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Thesis of Noah G. Cohen

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

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Approved: Thesis Committee

Major Professor: Dr. Matthew Johnston

Committee Member: Dr. Kenneth Krysko

Committee Member: Dr. Bernhard Riegl

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

EVALUATING THE ECOLOGICAL STATUS OF THE INTRODUCED NILE MONITOR (Varanus niloticus) IN FLORIDA: FORECASTING PRESENCE AND POPULATION EXPANSION USING COMPUTATIONAL GEOGRAPHIC INFORMATION SYSTEMS

Ву

Noah G. Cohen

Submitted to the Faculty of

Halmos College of Natural Sciences and Oceanography

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Abstract

The Nile monitor (*Varanus niloticus*) is a large, carnivorous lizard that has become a notorious invasive species in Florida, USA. Initially released in the 1980s from the pet trade, the species has since established at least three breeding populations and spread throughout much of southern Florida. While current control efforts have failed to eradicate *V. niloticus*, it is important to attain a better understanding of its invasive dynamics to guide and inform better control strategies. In this study, available georeferenced records of *V. niloticus* in Florida were compiled and linked to a habitat classification map to evaluate ecotype preferences. Factored with bioclimatic data, the regional spread of *V. niloticus* was modelled for contemporary and projected (i.e., in the year 2050) presence using Maxent and Mahalanobis Distance models. Study results indicate that *V. niloticus* maintains a strong presence in eastern Lee County on the southwestern coast. Populations in Palm Beach and Miami-Dade counties on the southeastern coast may be interconnected, contrary to current descriptions that they are separated from each another. Model forecasts of conditions for the year 2050 identify widespread expansion of *V. niloticus* in Florida, particularly northward with the establishment of a new population center in Pasco County in the western central peninsula. This is the first known modelling study of *V. niloticus* in Florida and identifies regions at greater risk for future population expansion.

Keywords: climate, Florida, GIS, habitat, invasive species, species distribution modelling, Varanidae

1.0 Introduction

The introduction of non-native species has become an increasingly common threat to ecosystems worldwide. Introduced (also known as non-native or exotic) species are organisms that have been introduced to an area outside of their native range. Invasive species are a smaller subset of introduced species, that have become established (i.e., reproducing populations) and are known to cause damage to cause harm to the environment, economy, or human health (Executive Order 13112, Invasive Species Advisory Committee 2006). Invasive species are second only to anthropogenic habitat alteration in their capacity to harm native species and ecosystems (Wilcove et al. 1998, Parker et al. 1999). As of the year 2005, the environmental cost of bioinvasions was estimated to be \$120 billion USD annually in the United States alone (Pimentel et al. 2005). Invasive species have been implicated as a contributing or even driving factor in the decline or extinction of native species and degradation of natural habitats (Fritts & Rhoda 1998, Gurevitch & Padilla 2004). Still, the negative impacts of introduced species are vast and often not well understood. The state of Florida, USA, is an epicenter of rampant introductions (Krysko et al. 2016) and identifying the threats posed by invasive species is critical to the management and protection of indigenous species and habitats (Semmens et al. 2004). Ferriter et al. 2006).

1.1 Invasive Species in Florida

Florida's warm climate, major ports of entry (e.g., Miami and Tampa), thriving captive wildlife industry, and available niches in human-altered habitats make the state especially susceptible to the introduction and establishment of a wide range of species (Corn et al. 2002, Hardin 2007, Krysko et al. 2011a). High volume shipping pathways and the offload of ballast water has been a frequent source of introduced and invasive species in Florida, notable examples include macroalgae (*Caulerpa taxifola*) (Walters et al. 2006), and red-imported fire ants (*Solenopsis invicta*) (Tschinkel 1998, 2006, Ascunce et al. 2011). Much of the goods received in Florida are associated with the wildlife and exotic plant trades. As a corollary of the wildlife industry, many introduced and invasive animal species in Florida are the direct result of pet trade animals being released intentionally and unintentionally into the wild. Notable examples of these invasive species in Florida include ornamental lionfish (*Pterois* spp.) in coastal reefs and the Florida Keys (Semmens et al. 2004, Johnston & Purkis 2011), spiny-tailed iguanas (*Ctenosaura*

similis) on Gasparilla and Keewaydin Islands (Krysko et al. 2003), and Burmese pythons (*Python bivittatus*) in the Everglades region (Snow et al. 2007, Krysko et al. 2008). Many plant species that have become rampant invasives in Florida were initially introduced as ornamental plants, such as the Brazilian pepper (*Schinthus terebinthifolus*) (Morton 1978), Australian carrotwood (*Cupaniopsis anacardiodes*) (Schmitz et al. 1997), and Chinese tallow (*Sapium sebiferum*) (Bruce et al. 1997, Schmitz et al. 1997). Hurricanes and tropical storms have also been implicated as a regional factor contributing to the establishment of invasive species in Florida (Horvitz et al. 1998, Bhattarai & Cronin 2014, Johnston & Purkis 2015). Notably, Florida has more introduced terrestrial, marine and freshwater species than any other region in the USA (Hardin 2007) and also ranks high in this respect globally, with breeding populations of new species regularly identified (Ferriter et al. 2006, Krysko et al. 2011a, 2016).

Given Florida's subtropical climate and large volume of exotic animal trade, it is no coincidence that a large proportion of Florida's invasive vertebrate species are reptiles. The subtropical climate of the Florida peninsula experiences a relatively stable warm temperature profile and humid conditions advantageous to herpetofauna from other tropical and subtropical latitudes. Likewise, the climate of southern Florida seldom falls below freezing temperatures, eliminating much of the risk of physiologically intolerable conditions for ectothermic organisms such as amphibians and reptiles.

The establishment of non-native herpetofauna has been documented in Florida for over 150 years (Cope 1863, Krysko et al. 2011a, 2016) and has accelerated in the last half century (Meshaka et al. 2004a, 2011; Krysko et al. 2016). Florida presently contains the largest number of established non-native amphibian and reptile species in the world (Butterfield et al. 1997, Krysko et al. 2011a, 2016). Indeed, the number of non-native lizard species breeding in Florida outnumbers, by a factor of three, native lizard species (Hardin 2007, Krysko et al. 2011a, 2016). Yet, the negative ecological, financial, and human impacts have been documented for only a few invasive reptile species in Florida, such as the Burmese python (Dove et al. 2011, Dorcas et. al 2012, McCleery et al. 2015), northern curly-tailed lizard (*Leiocephalus carinatus*) (Smith and Engeman 2004, Meshaka et al. 2005), black spiny-tailed iguana (*Ctenosaura similis*) (Avery et al. 2011, Nunez et al. 2016), and green iguana (*Iguana iguana*) (Meshaka et al. 2004b, McKie et al. 2005, Krysko et al. 2007, Sementilla et al. 2008). However, an invasive species of great concern in Florida that has been insufficiently studied is the Nile monitor (*Varanus niloticus*).

1.2 The Nile Monitor (Varanus niloticus)

The Nile monitor is the largest lizard species of its native African continent. Individuals in western African populations are known to reach 1.7 m total length (TL); whereas individuals in eastern and southern Africa grow much larger, up to 2.4 m TL in South Africa (Pianka et al. 2014). *Varanus niloticus* is characterized by having a light to dark brown dorsal coloration with yellow transverse bands on the head and limb; six to nine bands of yellow, rosette-like ocelli on the back; a light colored belly and throat, with varied patterns of black bars; and a laterally compressed tail (Lenz 1995, Pianka et al. 2004).

The native range of *Varanus niloticus* covers most of sub-Saharan Africa and, as its common name implies, follows the Nile River northward to Egypt. In its native range, *V. niloticus* occupies savannah, evergreen thicket, bushland, wetlands, mangrove forests, and swamps among other ecoregions. It preys upon various animals across ecotypes, including but not limited to fishes, birds, amphibians, reptiles, mammals, insects, and crustaceans. It exhibits an ontogenetic diet shift; it is primarily insectivorous in early life stages but shifts towards carnivory as it matures (Reipell & Labhardt 1979, Lenz 1995, Bennett 2002).

Populations have been frequently exploited and exported to satisfy demand from the exotic pet trade. *Varanus niloticus* accounted for 23% of all global trade among 28 species of varanid lizards monitored by CITES between 1975 and 2005, with the United States being the chief importer (Pernetta 2009). Despite being a popular import for the pet trade, industry experts and herpetologists note them to be unsuitable for most non-professional reptile keepers. The combination of their large size and captivity requirements can be difficult to provide, the inadequacy of such can lead to health issues and poor temperament. Such has been noted with the difficulty of keeping young individuals in captivity. With patience, proper care and handling, individuals can be tractable, but *V. niloticus* have a reputably poor temperament (Sprackland 2012). The combination of their generally intractable attitude and advanced captivity requirements are likely factors driving some less-than-responsible reptile keepers to intentionally release them outside their native range.

