Spatial distribution of the Nile crocodile (*Crocodylus niloticus*) in the Mariarano River system, Northwestern Madagascar

By

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Abstract

Little is known about the Nile crocodile (*Crocodylus niloticus*) population in Madagascar; however, its population is believed to be in decline resulting from hunting and habitat loss. This study maps the distribution of the Nile crocodile population in the Mariarano River in Northwestern Madagascar during the dry season (May-October) using the maximum entropy model Maxent. Four biophysical factors are included in the first model and the second model includes two additional anthropogenic factors of distance from roads and distance from villages to observe the effect of humans on suitable habitat for crocodiles. Data were collected in June-August 2011 and 2012. Model performance was assessed using the Receiving Operating Curve (ROC) and Area under the Curve (AUC), using 10 replicates of both models. Both models adequately predicted species occupancy using the test data: the anthropogenic model receiving model performance rating of excellent and the biophysical factor-only model receiving a rating of average. While the results initially indicated that the distance from roads was the most important variable to the model, other possible anthropogenic influences such as boat activity on the river and mangrove destruction were not included. The distribution map produced for the model can be used as a baseline for Nile crocodile distribution within the river and aid in conservation management decisions about the Nile crocodile in the region.

Chapter 1: Introduction

Purpose

The Nile crocodile (*Crocodylus niloticus*) is the most widespread of the three crocodilian species found in Africa, and is the only crocodilian species found in Madagascar. Conflict with humans and uncontrolled exploitation resulting from increased international demand for crocodile skin led to severe population declines throughout Africa beginning in 1945 after the end of World War II (Thorbjarnarson 1999). Today many sustainable harvest programs combined with captive breeding or ranching through crocodile farming have been established for other crocodile populations in mainland Africa (Thorbjarnarson 1999). The lack of knowledge about the Madagascar crocodile population, however, has limited effective conservation strategies in the country (Ottley et al. 2008). Hunting pressure for skins, conflict with humans, and an increasing rate of habitat degradation and destruction all pose potential threats to the Nile crocodile population in Madagascar (Ottley et al. 2008).

Nile crocodiles historically ranged throughout Africa and are typically the largest apex predator in their environment (Fergusson 2010). They often maintain and encourage biodiversity of wetlands; they can be considered an environmental indicator species especially concerning the build-up of contaminants; they can be a source of economic importance both for tourism and crocodile ranching/farming; and as apex predators they aid in the recycling of nutrients (Botha 2010). This status as an indicator species allows crocodiles to serve as proxies for the overall health of wetland ecosystems.

The Mahamavo region in northwestern Madagascar is not only home to the Nile crocodile but also several species on the International Union for Conservation of Nature (IUCN) red list, including the critically endangered Madagascar Fish Eagle (*Haliaeetus vociferoides*), yet the region receives no environmental protection (Figure 1; Birdlife International 2012; Harrison 2010). Harrison et al. (2009) conducted the first biodiversity and habitat assessment of the region and recommended designating the Mahamavo wetlands as a Bird Life International Important Bird Area or including it on the Ramsar list of Wetlands of International Importance. These recommendations resulted from the high number of threatened species as well as the increased threats to biodiversity from hunting and habitat deforestation (Harrison et al. 2009). Since 2010, the scientific group Operation Wallacea, in conjunction with the non-profit organization Development and Biodiversity Conservation Action for Madagascar (DBCAM), has been undertaking biodiversity surveys of all mammals, reptiles, amphibians, and birds in the Mariarano River and forest within Mahamavo every dry season from late June to early August (Dr. Peter Long pers. comm.). The goal of this project is to establish a baseline of the current biodiversity in the region, and to assess and monitor changes in biodiversity and species distributions over time.

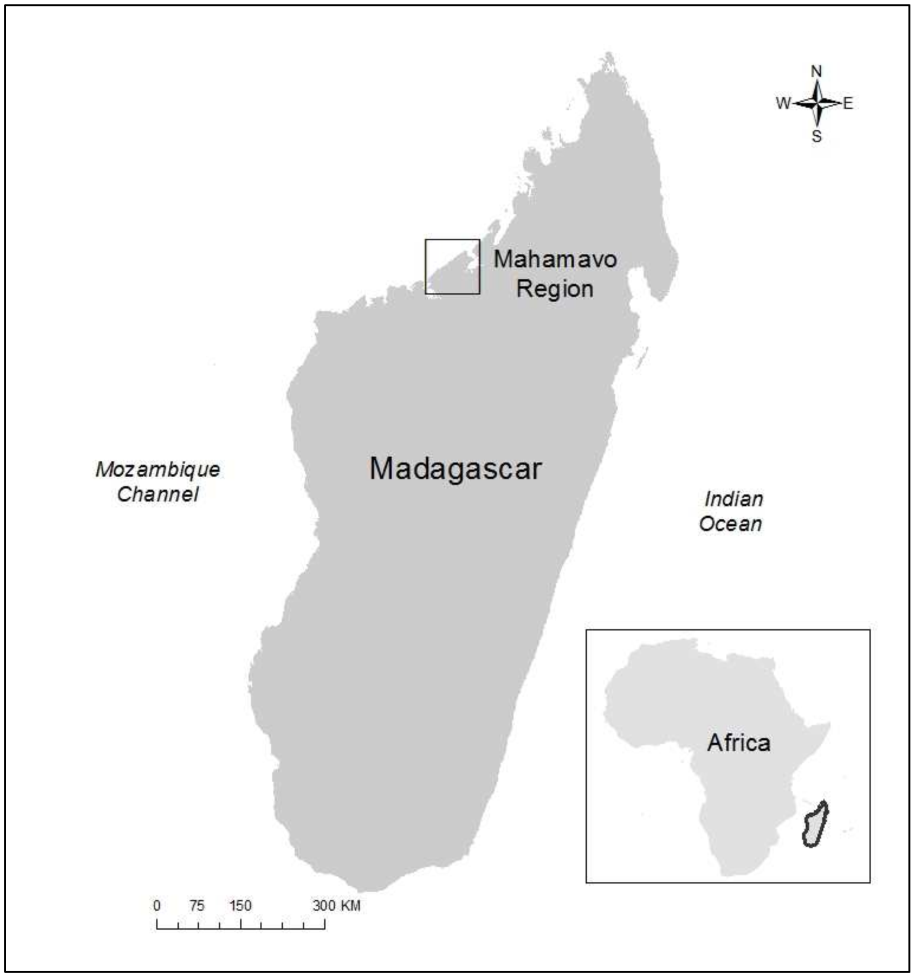


Figure 1. Location of the Mahamavo region within Madagascar. Inset: Location of Madagascar in relation to the African continent.

Examining the Nile crocodile population in Mahamavo will provide necessary information for a conservation management program in Madagascar. Illegal hunting and crocodile farming have long been issues in Madagascar, yet only one study has been conducted investigating the state of the current Nile crocodile population sponsored by the IUCN (Ottley et al. 2008). This study briefly surveyed several areas throughout Madagascar, and determined that though it appeared the population and overall distribution throughout the country was in decline, they did not have confidence in this assessment because of their short survey period and lack of historical data (Ottley et al. 2008).

The aim of this study was to determine suitable habitat for the Nile crocodile within the Mariarano River system and identify potential environmental factors affecting this habitat. A habitat suitability map was constructed using two models created in the computer program Maxent– the first with only biophysical factors; the second with anthropogenic factors included - distance of crocodile observations from roads and villages. The results of this study form a baseline habitat suitability map of the Nile crocodile within the Mariarano River system during the dry season which can serve as the basis for a long term Nile crocodile monitoring program and provide general information about the influence of anthropogenic factors on crocodile distribution that could be useful for crocodile management in other regions.

Organization

There are four chapters in this thesis after this introductory chapter.

Chapter 2 consists of a review of the literature explaining the history of Nile crocodile exploitation, critical issues when using species distribution models (SDMs) and a brief overview of Maxent modeling methods.

Chapter 3 describes the methodology used to collect field data and to perform the data analysis. Information about the study area and materials required are provided.

Chapter 4 presents the species distributions maps produced in Maxent, area under the curve values, and jackknife test results.

Chapter 5 discusses the results including the general performance and appropriateness of each modeling approach. It also provides recommendations for crocodile management and monitoring based on these results.

Chapter 2: Literature Review

This chapter briefly describes human-crocodile conflict, how this conflict has led to the decline of crocodilians throughout the world, and the recovery of some of these populations due to hunting regulations and crocodile farming (Bourquin and Leslie 2011; Caldicott et al. 2005; Ross 2000). The history of the Nile crocodile in Madagascar, how overexploitation and habitat degradation has led to their presumed decline, and the lack of knowledge about this population's ecology are discussed (Ottley et al. 2008). Species distribution modeling, its importance in ecology, and the different types of modeling available are explained, as well as the motivation for using Maxent modeling in this research (Franklin 2009). The probability of detecting crocodiles and the different types of detection bias encountered in a field survey are also examined (Shirley et al. 2012).

Human-crocodile conflict

Crocodilian species throughout the world are highly valued for their skin. The monetary value of their skin, as well as their constant conflict with humans makes them a target for hunting. In many regions, locals view crocodiles as a threat to their safety, and as competition for resources (Aust et al. 2009; McGregor 2005). Until the mid-1970s, which saw the formation of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), unregulated hunting led many crocodilian species to the brink of extinction. These species include the Nile crocodile (*Crocodylus niloticus*) in parts of mainland Africa, the saltwater crocodile (*Crocodylus porousus*) in Australia, and the black caiman (*Melanosuchus niger*) in South America – all of which are especially valued for their skin (Bourquin and Leslie 2011; Caldicott et al. 2005; Ross 2000).

Today many crocodilian populations have recovered with the help of both governmental and international protection through the IUCN and regulation under CITES (Fergusson 2010). CITES regulates the trade of crocodile skins and works with the IUCN Crocodile Specialist Group (CSG) and governmental agencies to monitor crocodile farms and to issue permits for annual skin exportation quotas.

Despite hunting regulations, trade restrictions, and international and government protection, human-crocodile conflicts persist — many crocodiles are hunted illegally and their eggs are taken to supply crocodile farms (Aust et al. 2009; McGregor 2005; Ottley et al. 2008). Bishop et al. (2009) found that although a previously exploited Nile crocodile population in the Panhandle region of the Okavango Delta in Botswana has partially recovered, the population remains at risk. The effective size of the Okavango population has decreased, meaning fewer individuals are contributing successfully to the gene pool, leading to a loss of genetic diversity in the population. In countries like Madagascar, which are permitted to export crocodile skins but do not possess adequate information on the wild Nile crocodile population and distribution, it is difficult to determine whether current harvest numbers are sustainable.

Since 1998, Madagascar has implemented a wild harvest program of its crocodile population, allowing the two crocodile farms in Madagascar to remove animals deemed a "nuisance" or threat to human livelihood (Ottley et al. 2008). The skins collected from those "nuisance" animals are then exported as "wild skins." Additionally, these two farms have received permits from CITES to export a specified number of farmed skins each year. Due to lack of enforcement of the export regulations imposed by CITES, however, as well as the perceived decrease in the country's wild crocodile populations, a six-month ban was imposed on crocodile skin exports in early 2010 (CITES 2010). This ban was still in effect in 2012 because the Madagascan government has not complied with the recommendations of the National Crocodile Management Workplan created by the CSG.

