov) site (as a factor, characterizing MKWS (site M) or RFs (site R) where M is the reference category. Human disturbance levels (hu_distubHc = heavily disturbed, hu_distubSc = slightly distubed, hu_distubOc = disturbed where hu_distubAb = absence of human disturbance as reference category. Observation covariates tested: survey time of a day (time). $_a$Confidence interval.

Table 4
Spatial Count (SC) model posterior summaries for saltwater crocodiles sampled in the Ayeyarwady delta from November, 2018 to March, 2019. Parameter values are presented as the mode with 95% Bayesian credible intervals (BCI).

#	Uninformative σ		Vague prior σ (0.135 km^2)		Informative σ (0.262 km^2)		Informative σ (0.046 km^2)	
	Mean (95% BCI)	SD	Mean (95% BCI)	SD	Mean (95% BCI)	SD	Mean (95% BCI)	SD
D[a]	0.185 (0.004, 0.547)	0.174	0.141 (0.017, 0.503)	0.123	0.458 (0.224, 0.576)	0.096	0.494 (0.311, 0.578)	0.073
λ_0[b]	0.02739 (0.000, 0.133)	0.040	0.042 (0.003, 0.299)	0.095	1.925 (0.030, 8.976)	2.567	3.578 (0.062, 9.575)	2.993
σ[c]	5.169 (0.201, 42.477)	12.030	0.732 (0.484, 1.033)	0.141	0.132 (0.085, 0.197)	0.029	0.090 (0.060, 0.127)	0.017
Ψ[d]	0.321 (0.007, 0.943)		0.244 (0.030, 0.865)	0.212	0.788 (0.385, 0.993)	0.166	0.850 (0.532, 0.995)	0.127
N[e]	95.787 (2, 283)	90.171	72.724 (9, 260)	63.634	237.069 (116, 298)	49.806	255.79 (161, 99)	37.926

[a] Density (saltwater crocodiles km^2).
[b] Baseline encounter probability for an individual whose activity center is located precisely at the trap.
[c] Spatial scale parameter determining the rate of decay in encounter probability.
[d] Proportion of individuals from the data augmented population.
[e] Total population size in the state space S.

Table 5
Numbers of crocodiles detected during the four repeated spotlight surveys in Meinmahlakyun wildlife sanctuary (MKWS), Pyindayae (PYD) and Kadonkani (KDK) reserved forests.

	MKWS	PYD	KDK
Juvenile	86	7	0
Sub-adult	18	1	2
Adults	6	1	2
Eye-shine only (EO)	13	0	5
Total [a]	123 (87%)	9 (0.06%)	9 (0.06%)

[a] Total number of crocodiles followed by frequency (%) in parentheses.

Table 6
Comparisons of saltwater crocodiles' size classes and mean encounter rates (the number of crocodiles observed per kilometre of survey route) observed during surveys of Meinmahlakyun wildlife sanctuary in 1999, 2003 and 2019.

Size class	1999	2003	2019
Juvenile	50	14	27
Sub-adult	4	8	9
Adults	2	0	4
Eye-shine only	5	1	5
Kilometers surveyed (km)	169.7	102.5	69.5
Mean encounter rate (crocodile/km)	0.234/km	0.22/km	0.64/km

which was followed by an estimate of 11.44 ± 2.00 (SE) in MKWS (Fig. 4c). Sub-adult population sizes were estimated at 26.864 ± 3.288 (SE) in MKWS, 12 ± 2.004 (SE) in PYD, and 26.782 ± 4.150 (SE) in KDK, respectively. The total population size of saltwater crocodiles including EO was estimated *c.*106 in the Ayeyarwady delta (Table F.1).

5. Discussion

This is the first study to investigate impacts from environmental parameters on saltwater crocodile occupancy and abundance in the Ayeyarwady delta. We use this data to estimate their population sizes by using alternative methods to address the well-known detection bias of crocodiles in the wild. Although mangrove cover did not determine the occupancy and abundance of saltwater crocodiles, we found saltwater crocodiles were more likely to occupy in MKWS than nearby RFs, and the human disturbance decreased abundance.

