

First evidence for a latitudinal body mass effect in extant Crocodylia and the relationships of their reproductive characters

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Received 1 October 2019; revised 21 December 2019; accepted for publication 23 December 2019

Relationships between distribution patterns and body size have been documented in many endothermic taxa. However, the evidence for these trends in ectotherms generally is equivocal, and there have been no studies of effects in crocodylians specifically. Here, we examine the relationship between latitudinal distribution and body mass in 20 extant species of crocodylians, as well as the relationships between seven important reproductive variables. Using phylogenetically independent contrasts to inform generalized linear models, we provide the first evidence of a latitudinal effect on adult female body mass in crocodylians. In addition, we explore the relationships between reproductive variables including egg mass, hatchling mass and clutch size. We report no correlation between egg mass and clutch size, upholding previously reported within-species trends. We also find no evidence of a correlation between measures of latitudinal range and incubation temperature, contrasting with the trends found in turtles.

ADDITIONAL KEYWORDS: biogeography – body size – crocodylians – generalized linear model – latitude – reproduction.

INTRODUCTION

The broad impact of climate on the body size of numerous vertebrate and invertebrate groups has been demonstrated across latitudinal (Ray, 1960; Wooller *et al.*, 1985; Graves, 1991; Kaspari & Vargo, 1995; Saunders & Tarling, 2018) and altitudinal (Bernadou *et al.*, 2016; Davis and Burtt, 2019; Yu *et al.*, 2019) gradients, insofar as these correlate with temperature gradients. While evidence for latitudinal size gradients is common in endotherms (Ashton, 2002a; Blackburn & Hawkins, 2004), the effect of latitude on ectotherm body sizes is more controversial (Ashton & Feldman, 2003; Pincheira-Donoso *et al.*, 2008). For example, amphibians (Ashton, 2002b; Adams & Church, 2008), lizards (Ashton & Feldman, 2003; Cruz *et al.*, 2005; Pincheira-Donoso *et al.*, 2008) and turtles (Ashton &

Feldman, 2003; Lindeman, 2008; Angielczyk *et al.*, 2015) have all been the subjects of studies with a diversity of findings. Strikingly, however, no previous studies have attempted to test whether this correlated variation applies to another major group of living reptiles, the crocodylians.

Crocodylians are a vital component of their ecosystems, often acting as keystone species in tropical regions (Ashton, 2010). They represent the last surviving pseudosuchian archosaurs, a clade that once inhabited every continent and that has persisted for at least 230 Myr (Irmis *et al.*, 2013; Turner *et al.*, 2017). Having survived the devastating Cretaceous–Palaeogene (K-Pg) mass extinction (Bronzati *et al.*, 2015; Puértolas-Pascual *et al.*, 2016), as well as a number of other, smaller or more protracted major extinction events (Hutchison, 1982; Markwick, 1993; Toljagic & Butler, 2013; Mannion *et al.*, 2015), crocodylians have demonstrated remarkable resilience to cataclysmic

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climate change and habitat loss (Toljagić & Butler, 2013). Despite this, half of all extant crocodylian species are currently threatened with extinction and, at the current rate, vertebrate species loss will soon equal or even exceed that of the K-Pg event (Barnosky *et al.*, 2011; Pievani, 2014; Lécuyer, 2018). To understand possible future trends in crocodylian diversity more fully, it is important that their current diversity, ecology and distribution are fully characterized (Fig. 1). Despite previous work in this area (Martin, 2007; Pierce *et al.*, 2008; Nicolai & Matzke, 2019), the nature of the relationship between geographical distribution and the reproductive biology of living crocodylians is unclear.

The resilience of crocodylians to historical mass extinctions is also much debated. Previous work has implicated many different factors in their survival, including diet (Sheehan & Hansen, 1986), aquaticism (Robertson *et al.*, 2013), famine resistance (Robertson *et al.*, 2013), induction of torpor at low air or water temperatures (Almandariz, 1975; Brisbin *et al.*, 1982; Sun *et al.*, 2019), and their propensity to burrow to take refuge from harsh environmental conditions (Thorbjarnarson, 1989; Mobaraki *et al.*, 2015). Another hypothesis concerns their unique reproductive biology (Charruau *et al.*, 2017). Crocodylians have no sex chromosomes and hatchling sex is thought to be fully controlled by incubation temperature. Temperature-dependent sex determination (TSD) systems have a threshold that yields an approximately 1:1 ratio of males and females at equilibrium (Escobedo-Galván

