



Major hurricanes affect body condition of American crocodile *Crocodylus acutus* inhabiting Mexican Caribbean islands

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ABSTRACT: Recent models suggest that anthropogenic global warming will lead to an increase in the number of major hurricanes, which have strong effects on ecosystems and may modify animal population characteristics. The goal of this study was to assess the body condition of American crocodiles *Crocodylus acutus* of Cozumel and Banco Chinchorro islands, Mexico, and use it as a tool to better understand short- and long-term effects of hurricanes on crocodylian populations. Changes in body condition (Fulton's *K*) of 392 crocodiles, captured between 2003 and 2015, were assessed and analyzed in response to a major hurricane through different environmental factors. Differences among populations and size classes, and between sexes, together with seasonal variation, were also evaluated. The body condition of crocodiles was generally good, with better condition for Banco Chinchorro, suggesting that these populations and the ecosystems they inhabit are healthy. Body condition for hatchlings and adults was higher than for other classes, with adults exhibiting the best condition. Body condition of Banco Chinchorro individuals varied seasonally, responding to reproductive events and environmental parameter fluctuations. We also found that *C. acutus* body condition is sensitive to the passage of tropical cyclones, most likely through their effects on salinity, temperature, and prey availability. Tropical cyclones have a 2-fold effect on populations. In the short-term, crocodile health is negatively affected by disturbance, while the species seems to maintain and improve its body condition over the longer term. An increase in strong tropical cyclone frequency could impede the recovery of populations, while causing a continual decrease in crocodile body condition.

KEY WORDS: Tropical cyclones · Crocodylian · Banco Chinchorro atoll · Health · Cozumel Island · *Crocodylus acutus* · Fulton's index

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1. INTRODUCTION

Recent models suggest that anthropogenic global warming could lead to an increased number of major hurricanes (Saffir-Simpson hurricane wind scale: categories 4 and 5) over the Atlantic Ocean by the end of the 21st century (Bender et al. 2010). Hurricanes exert strong effects by altering ecosystem vegetation, hydrology, physical structure, and biogeochemistry (Michener et al. 1997), which in turn could affect

animal population characteristics, such as reproduction, population structure and dynamics, diet, dispersal, and parasitism (Waide 1991, Michener et al. 1997, Pavelka et al. 2007, Ramírez-Barajas et al. 2012). Whether adverse impacts would be exerted only in the short-term or would require a longer period of recovery is determined not only by the frequency, timing, and wind speed (Saffir-Simpson rating) of these storms, but also by their distribution, duration, and intensity (barometric pressure drop,

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millibars). Yet, very few data are available to predict the effects of hurricanes on animal populations.

Quintana Roo is the Mexican state that is most affected by major meteorological disturbances; storms of all categories on the Saffir-Simpson wind scale cross its Caribbean coastline (Boose et al. 2003). The official cyclone season for the region occurs from 1 June to 30 November (Instituto Nacional de Ecología 2000). Within the timeframe of our study (2003–2015), 199 tropical storms with winds $\geq 65 \text{ km h}^{-1}$ that originated in the Atlantic entered the western Caribbean and contiguous Gulf of Mexico or were generated *in situ*. Of these, 22 tropical storms had tracked past or over the Yucatan Peninsula (National Hurricane Center, NOAA, Miami, FL, USA, <https://www.nhc.noaa.gov/>). Intense cyclonic storms exhibit maximum sustained wind speeds of 119 km h^{-1} and much higher. Indeed, 2 highly destructive hurricanes (Category 4 and 5) struck the coast of Quintana Roo in October 2005 (Wilma: maximum sustained velocity, 295 km h^{-1}) and August 2007 (Dean: 278 km h^{-1}).

The American crocodile *Crocodylus acutus* Cuvier, 1807 is distributed along the coastline of Quintana Roo and throughout the islands adjacent to the Yucatán Peninsula (Thorbjarnarson 1989), and is potentially susceptible to both the direct and indirect effects of such powerful storms. Using mark–recapture data, we compared crocodile body condition before and after landfall of Hurricane Dean on the atoll reef of Banco Chinchorro. We also examined indirect regional effects of tropical storms on crocodile body condition in terms of wind speed, precipitation, and accumulated cyclone energy (ACE) within the Caribbean Basin. ACE (Bell et al. 2000) is a useful measure of a storm's activity and destructive potential, but it takes into account only duration and wind speed (1 min sustained velocity ≥ 35 knots measured every 6 h).

Populations of American crocodile suffered from overexploitation and hunting between the 1930s and 1970s (Thorbjarnarson et al. 2006, Thorbjarnarson 2010). Currently, coastal populations are critically threatened by genetic introgression with the sympatric Morelet's crocodile *C. moreletii*, Duméril & Bibron, 1851 (Machkour M'rabet et al. 2009). The American crocodile is subject to further reductions in population size and habitat fragmentation and degradation that are due to accelerated coastal development (Cedeño-Vázquez et al. 2006, 2008, Machkour M'rabet et al. 2009, Charruau 2010). In contrast, island populations (Banco Chinchorro, Cozumel) of American crocodile have shown greater recovery from past overexploitation and little or no hybridization (Charruau et al. 2005, González-Cortés 2007,

Machkour M'rabet et al. 2009). Charruau et al. (2010) demonstrated that tropical cyclones can impose negative, short-term effects on crocodiles nesting on these islands, but these disturbances can also provide longer-lasting benefits by creating and maintaining open sandy nesting areas used by *C. acutus* (Charruau et al. 2010).

The American crocodile population of Banco Chinchorro atoll has been monitored annually since 2003. The atoll faced a major meteorological event, when Hurricane Dean travelled across it on 21 August 2007. Dean was a Category 5 hurricane (barometric pressure: 905 mb; National Hurricane Center), which was a very high-energy storm compared to the intensity of storms (typically ≥ 950 mb) preceding and following its passage. It passed directly over the atoll and reached the mainland at Mahahual with maximum sustained winds of 278 km h^{-1} (Franklin 2008). The effects of Hurricane Dean on Banco Chinchorro ecosystems have been mainly studied and measured in the offshore platform reefs (e.g. García-Salgado et al. 2008a,b), but very little research has been conducted in terrestrial and littoral systems where crocodiles live, i.e. the islands and their interior lagoons. Dean affected the coral reef by decreasing the cover of algae, soft corals, and reef-building corals, increasing the abundance of key invertebrates, altering fish diversity, assemblages, and biomass, and increasing the sedimentation of reef structures (Hernández et al. 2008). On Cayo Centro, the main cay of the atoll, strong winds and heavy waves inundated the terrestrial dunes, causing extensive damage to vegetation and human structures. The forest canopy suffered 100% defoliation, with toppling of 10% of the trees, which caused a marked increase in the canopy gap fraction (Charruau et al. 2010).

Crocodile populations on Cozumel Island were monitored from 2003 to 2015 on a less frequent basis than on Banco Chinchorro (González-Cortés 2007, Machkour M'rabet et al. 2009, Charruau & Hénaut 2012). Like Banco Chinchorro, Cozumel was subjected to the passage of 2 very active storms. First, Hurricane Wilma (Category 4, ACE = 38.92, intensity = 882 mb; Pasch et al. 2006) made landfall on the island on 21 October 2005. Second, Hurricane Emily (Category 4, ACE = 32.87; Franklin & Brown 2006) preceded the passage of Wilma in July of that year, but did not achieve landfall. Tropical storms, albeit very strong ones, can exert pronounced effects for considerable distances; for example, Wilma's high-velocity winds extended outward from its landfall on Cozumel (21 October 2005) for distances up to 135 km (Pasch et al. 2006). Moreover, torrential rainfalls associated with

hurricanes can remain dangerous to humans and animals alike even after the storms have made landfall and winds have begun to subside (Touma et al. 2019). Beaches and reefs of Cozumel Island were damaged by the passage of Emily and Wilma in quick succession (Álvarez del Castillo-Cárdenas et al. 2008, Álvarez-Filip et al. 2009, Rioja-Nieto et al. 2012). The terrestrial fauna and flora of the island and adjacent mainland were adversely affected by their passage (Goode & Allen 2008, Perdomo-Velázquez et al. 2017), but very little is known about recent hurricane responses of Cozumel's crocodile populations.

Crocodylians are affected by direct changes in environmental factors (and their interactions), such as water level, salinity, temperature, hydraulic disturbance, and other habitat alterations. These alterations potentially influence crocodile physical condition as well as the availability of their prey (Hutton 1987, Brandt 1991, Fujisaki et al. 2009, Mazzotti et al. 2012, Herrera et al. 2015). Given their ready response to environmental modifications, alligators and crocodiles were identified by Mazzotti et al. (2009) as useful ecological indicators. Indicator species are often used to evaluate condition and health of ecosystems, and can aid in distinguishing between human-induced and natural perturbations. In the context of global change, particularly increased frequency and strength of hurricanes, ecological indicators may have even greater importance, since they can be used to evaluate current and future impacts of increasing environmental change (Niemi & McDonald 2004).