5.1. Habitat use

About 37% of sampling sites within MKWS and RFs were occupied by saltwater crocodiles. Both likelihood-based and Bayesian results showed that the occupancy of saltwater crocodiles is lower in RFs than in MKWS. Saltwater crocodiles are not likely to occupy wide rivers with high salinity. Bayesian analysis is best used with prior information, but we had no previous knowledge about the coefficient of environmental parameter values for our study area. Our model outputs must, therefore, be interpreted with caution if the results are to be used in conservation decisions (Northrup and Gerber, 2018). We found no saltwater crocodiles in rivers near the sea mouth, which is several kilometres wide with high tides and no vegetation cover along the banks. Saltwater crocodiles were likely to occupy river creeks (sites with narrow river channels) within the wildlife sanctuary. Similarly, Mazzotti et al. (2007) found that crocodiles use narrow river channels (creeks) to access inland freshwater habitats such as mangroves or nesting habitats. Moreover, sub-adult and adult crocodiles in the Meinmahlakyun wildlife sanctuary largely occupied the tertiary and secondary water channels (creeks) (Thorbjarnarson et al., 2000). Mangrove vegetation cover did not affect site occupancy but negatively affected the abundance. Nevertheless, mangrove vegetation is regarded as poor nesting habitat for saltwater crocodiles (Magnusson et al., 1980; Webb et al., 1983; Evans et al., 2017). To nest, saltwater crocodile needs specific vegetation communities, particularly with *Melaleuca* species including *M. leucadendra*, *M. cajutupi*, and *M. viridiflora* in northern Australia (Brazaitis et al., 2009; Fukuda and Cuff, 2013). While conducting surveys in the study area, we observed four active and newly built nests in the vicinity of older unused nests, where three nests were in MKWS and one nest in the Kadonkani reserved forest. Those nests were mostly built with ferns (*Acrostichum aureum*) and shrubs (*Acanthus ilicifolius*) species. From the findings of most active nests inside the MKWS, the population is likely reproducing and breeding inside the sanctuary.

We found numerous human settlements and fishing nets setting up along the rivers within the two RFs. Presently, MKWS has less human interference than RFs where monoculture mangrove reforestation programs were initiated after the cyclone Nargis in 2008 (Oo, 2002; Leimgruber et al., 2005; Webb et al., 2014). The abundance of saltwater crocodiles was lower in areas heavily occupied by the human settlements than in less disturbed areas. However, the land-use intensity had little impact on *C. porosus* abundance compared to factors such as precipitation, temperature, and salinity in Northern Australia (Fukuda et al., 2008). However, poaching is often prevalent in areas with high human disturbance, thus the latter can only serve as temporary habitats for crocodiles (Musambachime, 1987; McGregor, 2005; Gramentz, 2008).

Although saltwater crocodiles are salt-tolerant species, we found that their site occupancy reduces with increasing salinity, and former studies also showed that for foraging and nesting, saltwater crocodiles commonly use hypo-saline (low salinity) areas (Fukuda and Cuff, 2013; Hanson et al., 2015; Evans et al., 2017; Adame et al., 2018). Moreover, crocodile relative density, hatchling growth, and survival are limited by higher salinities (Grigg et al., 1980; Mazzotti et al., 2007, 2019) and elevated salinity is associated with lower aquatic productivity (Lorenz, 1999). We found that the salinity of the rivers inside MKWS is lower than the rivers inside the two reserved forests. The higher aquatic productivity in lower salinity areas may bring potential prey items such as wild pigs (*Sus scrofa*), hawksbill turtles (*Eretmochelys imbricate*), and Asian wild dogs (*Cuon alpinus*) in MKWS (Oo, 2002). It is likely to increase prey accessibility for saltwater crocodiles which consume more terrestrial prey than riverine and marine prey (Adame et al., 2018). MKWS has favourable environmental conditions; moderate salinity, ample terrestrial prey, no human settlements, and therefore we suggest this may be the last optimal saltwater crocodile habitat in the Ayeyarwady Delta. Moreover, we found saltwater crocodiles were more likely to be active and detected in the early-morning time than during late-night. Given that crocodiles are primarily nocturnal hunters (Magnusson et al., 1987), this kind of crocodile activity pattern during the night is associated with the hunting behaviour to the prey (Evans et al., 2017). Currently, in MKWS, the survey protocol for rangers conducting annual spotlight surveys has not determined the survey start time which can influence the detection rate during surveys. Eversole et al. (2015) recommended to conduct nighttime surveys after midnight and early morning hours to maximize the sub-adult and adult crocodilian (American alligators) counts. Time of night may encompass all or most environmental variables attributing to saltwater crocodiles' detectability during a planned nighttime survey. Therefore, our findings are directly applicable in guiding future nighttime survey protocol to maximize detectability of saltwater crocodiles which can lead to more accurate estimates of population parameters.