In 2007 a three-year National Crocodile Management Workplan was created by the CSG in association with CITES and the IUCN. This workplan called for various management strategies, as well as a survey of the wild crocodile populations in Madagascar, which was done in 2008. The results of the survey indicated that locals often killed any crocodile encountered, and nests were frequently destroyed or collected for crocodile farms (Ottley et al. 2008). Additionally, crocodile populations in many of the rivers surveyed appeared to have diminished compared to surveys conducted in 1987, 1988 and 1997 although the low numbers of crocodiles observed made general comparisons difficult (Behra 1987; Behra and Hutton 1988; Games et al. 1997; Ottley 2008). By establishing a baseline crocodile distribution model in the Mariarano River region, future studies will be able to monitor the status of the distribution of crocodiles and identify priority areas for conserving crocodiles in the region.

Species Distribution Models

Species distribution modeling (SDM) is a commonly used technique to spatially identify and describe a species' suitable or available habitat, as well as provide a spatial understanding of a species niche (Franklin 2009). With the advent of powerful computers and the rise of Geographic Information Systems (GIS) in ecological and conservational applications, many SDMs have been developed and their techniques have been compared against each other (Guisan and Zimmerman 2000; Guisan and Thuiller 2005; Hernandez et al. 2006). Proper consideration, however, must be given when selecting an appropriate model since many SDM studies lack sufficient ecological theory and rationalization in the selection of variables and models (Austin 2002). Scale and type of available data play an important role when selecting a SDM (Austin 2002).

Before formulating the statistical aspect of the SDM it is essential to develop a strong conceptual model that incorporates the underlying ecological motivations and concepts (Guisan and Zimmerman 2000). This includes understanding the general biology and ecology of the species selected, the type of available data and predictors that should be incorporated, and the motivation for creating the model. How the model is to be used affects the data sampling strategy, sample scale and density, and spatial resolution of both the collected data and chosen covariates (Franklin 2009). Conversely, when using previously collected data, the type of available data (i.e. presence-absence versus presence-only) will play a key role in the choice of model. Another significant ecological consideration is whether or not the species is in equilibrium with its environment, meaning it is only found in areas deemed suitable and is not affected by biotic interactions, such as interspecific competition, or lack of dispersal ability (Pearson 2007). Guissan and Zimmerman (2000) and Austin (2002) address the drawbacks of assuming a high degree of equilibrium for a species in its environment, noting however that this assumption is often necessary in large-scale distribution models.

Franklin (2009) divided the most commonly used models into three categories based on the methodology used by each model: statistical, machine learning, and classification and distance methods. Statistical models incorporate modern regression methods, such as generalized linear models (GLMs), generalized additive models (GAMs), and multivariate adaptive regression splines (MARS). These three methods use statistical inference to estimate the parameters from the available data and the user chooses the distributional form. Machine learning methods include decision trees, artificial neural networks (ANNs), genetic algorithms (GAs), maximum entropy (Maxent) and support vector machines (SVM) – all of which use algorithms to learn the mapping rules set by the user from the provided training data. The last category, classification and distance methods, are based on presence-only data (absences were not recorded), and include some of the methods previously mentioned such as the GA framework underlying the genetic algorithms for rule production (GARP) and Maxent models, as well as other methods such as ecological niche factor analysis (ENFA) and environmental envelope methods (BIOCLIM, HABITAT).

Maximum Entropy Methods

The crocodile observational data collected for this study were collected for two years during the 2011 and 2012 field seasons (June-August) and can be considered presence-only data, as no absence data were available, and the sample size was relatively small (<75 observations). For presence-only modeling methods, maximum entropy models (using the software application Maxent) have been found to be the most capable, maintaining high predictive accuracy across a large range of sample sizes (Elith et al. 2006; Hernandez et al. 2006). Maximum entropy models do not require absence data, but use background environmental data throughout the study area and determines the probability distribution of maximum entropy, subject to covariates and observational records defined by the user (Pearson 2007; Phillips et al. 2006). The predictive power of the model is measured using the receiver operating curve (ROC) and its area-under-the-curve value (AUC; Phillips et al. 2006).

Detection Probability

In any study using observational species data there is always the issue of how likely the observer is to detect and record each animal in the given survey space, known as detection probability. Detection probability is affected not only by the skill/experience of the observer but also by the probability that detecting an animal decreases the further the animal is from the area/transects being surveyed (Bayliss et al. 1987; Hutton and Woolhouse 1989; Fujisaki et al. 2011; Shirley et al. 2012). The habitat being surveyed, weather at time of survey and behavior and morphology of the animal also affect the ability of an observer to detect an animal (Bayliss et al. 1986). Crocodiles are elusive creatures — their ability to submerge underwater, and preference for both open and dense vegetation can make them difficult to detect (Bayliss 1987; Hutton and Woolhouse 1989; Shirley et al. 2012). Submerging and concealment bias contribute greatly to how well an observer is able to detect a crocodile, but are difficult to quantify without absolute abundance already being known (Bayliss et al. 1987). Observer bias (based on experience/skill level) can be accounted for by using two independent observers on each survey — this method has been used successfully to survey American alligators (*Alligator mississippiensis*) in the Everglades National Park Florida, and to survey Nile crocodiles (*Crocodylus niloticus*) in Lake Nasser, Egypt (Fujisaki et al. 2011; Shirley et al. 2012). Unfortunately this method could not be used in this study as local guides would typically point out crocodiles before the observers were able to detect the crocodiles themselves.

Chapter 3: Methods

This chapter describes the field and analytical methodology used in the study. The study site and data collection procedures are described, for both the data collected in the 2012 field season and the previously collected data (the 2011 field season) from the Operation Wallacea database. The covariates used for the model and appropriate justifications are explained. Lastly, an overview of the Maxent modeling procedure is discussed, including the parameters and constraints of the model, as well as the performance measures used to assess the model.

Study Site

Surveys for the 2011 and 2012 field season took place for 6 weeks from late June to early August along the Mariarano River and several nearby lakes. The Mariarano River is located within the Mahamavo Peninsula in Northwestern Madagascar. The surveys occurred during the Madagascan winter (May-October), which is the driest season; the mean precipitation for the region in July is less than 1 mm per day. However, during the summer months (November-April) or wet season, the region receives greater than 10 mm per day, and extensive flooding occurs throughout the region (Washington et al. 2009, Washington 2010). Accessibility to the region greatly decreases during this time and often the only access is by boat. Due to budgetary and time constraints surveys were only conducted during the dry season.

Within the Mahamavo watershed there are four main river systems, and several inland lakes. The data for this thesis were collected along the Mariarano River and its tributaries along the eastern edge of the Mahamavo Peninsula. The Mahamavo peninsula consists of a mosaic of dry forest and wooded grassland/bush habitat. Deforestation is becoming a critical problem, and much of the area that was once forested is now savannah, especially areas near villages

(Washington et al. 2009). The four inland lakes surveyed were surrounded by such a mosaic. The habitat encompassing the Mariarano River consists of extensive mangroves; with evidence of habitat degradation due to cyclone damage and the use of mangrove wood as a source of charcoal by the local villages.

Data Collection and Methodology

Surveys of the Mariarano River were conducted in a 6 m fiberglass boat, during the day and at night, along fixed segments of the river named A through F (Figure 2). Each route was surveyed at least twice during the day and only the three closest routes to the jetty (A-C) were surveyed at least twice during the night due to fuel and safety constraints. During the daytime crocodiles were detected through the use of binoculars, and the data recorded included the date, time, distance and angle from observer location, and location (using a Global Positioning System (GPS)), as well as the estimated length of the specimen. The recorded location, distance (based on observer estimation) and angle (using a compass) from the observer were used to determine the true location of the animal (Buckland et al. 2000). Locations were only recorded if there was at least 10 m accuracy on the GPS receiver. At night crocodiles were detected by observation of eyeshine using Fenix E21 flashlights, and the same information was recorded as in the daytime surveys. On every survey at least two observers were present, as well as additional observers who were recording bird biodiversity along the river.

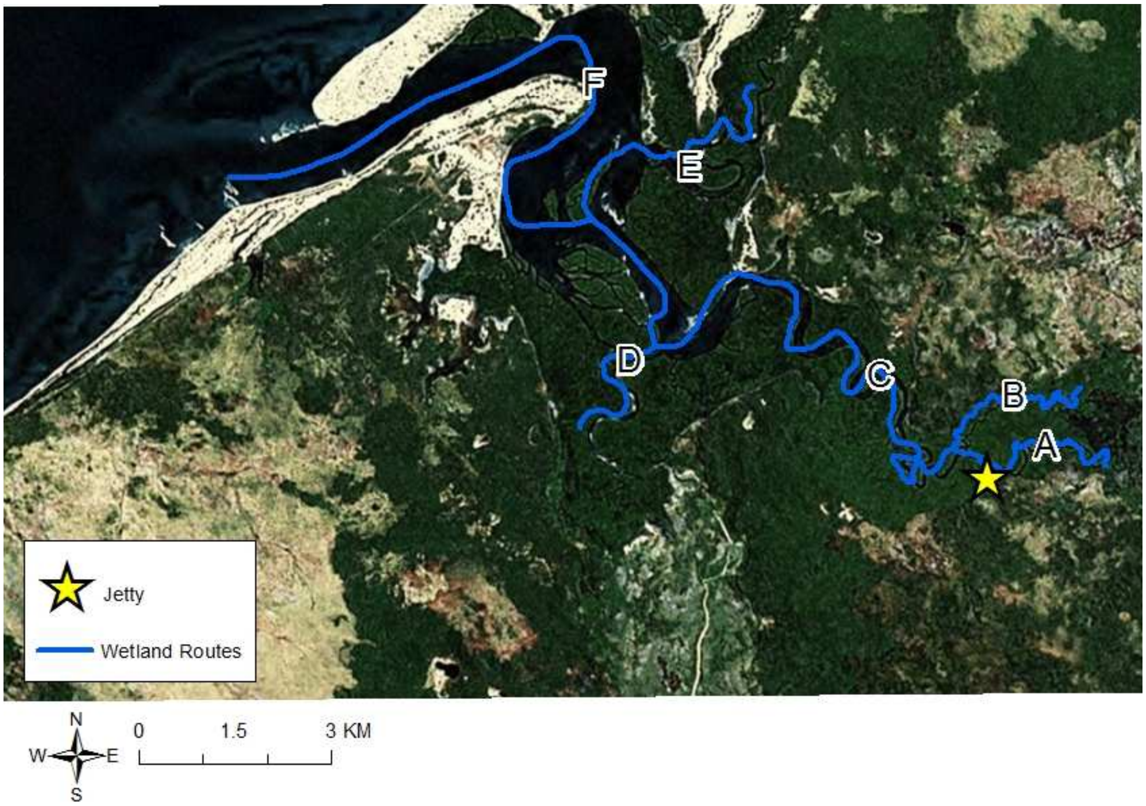


Figure 2. Map of the six boat routes along Mariarano River and its tributaries, and the location of the boat jetty used in the 2011 and 2012 field seasons.

Database

In addition to the data collected in the 2012 field season, observational crocodile data from the 2011 field season were also used to model crocodile distribution. The data were collected by various members of the scientific organization Operation Wallacea using similar methods to those outlined in the previous sections. The observational records for both field seasons are also included as part of a larger database used to measure the biodiversity within the Mahamavo region. All crocodile observations were input into the database, managed by Dr. Peter Long, a James Martin research fellow at the Institute of Biodiversity in the Department of Zoology at Oxford University working with Operation Wallacea. Dr. Long then calculated the true location of each species observation using the recorded coordinates of the observer and, distance and angle of the animal from the observer. The calculated true locations provided by Dr. Long were used for all analysis.