1.3 Presence of Varanus niloticus in Florida

Varanus niloticus is a relatively recent introduction to Florida. The earliest verified record in Florida is from 1981, collected from Lake Kanapaha, Gainesville, Alachua County (Krysko et al. 2016). This species has since been independently introduced throughout the state, and southern peninsular populations have spread southward to Key Largo, Monroe County (Krysko et al. 2011b). Breeding populations have been established since the 1980s in Miami and Homestead, Miami-Dade County, and the early 1990s in Cape Coral, Lee County (Enge et al. 2004, Campbell 2005, Ferriter et al. 2006). One genetic study linked the invasive populations of *V. niloticus* in Florida to individuals originating in western Africa, where their progenitors likely originated (Dowell et al. 2016). The source of both invasive populations is the pet trade with at least two possible scenarios for introduction (Enge et al. 2004, Campbell 2005): 1) individual lizards may have been released by ill-prepared pet owners that became incapable of managing these large, aggressive animals, and/or 2) a pet trader(s) may have intentionally released enough individuals to ensure its establishment in order to cull from the local population and thus avoid the costs of purchasing captive-bred individuals and/or regulatory aspects of importing animals (Enge et al. 2004, Campbell 2005).

Palm Beach County is another center of high activity for *Varanus niloticus*. Cohorts of all age classes have been observed and collected, with at least one record of a mating pair (Krysko et al. 2011b, EDDMapS 2015). Hence, the Florida Fish and Wildlife Conservation Commission (FWC) suggested that the Palm Beach County population is reproducing and self-sustaining (Florida Fish and Wildlife Conservation Commission 2015). *Varanus niloticus* has also been regularly observed since 1994 in Coral Springs and Tamarac, Broward County (Enge et al. 2004). Collier County is the site of the most recent invasion, first being recorded on 1 August 2015 (EDDMapS 2015). Other invaded counties include Sarasota, Pasco, Pinellas, Brevard, Seminole, Osceola, Orange and Monroe counties. Anecdotal observations have been noted from Fort Ogden, Arcadia, and Brownville in De Soto County (Enge et al. 2004), though no verified records exist from these areas in observational only databases.

Varanus niloticus has shown a remarkable capacity and adaptability in its successful expansion throughout Florida, including natural, aquatic dispersal from the mainland to barrier islands. For

example, in 1998, a Lee County Mosquito Control helicopter photographed an adult *V. niloticus* on Matlacha Pass, a small barrier island midway between Cape Coral on the mainland coast and Little Pine Island to the west (Enge et al. 2004, EDDMapS 2015). It is likely this individual either swam, a wellknown behavior in its native range, or traversed the road connecting Matlacha Pass to the mainland. A single *V. niloticus* was also observed among a group of black spiny-tail iguanas (*Ctenosaura similis*) on Gasparilla Island in 1999 (Enge et al. 2004). Though observations of *V. niloticus* on Sanibel Island date back to 1996 (Enge et al. 2004) there have only been three verified records from 2005–2008, which are thought to be of the same individual that migrated from the established population in Cape Coral (C. Lechowicz, pers. comm. 2015). There is also one record of an individual burrowing beneath plants on private property on Pine Island in 2011, (EDDMapS 2015). Additionally, two observations were reported in 2003 from Cayo Costa, an island west of Pine Island and south of Gasparilla Island (Enge et al. 2004).

The successful establishment of *Varanus niloticus* can, in part, be attributed to the lack of population controls (i.e., factors that may limit its spread) typically encountered in its native range. For example, there are no known predators of *V. niloticus* in Florida. Furthermore, a lack of natural, co-evolved parasites eliminates many issues associated with parasite load, as explained by the enemy release hypothesis (Torchin & Mitchell 2004, Liu & Stillings 2006, Huffaker 2012). While vulnerable to various parasites in its native range (Njagu et al. 1999, Hering-Hagenbeck & Boomker 2000, Pianka et al. 2004), *V. niloticus* captured in Cape Coral possessed no external parasites and few to no internal parasites, contributing to the overall good health across all individuals examined (Campbell 2005). The lack of such population controls elevates concern over the impacts of *V. niloticus* in Florida.

1.3 Threats posed by Varanus niloticus

As a generalist predator, *Varanus niloticus* has the capacity to negatively impact a wide range of species at different trophic levels. The invasive populations in Florida demonstrate much of the same dietary trend as indigenous individuals (Campbell 2005). The concern is that it is a generalist with no considerable population controls in Florida, posing a direct threat to numerous species and the trophic stability of Florida's ecosystems.

Established populations of *Varanus niloticus* in Charlotte, Lee, and Miami-Dade counties may pose a threat to indigenous crocodilians, such as the American alligator (*Alligator mississippiensis*) and American crocodile (*Crocodylus acutus*). In its native range, *V. niloticus* raids nests and eats eggs and

young crocodilians, sometimes using intelligent cooperative tactics to draw adult crocodilians away from their nests (Pianka et al. 2004). *Varanus niloticus* also competes with crocodilians in Africa for food resources (Cott 1960, Lenz 1995, Luiselli et al. 1999, Enge et al. 2004). *Crocodylus acutus* is a threatened species with a high proportion of nesting in Miami-Dade and Monroe counties (Krysko et. al 2011b), elevating the threat posed by the southern expansion of non-native *V. niloticus*.

Another species of particular concern is the burrowing owl (*Athene cunicularia*) – a state protected species whose habitat range includes the Cape Coral area (Enge et al. 2004, Campbell 2005). A *V. niloticus* predated a burrowing owl in 2005, confirming the invasive lizard could negatively impact the listed bird species (Campbell 2005).

There is also concern that Varanus niloticus may severely impact indigenous populations of turtles and tortoises. There is one recorded observation of V. niloticus eating the eggs of a Florida softshell turtle (Apalone ferox) as they were being oviposited (EDDMapS 2015), and turtle eggs were among the stomach contents identified in some captured lizard specimens (Campbell 2005). The gopher tortoise (Gopherus polyphemus) is another state protected species of critical importance. Its distribution includes that of known V. niloticus presence such as Cape Coral and coastal regions of southwestern Florida (FWC 2012). Direct predation on gopher tortoises by V. niloticus is of great concern, but even greater than that is the precipitated effect on other species. The burrows dug by gopher tortoises offer refuge for more than 360 species, and some like the eastern (Drymarchon couperi) and Gulf Coast (D. kolpobasileus) indigo snakes, and pine snake (Pituophis melanoleucus) are commensals of tortoise burrows (Lips 1991). The establishment of V. niloticus in Palm Beach County, expansion into Broward County, and an observation in Brevard County also raises concern of potential predation of sea turtle nests. These counties host major nesting beaches for loggerhead (Caretta caretta) and green (Chelonia mydas) sea turtles, and leatherback (Dermochelys coriacea), all of which are protected (Weishampel et al. 2003, Burnie & Ouellette 2005). Verified records of V. niloticus predating sea turtle nests have not yet been documented in Florida and it tends to stay closer to estuaries and freshwater sources rather than beaches (Campbell 2005). However, it has been noted as an occasional predator of sea turtle hatchlings in Equatorial Guinea (Tomas et al. 1999), and other varanid species have been documented predating sea turtle nests (Blamires 1999, 2003). Predation of V. niloticus on sea turtle hatchlings in its native habitat and freshwater turtles in both its native and introduced ranges leaves this possibility open (Lenz 1995, Pianka et al. 2004, Campbell 2005). Above are but a handful of species at risk of predation and therefore the need is urgent to understand the impact of V. niloticus on Florida's environment.

Compounding its generalist predatory behavior, *Varanus niloticus* thrives in a wide variety of habitats. Previous studies and the scientific literature describe *Varanus niloticus* as a terrestrial, semi-aquatic, or aquatic species (Lenz 1995, King & Green 1999, Pianka et al. 2004, Campbell 2005). Frequently established around permanent bodies of water, it likewise possesses adaptations that make it an adept swimmer and allow it to use its thick claws and muscular hind limbs to take advantage of arboreal habitats (Lenz 1995, Pianka et al. 2004). Not limited to natural habitats, it is also known to wander into urban and residential areas in its native range, often found basking on sidewalks and rooftops (Pianka et al. 2004). Its ecological plasticity affords *V. niloticus* the ability to exploit various prey across various habitats and complicates any general prediction of critical habitats in the absence of remote tracking or long-term field survey data.