et al., 2016). Higher temperatures produce a greater proportion of males, whereas lower temperatures produce more females (Deeming & Ferguson, 1989; González *et al.*, 2019). Counterintuitively, the highest tolerable incubation temperatures produce mostly females, although these frequently fail to thrive (Marco *et al.*, 2017). TSD was proposed as a possible buffer to extinction by Woodward & Murray (1993). Harsh environmental conditions are usually associated with a fall in ambient temperatures, and in species that utilize TSD these can result in a female-biased primary sex ratio (Tomillo *et al.*, 2014; Carter *et al.*, 2018). While lower temperatures may be consistent with the initial 'nuclear winter' effect of the end-Cretaceous bolide impact (Vellekoop *et al.* 2014, 2016), the longer-term warming resulting from increasing atmospheric greenhouse gas concentrations (Harrington, 2001; Turner, 2018) would be expected to skew sex ratios in favour of males. The latter scenario has been hypothesized as the most likely outcome of current trends in global warming (Miller *et al.*, 2004). Although TSD has been well documented within crocodylian species (Ferguson & Joanen, 1982; Deeming, 2004; Piña *et al.*, 2007), no comparisons of the effects of threshold temperature on development have been attempted across species, and little is known concerning the interrelationships between crocodylian reproductive characters.

The reproductive characters of crocodylians were first surveyed by Thorbjarnarson (1996). This work identified allometric relationships between egg mass,