Model Covariates

Selection of covariates was based on a literature review and expert opinion from Dr. Peter Long and Robert Gandola senior scientist of the Herpetological Society of Ireland and member of the IUCN Crocodile Specialist Group. Table 1 lists the purpose and source of each of the covariates.

Table 1. List, explanation and source of covariates used within the two Maxent models

Covariate	Explanation	Source
Elevation (m)	High elevations are believed to be a factor in determining suitable crocodile habitat (R. Gandola pers. comm)	USGS 2004, Shuttle Radar Topography Mission, 1 Arc Second scene SRTM_p161r071
Topographic Wetness Index (TWI)	Crocodiles require a certain amount of moisture and water for their survival and TWI measures water saturation capabilities in the soil (Franklin 2009; Rodder et al. 2010; Steel 1989; R. Gandola pers. comm.)	USGS 2004, Shuttle Radar Topography Mission, 1 Arc Second scene SRTM_p161r071

Wetland designation	Wetland designation is used as a limiting factor since this study only examines suitable habitat during the dry season (P. Long, pers. comm.)	USGS Landsat 7 satelite images: 7_p161r071_2012may04 LE71600712012125ASN00 & 7_p161r071_2012may20 LE71600702012141ASN00
Distance to water (m)	Crocodiles are dependent on water and can only travel so far from a water source (Rodder et al. 2010; Steel 1989; R. Gandola pers. comm.)	USGS Landsat 7 satelite images: 7_p161r071_2012may04 LE71600712012125ASN00 & 7_p161r071_2012may20 LE71600702012141ASN00
Distance to roads (m)	Roads allow for increased access to all regions, and can lead to deforestation and an increase in hunting (Pearson et al. 2002; Lindemeyer et al. 2000; R Gandola pers. comm.)	Foiben i Tsasarintanini Madagasikara (1951) Sarintany topografika 1:100000 LM38, N3738, L39, M39, N39, L40, M40, N40. Antananarivo.
Distance to villages (m)	Human settlements in suitable crocodile habitat can lead to human-crocodile conflict over safety & competition for resources (Pearson et al. 2002; Lindemeyer et al. 2000; Aust et al. 2009)	Foiben i Tsasarintanini Madagasikara 1951 Sarintany topografika 1:100000 LM38, N3738, L39, M39, N39, L40, M40, N40. Antananarivo.

Four of the covariates are “biophysical”: elevation, topographic wetness index, distance to water, and whether the area is a designated wetland. Climatic variables such as temperature and average rainfall were not included, because the available data resolution was too coarse to be useful for the small study site. Instead more local, high resolution data were used for the biophysical covariates.

Nearby roads and villages, whose locations are depicted in Figure 3, are considered important “anthropogenic” factors and are included in one of the final models as two distance metric covariates: distance to roads and distance to villages. The anthropogenic covariates were included as humans are thought to have a great impact on a crocodile’s movement and distribution, both in terms of hunting and human avoidance. Studies by Pearson et al. (2002) and Lindemeyer et al. (2000) have shown that such metrics affect the outcome of a species distribution model.

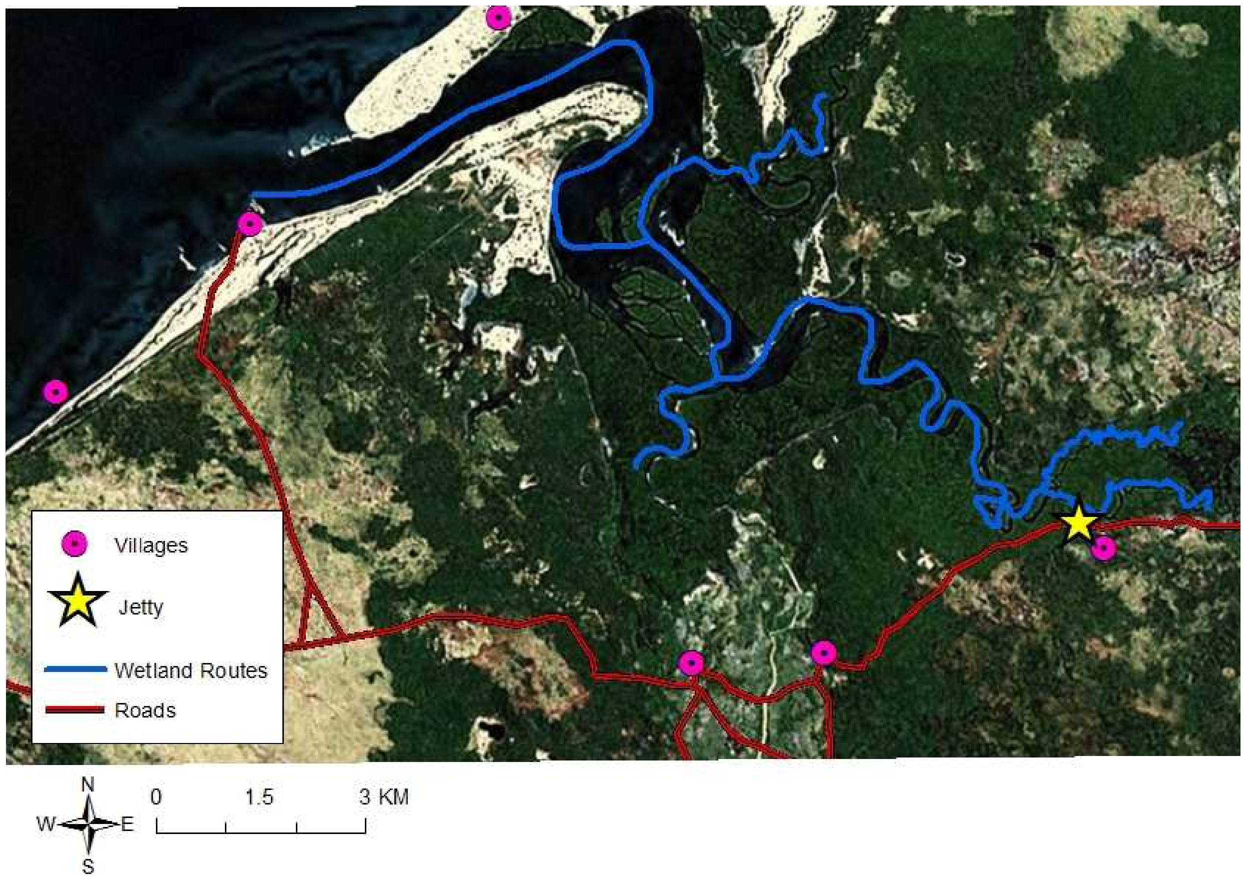


Figure 3. Road and village locations used to calculate the two anthropogenic distance metric covariates incorporated in the model

Some important issues about these covariates require additional explanation. The remaining paragraphs in this section provide additional detail about some of the covariates.

Distance to water and topographic wetness index (TWI) were incorporated into the model because, being semi-aquatic, crocodiles are dependent on water, especially during the dry season when there is limited water available (Rodder et al. 2010; Steel 1989; R. Gandola pers. comm.). The TWI is a method of measuring how water will be distributed across the landscape and how much water the ground is capable of absorbing before it becomes run-off (Franklin 2009). It is calculated using Equation 1.

$$TWI = \ln\left(\frac{a}{tan\beta}\right) \quad (1)$$

The variable *a* is defined as the upslope contributing area calculated using the watershed tool in IDRISI, while β is defined as the angle of the surface slope. The data used in calculating TWI came from a digital elevation model (DEM) at 30 m resolution from the Shuttle Radar Topographic Mission, 1 Arc Second scene SRTM_p161r071. The value of TWI can range from -6.68 (dry) to 18.12 (wet).

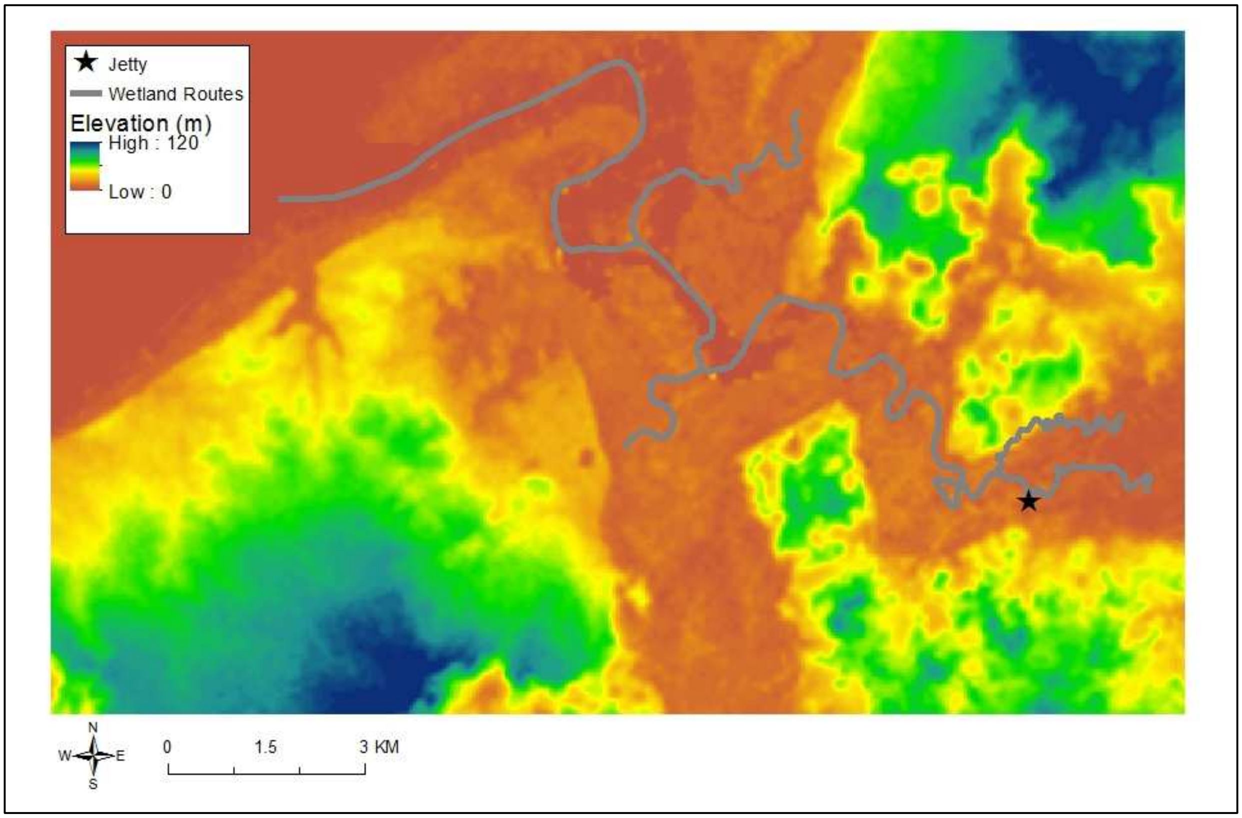
Elevation was included in the models as it has been considered a potential factor in the distribution of other crocodiles (R. Gandola pers. comm.). It is important to note that elevation is correlated with TWI as both covariates were derived from the same DEMs (Shuttle Radar Topographic Mission, 1 Arc Second scene SRTM_p161r071).

