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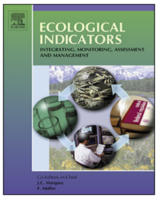

Influence of salinity on relative density of American crocodiles (*Crocodylus acutus*) in Everglades National Park: Implications for restoration of Everglades ecosystems

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ABSTRACT

The status of the American crocodile (*Crocodylus acutus*) has long been a matter of concern in Everglades National Park (ENP) due to its classification as a federal and state listed species, its recognition as a flagship species, and its function as an ecosystem indicator. Survival and recovery of American crocodiles has been linked with regional hydrological conditions, especially freshwater flow to estuaries, which affect water levels and salinities. We hypothesize that efforts to restore natural function to Everglades ecosystems by improving water delivery into estuaries within ENP will change salinities and water levels which in turn will affect relative density of crocodiles. Monitoring ecological responses of indicator species, such as crocodiles, with respect to hydrologic change is necessary to evaluate ecosystem responses to restoration projects. Our objectives were to monitor trends in crocodile relative density within ENP and to determine influences of salinity on relative density of crocodiles. We examined count data from 12 years of crocodile spotlight surveys in ENP (2004–2015) and used a hierarchical model of relative density that estimated relative density with probability of detection. The mean predicted value for relative density (λ) across all surveys was 2.9 individuals/km (95% CI: 2.0–4.2); relative density was estimated to decrease with increases in salinity. Routes in ENP's Flamingo/Cape Sable area had greater crocodile relative density than routes in the West Lake/Cuthbert Lake area and Northeast Florida Bay areas. These results are consistent with the hypothesis that restored flow and lower salinities will result in an increase in crocodile population size and provide support for the ecosystem management recommendations for crocodiles, which currently are to restore more natural patterns of freshwater flow to Florida Bay. Thus, monitoring relative density of American crocodiles will continue to be an effective indicator of ecological response to ecosystem restoration.

1. Introduction

The status of the American crocodile (*Crocodylus acutus*) has long been a matter of concern in Everglades National Park (ENP) and adjacent habitats due to its federal and state classification as a listed species and its recognition as a flagship species and ecosystem indicator (Ogden, 1978; Mazzotti, 1983, 1999; Mazzotti et al., 2007a,b, 2009). American crocodiles are indicators of regional hydrological conditions, especially freshwater flow to estuaries, which affect water levels, salinities, and prey availability (Mazzotti, 1983, 1989, 1999; Mazzotti et al., 2007a, 2009). Crocodilian population parameters most susceptible to changing hydrologic conditions are nesting effort and success, growth, survival, distribution, relative density, and body condition (Mazzotti et al., 2007a,b). Monitoring of these population parameters in southern Florida has been ongoing since crocodiles were identified as endangered in 1975. Results of long-term research and monitoring of these specific parameters have shaped species and land management decisions throughout southern Florida, provided the primary scientific

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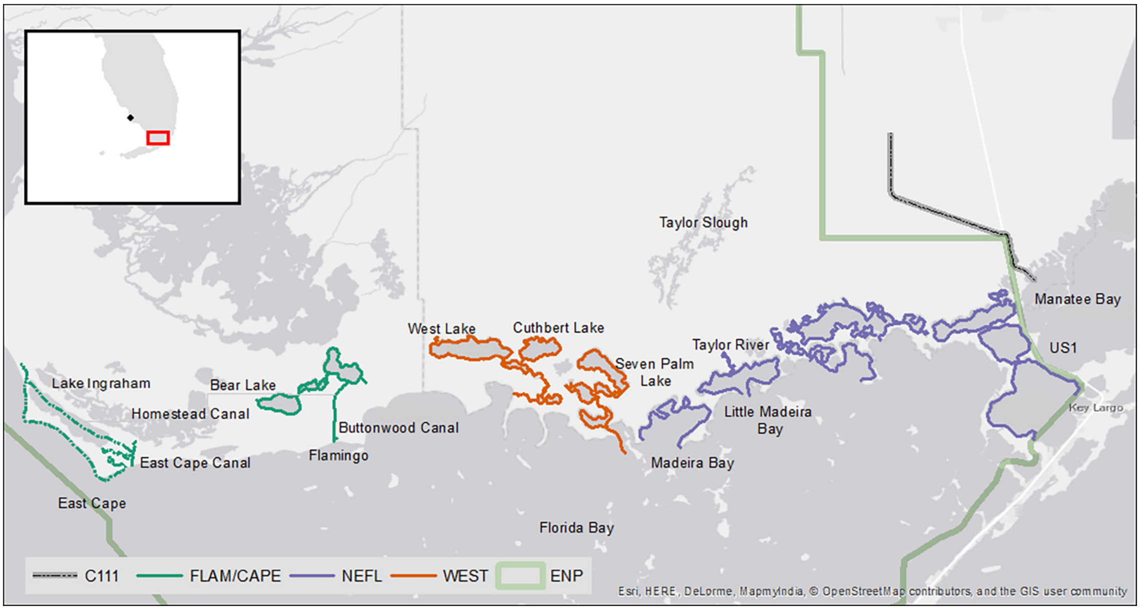

Fig. 1. This study examined count data of American crocodiles (*Crocodylus acutus*) within Everglades National Park (ENP), outlined in light green. ENP was subdivided into three main areas, each represented with a different color: Cape Sable to Flamingo and associated lakes (FLAM/CAPE), the middle lakes and creeks from West Lake to Seven Palm Lake (WEST), and Northeast Florida Bay (NEFB) from Madeira Bay to US1 on the eastern boundary of ENP. Survey routes not included in study are represented by a dashed line. Man-made canals of importance to *C. acutus* population include East Cape Canal, Homestead Canal, Buttonwood Canal, and C-111. Inset depicts location of study site within Florida (red box), point within subset identifies location of Rookery Bay.

evidence to support the 2007 reclassification of the American crocodile from endangered to threatened (United States Fish and Wildlife Service, 2007), and were used to establish the American crocodile as an indicator species for restoration of Everglades ecosystems (Mazzotti et al., 2009).

Efforts to restore more natural water flows in Everglades ecosystems have resulted in the most ambitious and expensive ecosystem restoration ever undertaken (Sklar et al., 2001). Use of improved, alternative water delivery methods into southern estuaries within ENP and ultimately Florida Bay may change resulting salinities, water levels, and water quality in receiving water bodies (see USACE and SFWMD, 2011, for example). Monitoring ecological response of indicator species with respect to hydrologic change is necessary to reduce uncertainty, improve models, and evaluate responses to restoration projects.

A system-wide monitoring and assessment plan (MAP), a component of Comprehensive Everglades Restoration Plan (CERP), has been developed to describe the monitoring necessary to track ecological responses to Everglades restoration (USACE, 2009). The MAP includes conceptual ecological models for how hydrologic indicators are linked to ecosystem restoration. The specific MAP hypothesis for crocodiles is that restoration of freshwater flows to and salinity regimes in southern coastal estuaries will improve their growth and survival (Mazzotti et al., 2009) and result in increases in relative density and body condition of crocodiles (Mazzotti et al., 2007a). Diverted freshwater flow and salinity patterns in northeast Florida Bay (NEFB) are currently the target of restoration (USACE and SFWMD, 2011).

Based on laboratory and field studies (Mazzotti, 1983, 1999; Mazzotti et al., 1986; Mazzotti et al., 2007a) stated that ecosystem restoration goals for crocodiles in NEFB should be to restore Taylor Slough as a main source of freshwater for NEFB and, specifically, to restore early dry season flow (October to January) from Taylor Slough to NEFB. Measurable objectives of success would be a fluctuating mangrove backcountry salinity that rarely exceeds 20 ppt, accompanied by an increase in relative density of crocodiles in areas of restored freshwater flow.

