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Shifts in hatching date of American crocodile (*Crocodylus acutus*) in southern Florida

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ABSTRACT

Globally temperature of marine environments is on the rise and temperature plays an important role in the life-history of reptiles. In this study, we examined the relationship between sea surface temperature and average date of hatching for American crocodiles (*Crocodylus acutus*) over a 37-year period at two nesting sites, Everglades National Park and Florida Power and Light Turkey Point Power Plant site in southern Florida. Our results indicate that hatch dates are shifting 1.5 days earlier every two years and at half that rate for the Turkey Point site, and with every 1 °C degree increase in temperature, hatching occurs about 10 days earlier in the Everglades and 6 days earlier at Turkey Point. Our results on shifting hatch dates for American crocodiles provide further details about the impacts of temperature change on crocodile life history and suggest that increased temperature may affect their phenology.

1. Introduction

Phenology is the study of seasonal biological processes and how climate and weather influence them. Warmer temperatures are often associated with earlier phenological events, and changes in phenology may indicate impacts of climate change on ecological communities (Asch, 2015). Evidence is growing that warming air and sea temperatures are affecting species' ranges and phenologies (Hughes, 2000), and understanding how protected species will respond is critical to prioritize vulnerable species to facilitate conservation and management (Williams et al., 2008). In response to recent changes in climate, studies have revealed earlier emergence and shifts in ranges of butterflies (Parmesan, 1999), earlier spawning in amphibians (Beebee, 1995) and shifts in earlier nesting patterns of oviparous species (Crick et al., 1997; Hughes, 2000; Solow et al., 2002; Walther et al., 2002; Weishampel et al., 2004; Pike et al., 2006; Schwanz and Janzen, 2008; Cadby et al., 2010; Lamont and Fujisaki, 2014).

Many aspects of crocodile reproduction are affected by environmental conditions including initiation of courtship, timing of nesting, nest temperature and length of incubation. Ecological studies have shown that a host of factors affect the timing of nesting in crocodilians, such as hormones, nutrition, water, temperature and photoperiod (Lance, 1987, 2003). There is a significant correlation of ambient air temperature with the timing of nesting (Joanen and McNease, 1989), importance of warmer water temperatures in triggering of spermatogenesis (Murphy, 1980) and during the incubation period, nest temperature plays a critical role in the rate of embryonic development, viability, body size and weight at hatching, abnormalities, and fitness and growth rates after hatching (Lance, 1987; Thorbjarnarson, 1989; Webb and Cooper-Preston, 1989; Janzen, 1994; Booth, 2006; Cadby et al., 2010; Parachu Marco et al., 2010). Further, nest temperature can be influenced by canopy cover, solar radiation, nest material, rainfall, nest depth and egg number and size (Charruau, 2012; Murray et al., 2016). However to date, studies on the effects of climate change on

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crocodilian biology have largely focused on the effect of temperature on sex determination, thermal regime of nests, duration of incubation period and size at hatching (Pina et al., 2003; Parachu Marco et al., 2010; Charruau, 2012; Elsey and Lang, 2014; Murray et al., 2016), but not on temperature's influence on date of hatching.

The American crocodile (*Crocodylus acutus*) is primarily a coastal crocodilian, occurring in Central and South America, the Caribbean, with the northern extent of its range in extreme southern mainland Florida and Florida Keys (Kushlan and Mazzotti, 1989; Thorbjarnarson, 1989; Mazzotti, 1999). Globally, it is classified by the International Union for Conservation of Nature as Vulnerable (Ponce-Campos et al., 2012), and by the U.S. Fish and Wildlife Service under the U.S. Endangered Species Act as Endangered range-wide except in Florida, where that distinct population segment is listed as Threatened (Federal Register 72: 13027 2007).