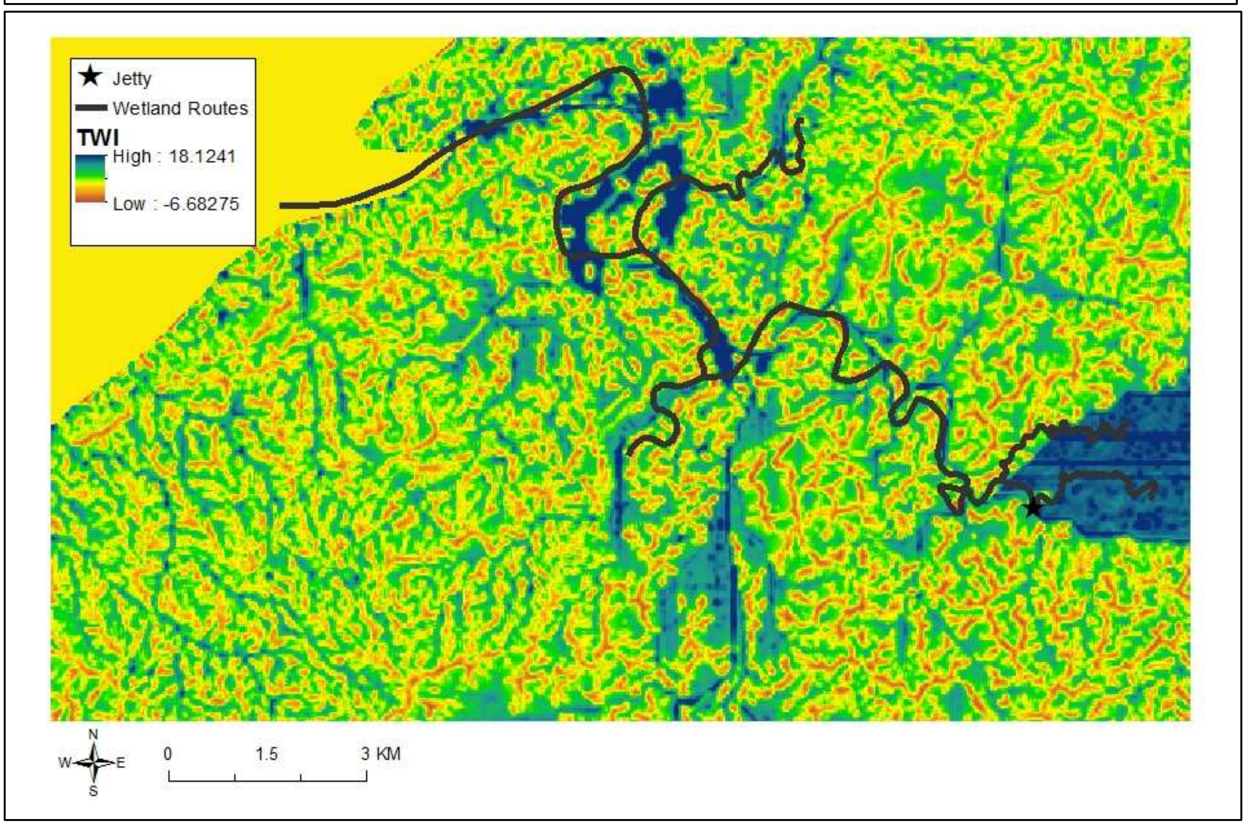
Since this study focuses on modeling *C. niloticus* distribution only during the dry season, wetland habitat designation is included as a potential limiting factor on species distribution and was used as a mask variable in the model. The areas designated as wetland habitat were extracted from a land cover dataset developed using a maximum likelihood classifier on high resolution satellite data from 2008 (Quickbird 2008 and Landsat 2008) and applied to Landsat 2012 data (P. Long pers. comm.). As this habitat suitability map is only for the dry season, areas designated here as wetland habitat include both open water habitat areas and areas classified as mangrove forest since the seasonally flooded areas are not underwater during the dry season. The designated wetland areas were then reclassified so that all designated areas received a value of 1, while all non-wetland areas received a value of no data, treating this covariate as a mask variable, and limiting the extent of the suitability analysis to only areas designated as wetlands (Phillips and Dudik 2008).

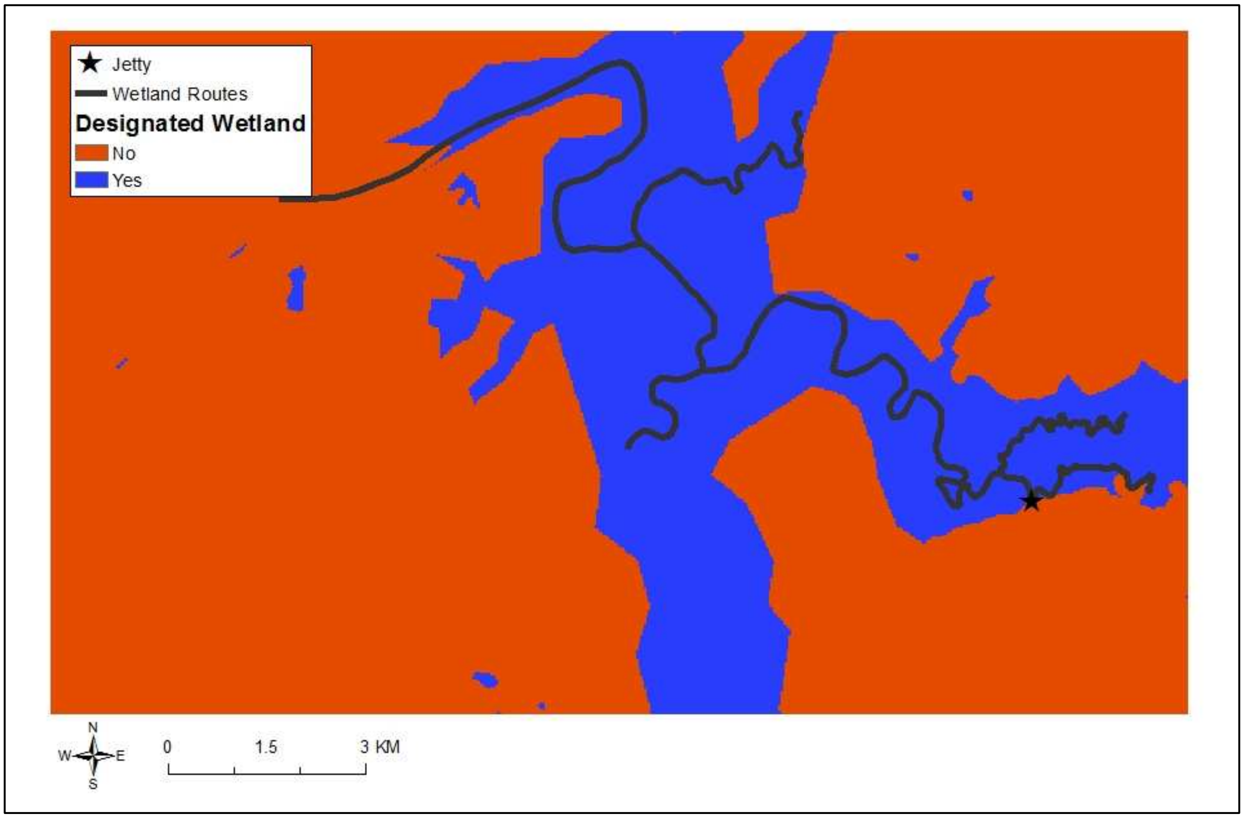
Including wetland habitat designation as a covariate does mean that distance to water and wetland habitat designation are correlated, as most of the water sources in the dry season are located within wetland areas, It is important to note that this correlation and the correlation between TWI and elevation covariates are not problems in this type of analysis since Elith et al. (2011) demonstrated that Maxent's set covariate regularization method allows for the use of correlated covariates, making removal of them unnecessary.

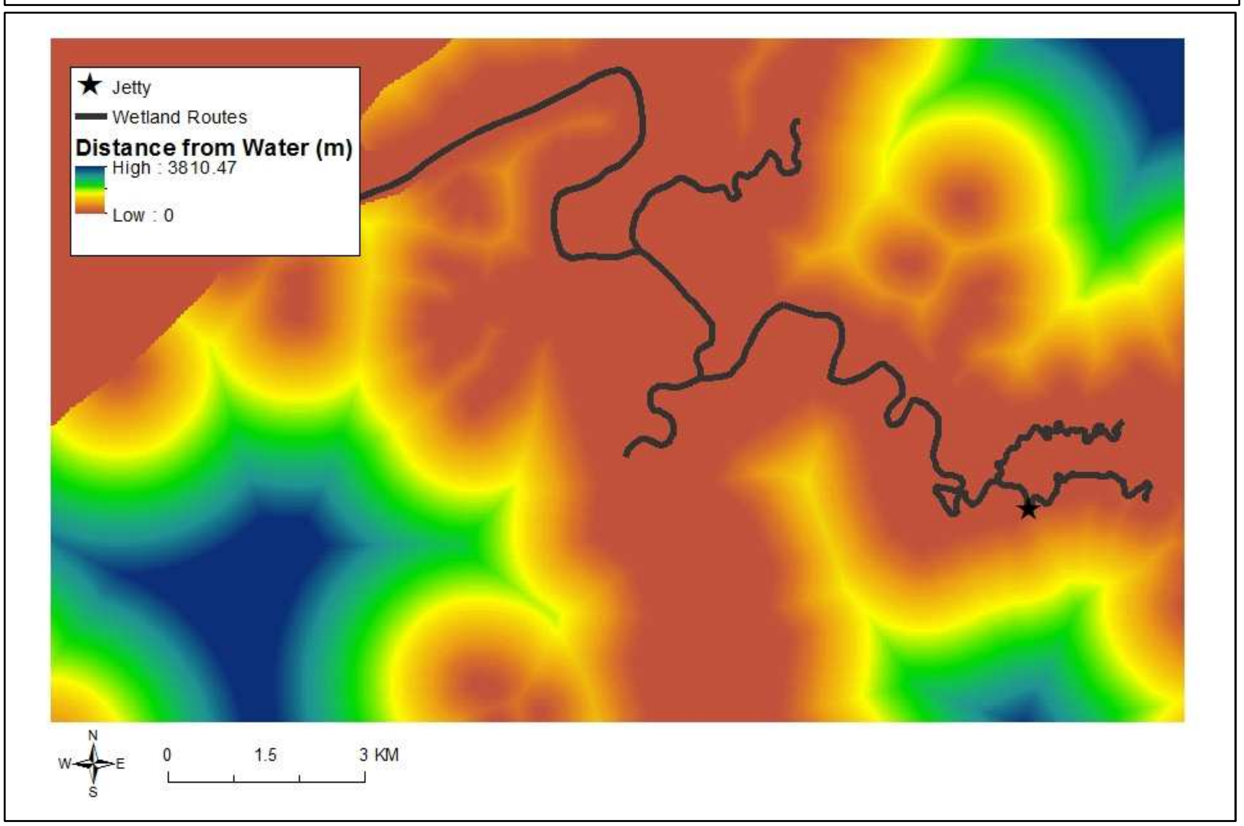
All distance metrics (distance from water, roads and villages) were calculated using the Euclidean distance analysis tool in Esri's ArcGIS 10.1. The tool created raster surfaces for the entire study area, with each cell value indicating the straight-line distance from the nearest water, road or village feature.