Despite ongoing eradication efforts through trapping programs in Lee and Palm Beach counties, *Varanus niloticus* still persists in these areas and continues to expand its distribution. Current data suggest that total eradication of this species from Florida is unfeasible using current control methods employed due to the financial costs and effort required, particularly for remote and densely vegetated areas difficult to access, and variable effectiveness of the control regimes (Enge et al. 2004, Campbell 2005). Though trapping efforts have provided successful capture rates in Cape Coral, these methods have proven less effective in Miami-Dade County (Ferriter et al. 2006). Furthermore, inadequate information on invasive *V. niloticus* distribution and behavior in Florida and a lack of regional, interagency coordination limits the effectiveness of control tools utilized by local and state officials. It is urgent to better understand the distribution and ecology of *V. niloticus* in Florida as the species has a high potential for ecological impacts and there has been inadequate study of its population sizes and dynamics (Enge et al. 2004, Campbell 2005, Mauldin 2010).

Common tools employed to help understand population expansion and predict the behavior of species are Species Distribution Models (SDMs). SDMs are varied in their computational analysis and output but can be generally simplified as such: SDMs link spatially-referenced data on species occurrence with maps of environmental variables such as climate, elevation, and habitat to create a statistical model predicting their behavior relative to environmental variables of concern. The species occurrence records may be a set of presence only or a set of presence and absence records, depending on sampling methods employed. Based on the results, depending on the model, inferences can be made on a species' realized niche and spatial extent. Applications of SDMs include predicting impacts of climate change and habitat loss, identification of corridors and reserve areas for conservation, and

predicting the spread of invasive species. To date, no studies have applied SDMs to study the invasive dynamics of *Varanus niloticus* in Florida. Some studies have simply proposed theoretical impacts based on known behavior in its native range, anecdotal accounts, and limited quantitative analysis on predation (Campbell 2005).

1.4 Purpose of Study

Given the lack of empirical and modeling studies of Varanus niloticus in Florida, the motivation of this study was to evaluate the ecological status of its populations and forecast potential distribution and future range expansion in Florida. Such information is critical to address the pervasive expansion of V. niloticus as presently there is a paucity of literature examples that may help to direct efforts to control and potentially eradication this invasive species. To accomplish this, verified, georeferenced specimens and observations were analyzed to determine the present distribution and spatio-temporal dynamics of V. niloticus populations. Through multivariate analysis of bioclimatic data and environmental niche modelling, physiological preferences and distribution correlations of this species were deduced. These data points were then linked to a habitat classification map to identify ecotype preferences. Knowledge of habitats presently utilized by *V. niloticus*, in combination with bioclimatic factors and projections on future climatic conditions, can inform corridors of population expansion and assess habitats and regions at greater risk for future population expansion. Identifying areas at risk for V. niloticus incursion and corridors of expansion will allow resource managers to act swiftly to prevent negative impacts to native fauna and establishment of further breeding populations. While V. niloticus is the focus of this endeavor, methods utilized herein may also be applied to other similar invasive species where such information is lacking, such as the Argentine black and white tegu (Salvator merianae).

2.0 Methods

2.1 Observation Data and Voucher Records

Georeferenced observation records and voucher specimens of *Varanus niloticus* in Florida prior to 1 January 2016 used were used to plot its historical introduction and range expansion, and serve as the basis for determining the monitors' preferred ecotypes. Records for vouchered specimens were provided by the Division of Herpetology, Florida Museum of Natural History, University of Florida (UF-Herpetology). Records and observational data were also taken from the FWC's nonnative species database, and Early Detection & Distribution Mapping System (EDDMapS), an open web-based database administrated by the University of Georgia's Center for Invasive Species. Additional observation records from Sanibel Island were provided by the Sanibel-Captiva Conservation Foundation (C. Lechowicz, pers. comm. 2015).

Individual records were first vetted for data quality. Records lacking or with inaccurate (i.e., low degree of specificity, high range of uncertainty) geospatial data, or insufficient information to consider credible (i.e., no photographic evidence, vague descriptions, etc.) were eliminated. In several cases, records had different database ID numbers with synchronous dates, identical GPS coordinates, but no measurements or specific descriptions to confirm as separate instances. In such cases, only one observation was used. Credible and confirmed observations were cross-checked between sources for duplicity to prevent distortion in statistical analysis or over-fitting of models. A total of 601 records for *Varanus niloticus* in Florida passed scrutiny and were used in subsequent analyses.

A geographic distribution map of data points from all sources was created in ArcMap (version 10.4.0.5524) (Figure 1). Records were compiled and plotted by month of incidence (Figure 2), thus measuring seasonal activity utilizing the R statistical program (R Core Team 2016). Utilizing the Spatial Statistics toolbox in ArcMap, distribution data were aggregated for clearer visualization of incident density (Figure 3). To accomplish this, a fixed grid was overlaid onto the map of *V. niloticus* incident in Florida. The pixel size selected for the grid was 224 x 224 meters, corresponding to the squared root of the 50,000 m² maximum home range noted for adult males in native habitats (Lenz 1995). This range was selected so that aggregated points would likely incorporate overlapping home ranges of individuals

of various life stages. All records situated within the same pixel were integrated into a quantityweighted point to illustrate the density of *V. niloticus* occurrence.

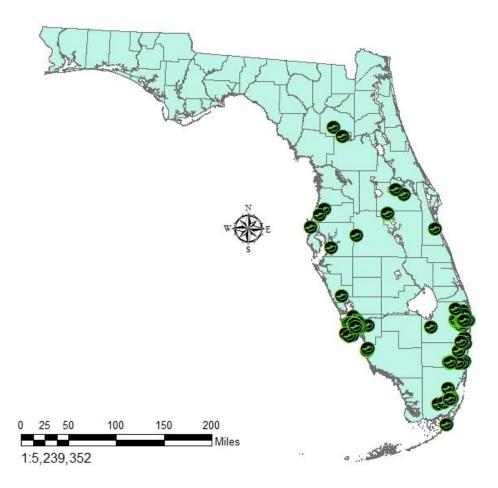


Figure 1. Varanus niloticus records (n=601) in Florida between 01 Jan 1981 and 31 Dec 2015. Data taken from FWC, UF-Herpetology, EDDMapS, and the Sanibel-Captiva Conservation Foundation.

2.1.1 Habitat Classification Map

Varanus niloticus distribution data were binned by habitat type based on the Florida Cooperative Land Cover (CLC) map version 3.1 to identify habitat utilization and possible corridors of expansion (Florida Fish and Wildlife Conservation Commission 2016). The CLC habitat classification map was developed cooperatively between FWC and Florida Natural Areas Inventory (FNAI) to delineate discrete habitat types within Florida. Criteria and classifications for natural, semi-natural, and disturbed habitats of the CLC map follows the Florida Land Cover Classification System (Kawula 2014). Distribution data were converted from WGS 1984 coordinates to FDEP Albers Harn, the state-specific geographic coordinate system used for the CLC. Linking distribution data to the habitat classification map demonstrates the range and distribution of verified observations of *V. niloticus* within Florida's ecotypes. All statistical analyses were performed using ArcMap statistics scripts and the R software language, version 3.1.1 (R Core Team 2016), and α values of < 0.05 for significance tests.

2.2 Bioclimatic Data

Observation record data were linked with climatic parameter data using computational Geographic Information Systems (GIS). As such, climatic data for present-day conditions were sourced from Worldclim version 2, compiled into a series of 19 bioclimatic factors calculated from mean monthly climate data for minimum, mean, and maximum temperature, and precipitation for the years 1970–2000 (Fick and Hijmans 2017). Bioclimatic data had a pixel size of 30 arc-seconds (~1 km) for maximum detail when modelling. The original 19 bioclimatic variables were subjected to tests for multicollinearity to prune the modelling parameters and eliminate potential problems with co-associated variables. Tests for multicollinearity were conducted using variable index factor (VIF) scores, eliminating variables scoring higher than 10.0, as specified with the materials for the 'usdm' package in R. The VIF threshold eliminated all but 7 bioclimatic factors; mean diurnal range, isothermality, mean temperature of the wettest quarter per annum, mean temperature of driest quarter per annum, annual precipitation, precipitation of wettest month per annum, and precipitation of warmest quarter per annum. The range and statistical correlations for locality preference and physiological tolerance in Florida were compared with data from the native range of *Varanus niloticus* as documented by Lenz (1995) to identify unique characteristics of the invasive population.