Since crocodylians can be affected by severe environmental perturbations that are caused by hurricanes (Michener et al. 1997, Elsey et al. 2006, Lance et al. 2010), we compared the body condition of animals that were captured prior to landfall of a major storm with those that had been recaptured during or after its passage. From mark-recapture records, we also examined changes in body condition of animals in the absence of direct storm effects. In the first case (direct effects), we predicted that recovery of body condition would strongly depend upon storm intensity (in this instance, Hurricane Dean), the disturbance that it incurs (i.e. changes in physical-chemical conditions), and the intervening recovery period that was required (significant positive slopes with time). In the second case (indirect effects), predicted changes in body condition were not related to time-to-recovery (slope = 0), except in terms of normal scheduled periods of growth and the onset of reproductive maturation.

Ecologists have developed a wide range of body condition indices to assess the physiological fitness of animals (Labocha et al. 2014). One of the oldest in-

dices, Fulton's K (Fulton 1904, cited by Nash et al. 2006) has mainly been applied to fish (Bolger & Connolly 1989, Froese 2006, Nash et al. 2006). This monitoring tool has been routinely used to quantify the effects of broad-scale perturbations on the health of aquatic reptiles such as crocodylians (Zweig 2003, Saalfeld et al. 2008, Cedeño-Vázquez et al. 2011, Mazzotti et al. 2012, Zweig et al. 2014).

Fulton's K is a non-invasive measurement that is made relatively rapidly. It can be used to compare the body condition of similar-sized individuals across several locations (Anderson & Neumann 1996, Froese 2006). Differences in K indices among sites can be used as indicators of their respective habitat qualities (Stevenson & Woods 2006). As a relative measure of condition, immediate changes in K both within and among individuals can signal the effects of abrupt environmental change, the potential for reproductive success within populations (Milenkaya et al. 2015), or a systematic change in developmental stage as the animal ages.

The principal goal of this study was therefore to assess the effect of hurricanes on the body condition of American crocodiles on islands off the Yucatán Peninsula. Using recaptured animals, we examined intra- and interannual changes in body condition at the level of both site (i.e. on the atoll and Cozumel Island) and individual. We further assessed the interaction between different environmental factors and crocodile body condition using recursive modeling, i.e. regression tree analysis (De'ath & Fabricius 2000). Possible further implications of an increased frequency and strength of hurricanes per year are discussed in terms of associations between their accumulated monthly or yearly cyclone energy (ACE; Goldenberg et al. 2001) and crocodile body condition. ACE aided the interpretation of crocodile responses in relation to *in situ* meteorological measurements, given that this metric incorporated neither precipitation nor storm area (spatial extent and air mass volume), which may be more difficult to quantify (Shepherd et al. 2007, Guo & Matyas 2016).

2. MATERIALS AND METHODS

2.1. Data collection

The research was conducted on Cayo Centro, an island that is part of the Banco Chinchorro Biosphere Reserve, and at the Punta Sur Ecological Park, which is located at the southern tip of Cozumel Island (for complete descriptions of these areas, see Charruau 2010). Cayo Centro, situated ~187 km south of Punta

Sur Ecological Park, is the largest of 4 cays that lie within the atoll reef, which is the largest in the Northern Hemisphere. Punta Sur Ecological Park is a complex of reefs, mangrove forest, beaches, and interior lagoons, the last of which are separated from the ocean by dunes.

Crocodiles were captured and marked between July 2003 and August 2015 during nocturnal spotlight surveys, which were conducted from a 4.27 m aluminum boat powered by a 15 HP outboard engine. Crocodiles were spotted by eye using handheld spotlights and headlights. Individuals were captured either by hand or with a self-locking wire snare, depending upon the size of and distance to the animal. Once crocodiles were captured and restrained, total length (TL), tail-base circumference (TC), snout–vent length (SVL), and head length (HL) were measured with a plastic measuring tape or calipers to the nearest 0.1 cm. Crocodiles were also weighed (M, g) using 1 of 3 electronic balances (5 kg ± 5 g; 40 kg ± 10 g; or 200 kg ± 200 g), depending upon their body size. Size classes proposed by Platt & Thorbjarnarson (2000) were used to classify captured crocodiles: hatchlings (class I), TL ≤ 30 cm; yearlings (class II), 30.1–60 cm; juveniles (class III), 60.1–120 cm; sub-adults (class IV), 120.1–180 cm; and adults (class V), TL > 180 cm. Whenever possible, individuals were sexed by cloacal examination (Brazaitis 1968). Caudal scutes were removed to mark individuals, following the code described by Platt & Thorbjarnarson (1997).

Once measurements were taken, each crocodile was freed at its capture site. For each capture, geographical coordinates were recorded using a global positioning system. Water salinity (ppt) and temperature (°C) at the capture point were taken using a hand-held refractometer (0–100 ppt) and mercury thermometer, respectively. These parameters were not measured for all animals that were captured. Precipitation (mm) and air temperature (°C) data were provided by the Comisión Nacional del Agua in Quintana Roo for Cozumel Island and Mahahual, the closest mainland location to Banco Chinchorro (31 km west; Charruau et al. 2015) for which meteorological records were most readily available.

2.2. Data analysis

2.2.1. Estimating Fulton's K

Crocodile body condition was assessed using Fulton's K , which is usually formulated as $K = 100 \times (M/L^3)$, where M is whole-body wet mass (g) and L is

body length (cm). The scaling factor of 100 ($n = 2$, see Eq. 2) typically is used to adjust K to a value close to 1 (Nash et al. 2006). Thus, body mass roughly increases with length cubed, essentially an estimate of body volume.

The data used to calculate Fulton's condition factor must satisfy 2 conditions. First, animals should exhibit isometric growth (Hayes & Shonkwiler 2001), where relationships between their surface areas, volumes, and lengths exhibit a constant shape, regardless of size (i.e. isometric scaling). Isometric scaling, which is rare in most species (Bolger & Connolly 1989), can be contrasted with the more frequent phenomenon of allometric scaling (Froese 2006), where an animal or its body parts change shape with increasing size (i.e. geometric similarity is not maintained). The assumption of isometric scaling can be verified by calculating the regression slope (β_1) between the natural logarithm of a morphometric measurement (L , cm) and the natural logarithm of the mass (M , g). This relationship is represented by the following equation, which is a linearized power function:

$$\ln M = \ln \beta_0 + \beta_1 \times \ln L \quad (1)$$

where β_0 and β_1 are the y -intercept and slope parameters, respectively. When the slope (β_1) does not significantly differ from 3, growth is considered isometric. The hypothesis of isometric growth ($H_0: \beta_1 - 3 = 0$) was verified with a 1-sample t -test.

Second, the intercept (β_0) estimate should be zero (Hayes & Shonkwiler 2001). This theoretical value is not routinely tested; the intercept is assumed to equal zero, and any departures from this value are the result of sampling error. Moreover, assumption 2 has been simply justified, given the fact that an animal with no length necessarily has no mass (Hayes & Shonkwiler 2001). Each of the slopes for the ln-transformed regressions of mass versus SVL, HL, or TC were tested to verify which of these length measurements conformed to isometric scaling (Zweig 2003, Cedeño-Vázquez et al. 2011).

Once morphometric measurements that followed isometric scaling were verified, the body condition index K was calculated using the equation:

$$K = M/L^3 \times 10^n \quad (2)$$

where n is the scaling factor, and all other variables are defined as before. As a measure of length (L), only SVL satisfied the isometric criterion (Table 1). The scaling factor usually takes a value between 0 and 5 to bring the body condition factor to a value close to 1 (Nash et al. 2006). We used a scaling factor of 5.

Table 1. Verification of isometric scaling for the calculation of body condition (Fulton's K), based upon regression relationships between body mass (M) and morphometric measurements of *Crocodylus acutus*. The slope coefficient (β_1) estimated from a linearized power function model was tested against the hypothesis of $\beta_1 - 3 = 0$. Snout-vent length satisfied the isometric criterion. All intercepts (β_0 s) significantly differed from zero ($p < 0.001$). SEE: Standard Error of the Estimate; TC: tail-base circumference ($n = 328$); SVL: snout-vent length ($n = 390$); HL: head length ($n = 389$)

| Relationship | β_0 (SEE) | β_1 (SEE) | r^2 | $\beta_1 - 3$ | t -test ($t > p$) |
|--------------|--------------------|--------------------|-------|---------------|--------------------------|
| M vs. TC | -6.777 (0.058) | 2.759 (0.012) | 0.994 | -0.241 | 20.083 (< 0.0001) |
| M vs. SVL | -10.739 (0.070) | 2.999 (0.013) | 0.993 | -0.001 | -0.077 (0.9387) |
| M vs. HL | -7.597 (0.190) | 3.123 (0.044) | 0.929 | 0.123 | 2.795 (0.0055) |

2.2.2. Effects of biotic and abiotic factors on body condition

In the second step of our analysis, we applied a regression tree model to Fulton's K using various nominal categorical and ordinal descriptors, and continuously distributed biotic and abiotic variables. The categorical variables that were employed in the analysis were site (Banco Chinchorro vs. Cozumel), crocodile size class (ordinal groups increasing from 1 to 5), and sex (male vs. female). We also included months (April to October) and year of collection (2003–2015) as predictors, together with reproductive (Repro = 1 for April and May) and non-reproductive (Repro = 0 for June, July, August, September, and October) periods. The latter also coincided with the onset of hurricane season. The continuous variables were salinity, air temperature, water temperature, and precipitation.

