



Regional warming and the thermal regimes of American crocodile nests in the Tempisque Basin, Costa Rica



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ABSTRACT

Spatial variation in global climate change makes population-specific responses to this enigmatic threat pertinent on a regional scale. Organisms with temperature-dependent sex determination (TSD) potentially possess a unique physiological susceptibility that threatens population viability if rapid environmental effects on sex ratios render populations non-viable. A heavily male-biased sex ratio for hatching American crocodiles of the Tempisque Basin, Costa Rica requires assessment of how nest temperature affects sex determination at this site, how females might compensate for these effects when creating nests, and how current patterns of climate change might alter future sex ratios and survival in hatchling cohorts. We demonstrate high within-nest variation in temperature but predict a female bias at hatching based on nest temperatures quantified here. Further, our data suggest that egg size and metabolic heating associated with this factor outweighs microhabitat parameters and depth in influencing nest thermal regimes. Finally, we document regional warming in the Tempisque Basin over the last 15 years and project that further heating over the next 15 years will not yield hatchling sex ratios as male biased as those currently found at this site. Thus, we find no support for nest temperature or climate change as likely explanations for male-biased American crocodile (*Crocodylus acutus*) sex ratios in the Tempisque Basin.

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1. Introduction

Research on physiological, ecological and evolutionary responses to climate change is critical for the diagnosis of population-level responses in relation to this enigmatic factor (Whitfield et al., 2007). Vertebrate populations are susceptible to range shifts (Colwell et al., 2008), physiological pressures (Huey et al., 2003) and reproductive transitions (Refsnider and Janzen, 2012) when exposed to shifts in temperature on a regional scale. Of particular concern are species with sex determination mechanisms that rely on environmental stimuli, such as organisms with temperature-dependent sex determination (TSD; Doody et al., 2006). Sex ratios are less self-correcting in vertebrates with TSD than in those species with genetic sex determination and species with TSD are also more susceptible to anthropogenic influences (Doody et al.,

2006). Alteration of nesting habitat, endocrine-disrupting compounds and global climate change are all factors that can alter developmental regimes and bias the resulting sex of vertebrates that exhibit TSD (Doody et al., 2006). While changes in nesting phenology or location may compensate for shifts in thermal regimes on a regional scale (Refsnider and Janzen, 2012; Doody et al., 2006), these may not be sufficient to thwart demographic changes that will risk population viability (Girondot et al., 2004).

As evidenced by both experimental and field studies, climate change can negatively affect sex ratios of numerous vertebrate populations. Ospina-Álvarez and Piferrer (2008) noted that climate change of a magnitude predicted by current models is capable of altering sex ratios of fish species with sex chromosomes based on a thermal override of genetic differentiation. Such a mechanism has proven common among vertebrates (Holleley et al., 2015). Among species with TSD, climate change may also prove detrimental to rare species (Hawkes et al., 2007; Huey and Janzen, 2008; Mitchell et al., 2008) as a result of limited environmental refugia from a warming microclimate and subsequent constraints on reproductive phenology and sex ratio shifts. Although species

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with TSD may alter nesting phenology to compensate for climate change, such compensation may fail to match the pace of climate change (Schwanz and Janzen, 2008). Aquatic apex predators, such as crocodylians, may be particularly susceptible to sex ratio shifts that alter their interaction with humans from both positive (increased ecotourism) and negative (increased attacks on humans) perspectives. For example, Charruau (2012) reports a male-bias in hatchling American crocodiles (*Crocodylus acutus*) in Banco Chinchorro Biosphere Reserve, Mexico and relates this to recent regional temperature increases. Further, Charruau (2012) issues a warning that the sex ratio shift will depend on the magnitude of temperature increase and its effect on the female-male-female (FMF) sex determination scheme characteristic of the American crocodile, a scheme in which 31 °C and 33 °C are the temperatures between which males can be produced (Lang and Andrews, 1994; Charruau, 2012).

Murray et al. (2015) and Bolaños-Montero (2012) report an unusually high male-bias in American crocodiles of the Tempisque Basin, Guanacaste, Costa Rica. This 3.4:1 male bias is one of the most extensive male biases within the genus *Crocodylus* reported to date (Thorbjarnarson, 1997). Charruau et al. (2005) recover a 6.8: 1 M: F sex ratio bias in *C. acutus* in Banco Chinchorro, Mexico among 53 individuals, however, mark-recapture techniques were not utilized. The Tempisque drainage population is large, rapidly growing and has been subject to frequent conflict with humans in recent years (Valdelomar et al., 2012). Here, we test the hypothesis that crocodile nest temperatures predict the male-biased hatchling sex ratio observed in Murray et al. (2015). We describe crocodile nest temperature profiles and test for correlations between nest thermal regimes and environmental variables to assess the compensatory effect of nest location as a variable that allows regulation of hatchling sex ratios. Further, we utilize current nest temperature profiles and patterns of temperature increase over the past 15 years to predict the sex ratio of offspring in the Tempisque Basin 15 years into the future.