2.3.1 Maxent

The current geographic distribution of Varanus niloticus in Florida was modelled utilizing the Maxent software program version 3.3.3k (<u>http://www.cs.princeton.edu/shapire/maxent/</u>). Maxent is a presence-only model that estimates the most uniform distribution ("maximum entropy") across a given study area (i.e., the probability that an occurrence at a given location is different from a randomly selected location given the constraints of environmental predictors). Maxent was selected as an ideal model for this study for several reasons. Maxent is a presence-only model that can utilize opportunistically reported observations were there is a lack of detailed sampling data recording both presence and absence in a given region. This is advantageous for V. niloticus data, which like other invasive species has lacking or nonexistent absence data (Gallien et al. 2010). Instead, Maxent randomly selects background points from the study area to serve as pseudo-absence data. Maxent incorporates both continuous and categorical variables, allowing for the possibility of measuring the effect of habitat on distribution. Maxent has been demonstrated as highly effective in modelling invasive species distributions (Wang et al. 2007, Ward 2007) and outperformed other modelling options (Hernandez et al. 2006, Pearson et al. 2007, Duan et al. 2014). Another reason for using Maxent was its output of both Receiver Operating Characteristic (ROC) curves and Area Under the Curve (AUC) as measures of model fit and accuracy. The ROC is a trendline plotting the values calculated for the values of specificity subtracted from 1 (i.e. false positive rate) against values for the sensitivity (i.e. true positive rate). The AUC is and the area calculated under the ROC curve, reflecting the fit of a model and its ability to make accurate predictions above random chance. The closer the AUC value is to 1, the better the predictive power of the model. Maxent is also freely available and user-friendly.

Of the three output options available from the Maxent software, the logistic model output was selected for ease of interpretation. Background data comprised 10,000 randomly selected points. Inclusion of multiple presence records in the same grid cell would distort model projections, therefore the option to remove duplicate records was selected. Furthermore, the β regularization parameter was set to 2.0 rather than the default 1.0 to optimize model performance and quality, reducing the potential for overfitting following Radosalvjevic & Anderson (2014). A total of 10 runs were conducted, each

randomly seeded with 4-fold cross-validation replicate runs. Cross-validation is a resampling technique where the data is divided into equal-sized portions, the number of which is denoted by the numeral k. To train the model, k-1 portions are used in combination first, with the final data portion subsequently used to obtain predictions from the trained model. The run with the greatest AUC value was retained. Jackknife analysis, a resampling method used to measure sampling bias associated with sample parameters, was performed to evaluate the influence of each bioclimatic factor in the probability of *Varanus niloticus* presence. The sum of the contribution of all predictor values is equal to 1, with greater values of individual predictors reflecting a stronger ability to predict presence.

2.3.2 Mahalanobis Distance Modelling

Mahalanobis distance modelling was performed with the dismo package in R (R Core Team 2015) and compared with outputs from Maxent. Mahalanobis distance is a presence-only model that analyzes clustering and distances of individual points from a mean distribution using eigenvectors, a set of vectors associated with a linear set of equations from a matrix (Mahalanobis 1936). Simply put and for the purpose of species distribution modelling, the Mahanalobis statistic (D²) indicates the relative distance any multivariate point in a defined space is from an ideal set of environmental conditions (Knick & Dyer 1997, Knick and Rotenberry 1998, Hamann & Wang 2006). The lower the D² value the closer a point is to an optimal location and more likely to test positive for the presence of the subject being modelled. Mahalanobis was selected for the same presence-only advantages provided by Maxent, robustness compared to other modeling options (Duan et al. 2014), and successful application in previous studies of invasive species (Etherington et al. 2009). Datasets for presence and background points were randomly seeded to develop training and testing datasets. The training data are a subset of the original data, analyzed by the software to identify ideal habitat conditions and to program the model to know how to calculate the Mahalanobis statistic. The test dataset is then subsequently used on the trained model to calculate the D² output for the Mahalanobis model. The Mahanalobis statistic output was analyzed by its AUC value and compared to the metric for Maxent. To evaluate probable areas of Varanus niloticus presence, a threshold must be applied to the D² statistic model output to filter for values with a lower D² value. The max threshold, the threshold at which the sum of sensitivity and specificity is highest, was applied to the raw Mahalanobis output to produce a probable distribution

map. The max threshold was selected because it minimizes the mean value of the error rate for positive observation values and negative observation values (Duan et al. 2014).

2.3.3 Projected Distribution by Global Climate Models

Future projections of *Varanus niloticus* presence in Florida were performed with Maxent utilizing projected bioclimatic data sourced from a global climate model. The global climate model selected was the projected 2050 dataset from the Community Climate System Model (CCSM4), having been reliably used in other species distribution projections (Stralberg et al. 2009, Boyd & Doney 2012). The CCSM4 global climate model also offers several representative concentration pathways (RCPs) for future climate scenarios interpolated to a 30 arc-second (~1 km) resolution. Representative concentration pathways are trajectories based on greenhouse gas concentrations adopted by the United Nations' Intergovernmental Panel on Climate Change (IPCC), used to describe possible climate futures. These climate scenarios range from the best case scenario requiring the cessation/mitigation of all greenhouse gas emissions immediately (RCP 26), to more moderate projections following current trends with peak emission rates in 2040 and 2080 respectively (RCP 45 and RCP60), and a more severe projection of climate change assuming continued increases in emission rates (RCP 85) (Meinshausen et al. 2011). All RCPs described were incorporated into Maxent projections, 10 runs for each, to forecast *V. niloticus* distribution in Florida by the year 2050 under various scenarios of climate change.

3.0 Results



3.1 Seasonal activity of Varanus niloticus

Figure 2. Varanus niloticus records in Florida by month between [day and month] 1981 and 31 Dec 2015 (by count). Data taken from FWC, UF-Herpetology, EDDMapS, and the Sanibel-Captiva Conservation Foundation.

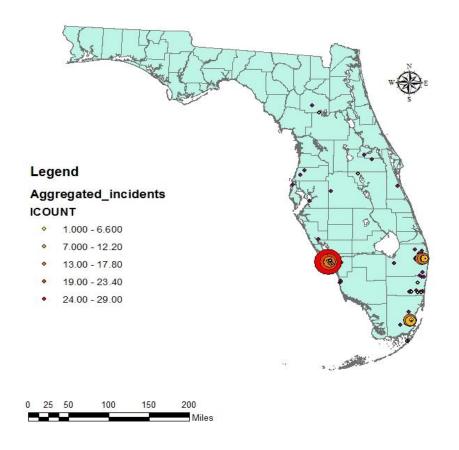
Plotting *Varanus niloticus* records by month in Florida illustrates seasonal activity gradually increases in March with a peak in May (n=105), followed by gradually declining through December (Figure 2). From November through March fewer animals were reported, suggesting the invasive populations may be less active in the late fall and winter months.

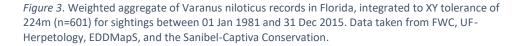
3.2 Population Density

Aggregated observation records illustrate three centers of *Varanus niloticus* activity in Florida; Cape Coral, Miami-Homestead, and southern portions of West Palm Beach and Westgate (Figure 3). These data suggest Cape Coral contains the greatest density of *V. niloticus* activity in Florida over the analysis period, with more than half of all the credible observations (n = 371) between 01 January 1981 and 31 December 2015 within city limits. *Varanus niloticus* was highly concentrated in western Cape Coral, decreasing in frequency and density southward and eastward to the Caloosahatchee River. A similar pattern in distribution was observed in previous surveys of the Cape Coral area (Campbell 2005). Additionally, there were scattered records on nearby islands.

West Palm Beach ranked second in density and frequency for *Varanus niloticus*, as records (n=104) were concentrated along the banks of or proximal (< 100 m) to the C-51 canal. Sporadic records were also found in residential areas to the south and the marshland/flatwoods perimeter of the Grassy Waters Preserve.

Varanus niloticus records from Miami-Dade County exhibited a moderately high density in the Homestead region. Records (n=40) were particularly concentrated around the Homestead Air Base, accounting for nearly all credible records available for the county. Other notable records were scattered near the marshlands to the west of the airbase with several southward in Key Largo. There were also clustered sightings in southern Broward County.





3.3 Habitat Preferences

A high proportion of *Varanus niloticus* records in this dataset were recorded in disturbed, urban land classes (Table 1). The most populated (n=312; 51.9%) land class by *V. niloticus* in Florida was High Intensity Urban, characterized by a commercial, industrial, or residential density of >2/acre. High activity was also noted within the Transportation class (n=126; 21.0%), comprising pathways and facilities used for the movement of goods and people (i.e., roads, airports, cargo docks, etc.). Canal systems and artificially modified streams, the Cultural-Riverine class, also were home to a relatively high proportion of *V. niloticus* records (n=90; 15.0%). Natural habitats all together accounted for a small proportion of records (n=18).

Table 1. Varanus niloticus records by land class determined by the Florida CLC map (version 3.1). Data taken from FWC, UF-Herpetology, EDDMapS, and the Sanibel-Captiva Conservation Foundation.