The package 'rpart' (Therneau & Atkinson 1997) implemented the regression tree model in R version 3.1.2 (R Development Core Team 2014) to predict body condition using the aforementioned independent variables. Regression tree analysis or modeling superficially resembles both cluster analysis and multiple regression analysis, but the regression tree also typically requires that in addition to model training, some portion of the data must be held back for its validation (20–30%). The dependent variable that is used to train the model is divided into smaller, more homogeneous groups to form clusters of very similar responses. Partitioning of responses within a given vertical stratum of the tree frequently is based upon different predictors; unlike regression analysis, these

splits represent interactions between predictor variables. Essentially, the splits are akin to large step-wise jumps in the predictors that are included in multiple regression models.

Fulton's K was partitioned based upon sequential binary splits of the predictors (Breiman et al. 1984). The motivation for using a regression tree model was 3-fold. First, Fulton's K was normally distributed, but variances that were associated with the responses were not homogeneous, based upon various combinations of the categorical factors. When we considered class size (5) crossed with levels of site (2) and sex (2), for example, the resulting treatment combinations were unbalanced (unequal numbers of observations) and incomplete (zero observations for many combinations). Under these crossed factors, Fulton's K was heteroscedastic (Levene's test: $F_{11,171} = 2.555$, $p = 0.005$). Recursive partitioning models in general, and regression trees in particular, are non-parametric, permutation-based procedures that are robust to such departures from parametric assumptions, including homoscedasticity (Legendre & Legendre 2012).

Second, relationships between Fulton's K and the predictors that we employed were not necessarily linear. Responses may exhibit strong correlations with the independent continuous variables, but only over a portion of the ranges of these variables. Hence, recursive partitioning can be used to obviate this problem and to exploit an intrinsic property of the dataset. Indeed, the strength or weakness of the response to individual predictors can serve as the criterion for estimating cut-points that result in dichotomous splits in the regression tree. The decision rule for a given node split is based upon ANOVA and the F -test that results from calculating the sums-of-squares for the node, and sums-of-squares for left and right daughters of that particular node (Therneau & Atkinson 1997).

Third, predictor variables in the body condition dataset may contain many missing observations. Missing values can be replaced through multiple or single imputation, although this strategy is not always successful. Hence, not all of the data are used. Further, independent variables in a recursive model may exhibit multicollinearity, a property of the data that can be used to the analyst's advantage. Indeed, 'rpart' uses a strategy that combines other independent variables to create surrogate variables, which are used to impute the missing values of the predictor(s) in question (Therneau & Atkinson 1997).

The strength of a given tropical storm (ACE) is a function of its duration and velocity (Bell et al. 2000).

To provide greater context to splits created by the regression tree using local salinity, temperature, and precipitation, we retrieved regional data from the National Hurricane Center to calculate ACE for 22 storms that had tracked past or made landfall on the Yucatan Peninsula from 2003 to 2015. Using multinomial ANOVA (see the Supplement at www.int-res.com/articles/suppl/m651p145_supp.pdf), we compared the proportions of storm strengths that were associated with individual captures among the terminal leaves into which the individual crocodile body condition responses had been partitioned.

2.2.3. Response of American crocodile body condition to landfall of a major hurricane

The third step of our analysis examined the effect of hurricane passage on body condition and duration of recovery. Recaptures ($n = 24$) were made over the course of the study from among the crocodiles that were initially captured on Banco Chinchorro (7% of captures for this site). Recaptures were divided into 2 groups: (1) those where the capture–mark–recapture operation occurred either prior to or following Hurricane Dean (Dean⁻); and (2) those where the intervening period included the passage of the hurricane (Dean⁺). Four recaptures were excluded from the Banco Chinchorro analysis, given that they were made within the same month (i.e. recovery interval = 0) and yielded no useful information (K was the same at recapture). We abandoned a similar analysis of the 7 recaptures from Cozumel (10% of captures on the site); only 2 observations included the passage of Hurricane Dean during the capture–recapture interval.

The response variable was the relative change in K (%) between capture and recapture: $\Delta K = 100 \times (K_{\text{recap}} - K_{\text{cap}})/K_{\text{cap}}$. These values were included in a 1-way ANCOVA. The 2 levels of the categorical factor (Dean⁻ vs. Dean⁺) were coded (0, 1) as 2 dummy variables. The covariate was duration (months) of the interval between capture and recapture. The actual covariate was not included in the model; rather, we used the factor code-by-time products to estimate 2 separate slope values, thereby testing whether there was a significant interaction between the main effect and covariate.

Estimates of Fulton's K for the hatchlings (size class I) underwent further analysis, because neonate body condition is strongly influenced by the point in time when they are captured after hatching and egress from the nest (Whitehead 1990). Nests were

visited frequently to determine their fates, while temperature loggers that were recovered from successful nests allowed us to determine the day of hatching (Charruau et al. 2010). Given the low number of nests that were surveyed and their wide spacing, we knew from which nest each group of hatchlings had emerged. Thus, hatchlings included in the analysis had known hatching dates ($n = 122$). We marked neonates that were captured during the hatching period.

Consistent with expectation, we predicted that neonate body condition varied with days since hatching, depending upon environmental conditions, availability of yolk reserves, and the assumption of feeding activity. Declines in their K values were also expected to occur when salinity increased or when precipitation and access to freshwater decreased. Unlike older crocodiles, hatchlings are very sensitive to changing salinity, given that their osmoregulatory capabilities are still developing, and their body displays a higher surface:volume ratio (Ellis 1981, Dunson 1982, Mazzotti et al. 1986, Mazzotti & Dunson 1989). These effects should manifest in subsequent modeling of the entire dataset (see Section 3), with possible segregation of the neonate responses from the larger size classes. Relationships among environmental descriptors (precipitation, salinity, water and air temperatures) and hatchling age (in days) were assessed using Kendall's rank correlation (τ) since they were not normally distributed or exhibited non-monotonic trends (Maidment 1993; Fig. A1 in the Appendix). A second-order polynomial regression was performed to assess effects of non-correlated descriptors on body condition of hatchlings. Normality of hatchling K -values was assessed using a quantile-quantile plot and a Shapiro-Wilk test ($p = 0.3266$). Homoscedasticity was confirmed graphically with a plot of residuals vs. fitted values (Legendre & Legendre 2012).

All statistical analyses were performed in R version 3.1.2 (R Development Core Team 2014). Significance was set to a threshold level of $\alpha = 0.05$.

3. RESULTS

3.1. Estimates of Fulton's K

Among potential isometric relationships, only M vs. SVL satisfied the first of the 2 conditions that were proposed by Hayes & Shonkwiler (2001) for isometric scaling (Table 1), i.e. $\beta_1 - 3 = 0$. Significant departures of slope coefficients from $\beta_1 = 3$ for morphome-

Table 2. Number and observed proportions (as percentage) of crocodiles in each category of body condition by size class and sex. Crocodiles from Banco Chinchorro and Cozumel were captured from 2003 to 2015 and from 2007 to 2013, respectively

| Body condition | Hatchlings (class I) | Yearlings (class II) | Juveniles (class III) | Sub-adults (class IV) | Adults (class V) | Males | Females | Total |
|------------------|----------------------|----------------------|-----------------------|-----------------------|------------------|-----------|-----------|------------|
| Total | 208 | 54 | 46 | 42 | 42 | 137 | 47 | 392 |
| Poor | 38 (18.3) | 10 (18.5) | 14 (30.4) | 7 (16.7) | 1 (2.3) | 27 (19.7) | 5 (10.6) | 70 (17.9) |
| Good | 138 (66.3) | 42 (77.8) | 32 (69.6) | 34 (81.0) | 18 (42.9) | 98 (71.5) | 28 (59.6) | 264 (67.3) |
| Excellent | 32 (15.4) | 2 (3.7) | 0 (0) | 1 (2.3) | 23 (54.8) | 12 (8.8) | 14 (29.8) | 58 (14.8) |
| Banco Chinchorro | 208 | 33 | 13 | 35 | 36 | 83 | 34 | 325 |
| Poor | 38 (14.7) | 4 (12.1) | 2 (15.4) | 6 (17.1) | 1 (2.7) | 9 (10.8) | 4 (11.8) | 51 (15.7) |
| Good | 138 (62.6) | 29 (87.9) | 11 (84.6) | 28 (80.0) | 15 (41.7) | 64 (77.1) | 19 (55.9) | 221 (68.0) |
| Excellent | 32 (19.4) | 0 (0) | 0 (0) | 1 (2.9) | 20 (55.6) | 10 (12.0) | 11 (32.4) | 53 (16.3) |
| Cozumel | 0 | 21 | 33 | 7 | 6 | 54 | 13 | 67 |
| Poor | 0 | 6 (28.6) | 12 (36.4) | 1 (14.3) | 0 (0) | 18 (33.3) | 1 (7.7) | 19 (28.4) |
| Good | 0 | 13 (61.9) | 21 (63.6) | 6 (85.7) | 3 (50.0) | 34 (63.0) | 9 (69.2) | 43 (64.2) |
| Excellent | 0 | 2 (9.5) | 0 (0) | 0 (0) | 3 (50.0) | 2 (3.7) | 3 (23.1) | 5 (7.5) |

tric relationships utilizing the other length measurements (TC, HL) suggested allometric scaling of body dimensions with body mass. In fulfilling the β_1 criterion, SVL was used to determine Fulton's K for each crocodile that was captured.