American crocodiles are typically found in freshwater or brackish coastal habitats (swamps, bays and creeks), characterized by low salinity, relatively deep water (>1m) and protection from wind and wave action. Kushlan and Mazzotti (1989) reported that in Florida, courtship was likely to occur in late January and into February, with nest preparation in March–May, egg laying at the very end of the dry season April–May, and hatching occurring during the wettest and hottest months of the year (July–August; Mazzotti, 1983). However, in recent years the onset of courtship and nest preparation have shifted earlier, with courtship activity being observed as early as late November (in 2018) and otherwise early to mid-December as the new normal at Flamingo in Everglades National Park (ENP; Mark Parry, National Park Service (ENP) 2019, personal communication) and nesting activity occurring mid-February in ENP (Seth Farris, University of Florida 2019, personal communication). The length of incubation is temperature-dependent (Mazzotti, 1983; Thorbjarnarson, 1989), with a reported incubation period in Florida averaging 90 days (Mazzotti, 1989).

In this study, we examined the relationship between sea surface temperature (SST) and average date of hatching over a 37-year period at two nesting sites, ENP and Florida Power and Light Turkey Point Power Plant (TP) in southern Florida, where hatching historically begins approximately two weeks earlier at TP than ENP. Water temperature during the summer months in Florida Bay average 10 °C lower than those at TP, where heated condenser cooling water is discharged into the system. We examined whether (1) sea surface temperatures have increased, (2) average hatch dates of the American crocodile have changed, and (3) changes in average hatch dates were correlated with changes in sea surface temperature. Our prediction was that hatch dates will be earlier as sea surface temperatures rise, with the change in hatching date at TP less responsive to changes in SST because water temperature at TP is less variable compared with water temperature in Florida Bay.

2. Methods

2.1. Study area

We conducted this study at the southern tip of mainland Florida in ENP and TP (Fig. 1). Within ENP, crocodiles nest along mangrove lined creeks, bays and ponds of Florida Bay, along mainland and island sandy beaches and along man-made canals and ditches draining into Florida Bay (Mazzotti, 1983, 1999). Vegetation in the study area is primarily mangrove swamp, with higher ground supporting tropical hardwoods (Olmstead et al., 1981). Water temperatures recorded from sites across Florida Bay (Fig. 1) average 28 °C and ranged from 11° to 39 °C during the breeding season (courtship: January–February, nesting: February–August).

The TP site comprises approximately 2830 ha and is occupied by a closed-loop cooling canal system (CCS) that is 8.2 km long, 4.2 km wide, and consists of 32 discharge and 6 return canals totaling 270 km in length (Fig. 1). Condenser cooling water is discharged into the north-eastern corner of the system and flows west, then south at a rate of about 4.5 m/min. It is collected at the south end of the system and is returned to the plant intake structures. A number of canals and berms within and adjacent to the cooling canal system are important to the crocodile population. Average water temperature is 38 °C and ranges from 34° to