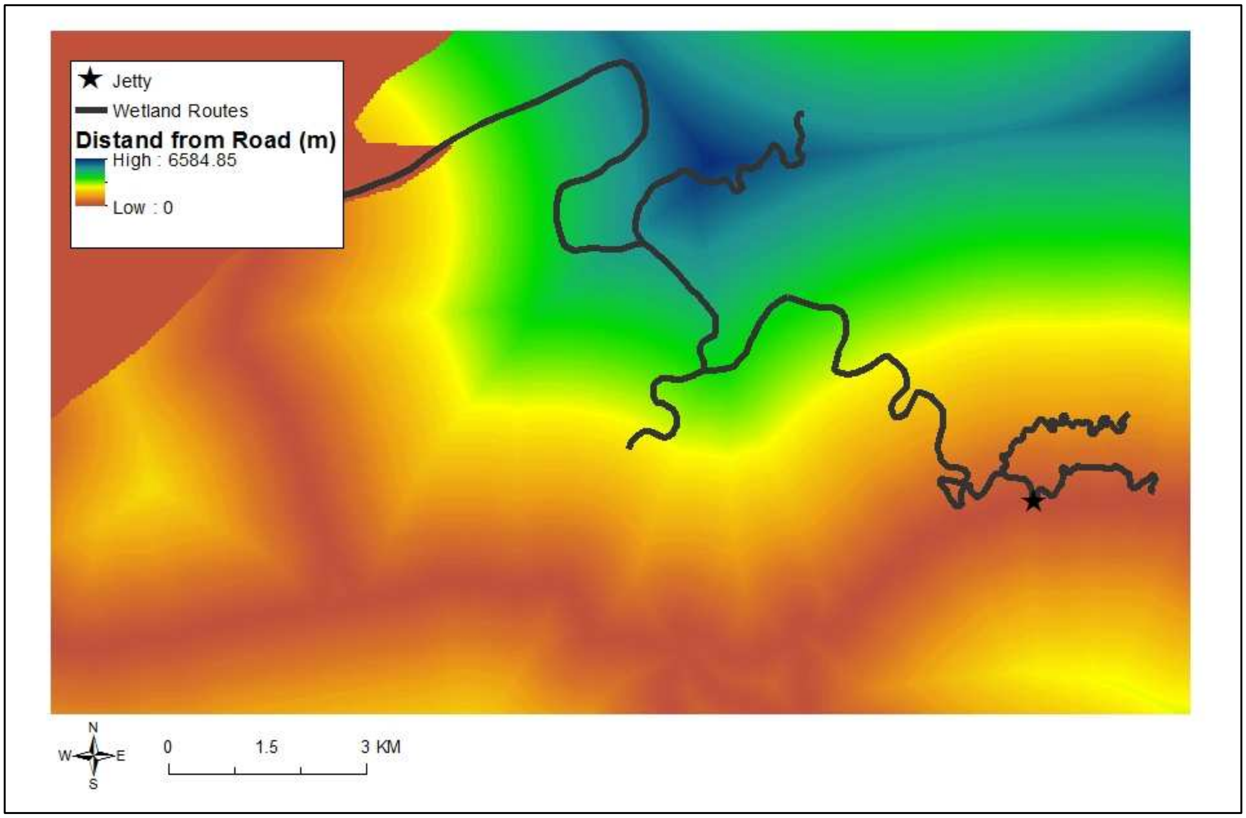
All covariate rasters used in the Maxent model were provided by Dr. Peter Long in association with Operation Wallacea. The rasters are all at 30m resolution with the projected coordinate system being UTM Zone 38S. Each covariate was co-registered to a common origin and orientation and clipped to a common extent: 670287-687437 and 8286487-8296867 that encompasses all the crocodile records from 2011-2012. The raster cell size is 30 m by 30 m or 900 m^2. The study area covered by the rasters (the bounding box) is a total area of 179.87 km^2. Figure 4 depicts each of the six covariate rasters.


Jetty
Wetland Routes
Elevation (m)
High : 120
Low : 0
N
W
E
S
0
1.5
3 KM


Jetty
Wetland Routes
TWI
High : 18.1241
Low : -6.68275
N
W
E
S
0
1.5
3 KM


Jetty
Wetland Routes
Designated Wetland
No
Yes
N
W
E
S
0
1.5
3 KM


Jetty
Wetland Routes
Distance from Water (m)
High : 3810.47
Low : 0
N
W
E
S
0
1.5
3 KM


Jetty
Wetland Routes
Distand from Road (m)
High : 6584.85
Low : 0
N
W
E
S
0
1.5
3 KM

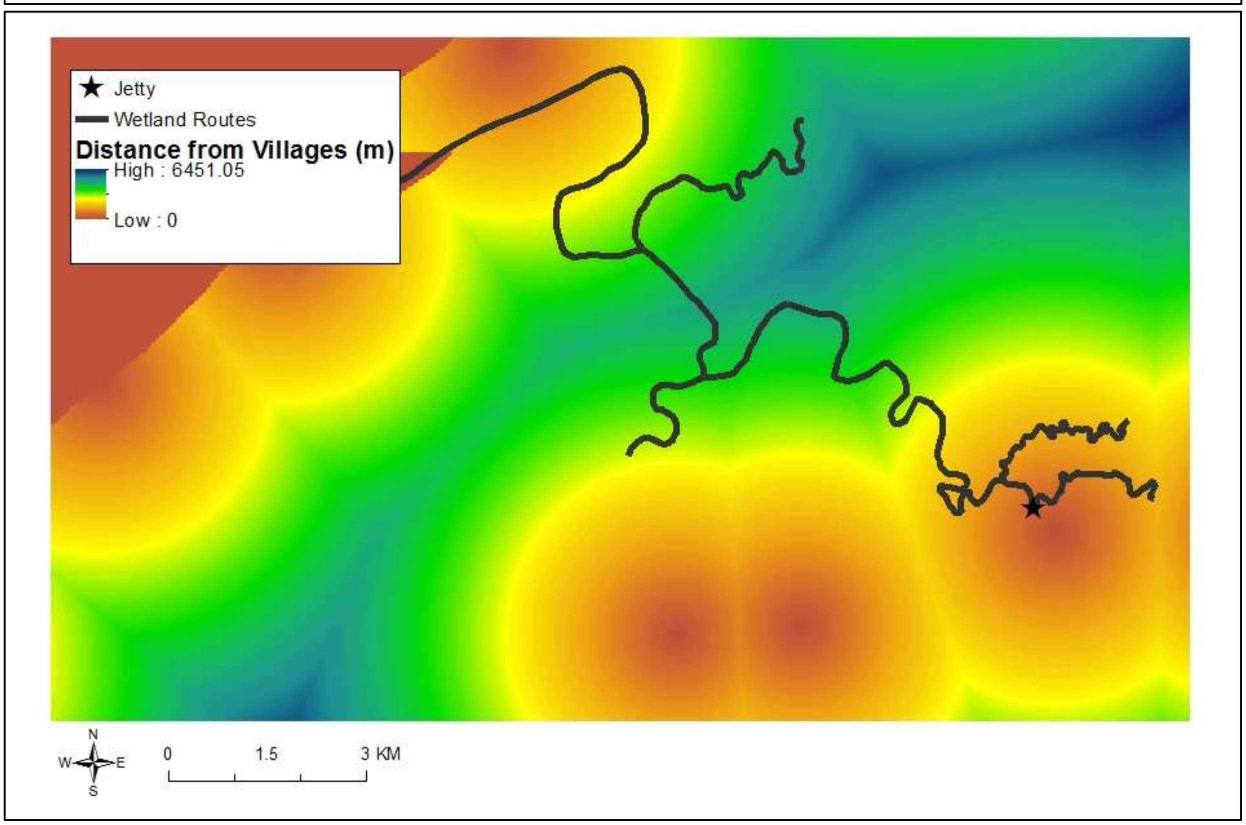

Jetty
Wetland Routes
Distance from Villages (m)
High : 6451.05
Low : 0
N
W
E
S
0
1.5
3 KM

Figure 4. Rasters of the six covariates used in the model (elevation, topographic wetness index, wetland designation, distance from water, distance from roads, and distance from villages). All rasters have 30 m pixel resolution.

Maxent Modeling Procedure

The free software program Maxent (version 3.3.3e, available at http://www.cs.princeton.edu/~schapire/maxent/) was used for all modeling and subsequent analysis. The program is based on a species distribution algorithm which uses maximum entropy methods (Phillips et al. 2006). The program requires two different input datasets. The presence data is input as a table listing the point locations of all observations. The second input is the set of covariates provided as a collection of rasters in ASCII grid format.

Two models were run: one with only the biophysical covariates, the other including the anthropogenic factors of distance to roads and villages. The regularization default settings presented by Maxent were used because Phillips and Dudik (2008) found that when using Maxent's default settings, the model performance showed little improvement from when the settings were altered to reflect the data. Table 2 displays the regularization parameters used for each model.

Table 2. Maxent model regularization parameters and applied model constraints

Number of Overall Samples	72
Regularization multiplier	1
Max number of background points	10000
Replicates	10

Maximum iterations	1000
Output format	Logistic
Convergence threshold	0.00001
Apply threshold rule	Minimum training presence

Model Performance Measures and Covariate Importance

Ten replicates were produced of the model using the cross-validation procedure. Cross-validation uses all of the occurrence data, with the data being split into 10 groups (the number of replicates) and one group used each time as the test data, while the other data is used to train the model. This procedure is then replicated 10 times, so that every group serves as a test group at least once. For each replicate Maxent produces a receiver operating curve (ROC) analysis, which determines the area under the curve (AUC) value, and this value is then averaged to obtain an average AUC value with a standard deviation.. The AUC was used to measure the predictive performance of the model of *C. niloticus* occurrences produced by Maxent. The AUC value ranges from 0 to 1, with 1 being the optimal value and 0.5 meaning the predictive performance of the model is no better than random. Araújo and Guisan (2006) provide a scale of the thresholds for the goodness of fit for the model which is presented in Table 3.

Table 3. Measure of the performance of the model produced by Maxent based on the AUC value (Araújo and Guisan, 2006)

AUC value	**Model Performance**
0.9 – 1.0	excellent
0.8 – 0.9	good

0.7 – 0.8	average
0.6 – 0.7	poor

When the model is produced in Maxent, an analysis is presented on the contributions of each predictor variable or covariate to the model. The percent contribution of each covariate is determined by examining which variable influences the model the most, and is dependent on the path used to obtain the optimal solution, thus caution is advised when interpreting the overall contributions (Phillips et al. 2006). The Maxent software also provided the option to run a jackknife test to measure the importance of each predictor variable/covariate in the model outcome. The jackknife test was used to identify which covariates contributed most to the model by running the model with each covariate being the only covariate in the model, and with each covariate being individually excluded from the model (all other covariates were present; Elith et al. 2011). However, it is important to note that highly correlated covariates can alter the contributions of each covariate to the model and increase the contribution of one of several correlated variables (Phillips et al. 2006, Baldwin 2009).

Chapter 4: Results

Survey Results

Crocodylus niloticus was observed on surveys 84 times in 2011-2012 (Figure 5). Twelve records were removed prior to analysis because their locations were believed to be inaccurate. The remaining 72 records were used in creating the habitat suitability map. Many observations were located in the southeast and southernmost parts of the Mariarano River system, due in part to the higher number of surveys in those regions. This creates bias for the distribution of crocodiles observed towards this region, however this bias does not affect the Maxent model, which is based on presence-only data (absence data are not included).