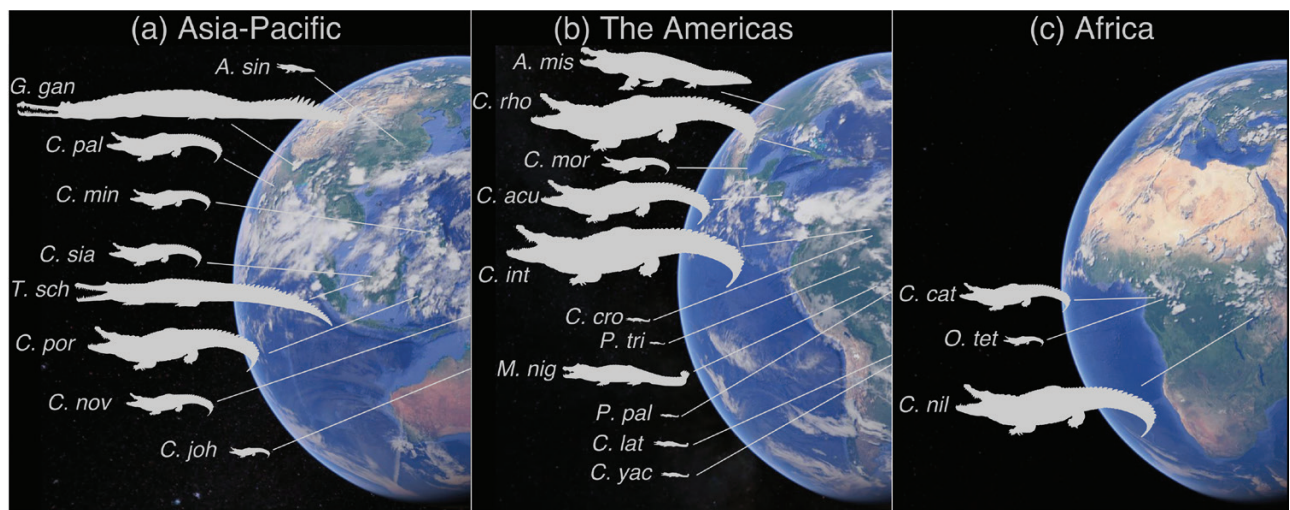


Figure 1. A representation of the relationship between the mean adult female body masses of 23 species of crocodylian and their latitudinal midpoint. Silhouette th scaled to body mass. (a) Asia-Pacific, (b) The Americas, (c) Africa. Abbreviations (Asia-Pacific): *Alligator sinensis*, *Gavialis gangeticus*, *Crocodylus palustris*, *Crocodylus mindorensis*, *Crocodylus siamensis*, *Tomistoma schlegelii*, *Crocodylus porosus*, *Crocodylus novaeguineae*, *Crocodylus johnstoni*. (Americas): *Alligator mississippiensis*, *Crocodylus rhombifer*, *Crocodylus moreletii*, *Crocodylus acutus*, *Crocodylus intermedius*, *Caiman crocodilus*, *Paleosuchus trigonatus*, *Melanosuchus niger*, *Paleosuchus palpebrosus*, *Caiman latirostris*, *Caiman yacare* (Africa): *Crocodylus cataphractus*, *Osteolaemus tetraspis*, *Crocodylus niloticus*. *Mesticops leptorhynchus*, *Crocodylus suchus* and *Osteolaemus osborni* were excluded due to lack of reliable female mass data.

clutch size, clutch mass and female length: patterns that had previously been observed in other vertebrate groups (Rohwer, 1988; Sinervo & Licht, 1991; Shine, 1992). However, the correlations and causal interactions between these reproductive variables were not the focus of this study.

Here, we used generalized linear models (GLMs) to test the relationships between the latitudinal distribution of extant crocodylian taxa and a variety of their important reproductive variables. We also tested whether there are significant relationships *between* those reproductive variables. In the context of these findings, we highlight some key questions concerning the reproductive biology, behaviour and social systems of wild crocodylians that could be addressed by future empirical and modelling work.

METHODS

DATA COLLECTION

We compiled data from the literature for seven morphological, environmental and reproductive variables across 24 extant crocodylian species (Supporting Information Appendix S1). We used the species list in Grigg & Kirschner (2015) (Fig. 1) and included one recently described species (*Mecistops leptorhynchus*) (Shirley 2018). Recent taxonomic uncertainty makes the attribution of some reproductive data unclear, and two species (*Crocodylus suchus* and *Osteolaemus osborni*) were therefore excluded (Shirley *et al.*, 2018; Hallmann and Griebeller, 2018; Isberg *et al.*, 2019). The data compiled were:

1. Maximum latitudinal range (°)
2. Midpoint of latitudinal range (°)
3. Mean mass of breeding-age female (kg)
4. Mean fresh egg weight (g)
5. Mean hatchling mass (g)
6. Threshold incubation temperature, or the temperature at which a clutch will produce ~50% males and 50% females (°C). The lower (female to male) threshold was selected in this case because females are often inviable at the higher (male to female) threshold.
7. Mean clutch size (number of eggs laid)
8. Mean duration of incubation (days)

We reviewed the literature in Google Scholar by searching for each species individually, coupled with appropriate terms (e.g. '*Crocodylus porosus* clutch size', '*Caiman yacare* body mass'). Variations on these were used as necessary (e.g. '*Caiman yacare*'/'*Caiman jacare*' + 'body mass'/'female mass'/'weight'/'kg'). These were searched until pages returned only irrelevant results. Data were collated into a single spreadsheet

(Supporting Information Appendix S1). Continuous variables (female mass, egg mass, hatchling mass, clutch size and duration of incubation) were averaged to smooth over outlier results that were unrepresentative. The literature contains data from individual captive-bred and wild-caught specimens, as well as values that are themselves averages from various heterogeneous samples. This constrains the precision of our data, but we believe that there is a homogeneous distribution of error. In addition, data on female mass were often derived from adults of different ages, and these were then averaged across multiple individuals and studies (Appendix S1). Data on latitudinal range were taken from the IUCN Red List of threatened species (IUCN, 2019).

For one species, *Tomistoma schlegelii*, there was insufficient information in the literature, and we therefore used data from our own observations. Hatchling mass data (see Supporting Information Appendix S1) were averaged from a captive-born clutch laid at 'Crocodiles of the World', Oxfordshire, UK. This clutch consisted of 17 eggs, of which 14 successfully hatched (although one infant failed to thrive and died shortly after hatching). Eggs were laid on 16 April 2016 by an imported farm-raised female measuring 2.3 m (snout-vent length). Eggs were separated and artificially incubated at 32.6 °C (three eggs), 32.0 °C (five eggs), 31.5 °C (five eggs) and 29.8 °C (four eggs), and hatched after 92, 94, 95 and 103 days, respectively. Hatchlings were weighed using a Marsden Super-SS B-100 waterproof electronic scale, accurate to 0.10 g.