5.2. Population size with methodological considerations

Across saltwater crocodiles' wide range, their population sizes have only been estimated in a few countries typically with either spotlight relative abundance indices or mark capture-recapture spatial models (Bayliss, 1987; Read et al., 2005; Brazaitis et al., 2009; Aziz and Islam, 2018). Via the spotlight relative abundance index approach, the population size of saltwater crocodiles in Ayeyarwady delta is estimated at c.106, which is almost the same population size as previously recorded for MKWS in 1999. Crocodiles may have been extirpated in PYD RF but a few adults and sub-adults were still present in KDK RF. The spotlight relative abundance index assumes that the population of saltwater crocodiles have a uniform distribution at all sites. However, this assumption is hard to meet unless the population is dense enough to record a large number of animals present in all the sampling units. It is not reasonable to estimate the population size of saltwater crocodiles across the whole study area which covers both MKWS and RFs because crocodiles did not occupy all sites within the study area. This highlights the importance of occupancy in quantifying the spatial distribution of animals particularly in areas with low population density but with high human disturbance. Moreover, submerged crocodiles may be missed if spotlight surveys were conducted only once at a site and that leads to major estimation biases (Marsh and Sinclair, 1989; Braulik et al., 2012).

Imperfect detection of crocodiles in the population size estimation is addressed in the N-mixture models by conducting repeated spotlight surveys—to estimate detection probability. The empirical unbiased maximum-likelihood estimate of population size was approximately 60 individuals in our study area. The total population size estimate was found to be similar to the population estimate of the juvenile crocodiles but both estimates were different from the estimates of adult and sub-adult crocodiles. The juvenile size-class (the most detected size-class) is likely to be dominant in population size estimation of N-mixture models. Depending on the nature of the species, this kind of size-class visibility bias can be raised by the survey methods used to monitor the species e.g. surveys following transects instead of setting up the traps randomly (Balaguera−Reina et al., 2018). Thorbjarnarson et al. (2000) suggested that adult crocodiles were more likely to be seen during the day than at night. In addition to the logistical constraints, the unequal probability of finding different size groups of crocodilians may occur due to the difference in site utilization/occupancy, or seasonal or daily movement of crocodiles (Balaguera−Reina et al., 2018).

With informative male and female home-range priors, the density estimates of saltwater crocodiles are reported to be 0.458 and 0.494 individuals per kilometre square respectively. The use of such prior knowledge in the Bayesian framework reported the estimates with high precision in the SC model (Chandler and Royle, 2013; Burgar et al., 2018). If we know the occupied areas, robust and spatially explicit population size estimates can be produced based on the SC model results. This is the first attempt using the spatial count (SC) model from camera traps detection data to estimate the density of crocodiles particularly for the *C. porosus* in the Ayeyarwady delta of Myanmar. Several limitations have been shown in the use of passive infrared sensor traps in studies of wild crocodilian populations including (1) fail in triggering if the subject in front of the camera has either low differential temperature, (2) false triggering by the movement of hot air or movement of vegetation in the detection zone (Chowfin and Leslie, 2014; Mohd-Azlan et al., 2016). However, when we carefully consider the placement of cameras (e.g. height, attachment, and distance from river bank), the density of cameras and data collection protocols (Mohd-Azlan et al., 2016), camera traps studies can provide encouraging results. Hence, the SC model produced 68 individuals as the population size estimate of saltwater crocodiles in MKWS (the only predicted high occupancy site in the Ayeyarwady delta). Although camera trap data can be limited to the adult or sub-adult crocodiles, *C. porosus* has no size-related spatial partitioning i.e. the activity space used by the crocodiles is not differentiated by body-size (Hanson et al., 2015). Hence, the SC model-based estimates describe the density of the pristine population of crocodiles which is typically dominated by the reproductively adult animals with comparatively low numbers of juveniles having higher mortality rates (Webb et al., 1987).