Relative density (crocodiles/km) estimated during nocturnal spotlight surveys is an established method for monitoring populations of crocodilians (Webb and Messel, 1979; Bayliss, 1987; Hutton and Woolhouse, 1989; Lentic and Connors, 2006). Long-term monitoring data using systematic surveys conducted throughout the landscape are potentially useful to describe spatial and temporal patterns of relative density of crocodilians (Fujisaki et al., 2011; Waddle et al., 2015). One limitation of spotlight survey data is the effect of variation in detection probabilities caused by uncontrollable factors, such as environmental conditions and observer differences. Water depth is a critical factor for monitoring as it affects movement patterns of crocodilians, and thus encounter rate during surveys (Woodward and Marion, 1978; Montague, 1983; Wood et al., 1985). Habitat type and vegetation density, both of which affect visibility, are also known to influence detection probability of crocodilians (Bayliss et al., 1986; Cherkiss et al., 2006). However, a two-stage hierarchical model has been developed to estimate both detection and changes in an animal's relative density from imperfectly observed data (Royle, 2004; Kéry and Royle, 2016).

Our purpose was to evaluate the expected outcome of restoring freshwater flow to Florida Bay on relative density of American crocodiles by using count data from 12 years (2004–2015) of crocodile spotlight surveys in ENP. Our objectives were to describe spatial and temporal patterns in crocodile relative density within ENP and to ascertain the relationship between salinity and relative density of crocodiles. We predicted that crocodile populations would have higher relative density with salinities less than the recommended restoration target of 20 ppt and that relative density would be lower in areas of higher salinity. Based on previous observations (Cherkiss et al., 2006), we predicted that habitat would affect detectability of crocodiles.

2. Materials and methods

2.1. Study area

The study was conducted at the southern tip of mainland Florida and included portions of Florida Bay, a shallow estuarine lagoon with an average depth of less than one meter (ranging in depth from emergent mud banks to greater than 2.5 m in depth) and total area of

2200 km^2, with 1800 km^2 within ENP (Rudnick et al., 2005). We subdivided ENP into three main areas: NEFB from US1 to Madeira Bay, West Lake to Seven Palm Lake (WEST), and Flamingo/Cape Sable (FLAM/CAPE) (Fig. 1). Survey routes included in the analyses for this study are from US1 to Bear Lake.

Coastal ENP has very low relief with exposed shorelines, creeks, ponds, small bays, and a few man-made canals and ditches draining into Florida Bay (Mazzotti, 1983, 1999). Exposed shorelines of Florida Bay front directly on the bay, affected by wind and wave action. The dominant vegetation on the shorelines is a mosaic of hardwood and buttonwood hammock and mangrove swamp (Olmstead et al., 1981; Mazzotti, 1983). The interior protected habitats include coves, ponds, and creeks that are located landward of the exposed shoreline and not exposed directly to effects of wind and wave action. The vegetation in these locations is primarily red and black mangrove (*Rhizophora mangle* and *Avicennia germinans*) with buttonwood (*Conocarpus erectus*), and hardwood hammocks habitats (Olmstead et al., 1981; Mazzotti, 1983). Marl banks that line creeks, canals, and sand beaches on mainland and island shorelines are important nesting habitat for crocodiles (Mazzotti, 1999).

The man-made canals and ditches mentioned above were dredged in FLAM/CAPE during the 1920s and 1930s and extended through a marl ridge from the coastline into the freshwater interior for navigation and to drain the area for agriculture and cattle grazing. These canals triggered substantial changes, altering salinity, deposition of sediments, and erosion patterns over the entire area, leading to several iterations of plugging man-made canals to reduce salt water intrusion (Mazzotti et al., 2007a), starting in 1986 and most recently in 2011.

2.2. *Spotlight surveys*

Nocturnal spotlight surveys were conducted by boat along canals, shorelines, coves, ponds, and creeks within the study area between February 2004 and December 2015. Surveys followed 22 distinct routes, each approximately 10 km in length. Surveys were performed quarterly following the calendar year (January - March, quarter 1; April-June, quarter 2; July-September, quarter 3; and October - December, quarter 4) from 2004 to 2009. Due to budget reductions, surveys were reduced to three times a year and performed during quarters 1, 2 and 4 in 2010 and 2011, and further reduced to quarters 1 and 4 in 2012 through 2015.

We used small 15–17 ft (~5 m) center console open fishing skiffs powered by 50–90 hp motors where possible and a smaller 10 ft (3 m) portable boat with 4–6 hp motor in shallow backcountry waters where access was limited to smaller vessels. We maintained a distance of 50–100 m offshore and a speed of 25–40 km/h in the center console skiffs when conditions permitted. Shallow water or obstructions such as rock or snags affected both survey speed and distance from shoreline. When surveying creeks and canals, we attempted to maintain a centerline route. Surveys were conducted only during the absence of environmental conditions such as full moon and high winds (> 25 km/h), which negatively affect detectability (Woodward and Marion, 1978). A 200,000 candle power quartz beam powered by a 12 V battery was used for illumination. Crocodiles were located by the reflective layer in their eyes (*tapetum lucidum*), which when illuminated produces a red, orange, or yellow "eyeshine." All eyeshines were approached as closely as possible to determine if it was a crocodile or an American alligator (*Alligator mississippiensis*), which are present in the study site. All non-hatchling crocodiles observed within 150 m of the center survey line were counted. Hatchling crocodiles were excluded from the analysis to avoid inflating the counts of crocodiles (Waddle et al., 2015). When crocodiles were observed, we recorded date, location (measured by global positioning system, GPS), water salinity (measured with an optical refractometer on a scale of 0–100 ppt), air and water temperatures (measured with a Taylor precision instant read dial thermometer), and habitat. Habitat was categorized as exposed shoreline, creek, cove, pond, or man-made canals (Mazzotti, 1983; Mazzotti, 1999). While we collected air temperature, water temperature, and salinity at each crocodile observation, our analysis required us to have these covariates along the entire survey route for every survey (see model details in Section 2.4 below), and we did not collect these data by hand. Therefore, we obtained existing environmental data from fixed monitoring stations in ENP and used spatial interpolation to obtain covariates across the entire study area.

2.3. *Environmental data*

Air temperature data were obtained from the EPA CASTNET station in ENP, which records data hourly (USEPA, 2017). The hourly temperatures were averaged from sunset over the next six hours (period of time in which surveys were normally performed) to obtain a mean survey air temperature.

Water temperature data were obtained from U.S. Geological Survey (USGS), ENP, and Audubon Florida, which all have fixed stations deployed throughout Florida Bay recording data daily. We used ordinary kriging to estimate water temperature for each segment of each survey route, on the day the survey was performed. We used data from a total of 51 stations for this interpolation. Kriging was done using functions from the R package "geoR" (Ribeiro and Diggle, 2001). We used maximum likelihood to fit the theoretical variogram using the function "likfit()" and then kriged the values for the segments using the function "krige.conv()". We used the kriged water temperature for each survey day as the model covariate.

Moon phase data were obtained from the U.S. Naval Observatory. Moon phase was expressed as a proportion of the lunar cycle, with 0 being the day after the full moon and 1 being the day of the following full moon, then converted to radians (θ) by multiplying by 2π. We used $\sin(\theta)$, $\cos(\theta)$, $\sin(2\theta)$, and $\cos(2\theta)$ as candidate model covariates, as suggested by deBruyn and Meeuwigg (2001) and Penteriani et al. (2011).