STATISTICAL ANALYSIS

For indicative purposes, non-phylogenetically controlled bivariate correlations between our seven variables are visualized in Figure 2. These were further tested using phylogenetic generalized least squares (PGLS). These results, and the literature on archosaur reproduction generally and crocodylians specifically were used to frame five hypotheses:

1. Adult female mass is positively correlated with latitudinal midpoint, maximum latitudinal range, egg mass, hatchling mass and/ or clutch size, as in some species of crocodylians (Verdade, 2001; Campos *et al.*, 2008; Murray *et al.*, 2013) and birds (Wendeln, 1997).
2. Egg mass is positively correlated with female mass, hatchling mass and/or clutch size, as in some species of crocodylians (Verdade, 2001; Murray *et al.*, 2013), birds (Wiebe & Bortolotti, 1995) and turtles (Wallace *et al.*, 2006).
3. Hatchling mass is positively correlated with adult female mass, latitudinal midpoint, maximum latitudinal range and/or egg mass, as in some

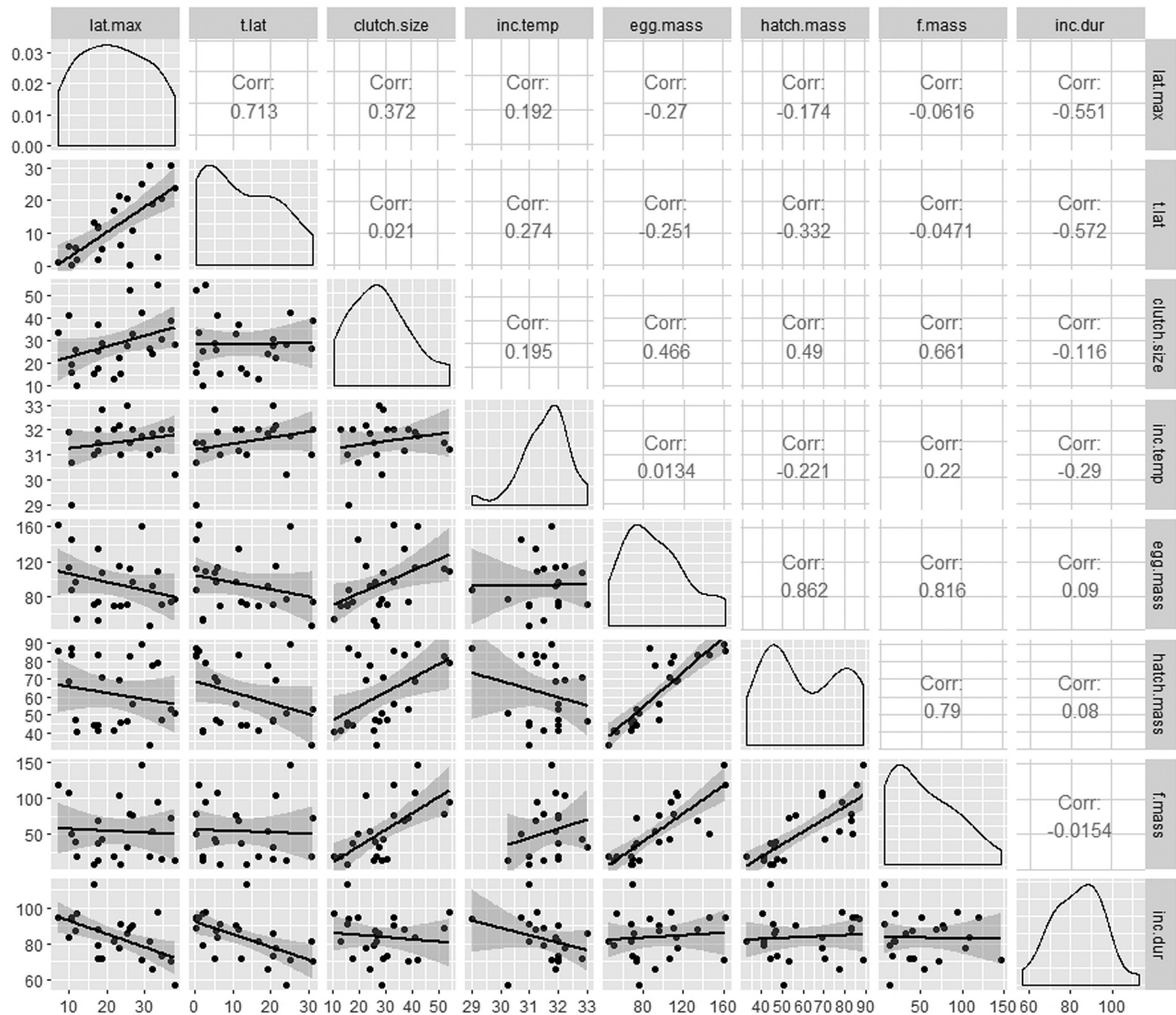


Figure 2. Spearman's correlation matrix indicating positive correlations between morphological reproductive traits (female mass, egg mass, hatchling mass), and negative correlations between latitudinal midpoint, threshold incubation temperature and incubation duration. Abbreviations: clutch.size, mean clutch size; egg.mass, log mean fresh egg weight; f.mass, log mean adult female body mass; hatch.mass, log mean hatchling mass; inc.dur, mean duration of incubation; inc.temp, threshold incubation temperature; lat.max, maximum latitudinal range; t.lat, latitudinal midpoint.

species of crocodylians (Verdade, 2001; Murray *et al.*, 2013), birds (Ricklefs, 1984; Smith *et al.*, 1993) and turtles (Roosenburg & Kelley, 1996; Wallace *et al.*, 2006).

4. Clutch size is positively correlated with adult female mass, egg mass, latitudinal midpoint, maximum latitudinal range and/or duration of incubation, as in some species of crocodylians (Verdade, 2001; Campos *et al.*, 2008; Murray *et al.*, 2013), birds (Erikstad *et al.*, 1993; Monaghan *et al.*, 1995) and turtles (Roosenburg & Kelley, 1996).