Overall mean K (\pm SD) was 2.202 ± 0.423 ($n = 392$). The categorical ranges for body condition were established as: poor, $K < 1.765$ ($= 2.202 - 0.423$); good, $1.765 - 2.642$; and excellent, $K > 2.642$ ($= 2.202 + 0.423$). Numbers and percentages of crocodiles that were captured during the study are summarized by body condition category. These responses were classified according to site, size class, and sex (Table 2).

Initial estimates of Fulton's K (pooled over time) suggested that mean body condition of Cozumel individuals ($K = 1.996 \pm 0.384$, $n = 67$) was lower than that of crocodiles from Banco Chinchorro ($K = 2.241 \pm 0.437$, $n = 325$). Many neonates were collected on Banco Chinchorro during August 2007 (Hurricane Dean), but their body condition was not affected by the passage of this major storm compared to other hatchlings that were captured during non-hurricane periods (2-sample t -test: $p = 0.40$). Even when hatchlings were excluded from this simple site comparison, mean body condition of Banco Chinchorro individuals was still higher than that of animals captured on Cozumel ($K = 2.212 \pm 0.410$, $n = 117$).

Body condition of non-hatchling *Crocodylus acutus* varied over 13 yr on Banco Chinchorro and Cozumel (Fig. 1, pooled across size class). Preliminary plots of K vs. reformulated values of time (months since July 2003, which is time zero) suggested different curvilinear responses of the body condition between the 2 sites over the course of the study. Mean population response on Banco Chinchorro slowly decreased from

initial collection through the period of hurricane disturbance, after which K increased. On Cozumel, Fulton's K progressively increased with time without displaying intervening negative effects of Hurricane Dean (data not shown). No animals were captured during direct passage of a Category 5 storm over Cozumel.

One-way ANOVAs exploring the time effect were conducted on the Banco Chinchorro data, given that the comprehensive record of captures for this site extended across the entire study. Ten time periods

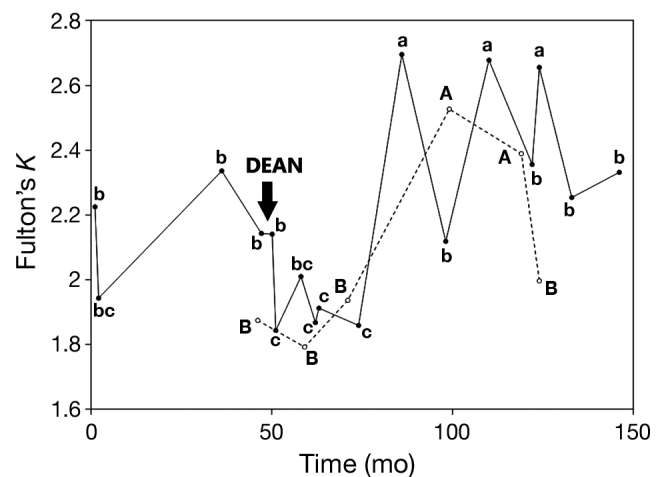


Fig. 1. Temporal variation in body condition (Fulton's K) for non-hatchling crocodiles that were captured on Banco Chinchorro atoll (black line) and Cozumel Island (dotted line) from July 2003 (0 mo) to August 2015 (145 mo). One-way ANOVA was followed by Tukey tests. Means with the same letter (lower case for Banco Chinchorro and uppercase for Cozumel) do not significantly differ at $p = 0.05$. The arrow indicates the August 2007 (49 mo) passage of Hurricane Dean over the atoll

were excluded, where there were zero captures at Banco Chinchorro (captures were made solely at Cozumel), or where captures consisted of hatchlings (Cozumel) and 1–2 non-hatchling individuals. The remaining data (with n for each capture period ranging between 3 and 18 individuals) satisfied homogeneity assumptions (Levene's test, $p = 0.609$). Fulton's K differed significantly among the 17 monthly sample periods (1-way ANOVA: $F_{16,95} = 3.766$, $p < 0.001$), following pairwise Tukey tests (Fig. 1).

3.2. Regression tree modeling of Fulton's K on size class, location, and site conditions

Recursive partitioning of K using the lowest relative error solution from cross-validation resulted in a dendrogram with 7 internal nodes and 8 terminal leaves (Fig. 2; Fig. A2). The regression tree model predicted leaf memberships using 80% of the data (312 of 392 captures). These data were split into more homogeneous groups based upon year of collection (node 1), size class (nodes 2 and 6), precipitation (nodes 3 and 4), salinity (node 5), and water temperature (node 7). Other predictors in the regression tree model that did not result in splits included breeding period, month, sex, site, and air temperature.

The first node partitioned the data into body condition measurements that were collected between 2003 and 2009 from those collected from 2010 to 2015. This accords with the trend for lower mean monthly K in the first group compared to the trend for those measured in the second group, as determined by

ANOVA and as shown in Fig. 1. The first group was split at node 2 to separate size classes II, III, and IV from I and V, leading to a terminal leaf for classes II, III, and IV with mean K of 1.89 ($n = 93$). Following the descendant splits down the left side of the regression tree, K increased with increases in precipitation (point-biserial correlation: $r_{pb} = 0.3563$, $p = 0.002$, $n = 104$). Indeed, data for classes I and V that were separated at node 2 were split at node 4 according to the rule: precipitation < 18.6 mm or precipitation ≥ 18.6 mm, yielding 1 terminal leaf (precipitation < 18.6 mm) where body condition was poor (mean $K = 1.73$; $n = 12$). About 92% of captures forming this leaf consisted of class I individuals (hatchlings). Despite higher levels of rainfall, body condition of the remaining individuals varied with salinity. Internal node 5 split these data according the rule: salinity ≥ 59.0 ppt versus < 59.0 ppt, leading to a terminal leaf for salinity ≥ 59 ppt, where body condition was good (mean $K = 1.97$, $n = 42$). When salinity decreased (< 59.0 ppt), body condition increased ($r_{pb} = 0.5791$, $p < 0.0001$, $n = 92$). Crocodiles that were included in this left-hand leaf were captured in hyper-saline water (60–79 ppt), and were mainly hatchlings (95%). For the right-hand terminal leaf, where salinity was reduced to < 59 ppt (5–58 ppt), average body condition of the crocodiles (85% hatchlings) was good and, indeed, about 21% higher than those in the adjacent leaf (mean $K = 2.39$, $n = 50$).

The 2010–2015 daughter of the regression tree (right-hand side) was repartitioned at node 3 to separate body condition based upon precipitation < 38.3 mm vs. precipitation ≥ 38.3 mm. Consistent with expectation, mean body condition was higher (excellent: $K = 2.92$, $n = 23$) for animals captured under high compared to low precipitation conditions ($r_{pb} = 0.580$, $p < 0.0001$, $n = 115$); 67% of the captures consisted of hatchlings. We could not make the same claim for decreasing salinity, given the scarcity of such data for the right-hand side of the regression tree (especially 2013 and onwards). However, under conditions of low rainfall (< 38.3 mm) and likely higher levels of salinity, classes I to IV (node 6) were split from class V, creating a terminal leaf for class V (adults) with excellent body condition (mean $K = 2.69$, $n = 17$). Finally, hatchlings to sub-adults (classes I to IV) that were split from adults at node 6 were separated into 2 terminal groups at node 7 according to the rule: water temperature $< 30.25^\circ\text{C}$ vs. water temperature $\geq 30.25^\circ\text{C}$. This final split led to

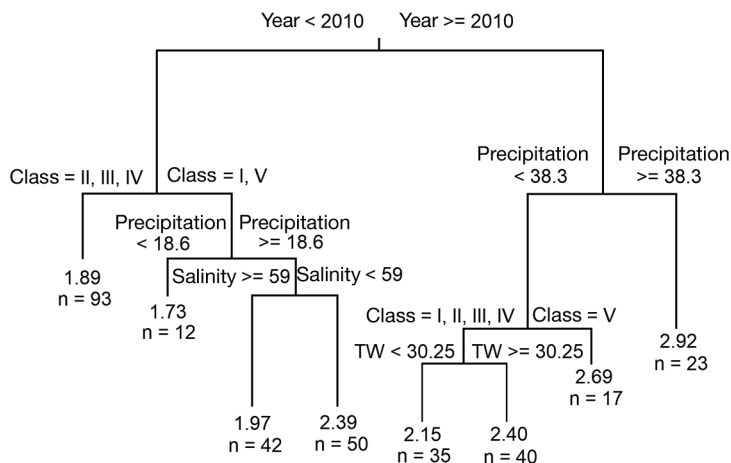


Fig. 2. Regression tree of body condition (Fulton's K) of American crocodiles from Yucatán Peninsula islands (data combined for Banco Chinchorro and Cozumel). TW: water temperature ($^\circ\text{C}$). Precipitation is given in mm, salinity in ppt

the left leaf (good: mean $K = 2.15$; $n = 35$) and the right leaf (good: mean $K = 2.40$; $n = 40$). Body condition increased with a modest increase (1.91°C) in water temperature ($r_{pb} = 0.429$, $p = 0.0001$, $n = 75$).