The habitat along each route was classified as either (1) Canal, (2) Cove, (3) Pond, or (4) Creek/River. Canals are human-made water passages with depth > 2 m. Coves are small, sheltered areas with depth < 1 m, open on at least one side. Ponds are small bodies of still water completely surrounded by land or vegetation and can be formed naturally or human-made. Creeks/rivers are sheltered natural waterways open on two sides, such as an inlet in a shoreline. Segment habitats were defined as the habitat with the greatest percentage along each segment, and since no route segments were dominated by Pond, that habitat classification dropped out before analysis.

Salinity data were obtained from the same monitoring stations as water temperature (USGS, Everglades National Park, and Audubon Florida; see above) and were interpolated using ordinary kriging, following the same procedure used for interpolating water temperature. Two additional monitoring stations had available salinity data, giving us a total of 53 stations from which to interpolate the salinity surface. We estimated salinity for each segment of each route on the day the survey was performed, and then we averaged those estimated salinities across all the surveys in that year to use as a model covariate.

The entire dataset contained a total of seven possible covariates: air temperature, water temperature, moon phase, survey route, habitat, salinity, and year. We calculated summary statistics for each of the continuous covariates (mean, SD, range) and the categorical covariates (mode and number of samples, n). The survey routes are shown in Fig. 1 and their codes are displayed in Fig. 5. Data are available upon request.

2.4. *Data analysis*

We used an N-mixture model to account for imperfect detection (Royle, 2004), which is a hierarchical model simultaneously estimating detection probability (p) and relative density (λ). The original formulation of this model assumed populations were closed (*i.e.*, that there were no births, deaths, immigration, or emigration). Subsequent extensions by Kéry et al. (2009) and Dail and Madsen (2011) relaxed this assumption by modeling the population growth rate, possibly as a Markovian process where the current population size was a function of the population size in the previous time step (where the time step of interest was often a year). In our approach, we assumed that λ was constant within a survey segment within a year, but we allowed λ to vary as a linear function of year, thus estimating a general trend and relaxing our assumption of population closure.

This type of hierarchical model requires extra information provided by both spatial and temporal replication to estimate detection probability and relative density. Survey routes were divided into 1.0 km segments, providing the spatial replication necessary to estimate relative density across the landscape. Segment size is a trade-off between replication and independence, and previous implementations of the N-mixture model for alligators have used 500 m segments (Fujisaki et al., 2011). Our decision to increase the size of our segments to 1.0 km was thus a conservative approach with respect to independence of counts. Surveys within the same year were treated as repeated visits to each segment, providing the temporal replication necessary to estimate detectability. Because each survey route segment was approximately 1.0 km in length, we interpreted λ as individuals/km. After dividing the survey routes into segments, we had a total of 251 segments along the 22 survey routes (all survey routes had at least one partial segment at the beginning or end).

We fit all models using the statistical platform R (R Core Team, 2016). We fit the N-mixture model using the function "pcount()" from the package "unmarked" (Fiske and Chandler, 2011). We first fit a full model, where p was modelled as a linear combination of air temperature, water temperature, and all four moon phase transformations; and where λ was modelled as a linear combination of survey route, habitat type, salinity, and year (see Table 1). We scaled and centered all the continuous variables except moon phase to improve model fitting by subtracting the mean from each measured value and then dividing by the standard deviation (Kéry and Royle, 2016). Survey route was included to account for spatial autocorrelation within each route.

The canonical N-mixture model typically uses a Poisson distribution to describe relative density; however, this statistical distribution has a variance equal to its mean, which is not always appropriate, as the data may be under-dispersed or over-dispersed. Generalizations of the Poisson distribution, the Zero-Inflated Poisson (ZIP), and Negative Binomial (NB) allow for over-dispersion (Kéry and Royle, 2016). To choose the appropriate variance structure, we fit the full model using each of those three distributions to describe relative density, and then evaluated the models using AIC scores.

After choosing the most appropriate variance structure, we then grew the model set using the chosen statistical distribution. We used backward selection, as suggested by Kéry and Royle (2016), removing variables with large p-values and then evaluating the model set using AIC. We iterated this process to obtain a top model, and then we re-evaluated the top model by including habitat type as a detection covariate. We did this to evaluate whether the model better fit our data if we considered habitat as affecting detection rather than relative density, and we note that the model would be unidentifiable if we tried to estimate the independent effect of habitat on *both* detection and relative density without another source of information (*e.g.*, telemetry). Lastly, we drew inference from the final top model. We also calculated R^2 for each model in the set using the method of Nagelkerke (1991), implemented by the function "modSel()" from the R package "unmarked" (Fiske and Chandler, 2011).

3. Results

The dataset consisted of 8497 survey records, which included 2928 segment years with 2–4 temporal replicates each. We observed 1449 crocodiles during the study. The summaries of the continuous model covariates were: mean air temperature = 20.9 °C (SD = 3.9, range = 7.6–28.2 °C), mean water temperature = 25.4 °C (SD = 4.0, range = 14.1–32.8 °C), mean moon phase = 3.0 rad (between last quarter and new moon; range = 0–2π radians), and mean salinity = 20.5 ppt (SD = 9.1, range = 0.8–47.0 ppt). The mode of route was Joe Bay (n = 504), and the mode of habitat was "Cove" (n = 2815).

We checked for collinearity among our continuous variables before proceeding. We found very low correlation ($r < 0.15$) between the predictors except between air temperature and water temperature ($r = 0.83$). We hypothesized *a priori* that both air and water temperature would affect crocodile detectability, so we followed the advice of Morrissey and Ruxton (2018) and kept both variables in our model.

To build our candidate model set, we chose the NB error structure over the Poisson or the ZIP. The full NB model strongly outperformed the ZIP (Δ AIC = 284.3) and the Poisson (Δ AIC = 416.6; Table 2).

Our top model from our full model set showed that detection varied as a function of air temperature, water temperature, and a sine transformation of moon phase; and relative density varied as a function of route, habitat, salinity, and year (the full model). The second best model (Δ AIC = 1.6) additionally included a cosine transformation of moon phase as a covariate for detection, and the third best model (Δ AIC = 2.3) additionally included the sine and cosine transformations of 2 × moon phase (*i.e.*, the full model). Together, these three models (differing only by included transformations of moon phase) received 82% of the model weight. The top seven models all contain the full variable set for λ and cumulatively receive 98% of the model weight, indicating strong support for all covariates of relative density. The top model had $R^2 = 0.30$ (Table 3).

The top model showed detection probability averaged across all surveys was 0.061 (95% CI: 0.050–0.073). Detectability increased with air temperature, decreased with water temperature, was highest during the moon's first quarter, and was lowest during the moon's last quarter (Fig. 2).

The mean predicted value for relative density across all surveys was 2.9 individuals/km (95% CI: 2.0–4.2). Relative density was estimated to decrease with increasing salinity, although average relative densities also varied across all habitat types and survey routes (Fig. 3). We found

Table 1
Covariates used to build N-mixture model set, simultaneously estimating detection probability (p) and relative density (λ; crocodiles/km) for American crocodiles in Everglades National Park, Florida. Variable names and their associated units are included, as well as variable type (continuous or categorical), use in modeling detection or relative density, and the data source. C = Celsius, ppt = parts per thousand, N/A = not applicable.