5. Threshold incubation temperature is positively correlated with latitudinal midpoint, maximum latitudinal range and/or hatchling mass, as in turtles (Ewert *et al.*, 2005).

The phylogeny of O' (Brien *et al.* 2019) was used to produce phylogenetically independent contrast (pic) values for each variable. These pic values (rather than our raw data) were used in the subsequent GLM analyses. This tree was constructed using multiple specimens representing each species and the tree was first pruned to remove duplicate

specimens ('Alligator_mississippiensis2', 'Alligator_mississippiensis3', etc.). The first entry was kept by default in each case. Rooting and branch lengths were kept consistent with those published by O' (Brien *et al.* 2019).

Before calculating the pic values, conspicuously non-normal continuous variables (female mass, egg mass and hatchling mass only) were log-transformed. Four species were excluded from our dataset because they were absent from the phylogeny of O' Brien *et al.* (2019) (*Crocodylus intermedius*, *Crocodylus moreletii*, *Caiman yacare* and *Masticops leptorhynchos*), leaving 20 species in the final analyses. We used the Akaike information criterion (AIC) to identify the minimum adequate model by backward stepwise deletion of poorly fitting variables. All models used the 'Gaussian' error family and 'identity' link function, and were implemented in the statistical software environment R, using the *GGally*, *ape* and *phytools* packages (version 3.5.3) (R Core Team, 2013).

We constructed five GLMs based on the phylogenetically independent contrasts of all variables (Table 1). Models 3 and 5 were produced from a modified phylogeny of 17 species, excluding *Crocodylus novaeguineae*, *Osteolaemus tetraspis* and *Tomistoma schlegelii*. This was because threshold incubation temperature data were not available for these species, and also because threshold incubation temperature was shown through our Spearman's rank test (Fig. 2) to correlate with hatchling mass (model 3), incubation duration and latitudinal values (model 5).