Proportions of ACE class counts were compared among the 8 terminal leaves created by the regression tree model (Fig. 2) using 2-way multinomial ANOVA (see the Supplement). For the primary tree split, the percentage of very energetic storms (cumulative ACE >20) was more than 8-fold higher for the 2003–2009 period (group 1: 36%) compared to 2010–2015 (group 2: 4.4%). Thus, the 2003–2009 and 2010–2015 periods formed 2 natural groups in the ANOVA, with 4 terminal nodes (leaves) per group (Supplement). Lower intensity storms were 2-fold lower in the 2003–2009 group compared to 2010–2015, for both class 0.1–5.0 (27.4 vs. 49.6%) and class 5.1–20.0 (12.2 vs. 27.8%).

These qualitative differences helped distinguish the behavior of terminal leaves 1 to 4 (left-hand side of regression tree) from leaves 5 to 8, as well as differences that were observed within the 2 groups (Supplement). Indeed, body condition across leaves 1 to 4 (Fig. 2) decreased from good (1, mean $K = 1.89$) to poor (2, 1.73) and increased back to Good (3, 1.97; 4, 2.39); this pattern of shifting body condition was accompanied by linear and quadratic trends in the proportions of the very intense ACE category (first-order contrast, Wald $\chi^2_1 = 6.82$, $p = 0.009$; second-order, Wald $\chi^2_1 = 9.70$, $p < 0.001$). In contrast, mean K increased steadily from leaf 5 to leaf 8 (Fig. 2), with ratings of good (5), good (6), excellent (7), and excellent (8). This progressive increase in body condition was accompanied by a strong shift in the proportion of moderate storms (first-order contrast, Wald $\chi^2_1 = 23.51$, $p < 0.001$; second-order contrast, Wald $\chi^2_1 = 10.34$, $p = 0.001$). We subsequently focused upon differences in ACE proportions that emerged in left and right daughters of the internal node splits.

Within the left-hand leaf cluster (Fig. 2), we compared storm proportions within leaf 1 with aggregate group 2-3-4, from which the first group split early in the regression tree analysis. Very high-intensity storms (ACE >20) constituted 50.5% of leaf 1 (Table S1), but decreased to 23.1% for the aggregate group; percentage captures in the absence of storms (ACE = 0) increased more than 6-fold in the latter group, from 6.5 to 40.4% (Wald $\chi^2_3 = 75.88$, $p < 0.001$). Terminal leaves 3 and 4 were differentiated (Wald $\chi^2_3 = 54.21$, $p < 0.001$) by increased low-intensity storms (ACE = 0.1–5) for the latter (0 to 52%), with simultaneous 2-fold decreases in captures with no measurable storm activity (64.3 to 30%) and cap-

tures associated with very intense storm activity (35.7 to 18.0%).

The right-hand cluster of terminal leaves (2010–2015) included fewer captures (115 animals) than the left-hand group (2003–2009; 197 captures). The former was characterized by few intense or very intense storms (ACE classes: 10.1–20.0 and >20.0 , respectively). This response was mirrored in leaves 5 and 6, which differed in their respective ACE proportions (Wald $\chi^2_3 = 33.22$, $p < 0.001$). Capture percentages where storm activity was absent increased from 0 to 19.1% (moving from leaf 5 to 6); storm activity decreased to zero, except for ACE class 0.1–5 (from 60.0 to 80.9%; Table S1). Leaves 5 and 6 (size class I–IV individuals), in turn, formed a larger group with leaf 7, which consisted only of adults (size class V). Under this internal split, adults were captured under moderately intense to intense (ACE: 5.1–20) and very intense storm (ACE: >20) conditions that increased 5-fold (shift from 5–6 to 7, 14.7 to 76.5%) and 3-fold (4.0 to 11.8%), respectively, relative to conditions experienced by the younger individuals (Wald $\chi^2_3 = 69.54$, $p < 0.001$). The final partition was formed between aggregate 5–6–7 vs. leaf 8. Storm class percentages between the aggregate group and leaf 8 differed (Wald $\chi^2_3 = 182.93$, $p < 0.001$). Indeed, individuals classified in leaf 8 exhibited the highest mean K among leaves and groups, a response that was reflected in the percentage of captures that were made under benign storm conditions. Yet, it also accords with higher levels of precipitation that were encountered and upon which this internal partition was based (Fig. 2). Counts of crocodiles captured in the absence of storms (ACE = 0) increased 10-fold from 5–6–7 to leaf 8 (from 6.5 to 65.2%), with a comparable drop in captures under moderate storm conditions (from 62 to 0%) and very intense storms (from 5.4 to 0%).

3.3. Hurricane effects on body condition

Prior to passage of Hurricane Dean in August 2007 (0 mo, mean $K = 2.141$), Fulton's K was higher in late spring to early summer of each year, before declining by late summer. Although a small, but non-significant recovery in body condition was observed in April 2008 (8 mo post-Dean, mean $K = 2.011$), mean K remained low in the aftermath of the hurricane until August 2009 (24 mo, mean $K = 1.860$). Body condition recovered substantially in August 2010 (36 mo, mean $K = 2.696$), fluctuating about a value of 2.477 until the end of the study (Fig. 1). In contrasting pre- and post-hurricane means, body condition prior to passage of

Hurricane Dean (August 2007) was lower than body condition in the post-hurricane period ($F_{1,95} = 4.421$, $p = 0.038$). The difference between respective means was small (2.136 vs. 2.207), suggesting that systematic effects imposed by Hurricane Dean on body condition were either weak or dampened by the occurrence of intra-annual fluctuations in crocodile body condition.

Trends in body condition indeed varied seasonally for crocodiles on Banco Chinchorro, based upon mean K responses for each month in which non-hatchling individuals had been captured (1-way ANOVA: $F_{6,177} = 3.011$, $p = 0.008$, $n = 184$). Homoscedasticity (Levene's test, $p = 0.197$) was maintained by pooling the yearly responses by the monthly categories (April to October) for this reanalysis. Mean K (\pm SD) increased from an April low (1.906 ± 0.246) to an intermediate value in May (1.993 ± 0.396), culminating in a June peak (2.361 ± 0.255). Following this peak, condition declined during July (2.192 ± 0.332) through August (2.225 ± 0.422) and into September (2.146 ± 0.424), before making a brief recovery in October (2.236 ± 0.468).

ANCOVA of the changes in Fulton's K (ΔK , %) revealed that passage of Hurricane Dean during the capture–recapture interval (Dean⁺) had a prolonged effect on the physiological recovery of individual animals. Body condition declined by $-19.537 \pm 6.891\%$ (Dean⁺, adjusted mean [\pm SEE, Standard Error of the Estimate]; $t_{13} = -2.799$, $p = 0.015$) in the presence of Dean, but significantly and progressively increased with time from this initial negative value (Dean⁺ by month interaction: slope = $0.599 \pm 0.132\%$ mo⁻¹; $t_{13} = 4.523$, $p = 0.001$). In the hurricane's absence (Dean⁻), a decline in body condition was evident for the intercept term for this treatment (adjusted mean = $-10.689 \pm 4.766\%$), but recovery was not sustained over time (Dean⁻ by month interaction: slope \pm SEE = $-0.162 \pm 0.132\%$ mo⁻¹; $t_{13} = 1.232$, $p = 0.240$). Overall, ANCOVA explained about 68.2% of the variation in % ΔK ($r^2_{\text{adjusted}} = 0.584$).