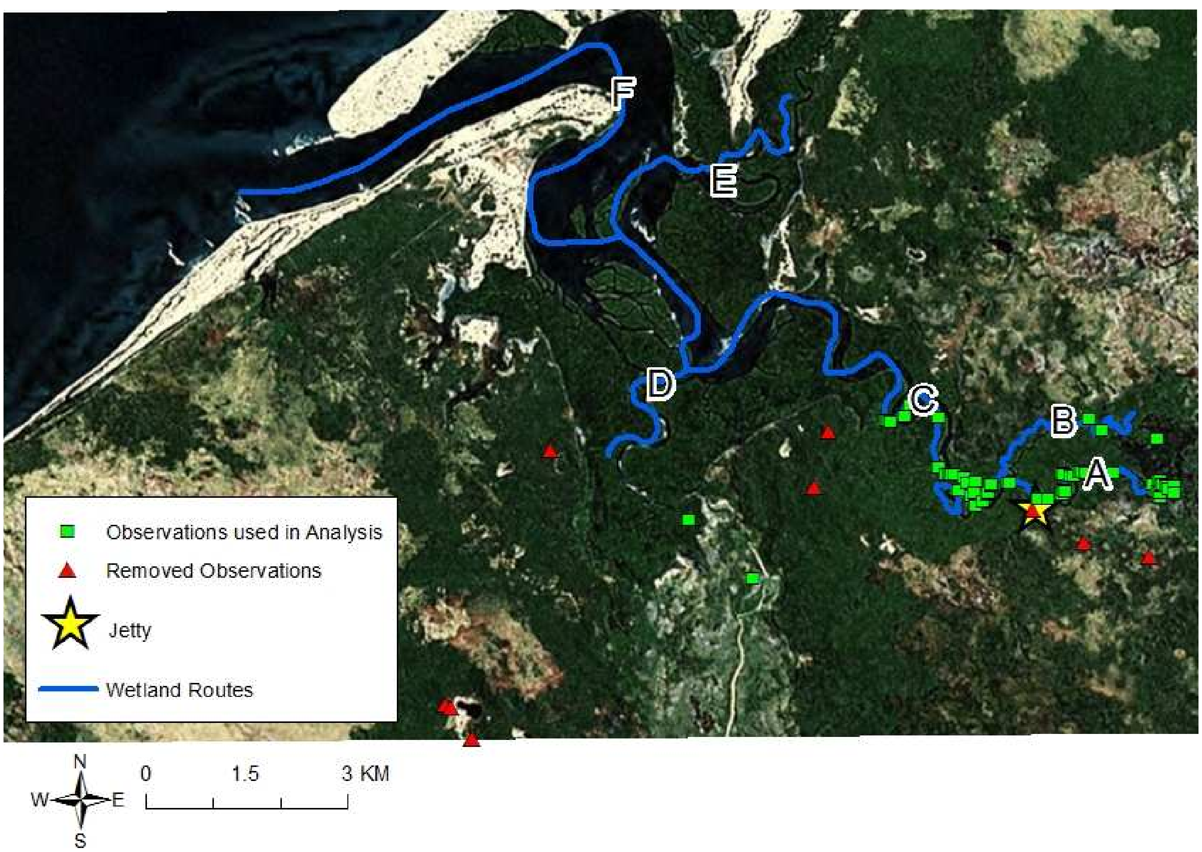


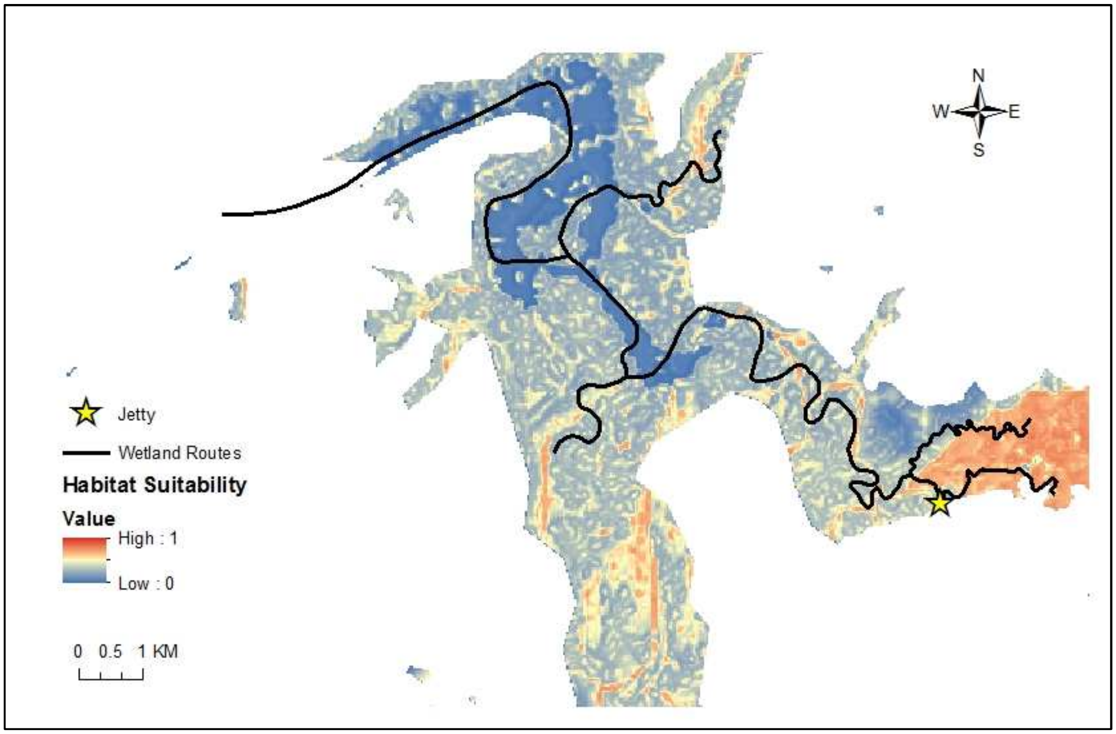
Figure 5. Crocodile observation locations used in creating *Crocodylus niloticus* habitat suitability maps

Nile crocodile (*Crocodylus niloticus*) Habitat Suitability Maps

Figure 6a represents the predicted *Crocodylus niloticus* habitat suitability map using only the four biophysical covariates: topographic wetness index (TWI), wetland designation, distance to water, and elevation. Both the habitat suitability map using the 4 biophysical covariates and the map using all 6 covariates were limited by the wetland designation covariate, which was used as a mask to remove the surrounding, non-wetland areas (total area of all wetlands 45.3 km^2). Areas of predicted high occupancy or habitat suitability are found in the southeast and southernmost parts of the Mariarano River system and along its banks.

Figure 6b represents the predicted *C. niloticus* habitat suitability map using all 6 covariates including distance from roads and distance from villages. Again areas of predicted high occupancy or habitat suitability are found in the southeast and southernmost parts of the Mariarano River system, however the areas along the edge of the system were deemed less suitable.

a)


N
W
E
S
Jetty
Wetland Routes
Habitat Suitability
Value
High : 1
Low : 0
0 0.5 1 KM

b)

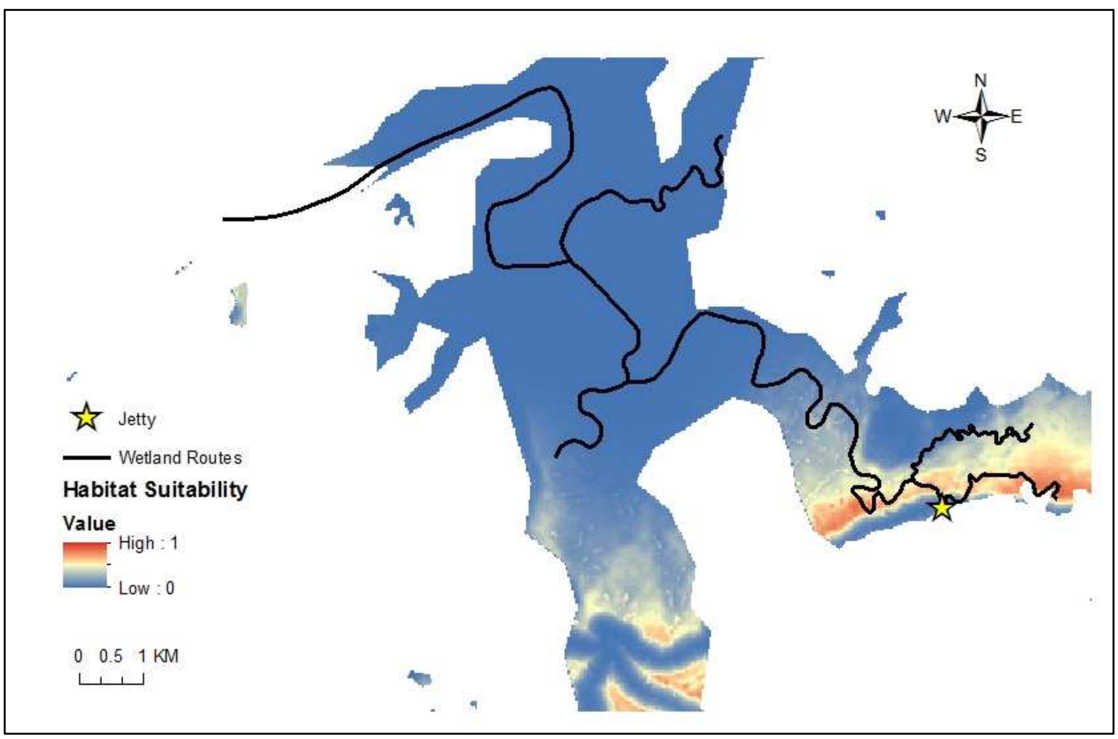

N
W
E
S
Jetty
Wetland Routes
Habitat Suitability
Value
High : 1
Low : 0
0 0.5 1 KM

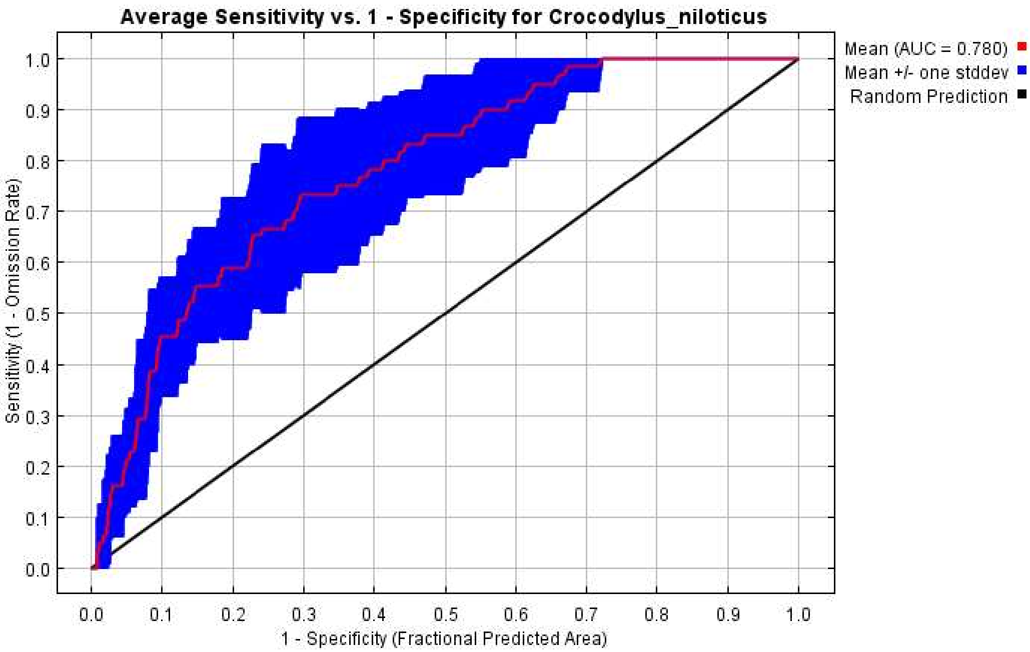
Figure 6. Representation of the predicted *Crocodylus niloticus* habitat suitability map based on the maximum value of 1 and minimum value of 0, with 1 being highly suitable habitat, and 0 being unsuitable habitat based on the different covariates included a) only the 4 biophysical covariates b) all 6 covariates including distance to roads and villages.