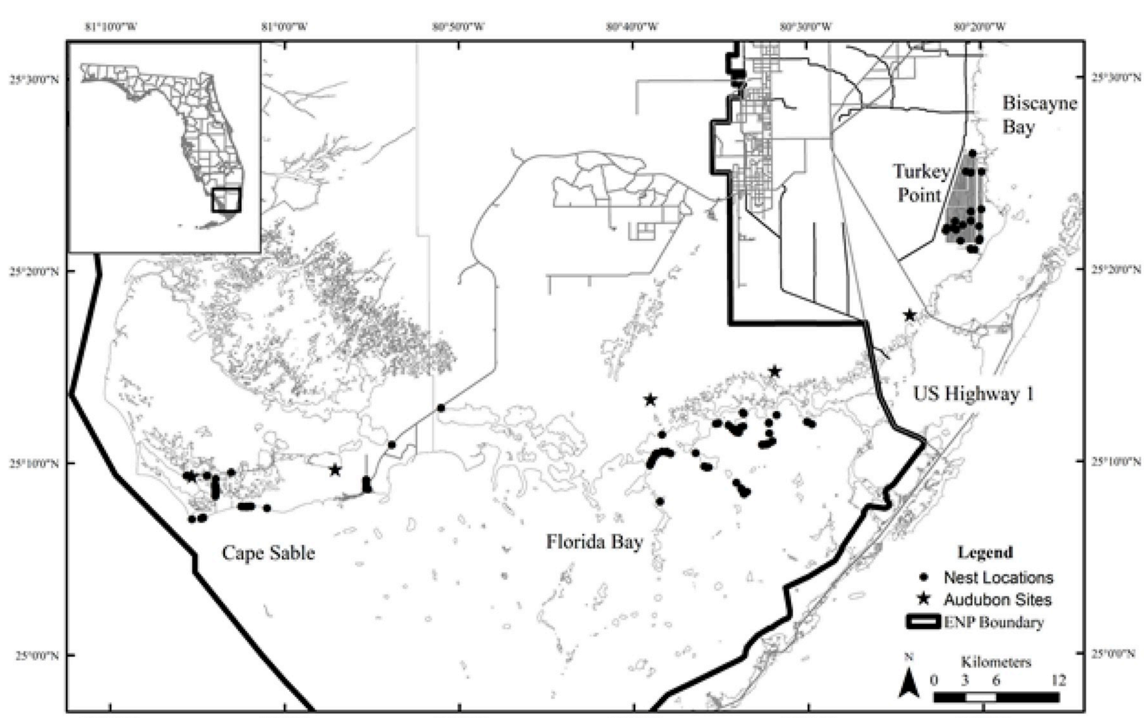

Fig. 1. Locations of all known American crocodile (*Crocodylus acutus*) nests in Everglades National Park and Turkey Point Power Plant site 1980-2016. Audubon water temperature stations that collected environmental data are indicated with stars.

42 °C during the breeding season (Brandt et al., 1995; see Gaby et al., 1985 for detailed description of TP site; Hughes et al., 2009).

2.2. Data collection

We monitored nests from 1980 to 2016 during the crocodile nesting season (April through August) as part of long-term American crocodile monitoring programs within ENP (since 1978) and TP (since 1983). Consistent survey methods under supervision of two investigators have been used to search known (historical) and potential nesting habitat at each site, within ENP (FJM) and at TP (FJM and JAW). Nests can be of mound or hole construction, located isolated away from others, or as close in proximity to within meters or the same mound in some instances. Searches were conducted by skiff, foot and canoe within ENP and by airboat and foot at TP. Nests were located during April and May (egg laying period) and monitored from June to August (hatching period). Evidence of nesting activity included tail drags, digging, or scraping.

During the hatching period nest sites were visually inspected during daylight hours or while performing surveys for hatchlings, which were conducted nightly at TP by airboat and one to five nights per week by skiff, kayak, or portaboat within ENP. Hatched nests were identified by the presence of an open hole and evidence of digging. Shells of hatched eggs or hatchlings located at an open nest were considered evidence of successful nests. A nest was considered successful if at least one hatchling was produced. Once a nest had completed hatching, the egg chamber was inspected for any remaining unhatched eggs which were then counted, this process ensured that multiple nests in close proximity that hatch in succession were not confused with each other. Hatch dates for all known nests within ENP and TP were determined when possible. If a nest site was not visited daily, hatch date was assigned the average date between the last date the nest was observed unhatched and the date it was observed hatched (up to a maximum of three days). Nests with longer than three days between visits were excluded from analyses, to keep hatch date estimates accurate. We chose hatch date over the date the first nest was laid each year, because we monitored known nests during incubation and could determine when nests hatched. It was not possible to determine when the first nest was laid with our monitoring methods.