On an individual treatment basis, the positive relationship between predicted changes in body condition and recovery time was stronger ($r^2 = 0.882$, $p = 0.0017$, $n = 7$; Fig. 3a) for crocodiles that had been captured prior to Hurricane Dean and recaptured afterwards (Fig. 3a), compared to the equation predicting the condition of individuals (Fulton's K) that had been captured and recaptured outside of the disturbance interval ($r^2 = 0.127$, $p = 0.31$, $n = 10$; Fig. 3b). The almost 20% drop in K required a recovery period of 32.5 mo (< 3 yr between capture and recapture) to restore body condition to the pre-disturbance value

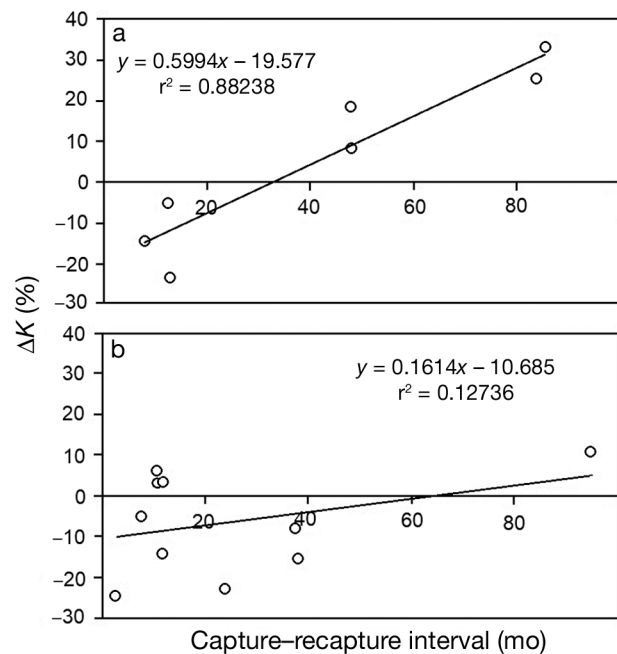


Fig. 3. Percentage changes in body condition (Fulton's K) of Banco Chinchorro crocodiles versus capture–recapture interval (months) that (a) included the passage of Hurricane Dean (Dean⁺) and (b) did not include the hurricane disturbance (Dean⁻)

(i.e. 0% change) when the interval included Hurricane Dean (Dean⁺, Fig. 3a). The longest interval of recovery from the hurricane (86 mo) that was recorded increased pre-disturbance body condition by 34% (Fig. 3a). According to ANCOVA, there were no significant, systematic increases in body condition with increasing duration of the capture–recapture interval (Fig. 3b) in the absence of hurricane disturbance. Relative changes in body condition of Cozumel crocodiles at recapture, which averaged -7.6% of values at initial capture, likewise did not significantly vary with duration of the intervening period ($p = 0.37$), which ranged from 5 to 13 mo.

Time-dependency in hatchling body condition was revealed by second-degree polynomial regression between Fulton's K estimates and hatchling age, in days ($F_{2,121} = 41.45$, $p < 0.001$, $r^2 = 0.407$; Fig. 4). According to Kendall's tau, other environmental factors had to be excluded from the analysis because they were all correlated with hatchling age (Fig. A1). Neonates comprised a substantial percentage of the crocodiles that were captured (55%). Hatchlings were only captured in July, August, and September, and only on Banco Chinchorro (Table 2). These young crocodiles generally exhibited good body condition ($K = 2.264 \pm 0.450$, $n = 208$). The sex of the young

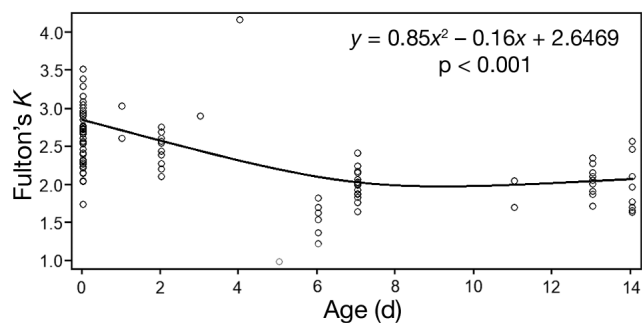


Fig. 4. Second-degree polynomial regression of body condition (Fulton's K) of American crocodile hatchlings from Banco Chinchorro versus age

could not be determined with certainty because of their small size.

4. DISCUSSION

4.1. Short- and long-term effects of hurricanes on American crocodile body condition

Crocodile populations of Banco Chinchorro and Cozumel were healthy, given their average, evidently good body condition. These observations confirm the good state of conservation of these populations, which has been observed in previous studies (Charruau et al. 2005, González-Cortés 2007).

With respect to our main objective, the pattern of mean K -values of the Banco Chinchorro population relative to Hurricane Dean suggests that major hurricanes can influence crocodile body condition. From 2007 to 2009, a strong decrease in mean body condition corresponded to a direct effect of this hurricane (Fig. 1). A significant increase in crocodile mean body condition was observed in 2010 (less than 3 yr after Dean), subsequently followed by values fluctuating about a higher mean body condition until the study ended (Fig. 1).

Results of recursive modeling mirrored temporal trends in mean body condition on Banco Chinchorro. K -indices were divided by 'rpart' into 2 main groups at the first internal node (Fig. 2): pre-2010 and earlier, with low mean body condition values; and 2010–2015, with higher mean body condition. During the first period (2003–2009), 3 consecutive years of hyperactive ACE (2003–2005) marked seasonal storm activity across the Atlantic Basin (including the Gulf of Mexico and the Caribbean Sea). The remainder of the period 2003–2009 was relatively quiet (National Hurricane Center bulletins), which was surprising given

the passage of Hurricane Dean over the Yucatan in August 2007. For the second daughter of the node (Fig. 2), the period 2010–2015 began with ACE hyperactivity (2010), which may account for the steep decline in mean K on Banco Chinchorro from August 2010 to August 2011 (Fig. 1; 85 and 97 mo from the beginning of the study). ACE decreased in subsequent years, to above normal activity, and then to below to near-normal activity (National Hurricane Center). The gradual decline in ACE was reflected in the relatively high (but fluctuating) K -indices that were maintained over this period (Fig. 1); however, a direct association between mean K and seasonal ACE was weak ($r_s = -0.273$, $p = 0.258$, $n = 19$). Estimates of ACE for storms that tracked across the western Caribbean Basin were more useful in the qualitative interpretation of the internal and external nodes (i.e. the terminal leaves) that resulted from regression tree modeling of body condition; indeed, shifts in ACE proportions among regression tree leaves reflected the above-mentioned high K -values that were obtained in the 2010–2015 period compared to 2003–2009.

The population trend was supported by data that were collected on recaptured individuals. Those individuals that were captured on Banco Chinchorro twice within the year when the hurricane struck the atoll (before–after comparison) showed a marked decrease in body condition (Dean⁺, Fig. 3a). Recovery to pre-disturbance body condition (zero change) at recapture required almost 3 yr (32.7 mo). In contrast, individuals that were captured and recaptured outside the period in which the hurricane passed (August 2007) exhibited no significant changes in body condition (Dean⁻, Fig. 3b). The contrast in these 2 results suggested a real effect of large-scale disturbance on crocodile body condition. In the regressions, size class I (hatchlings) was considered the reference condition.

Hurricanes are generally not a cause of mortality in crocodilians (except for hatchlings) (Charruau et al. 2010); however, they can cause substantial modifications to the environment (Michener et al. 1997). The effect of Hurricane Dean on crocodile body condition was amplified by the timing of the event, which coincided with the time of year where body condition usually has begun to increase (Fig. 5). Further, damage inflicted on vegetation by hurricanes, i.e. snapped boles, uprooted trees, and complete defoliation, as was observed on Banco Chinchorro following the passage of Hurricane Dean (Charruau et al. 2010), generally causes an increase in surface temperatures (Tanner et al. 1991). This response would increase evaporation and salinity, thereby negatively affecting

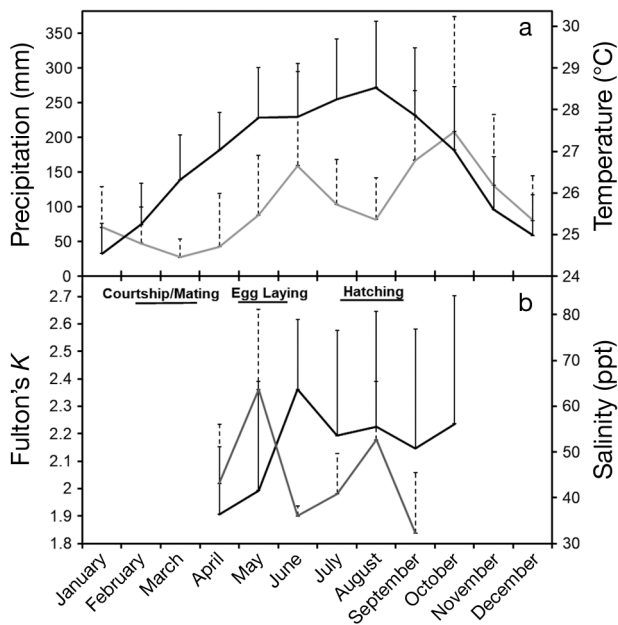


Fig. 5. Patterns of (a) temperature (black line) and precipitation (grey line) and (b) American crocodile body condition (Fulton's K , black line) and salinity (grey line) (b) over the course of a year on Banco Chinchorro. Bars represent standard deviations. Data are pooled across years

crocodile body condition, as indicated by our analyses and by previous studies (Dunson 1982). Increased precipitation also has accompanied hurricanes, particularly since 1995 (Trenberth 2005), but its spatial extent and intensity remain difficult to predict (Touma et al. 2019). Substantial inputs of freshwater that are caused by hurricanes should bring about decreases in salinity in closed basins, including isolated lagoons of Cozumel, thereby promoting increased crocodile body condition.