RESULTS

A Spearman's correlation matrix of our results is shown in Figure 2. The strongest positive correlations were between morphological reproductive characteristics [female mass vs. egg mass ($r_s = 0.85$, $P < 0.0001$), female mass vs. hatchling mass ($r_s = 0.79$, $P < 0.0001$), and egg mass vs. hatchling mass ($r_s = 0.94$, $P < 0.0001$)]. Other correlated traits were: (1) latitudinal midpoint vs. duration of incubation ($r_s = -0.60$, $P = 0.0007$); (2) female mass vs. clutch size ($r_s = 0.67$, $P = 0.0017$); (3) egg mass vs. clutch size ($r_s = 0.56$, $P = 0.0121$); (4) hatchling mass vs. clutch size ($r_s = 0.64$, $P = 0.0032$); (5) maximum latitudinal range vs. clutch size ($r_s = 0.045$, $P = 0.463$); and (6) latitudinal midpoint vs. duration of incubation ($r_s = -0.60$, $P = 0.0055$). PGLS analyses supported the following significant relationships: (1) female mass vs. egg mass ($P = 0.0008$); (2) female mass vs. hatchling mass ($P = 0.0003$); (3) egg mass vs. hatchling mass ($P < 0.0001$); (4) latitudinal midpoint vs. duration of incubation ($P = 0.0073$); (5) female mass vs. clutch size ($P = 0.0072$); (6) hatchling mass vs. clutch size ($P = 0.0154$); and (7) latitudinal midpoint vs.

duration of incubation. Some relationships were not supported by PGLS analysis: (1) egg mass vs. clutch size ($P = 0.0706$); and (2) maximum latitudinal range vs. clutch size ($P = 0.1213$).

FEMALE MASS

Model 1 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, egg mass, hatchling mass, clutch size and duration of incubation on female mass (Supporting Information Appendix S2 – initial and final models). The final model (Table 2) was the result of backward stepwise deletion based on AIC value as a measure of model efficiency. This model explained 85% of the deviance associated with adult female mass (D^2). Mean clutch size ($P = 0.0017$) was the most significant correlator to log mean female mass, followed by mean latitudinal range ($P = 0.0026$), log mean hatchling mass (0.0027) and maximum latitudinal range ($P = 0.0133$). Log mean egg mass and mean incubation duration both correlated poorly with log mean female mass and were dropped from the model.

EGG MASS

Model 2 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, female mass and clutch size on egg mass (Supporting Information Appendix S2). The final model (Table 3) explained 68% of the deviance associated with egg mass (D^2). Log mean female mass ($P < 0.0001$) was the only

Table 1. Initial structure of generalized linear models analysing relationships between phylogenetically independent contrasts in the reproductive characters of extant Crocodylia

Model number	Dependent variable	Independent variables
1	f.mass	Lat., egg.mass, hatch.mass, clutch.size, inc.dur
2	Egg mass	Lat, f.mass, clutch.size
3	Hatch.mass	Lat., f.mass, egg.mass, clutch.size, inc.temp, inc.dur
4	Clutch.size	Lat., f.mass, egg.mass, inc.temp.
5	Inc.temp.	Lat., egg.mass, hatch.mass, clutch.size, inc.dur

All models were conducted using the 'Gaussian' error family and 'identity' link function. Abbreviations: clutch.size, mean clutch size; egg.mass, log mean fresh egg weight; f.mass, log mean adult female body mass; hatch.mass, log mean hatchling mass; inc.dur, mean duration of incubation; inc.temp, threshold incubation temperature; lat.max, maximum latitudinal range; t.lat, latitudinal midpoint

significant correlator to log mean egg mass. Latitudinal midpoint and mean clutch size correlated poorly with log mean egg mass and were dropped from the model.

HATCHLING MASS

Model 3 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, female mass, egg mass, clutch size, threshold incubation temperature and incubation duration on hatchling mass (Appendix S2). The final model (Table 4) explained 90% of the deviance associated with hatchling mass (D^2). Log mean egg mass ($P < 0.0001$) was the only significant correlator to hatchling mass. Log mean female mass, latitudinal midpoint, mean clutch size and mean incubation duration correlated poorly with hatchling mass and were dropped from the model.

CLUTCH SIZE

Model 4 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal

range, female mass, egg mass and hatchling mass (Supporting Information Appendix S2). The final model (Table 5) explained 87% of the deviance associated with clutch size (D^2). The most significant correlators to mean clutch size were log mean female mass ($P < 0.0001$) and maximum latitudinal range ($P < 0.0001$), followed by latitudinal midpoint ($P = 0.0007$) and mean duration of incubation ($P = 0.1071$). Egg mass and hatchling mass were found to correlate poorly with clutch size, and were dropped from the model.

