



Thermal fluctuation within nests and predicted sex ratio of Morelet's Crocodile



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ABSTRACT

Understanding the interplay between thermal variations and sex ratio in reptiles with temperature-dependent sex determination is the first step for developing long-term conservation strategies. In case of crocodylians, the information is fragmentary and insufficient for establishing a general framework to consider how thermal fluctuation influence sex determination under natural conditions. The main goal of this study was to analyze thermal variation in nests of *Crocodylus moreletii* and to discuss the potential implications for predicting offspring sex ratio. The study was carried out at the Centro de Estudios Tecnológicos del Mar N° 2 and at the Sistemas Productivos Cocodrilo, Campeche, Mexico. Data was collected in the nesting season of Morelet's Crocodiles during three consecutive seasons (2007–2009). Thermal fluctuations for multiple areas of the nest chamber were registered by data loggers. We calculate the constant temperature equivalent based on thermal profiles among nests to assess whether there are differences between the nest temperature and its equivalent to constant temperature. We observed that mean nest temperature was only different among nests, while daily thermal fluctuations vary depending on the depth position within the nest chamber, years and nests. The constant temperature equivalent was different among and within nests, but not among survey years. We observed differences between constant temperature equivalent and mean nest temperature both at the top and in the middle of the nest cavities, but were not significantly different at the bottom of nest cavities. Our results enable examine and discuss the relevance of daily thermal fluctuations to predict sex ratio of the Morelet's Crocodile.

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1. Introduction

Climate projections undertaken over the last two decades have triggered speculation as to the ecological and evolutionary consequences of future environmental changes on some reptiles (Hulin et al., 2009; Janzen, 1994; Mitchell and Janzen, 2010; Mrosovsky and Godfrey, 2010; Refsnider and Janzen, 2012). Future climate conditions are of interest as most reptile lineages, including many turtles, all sphenodontians, a few lizards, and crocodylians, exhibit temperature-dependent sex determination during embryonic development (Bull, 1980; Pieau, 1996), whereby environmental conditions during incubation could lead to skewed sex ratios, and potentially an increased risk of local population extirpations (Hulin et al., 2009). Temperature-dependent sex determination patterns are characterized by showing a pivotal temperature (i.e., temperature which produces a balanced sex ratio at

constant incubation temperature) and a transitional range of temperature (i.e., the range of temperatures that yields both sexes in variable proportions). Thus, environmental conditions during reproduction represent a powerful driver of population sex ratio dynamics in TSD species (Janzen, 1994).

Available data demonstrates that some temperature-dependent sex determination species can shift the timing of nesting, nest depth, or nest-site, in response to changes in environmental conditions (Lang et al., 1989; Simoncini et al., 2011; Zhang et al., 2009). For instance, Doody et al. (2006) observed that a lizard with TSD (*Physignathus lesueurii*) selected different nesting sites across its range depending on thermal conditions, while Telemeco et al. (2009) observed that *Bassiana duperreyi* shift nest depth and laying season in response to environmental temperatures. However, these changes mainly occur prior to females laying their eggs, hence offspring phenotype and sex differentiation depends on microclimate nest conditions (e.g., Charruau, 2012; Telemeco et al., 2009). Our basic knowledge of thermal fluctuation within the nest suggests that a change of temperature above or below the pivotal temperature during the lability period of gonadal development

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would drastically alter offspring sex ratio. However, key aspects of this general framework remain largely unknown, such as the interplay between the daily temperature fluctuation and offspring sex ratio in species with temperature-dependent sex determination.

Crocodylians are considered as temperature-dependent sex determination species with female-male-female pattern (reviewed in Deeming, 2004). Observations of the American Alligator *Alligator mississippiensis* found that low and high incubation temperatures produced females, while a majority of males were produced at intermediate temperatures (Ferguson and Joanen, 1983). Subsequent studies in laboratory and some in field conditions showed a similar pattern among extant crocodylian species (Campos, 1993; Charruau, 2012; Lang and Andrews, 1994; Lang et al., 1989; Piña et al., 2003; Thorbjarnarson et al., 2001; Webb et al., 1987). Despite the effect of incubation temperature on embryos and hatchlings traits has been well studied (Allsteadt and Lang, 1995; Lang et al., 1989; Miranda et al., 2002; Parachú Marco et al., 2010; Piña et al., 1997, 2003), we still know surprisingly little about the thermal fluctuations within crocodylian nests. Indeed, data of temperature variation within and between nests in natural conditions are few and recently published, particularly with regard to Neotropical *Crocodylus* (Antelo et al., 2010; Charruau 2012; López-Luna et al., 2015).

For the Morelet's Crocodile *Crocodylus moreletii*, many aspects of the nesting and reproductive ecology has been documented both in captivity and wild conditions (Casas-Andreu and Rogel-Bahena, 1986; Casas-Andreu et al., 2011; Hunt, 1975; López-Luna et al., 2011, 2015; Pérez-Higareda, 1980; Platt et al., 2008); however, thermal fluctuations within nests in particular are unknown (López-Luna et al., 2015). Available data of thermal variation and climatic effects on nest temperature are needed to further develop a general framework for predicting how environmental changes impact crocodylians (Simoncini et al., 2014). Particularly, species-specific data on how temperature fluctuates within nests, and the implications for predicting offspring sex ratios, are necessary to understand the responses of crocodylians to changing environmental conditions, and construct effective management and conservation plans (de Marcovaldi et al., 2014).