Storm surge and saltwater intrusion, and increasing coastal inundation and flooding that is driven by high winds and accompanied by intense rains is likely to increase with climate change (Rezapour & Baldock 2014, Guo & Matyas 2016). Increased rainfall may diminish water salinity, but it is just as likely to heighten erosional losses, siltation and contaminant release in overland flow and flooding. Hurricanes can thus cause substantial physical damage to crocodile habitat, increase water pollution and decrease prey populations (Ensminger & Nichols 1957, Michener et al. 1997, Elsey et al. 2006, Charruau et al. 2010, Rezapour & Baldock 2014). Such conditions are only likely to worsen, as sea level continues to rise due to global warming and as storm surge penetration inland deepens.

Storm surges can be followed by periods of drought, which increases surface evaporation in wet-

lands and ponds that are not directly connected to or have restricted connections with the ocean, resulting in increased salinity and decreasing water depth. Drought following a tropical storm may hold an unintended benefit for crocodilians, by reducing both surface water depth and volume, thereby concentrating and increasing prey availability, as suggested by Fujisaki et al. (2009) for American alligator *Alligator mississippiensis* populations in the Florida Everglades (USA). Unlike crocodiles, however, alligators that experienced the aftermath of Hurricane Rita landfall in Louisiana, which included drought and increasing salinity levels, exhibited severe physiological stress, particularly due to effects of the latter (Lance et al. 2010). American crocodiles are tolerant of saltwater immersion, including hyper-saline conditions (Ellis 1981, Dunson 1982, Taplin et al. 1982, Thorbjarnarson 2010).

The atoll of Banco Chinchorro has a shallow lagoon (average depth = 6 m), but represents a very stable environment in terms of its physical and chemical characteristics, without exhibiting thermal or chemical stratification (de Jesús-Navarrete 2003). The state of interior lagoons of the individual cays is more dynamic, in contrast, given that they are small and very shallow (i.e. water temperature is more tightly coupled with air temperature), subject to variation in tidal influx, runoff, and evaporation. Indeed, Cayo Centro was inundated by ocean water during Hurricane Dean, introducing more salt to interior lagoons on the island.

Water salinity on Cayo Centro was likely subject to dramatic fluctuations in response to increased drought and, conversely, to episodic rainfall events, especially in its shallow, flat-bottomed interior lagoon. The highest salinity that was recorded during crocodile captures on Banco Chinchorro was 79 ppt (126% over the average of 35 ppt). Likewise, high salinity was observed in the dune-protected lagoons on Cozumel; the greatest value that we recorded during a capture on the island was 81 ppt (131% over 35 ppt), while the lowest values ranged from 0 to 5 ppt. Extremes of salinization have been observed in interior lagoons located on other Caribbean islands that have similar or more strongly restricted connections with the open ocean (Jarecki & Walkey 2006). American crocodiles are physiologically adapted to the challenge of living in brackish to hyper-saline habitats (Taplin et al. 1982), but environmental fluctuations and other habitat alterations mentioned above may help explain the short-term (3 yr long) lower body condition of *Crocodylus acutus* on Banco Chinchorro following the passage of Dean (Fig. 1).

According to Michener et al. (1997), new organic matter that is generated by the perturbation decomposes and increases the resource base for generalist consumers, such as crocodiles. When the environment recovers a few years after the hurricane, an irruption of invertebrates and small vertebrates can occur, providing crocodiles with abundant food, which may explain long-term increases in crocodile body condition on Banco Chinchorro after 2009. Lastly, a subsequent significant increase in body condition appeared in 2012, according to our results (Fig. 1). This variability could not be associated with any climatic events and probably was due to a low sample size (only 3 captures in 2012).

Our results revealed differences in mean body condition between the study populations. Body condition of the Banco Chinchorro population was higher than that of the Cozumel population. Hurricanes Emily and Wilma (Category 4 at landfall) struck Cozumel in 2005, substantially damaging the Punta Sur Park mangrove forests (comprising *Rhizophora mangle* and *Avicennia germinans*), which have yet to fully recover, unlike mangroves on Banco Chinchorro (Charrau et al. 2010). Indeed, mangrove forests are recognized as nursery sites for many species of fish and crustaceans (Robertson & Duke 1987, Nagelkerken et al. 2002, Koenig et al. 2007), which represent a major component of the diet of American crocodiles (Platt et al. 2013, Avila-Cervantes et al. 2017).

Unfortunately, Cozumel crocodiles have only been studied since 2007; therefore, no data are available for assessing patterns of crocodile body condition before and after hurricanes, as was done on Banco Chinchorro. In July and October 2005, hurricanes with very high sustained wind speeds (Emily, 290 km h⁻¹; Wilma, 295 km h⁻¹) made respective landfalls on the Yucatan Peninsula at Tulum (Emily) and at Cozumel (Wilma). Their landfalls likely transformed environmental conditions, especially altering temperature and moisture regimes (Tanner et al. 1991). Lower body condition of the Cozumel population, compared with that of Banco Chinchorro, could be explained by lower food resource availability, resulting from the passage of these 2 major hurricanes in quick succession.

Global change could eventually increase the frequency of such strong hurricanes (Category 4 and 5) in the Caribbean (Webster et al. 2005, Bender et al. 2010). According to our results, strong hurricanes may have short-term negative effects on crocodile body condition. Consequently, powerful storms that occur in rapid succession (every 2 or 3 yr) could retard or prevent recovery of both the population and

the environment, leading to a prolonged decrease in crocodile body condition. Collectively, the results of this study further support the utility of crocodiles as indicators of environmental health.

4.2. Further environmental, seasonal, sexual, and size effects on body condition

Body condition of hatchlings and adults was higher than for other classes, with adults exhibiting the best condition. Many reasons could explain differences in body condition among size classes. Banco Chinchorro atoll and Cozumel Island are relatively densely populated by crocodiles (Charrau et al. 2005, González-Cortés 2007), which contributes to intraspecific competition. Smaller individuals are less competitive, and they disperse from better quality sites during territorial conflicts (Thorbjarnarson 1989). Consequently, yearlings, juveniles, and sub-adults are often found in marginal habitats (Mazzotti 1983), such as hypersaline water or exposed shorelines (Gaby et al. 1985, Thorbjarnarson 1989), which contribute to decreases in their body condition. At Banco Chinchorro, smaller size classes are mainly found in the interior lagoon of Cayo Centro, where salinity levels are higher (Charrau et al. 2005). Furthermore, this dispersal phase imposes high energetic costs on young crocodiles (Thorbjarnarson 1989). High salinity makes osmoregulation more difficult and causes greater water loss for small individuals (Evans & Ellis 1977, Ellis 1981, Dunson 1982, Thorbjarnarson 1989).

Accordingly, we could hypothesize that hatchling body condition would be strongly affected by high water salinity and would therefore be lower than every other size class. Yet hatchling body condition did not seem to have been affected by environmental factors, but rather by life history characteristics of the species. Hatchling body condition in July is excellent, likely because neonates are provisioned with resources from the yolk sac, which continues to nourish them for several days following hatching (Ferguson 1985, Whitehead 1990). Hatchling body condition drops slightly in August, which is explained by the decrease in yolk reserves (Whitehead 1990). Once yolk resources are depleted, the young begin feeding for themselves, with a concomitant increase in their body condition, which provides one likely explanation for the curvilinear response shown in Fig. 4. Increased precipitation in late August–early September could also result in a decrease in water salinity, favoring better body condition. Even if hatchlings generally exhibit good body condition,

Charruau et al. (2010) observed a very low survival rate after Category 5 Hurricane Dean, whereas no mortality was associated with that particular hurricane for other size classes. Consequently, hurricanes may likely exert more deleterious effects on yearlings, juveniles, and sub-adults than on adults.

In general, females have a higher body condition than males, i.e. a greater proportion of individuals exhibit good to excellent ratings (Table 2). This was generally observed at Cozumel, but not at Banco Chinchorro. The apparent site difference could be explained in part by the capture of very few females compared to males during the reproductive (from courtship to egg-laying) period (from March to May, Charruau et al. 2010). Both males and females invest a great deal of energy in the reproductive period (Thorbjarnarson 1989) that results in decreased body condition, from which the animals in our study quickly recovered (Fig. 5). Males and females should have a different body condition for a few months during the year (especially during reproduction) due to differential investment and behavior during breeding and reproduction, according to literature reports (Lang 1987, Thorbjarnarson 1989).