Variable (units)	Type	Detection(p)/Relative density(λ)	Source
Air Temperature (°C)	Continuous	p	EPA CASTNET
Water Temperature (°C)	Continuous	p	USGS, NPS, Audubon
Moon Phase (radians)	Continuous (circular)	p	US Naval Observatory
Route (N/A)	Categorical	λ	N/A
Habitat (N/A)	Categorical	λ	This study
Salinity (ppt)	Continuous	λ	USGS, NPS, Audubon
Year (N/A)	Continuous	λ	N/A

Table 2

AIC table comparing full models for estimating detection probability and relative density for American crocodiles in Everglades National Park (2004–2015) assuming Poisson (Pois), Zero-Inflated Poisson (ZIP), and Negative Binomial (NB) variance structure. We selected the Negative Binomial model with which to build our full model set for inference.

Model	-LogLike	Parameters	AIC	Δ AIC	AIC Weight
Full NB	3168.9	34	6405.8	0.0	1
Full ZIP	3312.0	33	6690.0	284.3	0
Full Pois	3378.2	33	6822.3	416.6	0

support for a negative trend over time in relative density (Fig. 4). Finally, we found support for variability in relative density among routes (Fig. 5). Routes in FLAM/CAPE had greater relative density than routes in WEST and NEFB.

4. Discussion

As predicted, relative density of American crocodiles in ENP decreased as salinity increased in all habitats (Fig. 3). We found greater relative density along routes in FLAM/CAPE (Fig. 5). This is consistent with the increase in nesting that has occurred in the area (Mazzotti et al., 2007b), which we attributed to a simple restoration effort of plugging canals and ditches in the area (Mazzotti et al., 2007a). Plugging of canals reduced saltwater intrusion and freshwater runoff, and we previously hypothesized that this would lead to a lower salinity regime in FLAM/CAPE that concomitantly increased growth and survival of crocodiles and resulted in more crocodiles in the population (Mazzotti et al., 2007a, 2009). We attribute the relatively higher density of crocodiles in Buttonwood Canal, one of the routes in FLAM/CAPE, to the apparent proclivity of American crocodiles to occupy habitats consisting of permanent artificial deep bodies of water interspersed in more natural habitat (Brandt et al., 1995; Mazzotti et al., 2007a; Thorbjarnarson, 2010).

The lowest relative density of crocodiles occurred along survey routes in NEFB and WEST (Fig. 5). These areas suffer from diversion of freshwater that should flow into Florida Bay through Taylor Slough but is instead conveyed to Manatee Bay via C-111 Canal (McIvor et al., 1994; Rudnick et al., 2005). We predict that if the C-111 Spreader Canal Western Project is successful, water flow into Taylor Slough should be at least partially restored, resulting in lower salinities in NEFB (USACE and SFWMD, 2011) and an increase in relative density of crocodiles (Mazzotti, 2009).

Our top model explains 30% of the variation in relative density of crocodiles, so we can infer that factors other than route and salinity affect relative density. For example, Rosenblatt and Heithaus (2011) found that alligators moved to access higher prey abundance in full-strength seawater at the expense of exposure, and Evert (1999) found that relative density of alligators in Florida lakes was related to nutrient levels. Relating occurrence of crocodiles to distribution and relative density of prey items should improve our understanding of how crocodiles will respond to ecosystem restoration. We might also expect that crocodile relative density would be affected by other factors, such as social interactions and access to nesting habitat. For example, Mazzotti (1983) found that most sightings of crocodiles in higher salinities were females at nest sites. Our opinion is that explaining 30% of the variation in relative density of crocodiles with just environmental covariates is actually quite informative. Furthermore, we reiterate that our goal was to demonstrate the response of crocodile relative density to changes in salinity and not to fully explain the drivers of relative density of crocodiles in Florida.

We found support for a negative trend in relative density of crocodiles over time (Fig. 4), in contrast to Mazzotti et al. (2016) who found that relative density of crocodiles in ENP increased during 2004–2012. We recognize two factors that could contribute to this disparity. First, Mazzotti et al. (2016) did not take into consideration imperfect detection and used uncorrected estimates of relative density rather than a corrected estimate. However, estimates of probability of detection in this study were uniformly low and not affected by habitat or route, so this is not likely to have been a major driver of the difference. Second, Mazzotti et al. (2016) included East Cape Canal and Lake Ingraham in their analysis. East Cape Canal is a permanent artificial body of water

Table 3

AIC table for complete Negative Binomial model set for estimating detection probability and relative density for American crocodiles in Everglades National Park (2004–2015). R^2 was calculated using the method of Nagelkerke (1991). The full model for detection was p(airt, wt, sinM, cosM, sin2M, cos2M) and the full model for relative density was λ (route, hab, sal, yr). Covariate abbreviations are: airt = air temperature, wt = water temperature, sinM = sin(moon phase), cosM = cos(moon phase), sin2M = sin(2 × moon phase), cos2M = cos(2 × moon phase), route = survey route, hab = habitat type, sal = salinity, yr = year.

Model	-LogLike	Parameters	AIC	Δ AIC	AIC Weight	R^2	Cumulative Weight
p(airt, wt, sinM) λ (full)	3170.7	31	6403.5	0.0	0.5	0.30	0.46
p(airt, wt, sinM, cosM) λ (full)	3170.5	32	6405.1	1.6	0.2	0.30	0.67
p(full) λ (full)	3168.9	34	6405.8	2.3	0.1	0.30	0.82
p(airt, wt) λ (full)	3173.9	30	6407.9	4.4	0.1	0.30	0.87
p(wt) λ (full)	3175.1	29	6408.2	4.7	0.0	0.30	0.92
p(airt, wt, cosM) λ (full)	3173.3	31	6408.7	5.2	0.0	0.30	0.95
p(airt, wt, sin2M, cos2M) λ (full)	3172.4	32	6408.9	5.4	0.0	0.30	0.98
p(airt, wt, sinM, cosM) λ (route, hab, sal)	3174.9	31	6411.8	8.3	0.0	0.30	0.99
p(airt, wt) λ (route, sal, yr)	3178.1	28	6412.3	8.8	0.0	0.30	1.00
p(airt, wt) λ (route, hab, yr)	3178.2	29	6414.3	10.8	0.0	0.30	1.00
p(airt, wt) lambda(route, hab, sal)	3178.8	29	6415.6	12.1	0.0	0.30	1.00
p(airt, wt) lambda(hab, sal2)	3470.0	9	6957.9	554.5	0.0	0.12	1.00
p(full) lambda(hab, sal, yr)	3466.8	13	6959.5	556.0	0.0	0.12	1.00
p(airt, wt) lambda(hab, sal, yr)	3471.0	9	6960.1	556.6	0.0	0.12	1.00
p(airt, wt, cos2Moon) lambda(hab, sal)	3471.2	9	6960.3	556.8	0.0	0.12	1.00
p(airt, wt, sinMoon) lambda(hab, sal)	3471.9	9	6961.9	558.4	0.0	0.12	1.00
p(airt, wt) lambda(hab, sal)	3473.5	8	6963.1	559.6	0.0	0.12	1.00
p(airt, wt, cosMoon) lambda(hab, sal)	3473.0	9	6964.0	560.5	0.0	0.12	1.00
p(airt, wt, sin2Moon) lambda(hab, sal)	3473.2	9	6964.3	560.8	0.0	0.12	1.00
p(airt, wt) lambda(hab)	3476.2	7	6966.4	562.9	0.0	0.12	1.00
p(airt, wt) lambda(sal)	3616.0	6	7244.1	840.6	0.0	0.02	1.00
p(airt, wt) lambda(.)	3622.4	5	7254.8	851.3	0.0	0.02	1.00
p(wt) lambda(.)	3624.8	4	7257.7	854.2	0.0	0.01	1.00
p(airt) lambda(.)	3636.1	4	7280.2	876.7	0.0	0.01	1.00
p(.) lambda(.)	3644.1	3	7294.1	890.6	0.0	0.00	1.00