The present study aimed to assess thermal fluctuation within nests of the Morelet's Crocodile *Crocodylus moreletii*. First, we compared the nest temperature and daily thermal fluctuation within and between nests. Thereafter, we calculated the constant temperature equivalent based on thermal profiles among nests. Second, we evaluated differences between nests mean temperature and constant temperature equivalent of each nest depth (upper, middle and bottom). Third and finally, we examined the relevance of daily thermal fluctuations to predicted sex ratio, and discuss some ecological implications.

2. Methods

2.1. Study species

The Morelet's Crocodile, *Crocodylus moreletii*, is considered as an exclusively mound-nesting species (Campbell, 1972). The material for nests varies depending on choice of nesting site, and may consist of vegetation, soil, leaves, or woody debris, but in some cases is a mixture of mollusk shells, rocks, and sand, or even trash in areas with high levels of human activity (Casas-Andreu and Rogel-Bahena, 1986; Escobedo-Galván et al., 2009; López-Luna et al., 2011; Platt et al., 2008). This species can also build nests on a floating mat of grass (Escobedo-Galván et al., 2011; Pérez-Higareda, 1980; Platt et al., 2008). Morelet's Crocodile exhibits the TSD II pattern, in which females are produced at low and high

temperatures (< 31.5 °C, and > 33.5 °C), and males at intermediate temperatures (Lang and Andrews, 1994).

2.2. Data collection

The study was carried out at the Centro de Estudios Tecnológicos del Mar N° 2 (CETMAR) in Campeche City, and at the Biosistemas Productivos Cocodrilo (BPC), a local breeding farm operated by the Chiná community in Campeche State. At both sites crocodiles were kept in outdoor enclosures. The nests were not manipulated, facilitating incubation under natural conditions. In CETMAR females of *C. moreletii* built mounds mainly of sand, whereas at BPC females used leaves, grass, branches and soil to build mounds of vegetation.

Data from 17 nests of *C. moreletii* were collected during three consecutive nesting seasons from 2007 to 2009 (CETMAR, n=12; BPC, n=5). Clutch size was measured in only eight nests. After nest construction and oviposition was completed, the egg chamber of each nest was carefully opened, each egg was marked using a pencil on the top surface in order to maintain both the original position and orientation. In some cases, we evaluated the egg viability based on embryo development by banding (Ferguson, 1985). We placed dataloggers (UA-002-08, Onset Comp. Corp., Bourne, MA, USA) in each nest at the bottom, middle, and top of the egg chamber to measure daily thermal fluctuations under natural conditions. Dataloggers were placed the same day in all nests (the first record day varied among years), and were programmed to record nest temperature every hour until hatching. During the nesting season of 2007, we placed a datalogger at each study site (CETMAR and BPC) to record ambient temperature every hour in a shaded area at an average distance between nests. In addition, weather data of rainfall, and daily minimum and maximum temperature for Campeche City (19.8422 N, -90.5317 W, datum WGS84; elev. < 10 m) was provided by the Campeche Meteorological Station of the Comisión Nacional del Agua.

2.3. Data analysis

We did not have information on the time of oviposition, therefore we considered an approximate incubation period from the time the nest chamber was opened to hatching. We monitored incubation temperatures during an average of 57 ± 11 days (range 38 to 80 days, n=17) in each nest, which is more than half of the known incubation period of *C. moreletii*, and includes the thermo-sensitive period (Lang and Andrews, 1994; López-Luna et al., 2015; Platt et al., 2008).

Average daily nest temperature was used in statistical analysis and interpretation. Daily thermal fluctuation was calculated from the difference between maximum and minimum daily temperatures for each nest depth and by nests. Mean nest temperature was calculated from the three nest depths. After testing for normality and homogeneity of variances, a parametric one-way ANOVA test was used to examine differences in mean daily temperature and daily thermal fluctuation among nest depths within and between nests and years.

The ambient temperature was compared between study sites in 2007 using a two-sample *t*-test. Differences in ambient temperature (maximum and minimum) between years were tested using parametric one-way ANOVA; while a Kruskal-Wallis ANOVA was used to test differences in rainfall between years.

We used the model proposed by Georges (1989) to obtain constant temperature equivalents. This model transforms thermal fluctuation from natural nests into single value that is equivalent to a constant incubation temperature (Georges et al., 1994, 2004). We used one-way ANOVA tests to examine differences of constant temperature equivalent in different areas of the nest chamber (upper, middle and bottom), among nests and years. A two-sample *t*-test was applied to determine whether there were differences between mean nest temperature and constant temperature equivalents.

To compare and illustrate whether predicted sex ratios varied at different areas of the nest chamber (upper, middle and bottom) in response to thermal fluctuations, we used the mathematical model developed by Girondot (1999). This model is a standardized approach to determine the pivotal temperature that produces a balanced sex ratio at constant incubation temperature, and a transitional range of temperatures that yield both sexes in variable proportions, in order to describe patterns of temperature-dependent sex determination, and to predict sex ratio from nest temperature (Godfrey et al., 2003; Hulin et al., 2009). No data currently exists on the pattern of temperature-dependent sex determination for *C. moreletii*,

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