We obtained daily sea surface temperature data from two sources: one-degree grid cells for the study area from integrated global ocean station system (IGOSS; https://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.monthly/.dataset_documentation.html) and data collected by Audubon of Florida's Everglades Science Center from five sites in ENP (Fig. 1). The data provided by IGOSS was interpolated from a mix of satellite, buoy, and ship-measurements with most readings at a depth of one to several meters (See Reynolds et al., 2002 for further description) and Audubon data was collected from stations located within coastal creeks and wetlands. We averaged the daily data by month for the period 1 February to 31 August each year to coincide with the breeding season. However, prior to 1992 there was no local Audubon data for Everglades National Park. To create a complete set of water temperature data for the study period, we first confirmed that the relationship between SST from IGOSS and the Audubon dataset from ENP for the period of 1992-2010 was linear and positive (ANOVA, $F_{1,22} = 26.523$, $R^2 = 0.547$, $P < 0.001$, $y = 1.627 - 15.993x$). We then used the regression equation for the relationship between the two datasets to estimate SST values for the Audubon data during the period 1986-1991 based on IGOSS values. The final dataset used was the estimated data for the Audubon sites for 1986-1991 combined with the actual data for those sites from 1991 to 2016. We also obtained air temp, although there is no one station with a complete record for air temperature in south Florida and not one station that is representative of our study area. Therefore, we compiled a regional air temperature data set using eight weather stations as close to both study areas (ENP and TP) as possible. There were missing data in the record for individual stations but taking the average across all eight made it possible to fill in those gaps. We chose to use SST rather than air temperature because water temperature is buffered from the rapid fluxes that occur in air temperature, air and water temperatures are generally correlated and since crocodiles spend the majority of their time in water, water temperature is a likely driver of physiological and behavioral responses, such as the relationship found by Murphy (1980) with alligators living in artificially heated ponds.

2.3. Analytical methods

We used linear regression for all analyses using the stastitical platform R (R Core Team, 2019). We first created models to describe changes in SST by year, and the relationship between average hatching date in ENP since 1980 and at TP since 1983 through the 2016 nesting season using years with nests with a known hatch date. We then used the complete dataset for water temperature and the dataset obtained for air temperature and tested the relationship between SST and air temp separately for 1 February to 31 August across all years and the average hatch date for crocodile nests within ENP and TP. Finally, we used standard major axis regression to test for a difference between slopes, elevation and shift for the hatching – SST relationship between TP and ENP.

3. Results

The relationship between SST and year was significant and positive ($F_{1,24} = 12.427$, $P = 0.001$), indicating that SST has increased about 0.05 C per year from 1980 to 2016 (Fig. 2). The number of nests annually ranged from 5 to 138 for ENP and 1 to 25 for TP, with the percentage of nests for which the hatch date was known each year ranging from 0 to 59% for ENP and 93–100% for TP (Table 1 Appendix 1). Hatching dates ranged from June 16 to August 27 throughout the study period. In ENP, crocodiles have been hatching 0.78 days earlier per year (about 1.5 days every two years; $F_{1,24} = 28.706$, $R^2 = 0.5257$, $P < 0.001$; Fig. 3). The average hatch date has been trending earlier in TP as well, ($F_{1,31} = 4.636$, $R^2 = 0.102$ $P = 0.039$; Fig. 3), but the shift in hatching was about half the rate as ENP, about 0.38 days/year.

The trend in regressions between air temp and average hatching data are similar to the trends with SST. The result for TP has a P-value of 0.067, so significant at 0.10. The result for ENP was significant P-value of 0.014 and the R^2 values are lower than for SST. The trend in average hatching date is the same with air temp and SST, but relationships are stronger between hatching and SST, further justification for our decision to use SST. In ENP, for every degree that SST increased, hatching occurred about 10 days earlier ($F_{1,24} = 40.337$, $R^2 = 0.6114$, $P < 0.000$; Fig. 4). The trend for TP was less dramatic, indicating that for every degree SST increased, the average hatch date occurred earlier by about 6 days earlier ($F_{1,24} = 4.701$, $R^2 = 0.129$, $P < 0.040$; Fig. 4). The major axis regression tested for a difference between slopes for the hatching – SST relationship between TP and ENP and although the trend was not as strong in TP, the difference between slopes for the sites was not significant with a Likelihood ratio = 0.314, P = 0.575. Mean elevation for ENP was 2322.654 (range 1720.117–2925.190) and for TP was 2612.534 (range 1678.825–3546.243) and there was no evidence for a shift along the standardized major axes for the relationship between hatch date and year between Florida Bay and Turkey Point (Likelihood ratio = 2.859, P = 0.091).