Habitat	Observation (by count)
Cultural - Riverine	90
High Intensity Urban	312
Low Intensity Urban	33
Rural	10
Transportation	126
Cultural - Lacustrine	3
Cypress	1
Exotic Plants	3
Freshwater Forested Wetlands	1
Freshwater Non-Forested Wetlands	1
Mangrove Swamp	2
Marshes	3
Mesic Flatwoods	2
Mesic Hammock	1
Mixed Hardwood Coniferous	1
Pine Rockland	1
Praries and Bogs	1
Riverine	1
Salt Marsh	3
Vineyards and Nurseries	6
Total	601

3.4 Predicted Current Distribution

3.4.1 Maxent

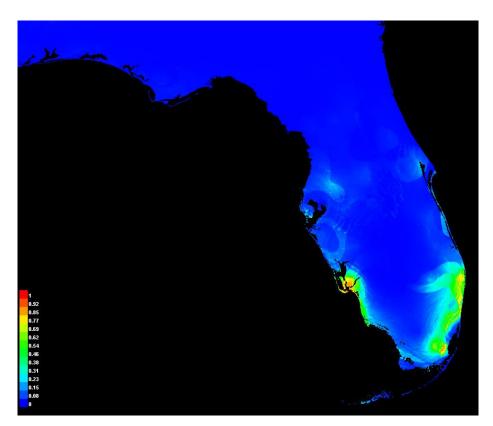


Figure 4. Maxent modelling output for areas of probable *Varanus niloticus* presence in Florida based on environmental predictor variables.

The Maxent projection for the current distribution of *Varanus niloticus* in Florida illustrates spread from previously noted areas of concentrated activity (Figure 4). The model output yielded an average Area Under the Curve (AUC) value for the test replicate runs of 0.956 with a standard deviation of \pm 0.013 (Appendix 2). The AUC value for the Receiver Operating Characteristic (ROC) curve and the analysis of the average test omission rate (Appendices 1, 2), closely following the predicted omission rate, both suggest the Maxent output to be a strong predictive model for *V. niloticus* presence in Florida.

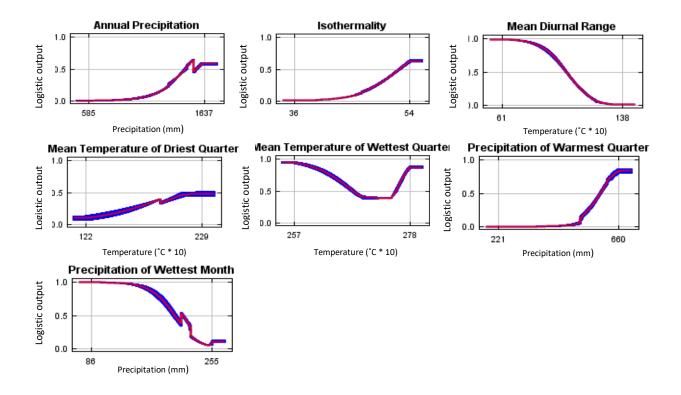


Figure 5. Marginal response curves for bioclimatic predictor variables incorporated into Maxent projection of current *Varanus niloticus* presence. Response curves incorporate mean trendline (red) with standard deviation (blue) for cross-validation runs. Bioclimatic data sourced from Worldclim 2.0.

Marginal response curves, measuring the singular effect of one variable with all others reduced to an mean sample value, suggest *Varanus niloticus* presence is positively correlated with Isothermality and Mean Temperature of Driest Quarter per annum (Figure 5). Though its presence is positively correlated with Annual Precipitation, there was a negative correlation based on the Precipitation of the Wettest Month per annum. Likewise, there was a negative correlation between Mean Diurnal Range. The Mean Temperature of the Wettest Quarter per annum exhibited a parabolic relationship with *V. niloticus* presence, initially exhibiting a negative correlation until the mean temperature reached 27.5 °C.

When accounting for the dependencies between a selected variable and correlations with other variables, the response curves undergo a notable change. The marginal response curve demonstrated a negative correlation between the Precipitation of the Wettest Month per annum and the logistic predictions of the model when considered in isolation. However, when aggregated with dependencies of other environmental predictors incorporated in the model, the relationship yields a positive correlation (Figure 6).

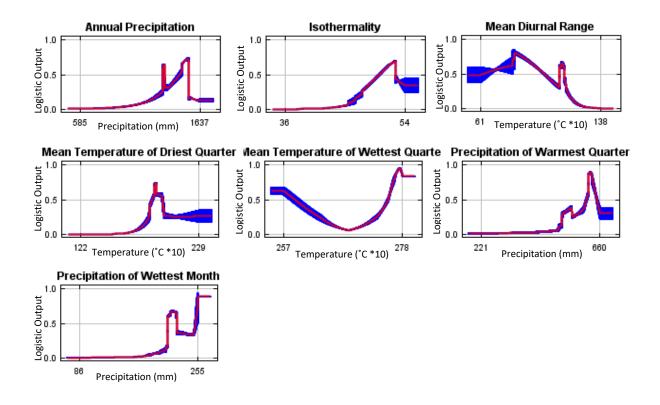


Figure 6. Response curves for bioclimatic predictor, incorporating correlations between bioclimatic variables, variables incorporated into Maxent projection of current *Varanus niloticus* presence. Response curves incorporate mean trendline (red) with standard deviation (blue) for cross-validation runs. Bioclimatic data sourced from Worldclim 2.0.

Jackknife analysis of the environmental predictor variables suggests Precipitation of the Wettest Month per annum to be the greatest predictor of *Varanus niloticus* presence (Figure 7). Precipitation of the Wettest Month, averaged across replicate runs, is responsible for a 30.5 percent contribution to the output of the model, identifying it as the most significant predictor. Mean Diurnal Range was calculated to contribute 21.2 percent to the model, followed in relative importance by the Mean Temperature of the Wettest Quarter (16.5 %), Mean Temperature of the Driest Quarter (14.4 %), and Precipitation of the Warmest Quarter (8.9 %). Isothermality and Annual Precipitation are found to be of lesser relative importance in the predictions of the Maxent model, contributing 5% and 3.4 %, respectively.

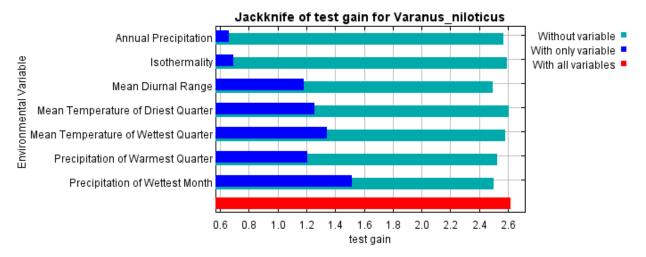
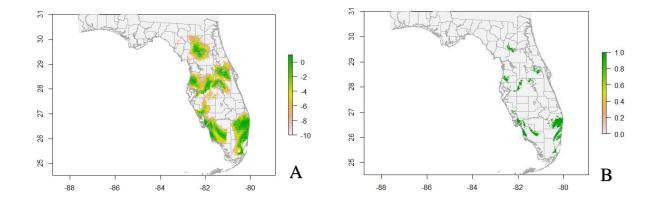


Figure 7. Jackknife analysis of relative contribution of bioclimatic variables in predictive output of the Maxent model for *Varanus niloticus* population spread in Florida.



3.4.2 Mahalanobis Distance

Figure 8. Mahalanobis D² statistic output (8A) and the probable presence of *Varanus niloticus* suggested by the application of the max threshold (8B).

The Mahalanobis Statistic output (Figure 8A) illustrates D^2 values calculated based on ideal conditions set by the training data (n = 481). The application of a max (kappa) threshold to the D^2 output using the test data (n = 120, absences = 50) produces a map of probable *Varanus niloticus* presence (see Appendix 15). The Mahalanobis predictive model produced an AUC value of 0.9942149 (Figure 8B).

3.5 Distribution projections of Varanus niloticus in the year 2050

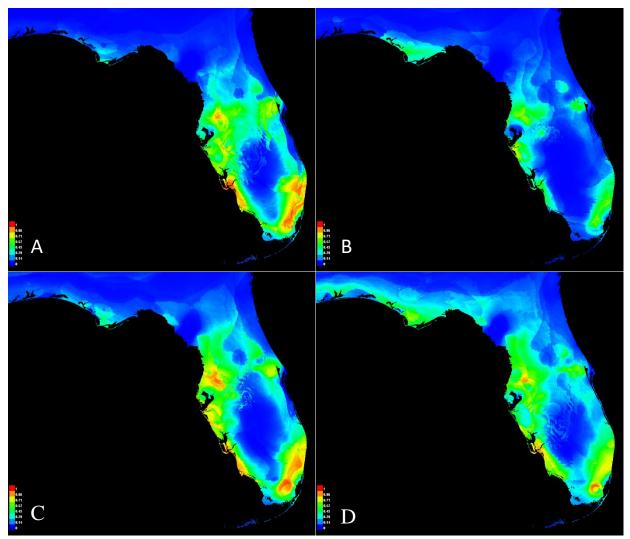


Figure 9. Forecasted Maxent modelling for areas of probable *Varanus niloticus* presence in Florida in 2050 based on RCP scenarios: RCP 26 (9A), RCP 45 (9B), RCP 60 (9C), and RCP 85 (9D).