THRESHOLD INCUBATION TEMPERATURE

Model 5 was constructed to account for the potential effects of latitudinal midpoint, maximum latitudinal range, female mass, egg mass, hatchling mass, clutch size and incubation duration on threshold incubation temperature (Supporting Information Appendix S2). The final model (Table 6) explained 42% of the deviance associated with threshold incubation temperature (D^2). The only significant correlator to threshold

Table 2. A generalized linear model (Model 1) describing the effect of latitudinal midpoint, maximum latitudinal range, hatchling mass and clutch size on the adult female mass of 20 species of crocodylian

Term	Coefficient	SE	<i>F</i>	<i>P</i>
t.lat	0.0421	0.0115	13.311	0.0026**
lat.max	-0.0365	0.0129	8.0132	0.0133*
log.hatch	1.1638	0.3206	13.175	0.0027**
clutch.size	0.0348	0.0090	15.047	0.0017**

$D^2 = 0.8510$. SE, standard error; *F*, *F*-value; *P*, *P*-value.

Table 3. A generalized linear model (Model 2) describing the effect of maximum latitudinal range and adult female mass on the fresh egg weight of 20 species of crocodylian

Term	Coefficient	SE	<i>F</i>	<i>P</i>
max.lat	-0.0074	0.0049	1.9114	0.1858
log.f.mass	0.5117	0.0809	33.295	<0.0001***

$D^2 = 0.6776$. SE, standard error; *F*, *F*-value; *P*, *P*-value.

Table 4. A generalized linear model (Model 3) describing the effect of female body mass and fresh egg weight on the hatchling mass of 17 species of crocodylian

Term	Coefficient	SE	<i>F</i>	<i>P</i>
lat.max	0.0052	0.0032	2.6903	0.1269
log.egg.mass	0.8348	0.0841	98.483	<0.0001***
inc.temp	-0.0751	0.0505	2.2103	0.1629

$D^2 = 0.8997$. SE, standard error; *F*, *F*-value; *P*, *P*-value.

Table 5. A generalized linear model (Model 4) describing the effect of adult female mass, latitudinal midpoint, maximum latitudinal range and incubation duration on the clutch sizes of 20 species of crocodylian

Term	Coefficient	SE	<i>F</i>	<i>P</i>
log.f.mass	11.9056	2.0480	33.796	<0.0001***
t.lat	-0.8362	0.1955	18.291	0.0007***
lat.max	1.0462	0.1804	33.623	<0.0001***
inc.dur	0.2435	0.1414	2.9650	0.1071*

$D^2 = 0.8662$. SE, standard error; *F*, *F*-value; *P*, *P*-value.

Table 6. A generalized linear model (Model 5) describing the effects of maximum latitudinal range, fresh egg weight, hatchling mass and duration of incubation on the threshold incubation temperature of 17 species of crocodylian

Term	Coefficient	SE	<i>F</i>	<i>P</i>
inc.dur	-0.0260	0.0081	10.201	0.0065**

$D^2 = 0.4215$. SE, standard error; *F*, *F*-value; *P*, *P*-value.

incubation temperature was mean incubation duration ($P = 0.0065$). Log mean female mass, log mean egg mass, log mean hatchling mass, mean clutch size, latitudinal midpoint and maximum latitudinal range all correlated poorly with threshold incubation temperature and were dropped from the model.

DISCUSSION

GENERAL OVERVIEW

A robust, positive correlation between latitude and body size has been well documented in endotherms (Gillman *et al.*, 2009; Torres-Romero *et al.*, 2016), but is much less compelling among ectotherms (Ashton & Feldman, 2003; Cruz *et al.*, 2005; Lindeman, 2008), and has never been tested for in crocodylians. Here, we demonstrate that, despite low overall correlation coefficients, both latitudinal midpoint and maximum latitudinal range correlate significantly with adult female mass once the effects of phylogeny and other potentially confounding reproductive variables are controlled for ($P = 0.0026$ and 0.0133 respectively, see Model 1). Furthermore, we describe significant relationships between some important morphological reproductive variables across crocodylians as a whole, a phenomenon that has previously been described only within species (Verdade, 2001; Campos *et al.*, 2008; Murray *et al.*, 2013). We demonstrate that these relationships are discrete with, for example, a significant effect of female mass on egg mass, and of egg mass on hatchling mass, but no direct effect of female

mass on hatchling mass. Female mass is a significant predictor of clutch size in crocodylians, as well as both the latitudinal midpoint and maximum latitudinal range. We did not detect any significant relationship between threshold incubation temperature and either latitudinal midpoint or maximum latitudinal range (see Model 5). Some of the most biologically significant relationships described by our models are presented in Figure 3.