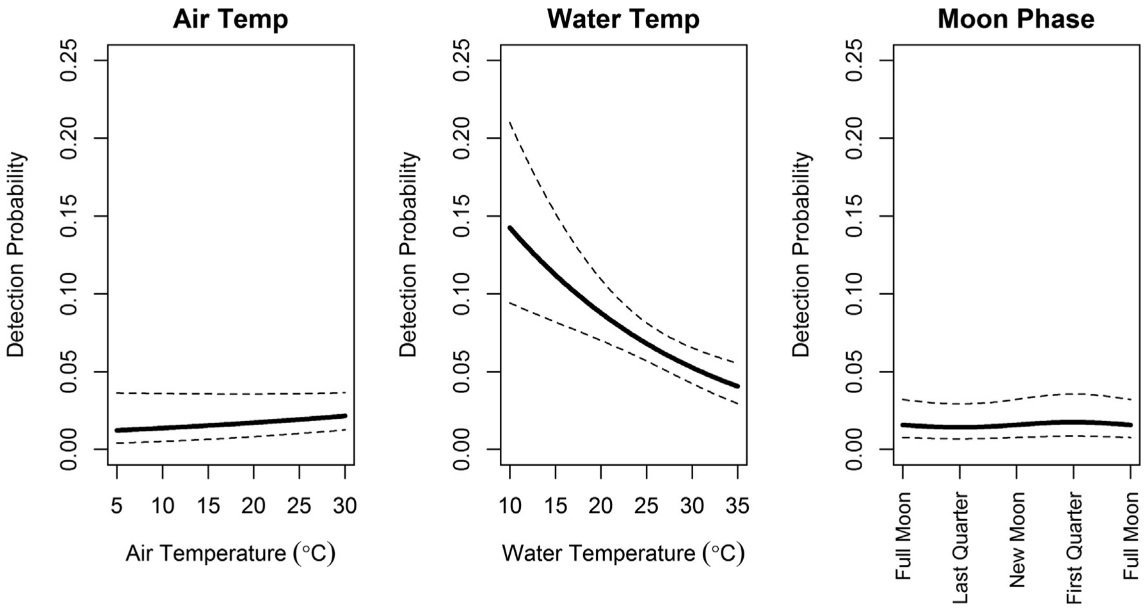

Fig. 2. Our top model indicated that detectability of crocodiles in Everglades National Park (2004–2015) increased with air temperature, decreased with water temperature, and varied throughout the lunar cycle. Envelopes show 95% confidence intervals. The other two covariates in each figure were held at a constant value for model predictions; air and water temperature were held constant at their mean and moon phase was held constant at $3\pi/2$ rad (*i.e.*, first quarter).

that was plugged, similar to Buttonwood Canal. East Cape Canal is also where most of the nesting increase in ENP has occurred (Mazzotti et al., 2007b). If East Cape Canal had been included, this may have changed the overall trend in relative density found in this study. We did not include East Cape Canalbecause those routes were on the edge of coverage by the salinity stations and we were concerned about boundary effect on our kriging analysis. The negative trend in relative density suggests that changes in relative density due to salinity are best thought of as occurring because of animal movement, not a change in the population size.

Estimates of relative density for the American crocodile vary across its range, as well as in adjacent Biscayne National Park, from 0.02 to 8 crocodiles/km (Seijas, 1988; Thorbjarnarson, 1988; King et al., 1990; Platt and Thorbjarnarson, 2000; Cherkiss et al., 2009). The ENP

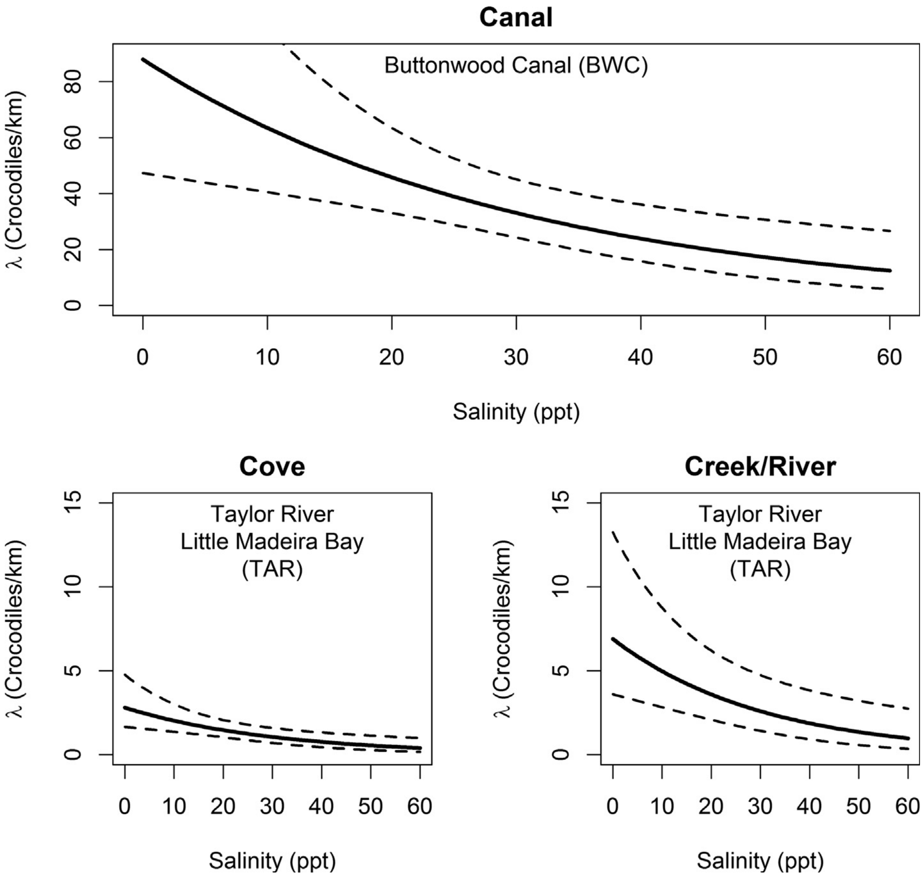

Fig. 3. Our top model indicated that relative density of crocodiles in Everglades National Park (2004–2015) decreased with salinity in all three habitat types. The survey route was held constant as “Taylor River Little Madeira Bay” for the two natural habitat types and held constant as “Buttonwood Canal” for the canal habitat type. Note the differing y-axis values between the canal habitat type and the natural habitat types. Dashed lines show 95% confidence intervals.