All projected model outputs for *Varanus niloticus* distribution in Florida illustrate range expansion beyond that indicated by the Maxent output for current distribution. For all RCP scenarios, regions of probable presence suggest northward future expansion. The ROC curves, AUC values and graphs of the test omission rates demonstrate all Maxent outputs to project areas of probable presence in 2050 far better than random chance. The Maxent output for the RCP 26 projection (Figure 9A) yields an average AUC of 0.954 with a standard deviation of 0.017. The RCP 45 Maxent projection produces an average AUC value of 0.953 with a standard deviation of 0.010, with far smaller regions of probable presence than other Maxent projections (Figure 9B). The Maxent projection based on the RCP 60 climate data yields and average AUC of 0.955 and standard deviation of 0.017 (Figure 9C). The final Maxent projection for the RCP 85 climate projection yields an average 0.955 with a standard deviation of 0.014 (Figure 9D).

4.0 Discussion

4.1 Seasonal Activity

According to this analysis, peak seasonal activity for *Varanus niloticus* in Florida occurs during the spring through summer, correlating with the breeding season and increases in day length and mean high temperature. In its native range, the breeding season of *V. niloticus* coincides with stages of the wet season, when monitors are known to be more active and expands its home range in search of mates (Lenz 1995, King & Green 1999). Similar behavioral patterns have been observed in other varanid species (Shine 1986). Findings suggest that the invasive populations in Florida exhibits the same pattern of increased activity in response to seasonal fluctuations of the local wet season, in preparation for breeding. In corroboration, the observed period of greater presence coincides with patterns of increased precipitation in Florida (Figure 10). Previous survey data of *V. niloticus* in Cape Coral (Campbell 2005) suggested that reproductive activity likely occurred during this same period, between the months of April and September. During this span, females exhibited egg development and distended oviducts, and males possessed enlarged testes. Increased activity by *V. niloticus* in the search and protection of mates during this time makes them more visible and therefore more likely to be reported.

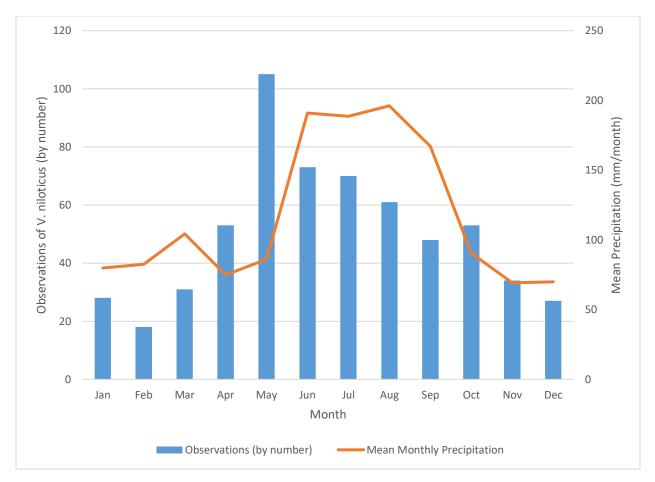


Figure 10. Records for *Varanus niloticus* factored against mean monthly precipitation in Florida between Jan 1981 and December 2015. Precipitation data sourced from the Florida State University's Climate Center.

4.2 Habitat Preferences

Varanus niloticus maintains a strong presence in disturbed habitats in Florida. Such behavior has frequently been observed in its native range (Lenz 1995, Pianka et al. 2004) as well as in its invasive range (Enge et al. 2004, Campbell 2005). No reliable conclusion can be made about habitat preferences of *Varanus niloticus* in Florida based on the available data analyzed herein. Much of the data, namely citizen-reported observations from EDDMapS, have inherit sampling bias explaining the high proportion of sightings in urban areas (Table 1). Disturbed habitats, such as urban centers and residential areas, are naturally where people are most densely populated and spend most of their time. Thusly, the majority of *V. niloticus* reported to EDDMapS came from these areas, as the probability of a chance encounter is greatest in these regions. Further study is needed to form valid conclusions about critical habitats and preferences of *V. niloticus* in Florida. Long-term field surveys, particularly in natural habitats and less

accessible regions, and tracking by acoustic or radio transmitters would provide the data necessary to identify critical ecotypes and, potentially, diurnal behavior patterns and specific pathways of spread.

Despite sampling bias, it can be hypothesized that there is an ontogenetic shift in habitat preference for *Varanus niloticus* in Florida. Hatchlings likely prefer sheltered ecotypes such as mangroves, dense brush, hammock and other arboreal habitats that dualistically offer refuge from predation, larger conspecifics and provide a reliable source for many species insect and arthropods to feed upon. Such ontogenetic shifts are observed in other varanids (King & Green 1999, Pianka et al. 2004, Imansyah et al. 2008, Karunarathna et al. 2017) and other large lizards such as iguanids (Knapp and Owens 2005). Dense landscaping in residential areas could also fulfill the same habitat requirements, where credible sightings of juvenile *V. niloticus* have been observed (EDDMapS 2015, UF Herpetology 2016). As varanids mature, they expand their home ranges as increased energy reserves allows them to roam large areas and exploit a larger pool of prey types (Christian et al. 1995, King & Green 1999). It is important to emphasize that for the populations of *V. niloticus* in Florida this pattern of behavior is merely speculative. There is insufficient data available for *V. niloticus* with specific measurements placing them in this age class for a conclusive statement.

4.2.1 Theoretical corridors for range expansion

The distribution of records suggests canal networks may be a corridor of expansion for *Varanus niloticus*. Indeed, the Cultural-Riverine land class is home to a notable proportion of records (n = 90, 15.0%), especially for a habitat class that is characteristically narrow physically and is a relatively small overall proportion of the study area. GPS coordinates place an additional majority of records (n = 359, 53.7%) in other land classes that physically flank (<100 m) habitats of the Cultural-Riverine class (Figure 1). *Varanus niloticus* tends to live near permanent bodies of water in its native range (King &Green 1999, Pianka et al. 2004) and the home ranges all individuals surveyed by Lenz (1995) in Gambia contained at least 1 permanent source of water. Canals offer a freshwater source and a convenient means of retreat, as has been noted in observations (EDDMapS 2015). Furthermore, the concrete banks and sidewalks lining much of the canal network offer attractive basking spots.

4.3 Modelling outputs

4.3.1 Potential distribution from Maxent

A significant result from the Maxent analysis of *Varanus niloticus* distribution in Florida is that populations between West Palm Beach and Miami may now be interconnected. The projected distribution (Figure 4) shows an extended region of probable presence well into southern Broward County and branches into Miami-Dade County. Previous studies segregate the two populations as distinct (Enge et al. 2004, Dowell et al. 2016), however the data used herein suggest there may be an exchange of individuals between the two or they may even now represent a single population. Genetic analysis suggests that individuals from all breeding populations are sourced from the western clade in their native habitat (Dowell et al. 2016), but no genetic studies have been published between invasive populations in Florida. Further seasonal tracking studies and genetic tests are required to confirm the degree of genetic overlap between the Miami-Dade and West Palm Beach populations.

The Maxent projection identifies the neighboring regions around Cape Coral and the islands adjoining Lee County as sites of highly probable presence. Predictably, the entire area of Cape Coral is identified by Maxent as the area with the highest probability of *Varanus niloticus* presence in Florida (Figure 4). More interesting is the identification of eastern Lee County as a region of highly probable presence. To date, credible and/or confirmed sighting of *V. niloticus* on the eastern side of the Caloosahatchee River have been rare, in contrast to the extreme density of records in Cape Coral. It is possible the lack of records from these areas is the result of survey efforts and frequent public service announcements exclusively focused in the Cape Coral region. Still, the aquatic capabilities and adaptations of *V. niloticus* have been established (Ingleton 1929, Wood & Johansen 1974, Lenz 1995, Pianka et al. 2004) and so it is reasonable to suggest that individuals could cross the Caloosahatche River as a means of range and niche expansion and to avoid resource competition with conspecifics.

The additional forecast of continued and expanded presence upon islands neighboring Lee County is worth noting. Though few sightings from the islands in the past 10 years exist (EDDMapS 2015, UF Herpetology 2016), researchers investigating the invasion suggest that recurring incursion by *V*. *niloticus* from the Cape Coral population to nearby islands such as Sanibel is inevitable (C. Lechowicz, pers. comm. 2015).

The Maxent projection shows a region of probable presence branching southward from Cape Coral into Collier County. It is only recently that several sightings have been confirmed throughout

Collier County, but the forecast done here suggests that *Varanus niloticus* may be more widespread in the area than records currently indicate. Likewise, such sightings could represent an expansion from the core Cape Coral population to other regions as overlapping home ranges or other factors push individuals to explore new territories.