5.3. Conservation implications

We explored a suite of species-occupancy-abundance relationships for saltwater crocodiles in the Ayeyarwady delta of Myanmar. A growing human footprint around the wildlife sanctuary affects the current abundance of crocodiles in the Ayeyarwady delta. We reported c.106 as the overall spotlight absolute population size of saltwater crocodiles over the three sites: MKWS, KDK, and PYD in the Ayeyarwady delta. However, the overall population size of 106 individuals still has not integrated the occupancy areas and home range behaviour of saltwater crocodiles, and in addition, the more detected crocodiles (juveniles) can influence the overall population size estimates. Saltwater crocodiles were predicted to occupy inside MKWS relative to the reserved forests. Therefore, the population size estimates of the MKWS, predicted high-occupancy area by the saltwater crocodiles in the Ayeyarwady delta, were 75, 58, and 68 from the spotlight index, N-mixture, and SC models respectively. Thorbjarnarson et al., (2000), 2006 reported different encounter rates of saltwater crocodiles per kilometre of surveyed rivers inside MKWS and the total population was estimated to be < 100 non-hatchling crocodiles in the MKWS. Although the current encounter rate of crocodiles in MKWS was higher than the rates derived in 1999 and 2003 (Table 6), the estimated spotlight population size of MKWS was 75 individuals which are still lower than the previous estimate of Thorbjarnarson et al. (2000). Therefore, our study highlights the small population sizes of saltwater crocodiles which were now restricted to MKWS. Therefore, future surveys and analyses should use the data collected herein as priors for adaptive management strategies in MKWS and the Ayeyarwady delta. Saltwater crocodile occupancy was predicted to be high inside MKWS rather than outside sanctuary, which highlights the importance of protected areas in conservation. Furthermore, unprotected mangroves in the Ayeyarwady region are projected to be lost in the next few decades if agricultural expansion continues (Webb et al., 2014). MKWS is the only protected area in the Ayeyarwady delta that has successfully conserved mangroves and saltwater crocodiles—but for how long? Continued land-use change surrounding MKWS could pose substantial threats to an already small number of crocodiles in the Ayeyarwady delta.

Given the substantial lack of reliable population estimates and ecological information on the only Crocodilian species left in Myanmar, we found alarmingly small population sizes of saltwater crocodiles which is now limited to a single protected area. We believe that the estimated population still does not exceed the carrying capacity of MKWS if there is no competition between crocodiles and humans for resources within the wildlife sanctuary. Apparently, as the relatively small area of saltwater crocodile habitats in MKWS is under legal protection, better land-use planning around the MKWS should safeguard the habitat loss and degradation of saltwater crocodile populations by human activity. Our study provides a reliable, but smaller population size estimate of saltwater crocodiles than former studies (Thorbjarnarson et al., 2000) and shows they are now largely restricted to the MKWS of the Ayeyarwady delta. Hence, the population monitoring programs of saltwater crocodiles by the wildlife sanctuary should be re-evaluated using our study as the baseline for monitoring the long-term population trend of saltwater crocodiles in MKWS to provide more reliable and consistent data than the current annual surveys. Our findings could also be used to develop a habitat restoration plan, such as establishing buffer zones around the MKWS, including some parts of the RFs to conserve saltwater crocodiles and their associated habitats in Myanmar and prevent further population declines.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01206.

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