4. Discussion

Globally, average temperatures of marine environments have risen (Walther et al., 2002), and temperature plays an important role in the life histories of reptiles (Shine, 2005). Our study is novel in that we were able to utilize 37 years of American crocodile nesting data from two nesting sites collected in a standardized manner, with consistent effort,

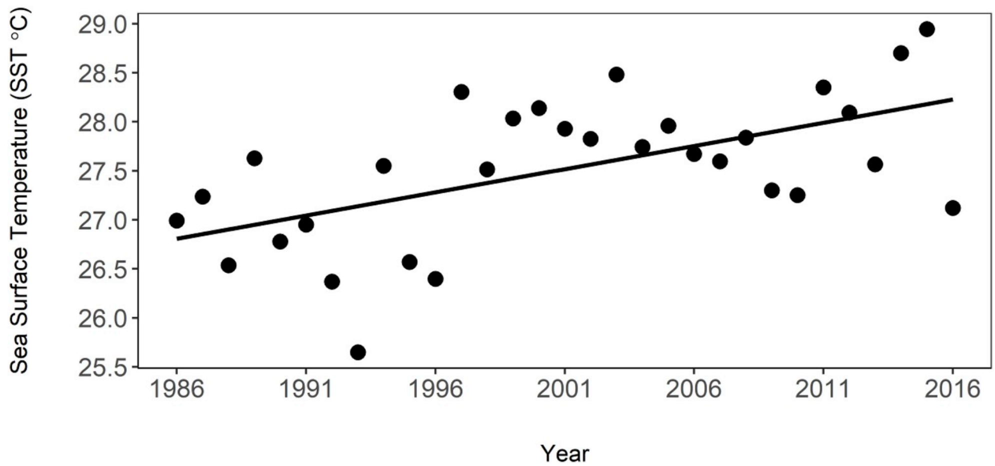

Fig. 2. Relationship between sea surface temperature (SST) in southern Florida and year, ($F_{1,24} = 12.427$, $P = 0.001$, $y = 0.0473x-67.0253$), indicating that SST has increased about 0.05 C per year.