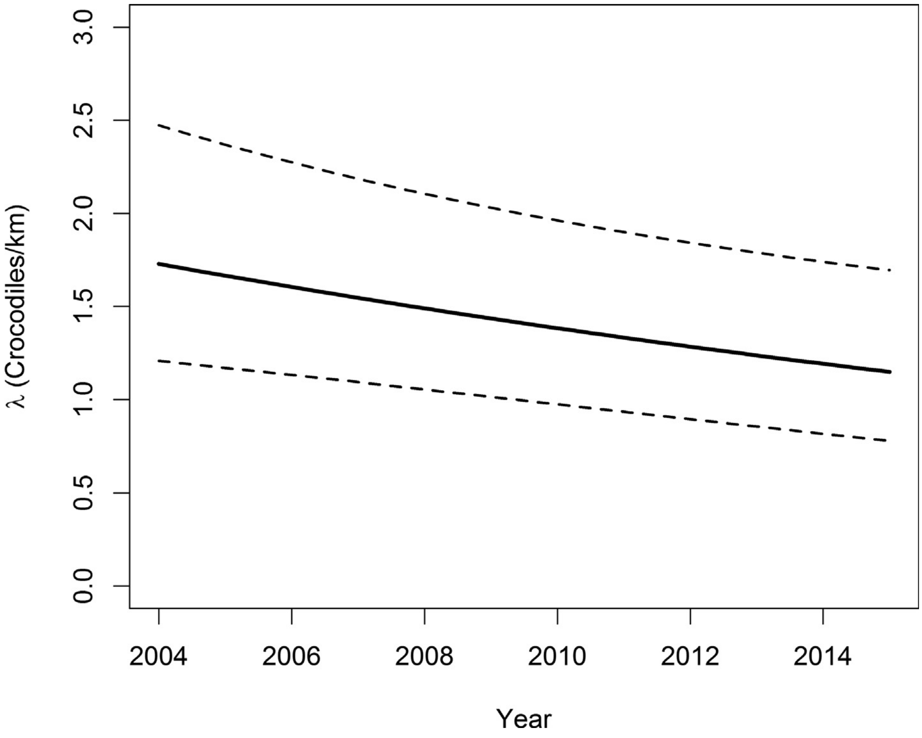

Fig. 4. Our top model indicated that relative density of crocodiles in Everglades National Park (2004–2015) has decreased over time. For this model prediction, salinity was held constant at its mean (20.5 ppt), habitat was held constant at its mode (the cove habitat type), and route was held constant as "Taylor River Little Madeira Bay." Dashed lines are 95% confidence intervals.

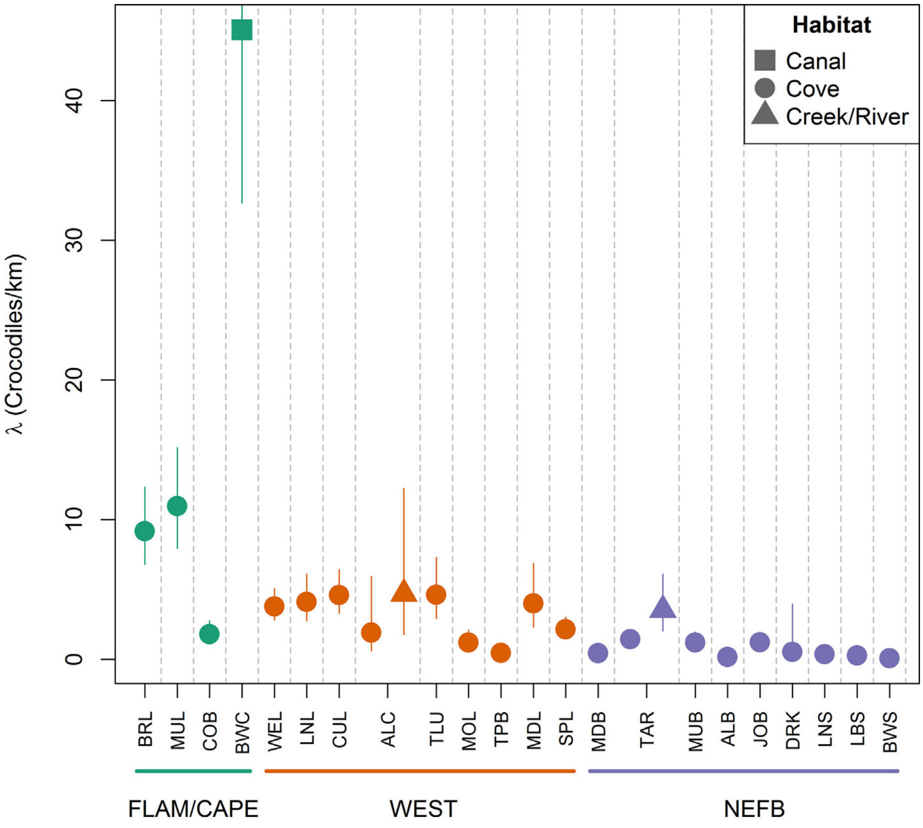

Fig. 5. Our top model of American crocodile relative density in Everglades National Park (2004–2015) indicated significant variation among survey routes. Survey routes include those in the Flamingo/Cape Sable area (FLAM/CAPE): Bear Lake (BRL), Mud Lake (MUL), Coot Bay (COB), Buttonwood Canal (BWC); the middle lakes and creeks (WEST): West Lake (WEL), Long Lake (LNL), Cuthbert Lake (CUL), Alligator Creek (ALC), the Lungs (TLU), Monroe Lake (MOL), Terrapin Bay (TPB), Middle Lake (MDL), Seven Palm Lake (SPL); and those in Northeast Florida Bay (NEFB): Madeira Bay (MDB), Taylor River (TAR), Mud Bay (MUB), Alligator Bay (ALB), Joe Bay (JOB), Deer Key (DRK), Long Sound (LNS), Little Blackwater Sound (LBS), and Blackwater Sound (BWS). Predicted values for each survey route are shown, with habitat-type color coded. Only habitats that occur along each particular survey route are shown. Salinity was held constant at its observed mean (20.5 ppt) and year was held constant at 2009 (approximate midpoint of our study period). Bars represent 95% confidence interval of the model prediction. Extreme uncertainty in upper limit for canal habitats not shown.

crocodile population relative density estimate of 2.9 crocodiles/km is in the middle of this range of estimates. We caution against directly comparing relative densities of crocodiles in different geographic locations, as different measurement and analysis techniques may produce incongruous estimates. For example, we used an estimate of corrected relative density (*i.e.*, corrected for detection probability), whereas other authors (Seijas, 1988; Thorbjarnarson, 1988; King et al., 1990; Platt and Thorbjarnarson, 2000; Cherkiss et al., 2009) used uncorrected estimates of relative density. In addition, we have no estimate of the proportion of the population observed during spotlight surveys. Factors that affect the proportion of crocodiles observed during a spotlight survey include water levels, air and water temperatures, and inaccessibility of habitat (Hutton and Woolhouse, 1989; Sai et al., 2016). Hutton and Woolhouse (1989) found that the proportion of Nile crocodiles observed during surveys ranged from 10% to 63%.

Contrary to our prediction, probability of detection was not affected by habitat. We expected that the winding, narrow, overgrown nature of creek habitats would have a lower probability of detection than the more open and less obstructed habitat found along banks and shorelines of canals and coves. We were also surprised that probabilities of detection were uniformly low for all habitats and routes given that crocodile eyes shine like bicycle reflectors. Wariness of humans by crocodiles can affect detection of crocodiles (Webb and Messel, 1979; Ron et al., 1998). Perhaps American crocodiles are even more shy than previously thought. Alternatively, this low probability of detection could be attributed to unidentifiability in the model (*i.e.*, we have no way to distinguish between whether an observed effect of habitat is actually affecting detection or relative density). The high relative density of crocodiles estimated in Buttonwood Canal may be due to increased detectability. Furthermore, the high estimated density in Buttonwood Canal could be biasing the overall estimates of detectability. As we mentioned above, the model allowed relative density to vary with habitat, but not detection, as this model would be over-specified and unidentifiable. Therefore, the detection probability that we estimated can be thought of as an average detection probability across all habitat types (given the environmental covariates we did include in the model). The potential exists for Buttonwood Canal to have a different detection probability than the other routes, but this will have to be the subject of future investigation. We caution against placing too much faith in the very high estimates of relative density in the canal habitat, but we have confidence in the more reasonable estimates for the natural habitats that comprise the overwhelming majority of our dataset.