4.3.2 Potential distribution from Mahalanobis

The regions of probable presence identified by the max threshold applied to the Mahalanobis Distance model coincide with many of the regions identified within the Maxent projection (Figure 8). The Mahalanobis output likewise shows the population in West Palm Beach extending throughout Palm Beach County and well into Broward County. However, unlike the output from Maxent, the regions of probable presence between the Miami and West Palm Beach populations are not contiguous connection. It is still possible that migration of individuals exists between the two regions in this scenario but seemingly less likely. Furthermore, the Mahalanobis output also portrays *Varanus niloticus* expanding eastward across the Caloosahatchee River to Fort Myers.

Given the similarities in the outputs between the two models, the projection produced by the Mahalanobis Distance model does yield some key differences. For example, unlike the Maxent model output, the Mahalanobis model identifies areas of probable presence within Polk and Pasco counties. Areas of probable presence of *Varanus niloticus* are also identified around Seminole and Alachua counties. This result is unexpected as sightings in these areas are rare, but do encompass areas with greater values for Precipitation of the Wettest Month compared to surrounding areas, more attractive to *V. niloticus* during breeding season. The Mahalanobis output predicts probable *V. niloticus* presence around Orange and Seminole counties. Sightings after the date range for records incorporated into this study lend credence to the prediction. FWC records include an individual photographed on 4 September 2016 in northern Orlando.

4.3.3 Implications of 2050 distribution projection

The 2050 projections for all RCP scenarios suggest range expansion of *Varanus niloticus* from contemporary population centers, with the establishment of a new population center in Pasco County (Figure 9 A – D). All RCP projections for 2050 show continuous regions of probable presence from Lee County northward to Hillsborough and Pasco counties. Furthermore, all but the RCP 45 Maxent projection identify a concentrated region of highly probable presence in eastern Pasco County, suggesting the area could become home to an established breeding population. Similar to the Maxent projection for current presence (Figure 4), jackknife analysis indicates the environmental predictor of greatest relative importance is the Precipitation of the Wettest Month (Appendices). It is suggested that current survey and trapping efforts are expanded to this region with the aim of inhibiting or even preventing the establishment of a new breeding population in the area. Maxent projections for RCP scenarios also suggest southward range expansion and establishment within Collier County.

RCP 85 shows probable distribution near Apalachicola National Forest in the panhandle (Figure 9D), suggesting the region to contain suitable habitats and conditions for establishment. To date, there is an absence of records for *Varanus niloticus* from this region, and model projections from this study illustrate no projected presence in adjacent areas. Consequently, the method of ingress by *V. niloticus* to the panhandle region as suggested in the RCP 85 projection is unclear. It is possible that *V. niloticus* may expand into to the panhandle from an established presence in the regions around Alachua County. The Mahalanobis output (Figure 8B) forecasts contemporary, regional presence of *V. niloticus* around Alachua County. Data collected after the study period lends credence to this suggestion. A confirmed observation was noted in Suwannee County in 29 December 2016, northwest of the regional presence forecasted bioclimatic data for factors strongly correlated with *V. niloticus* presence (Precipitation of Wettest Month per annum, Temperature of Wettest Quarter per annum, Temperature of Driest Quarter per annum) show a region of preferential conditions connecting the two regions, serving as bridge for range expansion.

Confirmed and credible sightings collected after the study period likewise coincide with other regions identified in the 2050 Maxent projections. The projection for the RCP 26, 60 and 85 scenarios yield regions of probable presence in northern Florida around the intersection of Brevard, Seminole and Volusia counties (Figure 9A, C, D). This is another region were credible records have been exceptionally rare. However, there was a confirmed sighting in the Doris Leeper Preserve in Volusia County on 25 February 2017.

4.4 Suggestions for Future Research

Information yielded from this study provides new insight into the behavior of *Varanus niloticus* in Florida and implications for their potential expansion and management. With that in mind the findings here leave many questions open and unanswered that merit further study.

Understanding the diurnal behavior and locomotion of *Varanus niloticus* would be critical to developing better control strategies. It is currently unknown if the invasive *V. niloticus* populations exhibit the same home range extent as in its native habitat. Of additional concern is the effect of the breeding season on movement patterns. While it tends to expand its home range in search of mates, it is unknown once a mate has been found if it continues to roam large areas to ward off competitors and search for additional mates or, alternatively, prefers to intimately guard a small area with a single mate. Both behaviors have been observed from the Andros Island iguana (*Cyclura cyclura cyclura*) (C. Knapp pers. comm. 2017). Radio-tracking studies of established breeding populations could inform diurnal and seasonal movements and provide valuable information relevant to their management and eradication. Such methods have been successfully implemented with other invasive species, such as the cane toad (Llewelyn et al. 2010) and domesticated goats (Taylor & Katahira 1988). Radio tracking can also inform dispersal rates, allowing for more detailed modelling of the mechanics of invasive behavior (Alford et al. 2009, Llewelyn et al. 2012).

Inter-population genetic studies of *Varanus niloticus* in Florida can also provide key information necessary for effective population control. Distribution modelling projections from this analysis draw questions about whether the Palm Beach and Miami-Homestead populations are connected. Conclusive determination of the genetic relationship between Florida's invasive populations and the transfer of individuals between them is key to better targeting strategies for population control.

Ontogenetic development and behavioral changes are seldom studied in *Varanus niloticus* in its native range. While analysis has been done to evaluate the changes in diet and dentition with maturation (Rieppel & Labhardt 1979, Bennett 2002), no detailed analysis is known regarding potential shifts in habitat preferences or the survival rates of different population demographics. The sensitivity of survival rates at different life stages can vary, making extermination of individuals of a particular age class most effective for eradication efforts (Govindarajula et al. 2005). Likewise, if young monitors frequent different habitats than older conspecifics, it will influence control strategies for invasive populations.

Conclusion

Varanus niloticus is a highly successful invasive species, whose seasonal activity in Florida are associated with patterns of precipitation. It has successfully exploited a wide range of habitats, potentially utilizing Florida's canal networks to spread to new areas. Known to be highly concentrated within Cape Coral, modelling indicates *V. niloticus* maintains a strong presence in eastern Lee County. Furthermore, there may be an exchange of individuals or even contiguousness between the population centers in West Palm Beach and Homestead. Model forecasts of conditions for the year 2050 suggests strong range expansion, particularly northward with the establishment of a new population center in Pasco County. Further study of the diurnal behavior and developmental biology of the invasive populations can better inform resource managers of how to better target individuals and incorporate more effective control methods. The techniques used and suggested for further study here can be applied to other introduced and invasive species in Florida such as the Argentine black-and-white tegu (*Salvator merianae*) and savannah monitor (*Varanus exanthematicus*).

Acknowledgements

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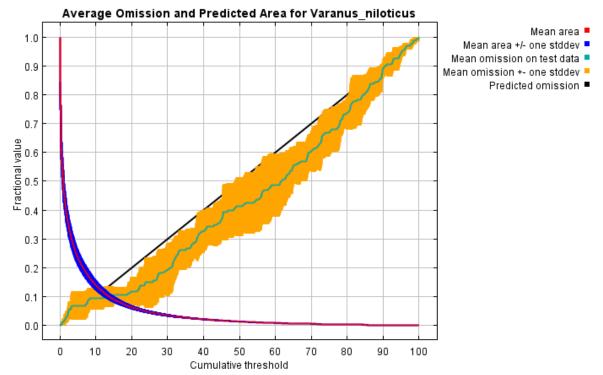
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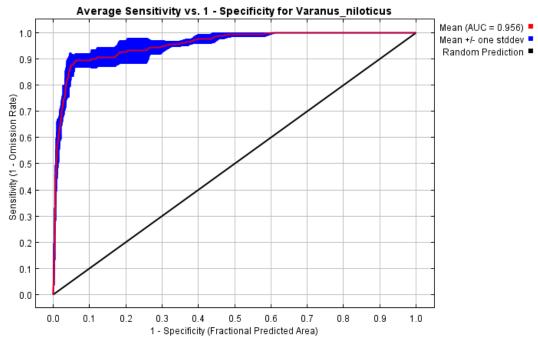
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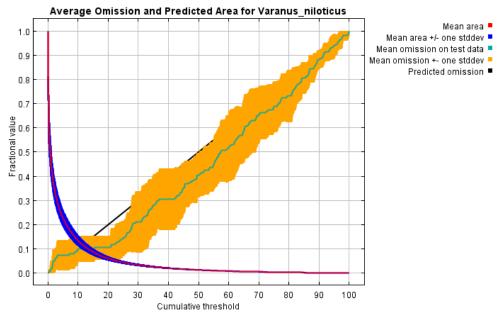
Appendices



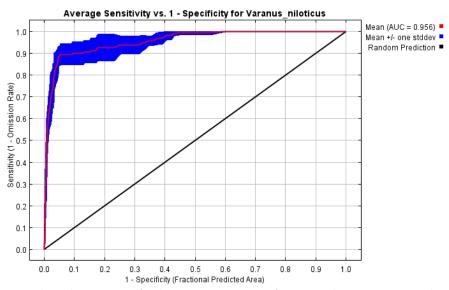
Appendix 1. The test omission rate and predicted area as a function of cumulative threshold for forecasted current Varanus niloticus presence.