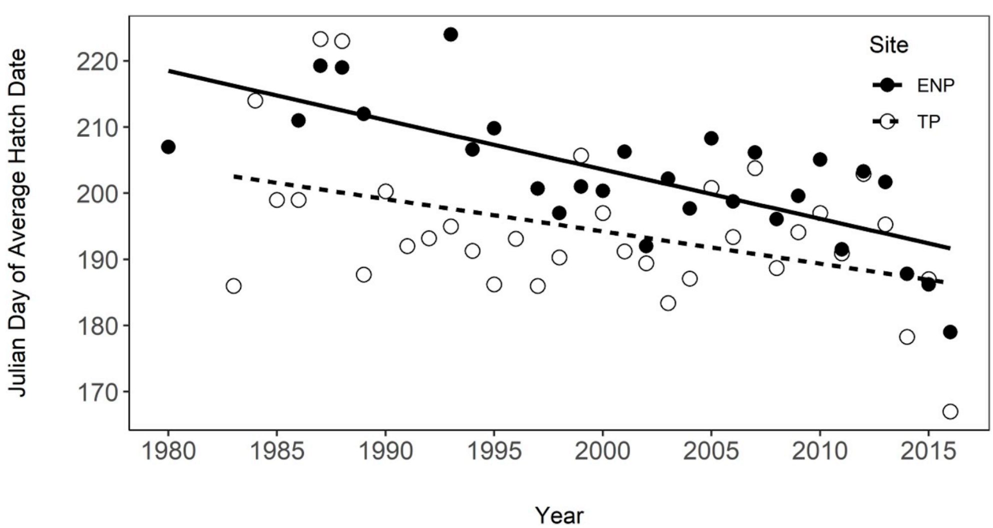

Fig. 3. Temporal change and trend in Julian day of average hatch date for American crocodiles (*Crocodylus acutus*) in Everglades National Park (F1,24 = 28.706, P < 0.000, y = − 0.7814x + 1767) and at the Turkey Point Power Plant site (F1,31 = 4.636, P = 0.039, y = −0.3781x + 951) indicating a change in hatching of 1.5 days earlier every two years in Everglades National Park and at half that rate for the Turkey Point site, and with every 1 °C degree increase in temperature. Slopes are not different between the two sites with a Likelihood ratio = 0.314, P = 0.575.

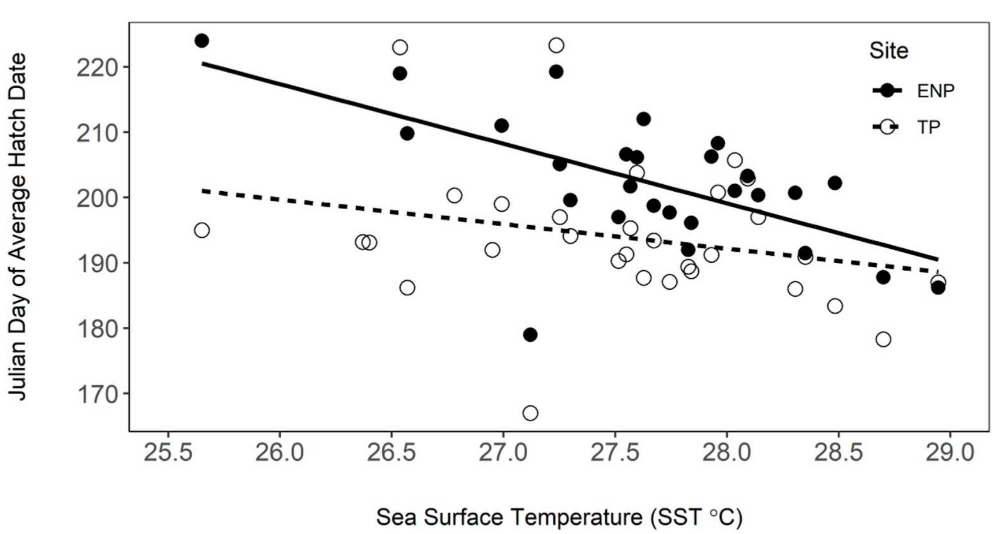

Fig. 4. Change and trend in Julian day of average hatch date for American crocodiles (*Crocodylus acutus*) in Everglades National Park ($F_{1,24} = 40.337$, $R^2 = 0.6114$, $P < 0.000$) and at the Turkey Point Power Plant site ($F_{1,24} = 4.701$, $R^2 = 0.129$, $P < 0.040$) indicating for every degree that SST increased, hatching occurred about 10 days earlier in Everglades National Park and decreased by about 6 days earlier for the Turkey Point site and with every 1 °C degree increase in temperature. Slopes are not different between the two sites with a Likelihood ratio = 0.314, P = 0.575.

to analyze patterns in phenological shifts. We found compelling evidence that crocodile nesting exhibited phenological sensitivity to changing water surface temperatures. In addition, results of this study show that crocodiles may responded differently to increasing water surface temperatures between a natural (ENP) and an artificially heated man-made system (TP). Our results indicate that hatch dates are shifting approximately 1.5 days earlier every two years in ENP and at half that rate for TP compared with historical (1980's) hatching dates. Further, with every 1 °C degree increase in temperature, hatching occurs about 10 days earlier in ENP and 6 days at TP.