Model Validation

The mean area under the curve (AUC) for the test data using the model with only biophysical covariates was 0.780 with a standard deviation of 0.065 (Figure 7a). According to the AUC classification by Araújo and Guisan (2006) this ranks the model as "average" in terms of predictive performance. The AUC value for the test data using the model with all of the covariates was 0.913 with a standard deviation of 0.028, ranking the model as excellent (Figure 7b). The receiver operating curve (ROC) produced by both models plots the sensitivity (true positive) against the 1 - specificity (false positive), as well as the corresponding AUCs, indicating model performance (Figure 7). The red line shows the mean AUC value, while the blue shaded areas represent the standard deviation from the mean value. The closer the red line is to the left (closer to 1) and the smaller the standard deviation value the better the model performance.

a)

Biophysical Model



b)

Anthropogenic Model

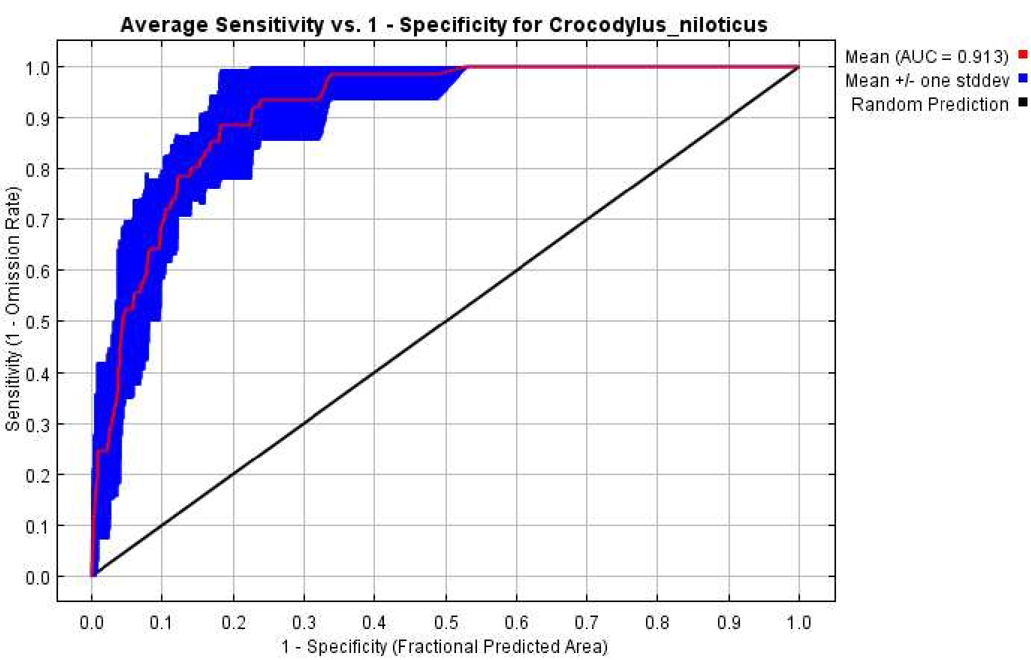


Figure 7. Receiving Operation Curve (ROC) with corresponding area under the curve (AUC) values for the Maxent models produced a) using only biophysical covariates as predictor variables b) using all covariates as predictor variables including distance to roads and villages

Variable Contribution and Importance

The TWI contributed the most (63.7%) to the model containing only biophysical covariates, followed by elevation (35.3%; Table 4). Distance from water only contributed 1% to the model, while the wetland designation mask contributed nothing (as expected). When considering all six covariates, distance from roads had the highest contribution (88.7%), while distance from villages contributed 4.9% (Table 5). Elevation had the second highest contribution at 5.6%, while the other three covariates combined contributed less than 1% to the model.

Table 4. Percent contribution of each predictor variable, including only biophysical covariates in the model

Variable	**Percent contribution**
Topographic Wetness Index	63.7
Elevation	35.3
Distance from water	1
Wetland designation	0

Table 5. Percent contribution of each predictor variable, when all covariates were included in the model

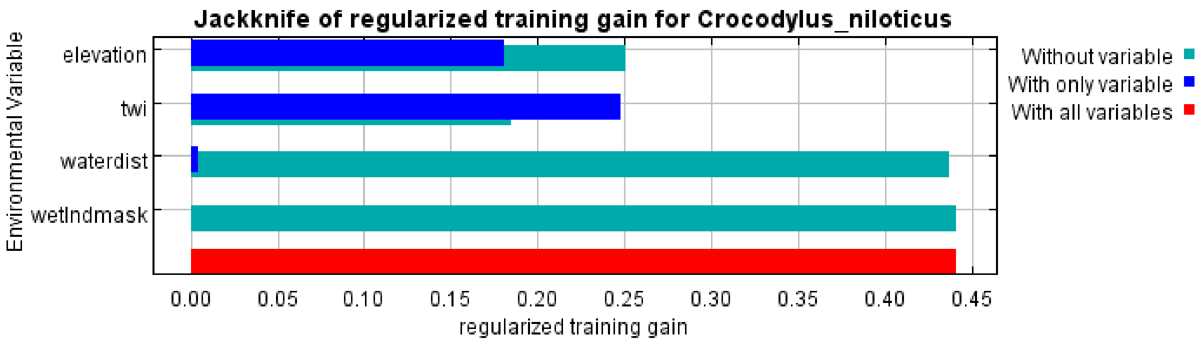
Variable	**Percent contribution**
Distance from roads	88.7
Distance from villages	4.9
Elevation	5.6
Topographic Wetness Index	0.5
Distance from Water	0.4
Wetland designation	0

Predictor Variable (Covariate) Importance

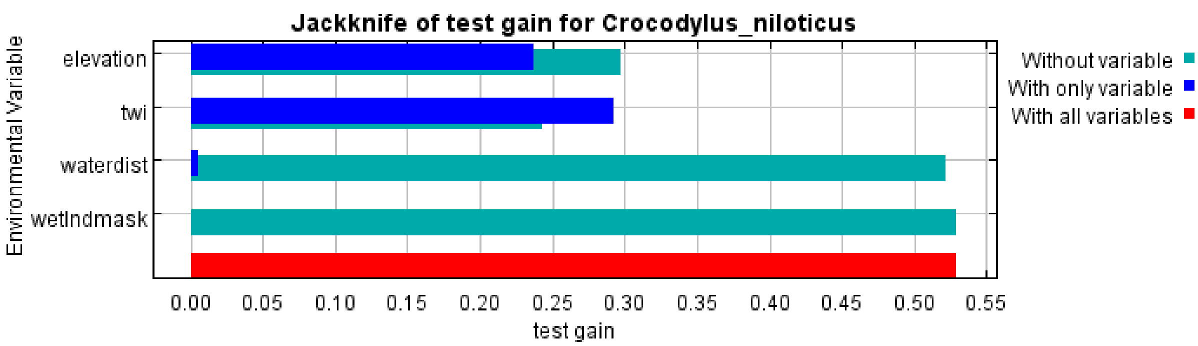
The jackknife test showed that when considering environmental variables, the topographic wetness index was the most important variable in training, test, and AUC evaluation of model prediction and performance (Figure 8a-c). Without the TWI variable, the gain of the model (or how well the model fits the data) experienced the greatest decrease, while experiencing the greatest gain when TWI was the only predictor variable. The wetland designation variable (wetland) did not affect the gain in any of the three evaulations when excluded, and caused no gain at all when it was the only variable used in the model.

Figure 9 a-c displays that distance from roads was the most important variable for all three model evaluations when including all six covariates. When not included in the model, the training gain decreased the most for all three evaluations, and when distance from road was the only variable used, the model experienced the most gain for all three evaluations.

a)



b)



c)

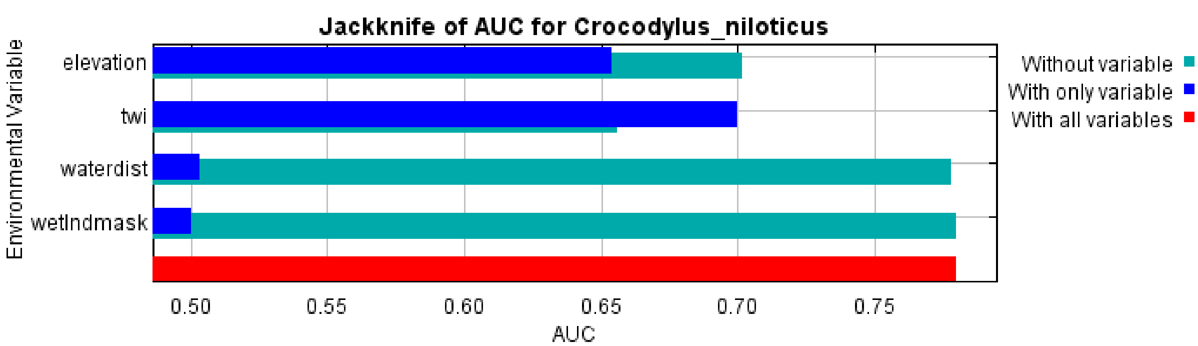
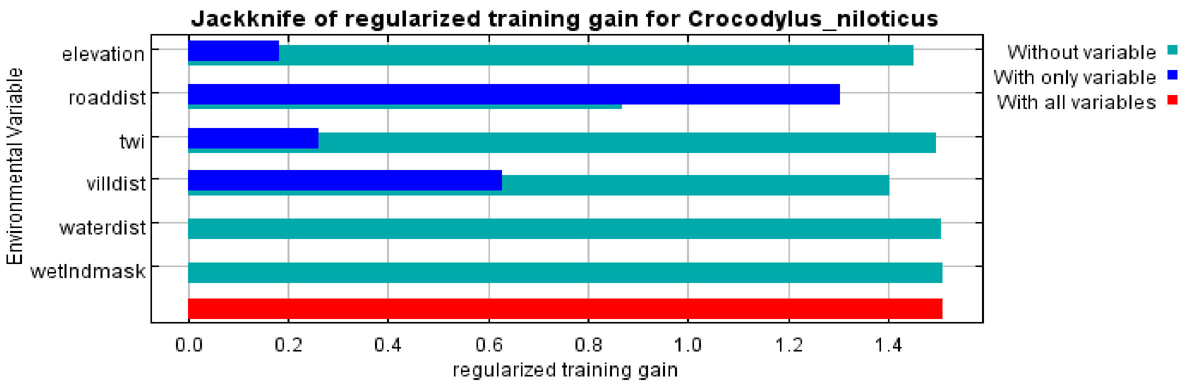
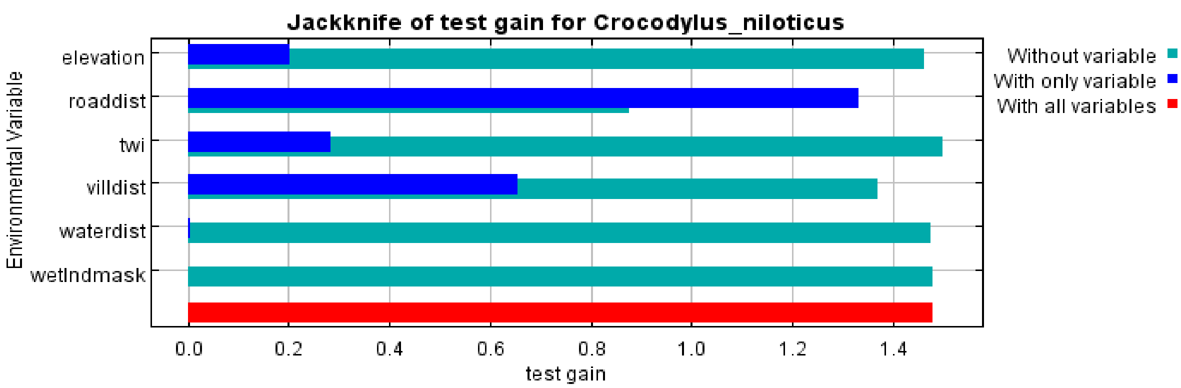