While we suspect that a route with much higher relative density of crocodiles could have biased our overall estimates of detection probability, it is worth pointing out that the converse can be true – low estimates of detection probability can cause a bias in relative density estimates, particularly when the number of sampling occasions is low (Dennis et al., 2015). Our dataset has many sampling occasions ($N = 2928$), but because of a very low estimate of detectability ($\hat{p} = 0.06$), it is possible that our estimates of relative density are biased. In the context of this study, we place more faith in our estimated relationship between density and salinity than we do on the absolute number of crocodiles encountered.

Probability of detection increased with air temperature, decreased with water temperature, and fluctuated with moon phase (Fig. 2). We expected that crocodiles would be more active and more detectable with warmer temperatures. In the case of air temperature, crocodilians tend to be more active, more detectable, and have a higher relative density with warmer temperatures (Hutton and Woolhouse, 1989; Lutterschmidt and Wasko, 2006). Interestingly, results with water temperature are mixed. Sometimes there is a positive relationship between water temperature and detectability and relative density (Hutton and Woolhouse, 1989), and sometimes the opposite is true (Waddle et al., 2015). It may be that crocodilians are not only more active but spend more time submerged at warmer water temperatures (Bugbee, 2008).

5. Summary and implications

Relative density of crocodiles increases as salinity decreases and crocodile relative density is currently greater in areas where ecosystem restoration activities have occurred. These results confirm the MAP hypothesis that restored freshwater flow and lower salinities will result in more crocodiles in restored areas; our results provide support for the ecosystem management recommendations for crocodiles (*i.e.*, to restore Taylor Slough as a main source of freshwater for NEFB; to restore early dry season flow (October to January) from Taylor Slough to NEFB). Measurable objectives of success would be a fluctuating mangrove backcountry salinity that rarely exceeds 20 ppt accompanied by an increase in relative density of crocodiles. Monitoring relative density of American crocodiles will continue to be an effective indicator of ecological response to ecosystem restoration.

This study emphasizes importance of long-term data sets when monitoring ecological responses on the spatial and temporal scales upon which ecosystem restoration occurs. Our ability to hypothesize that crocodiles would respond positively to ecosystem restoration efforts that restored more natural salinity patterns to Everglades estuaries and to inform specific restoration components was based on data collected starting in 1978. As restoration of freshwater flow to southern coastal systems continues to occur, we predict that relative density of American crocodiles will increase in areas where they occur now in apparent low relative density such as the west coast river system and Ten Thousand Islands between Cape Sable and Rookery Bay (Fig. 1). Initiating monitoring programs in those areas now will allow us to evaluate impacts of ecosystem restoration on American crocodiles in the future.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.03.002.

References

Bayliss, P., 1987. Survey methods and monitoring within crocodilian management programmes. In: Webb, G.J.W., Manolis, S.C., Whitehead, P.J. (Eds.), Wildlife Management: Crocodiles and Alligators. Surrey Beatty and Sons Pty Ltd., Chipping Norton Australia, pp. 157–175.

Bayliss, P., Webb, G.J.W., Whitehead, P.J., Dempsey, K., Smith, A., 1986. Estimating the abundance of saltwater crocodiles, *Crocodylus porosus*, Schneider, in tidal wetlands of the Northern Territory; a mark-recapture experiment to correct spotlight counts to absolute numbers, and the calibration of helicopter and spotlight counts. Australian Wildlife Res. 13 (2), 309–320. https://doi.org/10.1071/WR9860309.

Brandt, L.A., Mazzotti, F.J., Wilcox, J.R., Barker, P.D., Hasty, G.L., Wasilewski, J., 1995. Status of the American crocodile (*Crocodylus acutus*) at a power plant site in Florida, USA. Herpetol. Nat. History 3 (1), 29–36.

Bugbee, C.D., 2008. Emergence dynamics of American alligators (*Alligator mississippiensis*) in Arthur R. Marshall Loxahatchee National Wildlife Refuge: life history and application to statewide alligator surveys. M.S. Thesis. University of Florida.

Cherkiss, M.S., Mazzotti, F.J., Rice, K.G., 2006. Effects of shoreline vegetation on visibility of crocodiles during spotlight surveys. Herpetol. Rev. 37 (1), 37–40. https://pubs.er.usgs.gov/publication/70030225.

Cherkiss, M.S., Romanach, S.R., Mazzotti, F.J., 2009. The American Crocodile in Biscayne Bay, Florida. Estuaries Coasts. https://doi.org/10.1007/s12237-011-9378-6.

Dail, D., Madsen, L., 2011. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67, 577–587. https://doi.org/10.1111/j.1541-0420.2010.01465.x.

deBruyn, A., Meeuwigg, J., 2001. Detecting lunar cycles in marine ecology: periodic regression versus categorical ANOVA. Mar. Ecol. Progr. Ser. 214, 307–310. https://doi.org/10.3354/meps214307.

Dennis, E.B., Morgan, B.J.T., Ridout, M.S., 2015. Computational aspects of N-mixture models. Biometrics 71 (1), 237–246. https://doi.org/10.1111/biom.12246.

Evert, J.D., 1999. Relationships of alligator (Alligator mississippeinsis) population density to environmental factors in Florida lakes. M.S. Thesis. University of Florida, Gainesville, pp. 122.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Software 43. http://www.jstatsoft.org/v43/i10/.

Fujisaki, I., Mazzotti, F.J., Dorazio, R.M., Rice, K.G., Cherkiss, M.S., Jeffery, B., 2011. Estimating trends in alligator populations from nightlight survey data. Wetlands 31, 147–155. https://doi.org/10.1007/s13157-010-0120-0.

Hutton, J.M., Woolhouse, M.E.J., 1989. Mark-recapture to assess factors affecting the population of a Nile crocodile population seen during spotlight counts at Ngezi, Zimbabwe, and the use of spotlight counts to monitor crocodile abundance. J. Appl. Ecol. 26, 381–395. https://www.jstor.org/stable/2404068.

Kéry, M., Dorazio, R.M., Soldaat, L., Van Strien, A., Zuiderwijk, A., Royle, J.A., 2009. Trend estimation in populations with imperfect detection. J. Appl. Ecol. 46, 1163–1172. https://doi.org/10.1111/j.1365-2664.2009.01724.x.

Kéry, M., Royle, J.A., 2016. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS. Elsevier, Amsterdam.

King, F.W., Espinosal, M., Cerrato, C.A., 1990. Distribution and status of the crocodilians of Honduras. In: Crocodiles: Proceedings of the 10th Working Meeting of the Crocodile Specialist Group, 313–354. Gland: IUCN–The World Conservation Union.

Lentic, M., Connors, G., 2006. Changes in the distribution and abundance of saltwater crocodiles (*Crocodylus porosus*) in the upstream, freshwater reaches of rivers in the Northern Territory, Australia. Wildlife Res. 33, 529–538. https://doi.org/10.1071/WR05090.

Lutterschmidt, W.I., Wasko, D.K., 2006. Seasonal activity, relative abundance, and size-class structure of the American alligator (*Alligator mississippiensis*) in a highly disturbed inland lake. Southwestern Nat. 51 (3), 346–351. https://doi.org/10.1894/0038-4909(2006) 51[346:SARAAS]2.0.CO;2.