This phenology shift in nesting related to environmental factors is consistent with our understanding of crocodilian reproductive patterns. Reproduction in crocodilians is tied to environmental factors including temperature (Murphy, 1980; Lance, 2003). The ability of crocodilians to shift with environmental conditions ensures hatchlings access to freshwater, abundant food resources of the appropriate size, and ample habitat to avoid predation (Brazaitis and Watanabe, 2011). Much of the work on timing of crocodilian nesting has focused on the relationship between precipitation and wetland water levels, to nest flooding and food availability. Work on effects of temperature and nest behavior has focused on how changes in oviposition timing can modify offspring phenotypic characteristics affecting sex (Pina et al., 2003; Parachu Marco et al., 2010; Charruau, 2012; Simoncini et al., 2014; Elsey and Lang, 2014; Murray et al., 2016), post hatching patterns of thermoregulation (Lang, 1987), growth and survivorship (Joanen et al., 1987; Webb and Cooper-Preston, 1989; Pina et al., 2003; Parachu Marco et al., 2010), hatchling size (Lance, 1987; Parachu Marco et al., 2010) and to a lesser extent how temperature affects timing of reproduction.

Murphy (1980) noted that adult alligators (*Alligator mississippiensis*) living in ponds artificially heated by effluent from a nuclear reactor produced sperm two weeks earlier than adults living in adjacent natural ponds and hypothesized this could prevent animals within the cooling pond from mating with animals from outside. Further, Murphy (1980) reported on the importance of warmer water temperatures in triggering spermatogenesis. In addition, warmer spring air temperatures result in earlier breeding of alligators in Louisiana (Joanen and McNease, 1979, 1989), Florida (Jacobson and Kushlan, 1986), and North Carolina (Lance, 1989). Exact timing may vary from year to year based on temperature (Lance, 2003). For the Chinese Alligator (*Alligator sinensis*), courtship begins as temperatures rise, but it can also be altered and delayed by unusually cool weather conditions (Thorbjarnarson et al., 2001). Similar relationships with temperature were also determined for the Saltwater crocodile (*Crocodylus porosus)* in Australia (Webb and Cooper-Preston, 1989) and Broad-snouted caiman (*Caiman latirostris)* in Argentina (Simoncini et al., 2013). Because the crocodiles nesting at TP are in warmer water most of the time they historically bred and nested earlier than crocodiles in ENP; however, since they are not restricted to cooling canals year-round they might additionally be affected by the warmer SSTs, though not as much as animals in ENP because the thermal differential is less.

Many species are known to have the ability of adjusting nesting behavior in response to environmental conditions and gradients, and this plasticity potentially facilitates acclimating to climate change (Schwanz and Janzen, 2008; Mainwaring et al., 2016). This plasticity also is exhibited by crocodiles, as captive crocodiles from Jamaica in Florida follow the Florida nesting schedule of nesting in April/May (Garrick and Lang, 1977) rather than the March/April schedule observed in Jamaica (Thorbjarnarson, 1989). This ability of crocodiles to adjust nesting phenology based on temperature provides an immediate way to mitigate potentially negative effects of changing temperature.

In Florida, courtship and initial nest digging exploration have been occurring earlier (Mark Parry, National Park Service (ENP) 2019; Seth Farris University of Florida 2019, personal communications). However, because date of nest laying is not always available, we cannot use date of nest deposition in analyses. Based on observations noted above we believe that crocodiles in southern Florida are exhibiting plasticity of breeding initiation in response to local climate variables and initiating courtship, breeding and nesting earlier than when the monitoring began in the early 1980s. It is also possible that the incubation period is shortening as laboratory studies for crocodilians have shown that length of incubation period is negatively correlated with incubation temperature: as temperature increases development is accelerated and incubation time decreases (Lang et al., 1989; Webb and Cooper-Preston, 1989; Pina et al., 2003). Although a similar relationship probably exists in the wild (Webb and Cooper-Preston, 1989), it has not been quantified precisely, precluding us from making inferences about the length of incubation in the American crocodile, in addition to the recent shifts observed in courtship and nesting, leading us to believe the incubation period is not shortening in southern Florida.