Figure 8. Jackknife test of variable importance with the inclusion of only biophysical covariates for a) regularized training gain b) test gain c) area under the curve (AUC)

a)



b)



c)

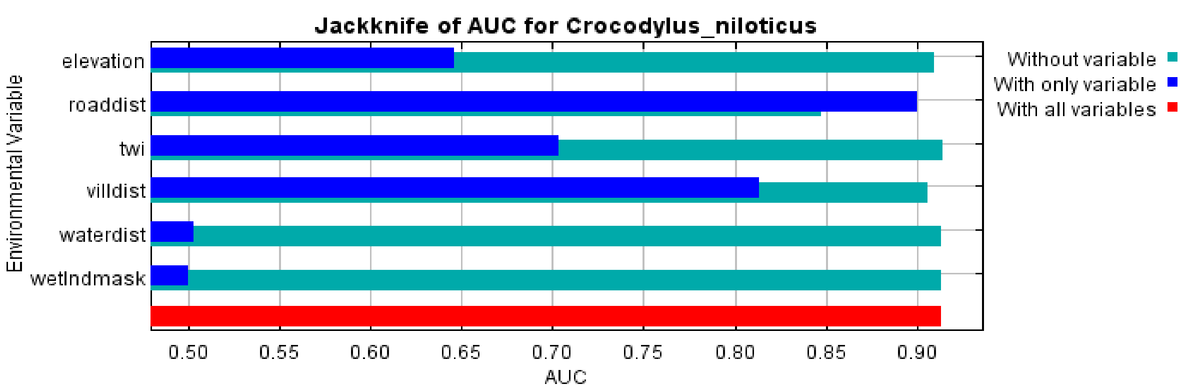


Figure 9. Jackknife test of variable importance with the inclusion of all covariates for a) regularized training gain b) test gain c) area under the curve (AUC).

Chapter 5: Discussion

Chapter 5 describes the field data used in the model and provides an overview of the model strengths and conclusions drawn from the results of the model, together with a discussion about the most influential variables for each model (biophysical and anthropogenic). The limitations of the model are presented, including concerns with species detectability and potentially insufficient anthropogenic covariates. Lastly, future research directions are described as well as how the results and conclusions of this study may be used in crocodile management practices.

Field Data

The use of 72 presence-only records to create the habitat suitability maps were sufficient as Maxent is equipped to deal with a wide range of sample sizes (Elith et al. 2006; Hernandez et al. 2006). The unequal survey effort due to time and safety constraints (only routes A, B, and C were surveyed at night – D through F were not; see Figure 2), as well as the issue of species detectability (see Model Limitations) may have resulted in an increase in observations in the south and southwestern portions of the study area. However, according to locals, crocodiles are not found in the areas near routes D through F, and it was believed by them to be a waste of time surveying these portions of the river (Mamy Rabenero, pers. comm.). As no crocodiles were recorded in these areas, the unequal survey efforts are believed not to have impacted the overall findings of the study.

Model Strengths and Conclusions

Using the AUC classifications presented by Araújo and Guisan (2006) both models performed very well, with the first model containing only the biophysical covariates scoring a rating of “average” (AUC = 0.780), while the second model with the anthropogenic factors (distance from roads and villages) scored a rating of “excellent” (AUC = 0.913). The inclusion of the anthropogenic factors not only increased the resulting AUC value of the model, implying that the model had better predictive performance than without those two predictive variables, but also greatly reduced the amount of predicted crocodile habitat within the Mariarano River system.

The results of the jackknife test indicated that without the inclusion of anthropogenic factors, the most influential variable was the topographic wetness index (TWI), which is used to predict water accumulation within a distinct area. The areas deemed as highly suitable crocodile habitat corresponded with high levels of TWI, indicating that *C. niloticus* may prefer areas with higher soil moisture content. Studies that have incorporated TWI when considering suitable habitat for crocodilians normally consider it based on nest site suitability rather than suitability for the animal itself (Lutz and Dunbar-Cooper 1982; Kushlan 1982). However if *C. niloticus* does prefer high levels of TWI, this may not be due to nesting site preference as other studies have found that *C. niloticus* prefer dry, sandy areas as nesting sites (Steel 1989; Shacks 2006). Elevation also played an important role not only according to the jackknife test results but also in the percent contributed by the variable to the model’s performance. Wetland designation and distance to water contributed little to the model. Distance to water may have added little to the model because it was related to wetland designation, which was used as a mask for the model.

However, once the anthropogenic factors of distance from roads and distance from villages were included, distance from roads became the most important variable, contributing 88.7% to the model predictions and causing the largest decrease in model gain when excluded from the model and the largest increase in model gain when it was the only covariate included in the model. Topographic wetness index contributed very little to the anthropogenic model. This minimized role may have been due to the greater influence of distance to roads. Human-crocodile conflict occurs where humans and crocodiles overlap, and increased access to crocodile habitat by roads may negatively affect their distribution (Aust et al. 2009; Thorbjarnarson et al. 1999; R. Gandola pers. comm.). While this may indicate that humans play an influential role in limiting crocodile distribution within the Mariarano River, there may be other anthropogenic and biological factors missing from the model.

Though roads may allow for greater access to crocodile habitat, the large percent contribution of the distance to road covariate (88.7%) may also be due in part to co-linearity of the independent variable with the predictor variable (i.e. crocodile observations). Though Maxent is not a statistical technique and the overall output is not affected by co-linearity among variables, the contributions of individual variables to the model as determined by Maxent can be affected though co-linearity (Phillips et al. 2006; Baldwin 2009). This possible co-linearity between the distance to roads and crocodile observations may have caused the greater contribution of the distance to roads covariate, decreasing the contributions of other covariates such as TWI, which had previously had a higher contribution in the biophysical model.

Model Limitations

Species detectability is a source of error that could have possibly biased recorded observations. Crocodiles are often very elusive and behavioral factors (such as submersion) and environmental factors (habitat, weather, observer bias) can influence detectability (Shirley et al. 2011; Hutton and Woolhouse 1989). Environmental factors may have caused variability in the detectability of crocodiles within the river, causing an increase in observations in certain areas of the river. This may have influenced any spatial autocorrelation present in the data. By using the cross-validation procedure available in Maxent using ten replicates, all sets would experience the same spatial autocorrelation which would contribute to the same error (Fielding and Bell 1997; Stockwell 1992). Although spatial autocorrelation is a common issue in all species distribution models, it was not addressed here due to the disparities in addressing this issue in the literature (Hijmans 2012, Lennon 2000, Liu et al. 2011, Václavík et al. 2011). Václavík et al. (2011) did find that while accounting for spatial autocorrelation improved the performance of the models produced by Maxent, it did not decrease the amount of residual autocorrelation.

Using the wetland designation covariate as a mask for the model limited the effectiveness of the model, as it expanded the habitat suitability analysis beyond the extent of the surveyed areas. While Maxent is equipped to perform projections of the original model, extending its overall area analyzed, those procedures were not performed in this analysis, limiting the use of the results of the biophysical and anthropogenic models created in this study (Phillips and Dudik 2008). Thus while the two models originally may have been seen as the potential suitable habitat for crocodiles in the Mariarano River area (biophysical model) and the realized suitable habitat for crocodiles (anthropogenic model), the use of the wetland designation as a mask rather than the areas surveyed reduces the viability of the model.

The variables of distance from road and village contributed 88.7% and 4.9% respectively to the model, and were the two most important variables identified in all three model evaluations using the jackknife test. However, these results may not accurately reflect the effects of anthropogenic activities on *C. niloticus* distribution along the Mariarano River. For example while roads may increase accessibility to waterways, other anthropogenic factors not included in this model, such as boat traffic along the river may be a greater contributing factor to *C. niloticus*'s distribution. The habitat suitability model created for *C. niloticus* nesting sites included boat traffic and burning activity as additional anthropogenic factors affecting the location of suitable nesting sites (Shacks 2006). Thus, although the model may have been ranked as excellent based on its resulting AUC value, its lack of inclusion of all of the potential anthropogenic factors may limit its usefulness in creating an appropriate habitat suitability map for *C. niloticus* in the region.

Future Research Directions

Future work on examining *C. niloticus* distribution within the Mariarano River system should include additional anthropogenic factors such as boat traffic along the river, as well as areas of high fishing intensity, and mangrove deforestation. Shacks (2006) determined that in the Okavango Delta, 59% of previously suitable habitat had been disturbed by humans at the time of study, specifically by boat traffic, fire disturbance, vegetation harvesting and cattle grazing. Determining which anthropogenic disturbances affect crocodile distribution would aid future monitoring programs of crocodiles in the region, as well as potentially contributing to knowledge about crocodile distributions in other regions of Madagascar.

Further surveys should also be conducted in the wet season (November-April), because extensive flooding occurs throughout the region, making many areas inaccessible except by boat, and connecting the Mariarano River to many of the surrounding lakes. The amount of rain received and subsequent flooding dramatically alters the landscape, which should increase the distribution of *C. niloticus* during this season. Understanding how *C. niloticus* distribution in the region changes between the dry and wet season will aid in future conservation management measures.

Future Uses

This study was conducted under the advisement of Operation Wallacea, an organization that runs biological and conservation management science programs throughout the world. The Mariarano River system and surrounding areas have acted as a field site for the organization since 2010, and will continue to be used in future field seasons. By establishing a species distribution model for the Nile crocodile, this will aid in the project site's long term monitoring goals through the creation of a baseline crocodile distribution map for the area (P. Long pers. comm.). Additionally, the model limitations outlined, and the future work and modifications suggested in this thesis, will aid researchers in the monitoring of the Nile crocodile population in the Mariarano River System.

On a larger scale, this is one of the first studies conducted on Nile crocodiles in Madagascar that has spanned over the course of two years, and the only study conducted on Nile crocodiles in Madagascar in 2012 (R. Gandola pers. comm.). With the ban on exporting crocodile goods put in place by the International Union for Conservation of Nature (IUCN) and a lack of information about the status of the Nile crocodile throughout the country, the findings of this study will provide future motivation to continue monitoring crocodiles in the Mariarano region and possibly provide information on conservational management practices that may be used in other regions.

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