Mazzotti, F.J., 1983. The Ecology of Crocodylus acutus in Florida. Unpubl. Ph.D. diss. Pennsylvania State University, University Park.

Mazzotti, F.J., 1989. Factors affecting the nesting success of the American Crocodile, *Crocodylus acutus*, Florida Bay. Bull. Mar. Sci. 44 (1), 220–228.

Mazzotti, F.J., 1999. The American Crocodile in Florida Bay. Estuaries 22, 552–561. https://doi.org/10.2307/1353217.

Mazzotti, F.J., Bohnsack, B., McMahon, M.P., Wilcox, J.R., 1986. Field and laboratory observations on the effects of high temperature and salinity on hatchling Crocodylus acutus. Herpetologica 42 (2), 191–196.

Mazzotti, F.J., Brandt, L.A., Moler, P.E., Cherkiss, M.S., 2007a. American Crocodile (*Crocodylus acutus*) in Florida: recommendations for endangered species recovery and ecosystem restoration. J. Herpetol. 41, 121–131. https://www.jstor.org/stable/4498560.

Mazzotti, F.J., Cherkiss, M.S., Parry, M.W., Rice, K.G., 2007b. Recent nesting of the American crocodile (*Crocodylus acutus*) in Everglades National Park, Florida, USA. Herpetol. Rev. 38, 285–289. https://pubs.er.usgs.gov/publication/70030721.

Mazzotti, F.J., Best, G.R., Brandt, L.A., Cherkiss, M.S., Jeffery, B.M., Rice, K.G., 2009. Alligators and crocodiles as indicators for restoration of Everglades ecosystems. Ecol. Indicat. 9, 137–149. https://doi.org/10.1016/j.ecolind.2008.06.008.

Mazzotti, F.J., Cherkiss, M.S., Parry, M., Beauchamp, J., Rochford, M., Smith, B., Hart, K., Brandt, L.A., 2016. Large reptiles and cold temperatures: do extreme cold spells set distributional limits for tropical reptiles in Florida? Ecosphere 7 (8), e01439. https://doi.org/10.1002/ecs2.1439.

McIvor, C.C., Ley, J.A., Bjork, R.B., 1994. Changes in freshwater inflow from the Everglades to Florida Bay including effects on biota and biotic processes: a review. In: Davis, S.M., Ogden, J.C. (Eds.), Everglades: The Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, pp. 117–146.

Montague, J.J., 1983. Influence of water level, hunting pressure and habitat type on crocodile abundance in the Fly River Drainage, Papua New Guinea. Biol. Conserv. 26, 309–339. https://doi.org/10.1016/0006-3207(83)90095-2.

Morrissey, Michael B., Ruxton, Graeme D., 2018. Multiple regression is not multiple regressions: the meaning of multiple regression and the non-problem of collinearity. Philos. Theory Practice Biol. 10, 3. https://doi.org/10.3998/ptpbio.16039257.0010.003.

Nagelkerke, N.J.D., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691–692. https://doi.org/10.2307/2337038.

Ogden, J.C., 1978. Status and nesting biology of the American crocodile, Crocodylus acutus, (Reptilia, Crocodilidae) in Florida. J. Herpetol. 183–196.

Olmstead, I.C., Loope, L.L., Russell, R.P., 1981. Vegetation of the southern coastal region of Everglades National Park between Flamingo and Joe Bay. National Park Service, South Florida Research Center Report T-603.

Platt, S.G., Thorbjarnarson, J.B., 2000. Status and conservation of the American crocodile, *Crocodylus acutus*, in Belize. Biol. Conserv. 96, 13–20. https://doi.org/10.1016/S0006-3207(00)00038-0.

Penteriani, V., Kuparinen, A., Delgado, M. del M., Lourenço, R., Campioni, L., 2011. Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. Animal Behav. 82, 413–420. https://doi.org/10.1016/j.anbehav.2011.05.027.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org.

Ribeiro Jr., P., Diggle, P.J., 2001. geoR: A package for geostatistical analysis. R-News. 1, 15–18. http://cran.r-project.org/doc/Rnews/Rnews_2001-2.pdf.

Ron, S.R., Vallejo, A., Asanza, E., 1998. Human influence on the wariness of *Melanosuchus niger* and *Caiman crocodilus* in Cuyabeno, Ecuador. J. Herpetol. 32 (3), 320–324. https://www.jstor.org/stable/1565444.

Rosenblatt, A.E., Heithaus, M.R., 2011. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? J. Animal Ecol. 80 (4), 786–798. https://doi.org/10.1111/j.1365-2656.2011.01830.x.

Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60, 108–115. https://doi.org/10.1111/j.0006-341X.2004.00142.x.

Rudnick, D.T., Ortner, P.B., Browder, J.A., Davis, S.M., 2005. A conceptual ecological model of Florida Bay. Wetlands 25 (4), 870–883. https://doi.org/10.1672/0277-5212(2005) 025[0870:ACEMOF]2.0.CO;2.

Sai, M., Utete, B., Chinoitezvi, E., Moyo, G.H., Gandiwa, E., 2016. A survey of the abundance, population structure, and distribution of Nile crocodiles (*Crocodylus niloticus*) using day ground surveys in Sengwa Wildlife Research Area, Zimbabwe. Herpetol. Conserv. Biol. 11, 426–433.

Seijas, A.E., 1988. Habitat use by the American crocodile and the spectacled caiman coexisting along the Venezuelan coastal region. MSc thesis. University of Florida.

Sklar, F.H., Fitz, H.C., Wu, Y., Van Zee, R., McVoy, C., 2001. South Florida: the reality of change and the prospects for sustainability: the design of ecological landscape models for Everglades restoration. Ecol. Econ. 37 (3), 379–401.

Thorbjarnarson, J.B., 1988. The status and ecology of the American crocodile in Haiti. Bull. Florida State Museum Biol. Sci. 33, 1–86.

Thorbjarnarson, J.B., 2010. American crocodile Crocodylus acutus. Crocodiles: Status Survey and Conservation Action Plan, pp. 46–53.

USACE, 2009. CERP Comprehensive Monitoring and Assessment Plan. http://141.232.10.32/pm/recover/recover_map_2009.aspx.

USACE and SFWMD, 2011. Central and Southern Florida Project Comprehensive Everglades Restoration Plan C-111 Spreader Canal Western Project Final Integrated Project Implementation Report and Environmental Impact Statement. United States Army Corps of Engineers, Jacksonville, FL, and South Florida Water Management District, West Palm Beach, FL.

USEPA, 2017. Clean Air Status and Trends Network (CASTNET) (accessed 21 Sep 2017). www.epa.gov/castnet.

Waddle, J.H., Brandt, L.A., Jeffery, B.M., Mazzotti, F.J., 2015. Dry years decrease abundance of American alligators in the Florida Everglades. Wetlands 35 (5), 865–875. https://doi.org/10.1007/s13157-015-0677-8.

Webb, G.J.W., Messel, H., 1979. Wariness in *Crocodylus porpsus* (Reptilia: Crocodilidae). Australian Wildlife Res. 6, 227–234. https://doi.org/10.1071/WR9790227.

Wood, J.M., Woodward, A.R., Humphrey, S., Hines, T.C., 1985. Night counts as an index of American alligator population trends. Wildlife Soc. Bull. 13, 262–302. https://www.jstor.org/stable/3782490.

Woodward, A.R., Marion, W.R., 1978. An evaluation of factors affecting night-light counts of alligators. In: Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies, vol. 32, pp. 291–302.