As with most species-level changes related to climate change, the implications of earlier hatching in terms of conservation, and ecosystem level interactions are speculative. American crocodiles in Florida are restricted to a narrow coastal band of habitat at the northernmost extent of its range (Mazzotti et al., 2007) and are potentially at risk from sea level rise due to vulnerability of natural nest sites due to increases in water levels (Mazzotti, 1999). This restriction in habitat is, in part, due to altered water management practices, which have changed the natural patterns of freshwater flow into crocodile habitat. These hydrological alterations have impacted salinity in the estuary, and impacted crocodile distribution, relative abundance, nesting, growth and survival (Mazzotti et al., 2007).

The effects of sea level rise on crocodiles in Florida should be of concern and requires further evaluation. Hatching in Florida is currently timed with the middle of the rainy season (Mazzotti, 1983; Thorbjarnarson, 1989). With hatching occurring earlier, hatchlings may not be biologically prepared for the differences in food supply and access to fresh water resulting from earlier emergence. However, increased survival attributed to reaching a critical threshold before the onset of the dry season was reported by Moler (1991). Mazzotti (1983) reported that American crocodiles in Florida exhibit faster growth in comparison to other crocodilians. Perhaps rapid growth combined with earlier hatching would allow additional hatchlings to grow to critical mass before the onset of the dry season, thereby increasing hatchling survival. This study underscores the importance of long-term monitoring programs and demonstrates how our ability to interpret population parameters is related to a consistent monitoring effort. Continued monitoring is critical to monitor changes in nesting effort and success as it relates to changing environmental characteristics.

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Declaration of competing interest

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the author(s) and the U.S. Geological Survey but do not necessarily represent the views of the U.S. Fish and Wildlife Service.

CRediT authorship contribution statement

Michael S. Cherkiss: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing - original draft. **James I.**

Watling: Conceptualization, Methodology, Validation, Formal analysis, Visualization, Writing - original draft. **Laura A. Brandt:** Conceptualization, Methodology, Formal analysis, Writing - original draft. **Frank J. Mazzotti:** Conceptualization, Methodology, Investigation, Funding acquisition, Supervision, Project administration, Writing - original draft. **Jim Lindsay:** Methodology, Funding acquisition, Writing - original draft. **Jeffrey S. Beauchamp:** Methodology, Investigation, Writing - original draft. **Jerome Lorenz:** Methodology, Investigation, Writing - original draft. **Joseph A. Wasilewski:** Methodology, Investigation, Writing - original draft. **Ikuko Fujisaki:** Methodology, Formal analysis. **Kristen M. Hart:** Conceptualization, Methodology, Funding acquisition, Supervision, Writing - original draft.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2020.102521.

Appendix 1

Table 1
Number of nests annually (1980–2016) for which a nest hatching date is known for Everglades National Park and Turkey Point Power Plant.

Year	Everglades National Park	Turkey Point
1980	1	0
1981	0	0
1982	0	0
1983	0	1
1984	0	2
1985	0	1
1986	2	3
1987	8	4
1988	3	3
1989	1	6
1990	0	8
1991	0	5
1992	0	6
1993	2	9
1994	8	10
1995	5	15
1996	0	16
1997	7	11
1998	1	10
1999	9	15
2000	11	16
2001	8	13
2002	8	17
2003	22	17
2004	26	17
2005	23	24
2006	24	24
2007	51	21
2008	50	27
2009	33	24
2010	48	15
2011	21	14
2012	7	18
2013	56	24
2014	30	24
2015	63	9
2016	37	8

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