2. Methods

2.1. Field methods

Between 2012 and 2014 twenty-five *Crocodylus acutus* nests were located along waterways surrounding Palo Verde National Park. These drainages included the irrigation drain on the north-west border of the park, the Tempisque River between El Viejo sugarcane farm and the Bebedero River junction, and the Bebedero River between the northeast border of the park and the Tempisque River [see Murray et al. (2015) for detailed description of the study site]. Nests were located from a boat via visual inspection of the bank for slides, cleared areas, and suitable substrate. The banks of all potential nesting waterways were searched every other day ensuring that all nests were discovered within 2 days of construction and egg deposition.

Canopy cover at each nest was quantified using the canopy-scope method (Brown et al., 2000), a more nest-specific quantification compared to the methodology of Doody et al. (2006). Laying face-up on the nest surface looking directly perpendicular to the ground, the grid is held 20 cm away from the eye, standardized by a measured string attached to the scope. The proportion of canopy foliage intersecting the line of sight between the scope and sky was recorded. Solar radiation was not recorded because all nests were situated on flat surfaces. Each nest cavity was excavated by carefully removing the loose dirt over the nest hole and nest depth, egg size (pole diameter to nearest mm) and number of eggs were recorded. Nest depth was recorded post-excavation as the distance from the soil surface to the bottom of the deepest egg. Eggs were

carefully removed and their orientation marked with a pencil to avoid rotation during nest excavation. They were then replaced in the nest, along with a set of Ibutton thermal data loggers (model: DS1922L, accuracy: -40 °C to $+85$ °C, precision: ± 0.5 °C, Maxim Integrated, INC.), and covered as similarly as possible to the original nest structure. The thermal data loggers were sealed in beeswax and placed in plastic eggs half filled with water and sealed with waterproof tape. To test this logger system, Ibuttons were inserted into a small rectangular hole cut in infertile chicken eggs. This hole was covered and plastic egg and infertile chicken egg designs were paired and laid on a windowsill. The plastic egg design matched the thermal fluctuations of infertile chicken eggs in these lab trials. Four loggers were placed in each nest, one at the bottom, center, top, and on the side nearest the water. Each logger recorded temperature every 30 min for a minimum of two weeks and a maximum of 3.5 weeks during the 4 weeks of the middle third of incubation (days 30–60 of a 90-day incubation period; Charruau, 2012). Because the date of egg deposition was known and nest variables were quantified during the middle third of incubation, our loggers, inserted after the first third of incubation, recorded the thermal regime during the portion of development when sex is determined (Georges et al., 2004). Loggers were recovered by re-excavating nests. Only thirteen of the 25 nests were available for data collection due to predation of the remaining nests. The eggs were covered after re-excavation so that the nests could continue to be monitored for aspects of a separate study.

In 2014, reference thermal loggers were buried one meter away from the center of each of four nests, with the reference logger placed at the same depth and same distance from water as the center of the paired nest. Nest hole substrate and canopy cover did not qualitatively differ among these four nests. Thereby, these loggers provide a control against which metabolic heat produced by a clutch might be compared. One reference logger was not recovered, so the sample size was three for this analysis.

2.2. Thermal analyses

Trends in nest thermal regimes were assessed in two ways. First, we used data from the thermal loggers to characterize the mean temperature for each location within a nest, and the variation around that mean. These summary statistics were used to describe the thermal environment within and between nests. Top, center, and bottom recordings characterized thermal profiles in the vertical axis and side temperatures were extrapolated to all sides of the nest along the horizontal axis (Fig. 1). Second, we used data pooled for all loggers within a nest to explore the influence of nest parameters on nest temperature and temperature variance. For this analysis, multiple linear regression was performed in R (R Development Core Team, 2011) using mean temperature and variance as dependent variables and canopy cover, nest depth, egg number, and egg size as independent variables. We also tested these independent variables against the average logger temperature at the top position of the nest, assumed to be the most environmentally influenced location of the nest (Charruau, 2012). A Welch's *T* test was implemented in R (R Development Core Team, 2011) to explore relationships between important nest parameters and nest temperatures.

We used data from the thermal loggers to predict the sex of offspring expected to hatch from each nest. To do this, the mean temperature for each location was converted to a constant temperature equivalent (CTE), the temperature above and below which half of embryonic development is estimated to have occurred (Georges et al., 1994, 2004). Developmental rates among incubation thermal regimes are not available for *Crocodylus acutus*. Instead, data from Lang and Andrews (1994) on alligator development were used as a proxy for crocodylian developmental rates

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