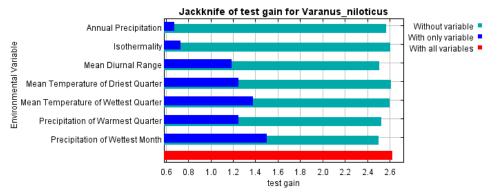




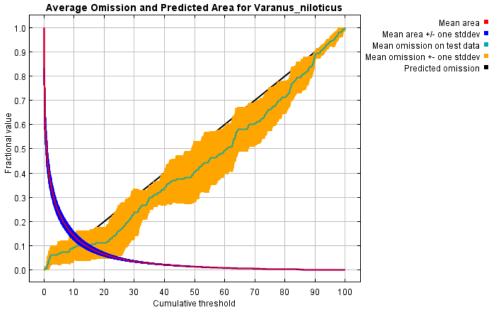
Appendix 3. The test omission rate and predicted area as a function of cumulative threshold for Varanus niloticus presence under the RCP 26 forecast for the year 2050.



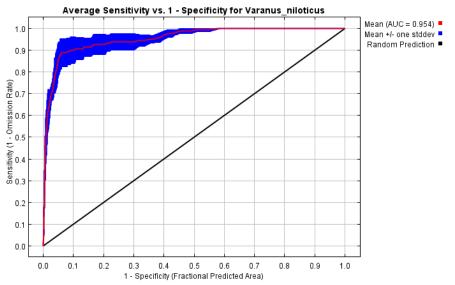
Appendix 4. The ROC curve for the Maxent projection of Varanus niloticus presence under the RCP 26 forecast for the year 2050.



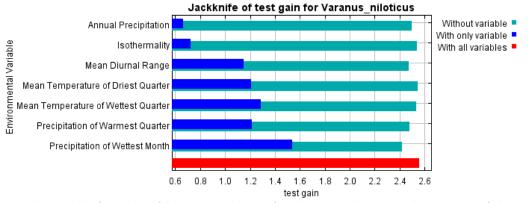
Appendix 5. Jackknife analysis of relative contribution of bioclimatic variables in predictive output of the Maxent model for Varanus niloticus population spread in Florida for the year 2050 under RCP 26 forecasted conditions.



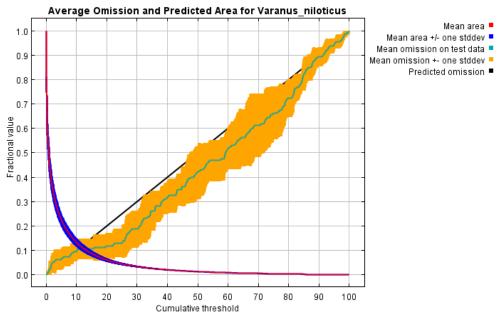
Appendix 6. The test omission rate and predicted area as a function of cumulative threshold for Varanus niloticus presence under the RCP 45 forecast for the year 2050.



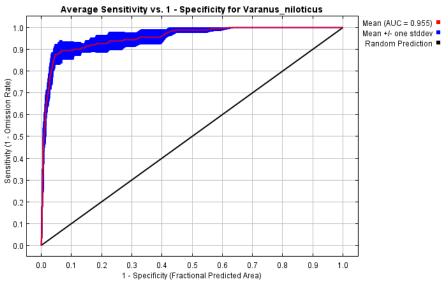
Appendix 7. The ROC curve for the Maxent projection of Varanus niloticus presence under the RCP 45 forecast for the year 2050.



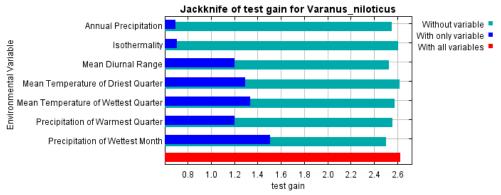
Appendix 8. Jackknife analysis of relative contribution of bioclimatic variables in predictive output of the Maxent model for *Varanus niloticus* population spread in Florida for the year 2050 under RCP 45 forecasted conditions.



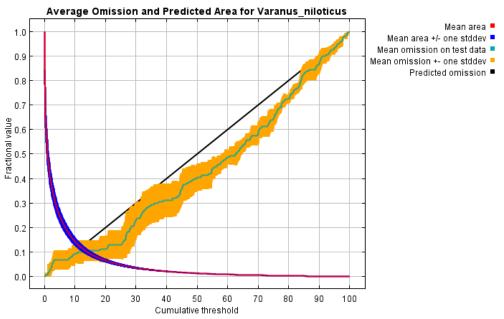
Appendix 9. The test omission rate and predicted area as a function of cumulative threshold for Varanus niloticus presence under the RCP 60 forecast for the year 2050.



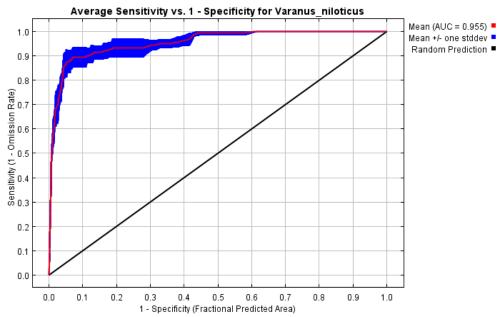
Appendix 10. The ROC curve for the Maxent projection of Varanus niloticus presence under the RCP 60 forecast for the year 2050.



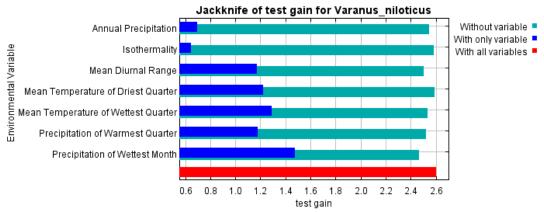
Appendix 11. Jackknife analysis of relative contribution of bioclimatic variables in predictive output of the Maxent model for *Varanus niloticus* population spread in Florida for the year 2050 under RCP 60 forecasted conditions.



Appendix 12. The test omission rate and predicted area as a function of cumulative threshold for Varanus niloticus presence under the RCP 85 forecast for the year 2050.



Appendix 13. The ROC curve for the Maxent projection of Varanus niloticus presence under the RCP 85 forecast for the year 2050.



Appendix 14. Jackknife analysis of relative contribution of bioclimatic variables in predictive output of the Maxent model for Varanus niloticus population spread in Florida for the year 2050 under RCP 85 forecasted conditions.

#create presence train and test data
set.seed(RandomSeed)
group<-kfold(Nile_monitor, 5)
pres_train<- Nile_monitor[group !=1,]
pres_train\$Species<-NULL
pres_train<- pres_train[,c("Longitude Decimal", "Latitude Decimal")]
colnames(pres_train)<- c("lon","lat")
pres_train<-data.matrix(pres_train)</pre>

pres_test<- Nile_monitor[group ==1,]
pres_test\$Species<-NULL
pres_test<- pres_test[,c("Longitude Decimal", "Latitude Decimal")]
colnames(pres_test)<- c("lon", "lat")
pres_test<-data.matrix(pres_test)</pre>

#create background train and test data
set.seed(RandomSeed)
backg<-randomPoints(pred_bio, n=1000)
group<-kfold(backg, 5)
backg_train<- backg[group !=1,]
backg_test<- backg[group ==1,]
colnames(backg_test)<-c("lon","lat")
colnames(backg_train)<-c("lon","lat")</pre>

#plot background and train data
r<-raster(pred_bio, 1)
plot(!is.na(r), col=c('white', 'light grey'), legend=FALSE)
points(backg_train, pch='-', cex=0.5, col='yellow')
points(backg_test, pch='-', cex=0.5, col='black')
points(pres_train, pch= '+', col='green')
points(pres_test, pch='+', col='blue')</pre>

#Add Florida shapefile FL<-shapefile("FL_shapefile_location.shp") plot(FL) #Mahalanobis distance modelling
mm <- mahal(pred_bio, pres_train)
e <- evaluate(pres_test, backg_test, mm, pred_bio)
e</pre>

pm<-predict(pred_bio, mm, ext=FL)

#Apply max threshold

par(mfrow=c(1,2))
pm[pm < -10] <- -10
plot(pm)
plot(FL, add=TRUE, border='dark grey')
tr <- threshold(e, 'kappa')
plot(pm > tr)
plot(FL, add=TRUE, border='dark grey')

Example R code for Mahalanobis Distance modeling of Varanus niloticus presence in Florida.