These previous explanations are consistent with observations of crocodile body condition patterns over a year. In fact, their body condition appears to be at its lowest in April and May. Mating, nesting site selection and egg laying occur during these months (Charruau et al. 2010, 2011), and crocodiles invest a great deal of energy in these activities (Lang 1987, Thorbjarnarson 1989), thereby incurring a decrease in their body condition. Males invest energy in courtship, mating, and territorial extension and defense, while females invest in nest building, mating, egg production, and protection (Lang 1987, Thorbjarnarson 1989). In crocodylians, both males and females neglect feeding during this period (Álvarez del Toro 1974, Lang 1987, Barão-Nóbrega et al. 2016). Furthermore, April and May represent the end of the dry season, which is characterized by high salinity (Fig. 5) and a less productive habitat (Thorbjarnarson 1989). Our results show that *C. acutus* body condition decreases when salinity increases. In June, body condition increases, which can be attributed to the end of the reproductive period for males, the beginning of the rainy season, and a decrease in salinity. A subsequent 3 mo decrease is notable from July to September. This decrease may be caused by a brief drought, which occurs in the Caribbean around July and August (Charruau et al. 2010). High temperatures, decreased precipitation, and increased salinity characterize this period. With returning October rains,

crocodile body condition appears to recover. Yet, mean *K* responded more strongly to decreasing salinity ($r_s = -0.309$, $p = 0.184$, $n = 20$) than to increasing precipitation ($r_s = -0.093$, $p = 0.697$; but see Fig. A1).

The fact that males and females might exhibit different body condition for a few months during the year (especially during reproduction), as a result of differential investment and behavior during breeding and reproduction (Lang 1987, Thorbjarnarson 1989), is important to consider when evaluating the effect of hurricanes on crocodile body condition. Reproduction certainly adversely affects body condition. The addition of short-term negative effects of a hurricane could further diminish body condition; this effect may be even more important for females. Also, the end of the laying period coincides with the beginning of Caribbean hurricane season. As a result, crocodiles could be strongly affected by the onset of a hurricane very early in the season (e.g. Hurricane Emily; Franklin & Brown 2006), having likely reached their lowest body condition in previous months.

As previously mentioned, ongoing global change is likely to increase the frequency of strong hurricanes (category 4 and 5) in the Caribbean (Webster et al. 2005, Bender et al. 2010). From their economic analysis of tropical storm effects on human populations and infrastructure, Grinsted et al. (2019) found that in terms of area of total destruction, hurricanes are becoming progressively more dangerous and damaging, at least in the USA; furthermore, the authors asserted that the frequency with which the most damaging hurricanes occur has markedly increased (330% per century). Hurricane damage will likely similarly increase as economic development proliferates along the Mayan Riviera, while further compromising remaining crocodile habitat.

According to our results, individual strong hurricanes may have short-term negative effects on crocodile body condition; consequently, closely spaced and powerful storms (every 2 or 3 yr) might not allow the population to fully recover and could cause a prolonged decrease in their body condition. However, American crocodile body condition at Cozumel and Banco Chinchorro is generally good, which suggests that these populations are healthy. These responses also suggest good quality and health of their ecosystems, given that crocodiles are viable candidates for serving as proxies or indicators of ecosystem status. According to the International Union for Conservation of Nature (IUCN), the status of the species remains Vulnerable (Ponce-Campos et al. 2012). For this reason, particular attention should be paid to conservation. The present study showed that body

condition of *C. acutus* is sensitive to the effects of tropical cyclones, most likely through their effects on salinity, temperature, and prey availability. Tropical cyclones can exert short-term negative effects on crocodile body condition, but they also may have a beneficial effect on body condition over the longer term. Short-term negative and long-term beneficial effects of tropical cyclones have been previously observed by Charruau et al. (2010) with regard to the reproductive ecology of *C. acutus*. Furthermore, hurricanes differentially affect size classes and sexes, depending upon the time of year in which the hurricane occurred. Continual monitoring of these populations is important, especially in the context of ongoing global change. An increase in strong tropical cyclone frequency (every 2 or 3 yr) could impede the recovery of populations, while causing a continual decrease in crocodile body condition.

Acknowledgements. Fieldwork conducted from 2003 to 2015 was funded by El Colegio de la Frontera Sur, Fundación de Parques y Museos de Cozumel, Proyecto PAPIIT UNAM (IN215011-3), the Xcalak to Chinchorro Dive Center, Transbordadores del Caribe, and the Centro del Cambio Global y la Sustentabilidad en el Sureste A.C. P.C. received a bilateral Mexico–France doctoral scholarship (22/BFE/2005 457761B) from the Secretaría de Relaciones Exteriores de México and the Ministère des Affaires Étrangères de France (2006–2008), together with a post-doctoral scholarship from the Programa de Becas Posdoctorales, Universidad Nacional Autónoma de México (2011–2013). We thank Banco Chinchorro Biosphere Reserve, and the Fundación de Parques y Museos de Cozumel and their staff for logistical support, together with all of the volunteers who helped sample and capture crocodiles over 13 yr. The Secretaría de Medio Ambiente y Recursos Naturales of Mexico provided the scientific research permits for crocodile captures (Oficios no. SGPA/DGVS/ 02932/06, 02188/07, 02066/08, 02516/09, 00724/10, 04528/11, 03366/12, 03080/13). We are grateful to A.H. Escobedo-Galván for his comments on an earlier version of the manuscript.

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Appendix. Additional analyses

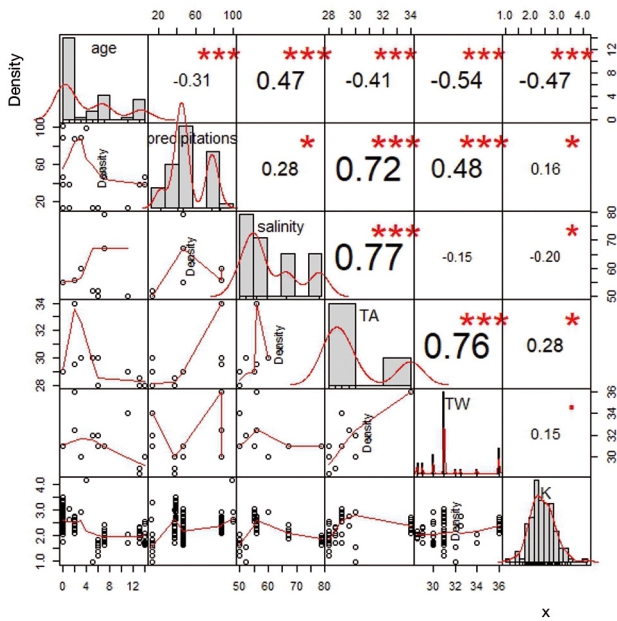


Fig. A1. Kendall's tau trellis chart of studied variables for the regression of hatchling age vs. body condition in American crocodiles. x: range of values of each variable, Density: relative frequency of values, TA: air temperature, TW: water temperature

Editorial responsibility: Robert M. Suryan, Juneau, Alaska, USA

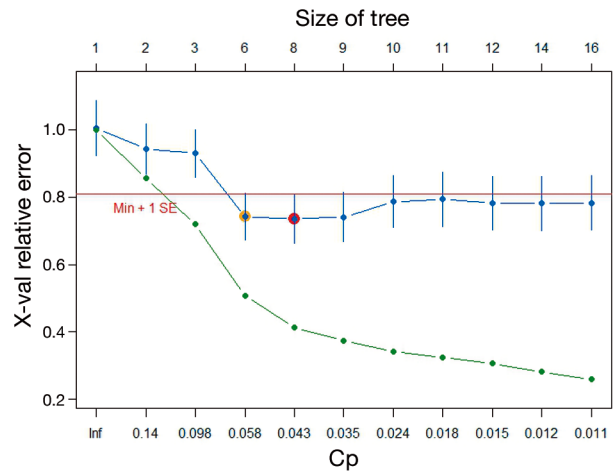


Fig. A2. Cross-validation of the regression tree to select the number of terminal leaves. The Cp term plotted along the x-axis is Mallows' Cp, which is a statistic used in multiple regression analysis to assess the fit of individual models by ordinary least squares. Cp provides a stopping rule in step-wise regression to avoid overfitting and, like AIC, is used in selecting an appropriate model among a set of candidates—probably ranging from a saturated model (all predictors in the model) to the null model case (estimate of the intercept). The green line represents the relative error, the blue line represents the cross-validated relative error (CVRE), and the red line the addition of one to the minimum value of relative error. An appropriate size of tree is achieved when cross-validation relative error is minimized; the red dot shows the solution with the lowest CVRE (number of leaves) while the orange dot shows the minimum size within one standard error of CVRE (number of nodes) in the final tree (Fig. 2)

Submitted: January 10, 2020; Accepted: July 14, 2020
 Proofs received from author(s): September 15, 2020