IMPLICATIONS OF RESULTS

The strongest associations in our study are between morphological reproductive variables (Models 1, 2 and 3). These include adult female mass, fresh egg weight, hatchling mass and clutch size (Fig. 3). Intraspecific relationships of this kind have previously been documented in the American alligator (*Alligator mississippiensis*) (Murray *et al.*, 2013) and in the broad-snouted, spectacled and Yacare caimans (*Caiman latirostris*, *Caiman crocodilus* and *Caiman yacare*) (Verdade, 2001; Larriera *et al.*, 2004; Campos *et al.*, 2008). Here, we verify the same trends across extant crocodylians as a whole. We report a significant positive effect of female mass upon clutch size (Model 4), a result that contrasts with the findings of previous species-level studies (Verdade, 2001). We find no evidence for any correlation between egg mass and clutch size, which is a biological trade-off that has been described in many other taxa (Lack, 1967; Sinervo & Licht, 1991; Rowe, 1994).

We found no significant relationship between threshold incubation temperature and hatchling mass (Models 3 and 5), suggesting that the temperature required to produce an even sex ratio is not significantly different in crocodylian species that produce large hatchlings compared with those that produce small hatchlings. This result is consistent with previous studies that examined trends within species (Joanen & McNease, 1989; Campos, 1993). The effects of contemporary climatic warming on the reproductive biology of crocodylians have yet to be examined (Zhang *et al.*, 2009; Simoncini *et al.*, 2014), but based on deep-time associations between crocodylian distributions

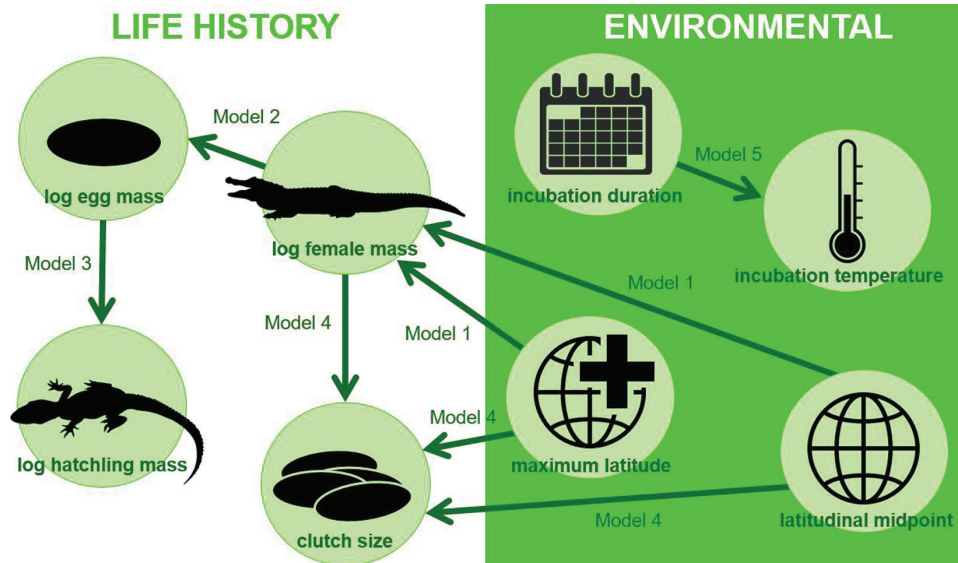


Figure 3. Map of the interactions between some important reproductive variables in Crocodylia. Positive relationships shown are between latitudinal midpoint and log mean female mass ($P = 0.0026$); maximum latitudinal range and log mean female mass ($P = 0.0133$); log mean egg mass and log mean female mass ($P < 0.0001$); log mean egg mass and log mean hatchling mass ($P < 0.0001$); log mean female mass and mean clutch size ($P < 0.0001$); maximum latitudinal range and mean clutch size ($P < 0.0001$); latitudinal midpoint and mean clutch size ($P = 0.0007$); and mean incubation duration and threshold incubation temperature ($P = 0.0065$).

and climate change (Markwick, 1998; Quintero & Wiens, 2013; Mannion *et al.*, 2015), it is plausible that all crocodylians are vulnerable to rapid warming, and that this should be considered a threat to local populations (Dudgeon, 2014).

Our results suggest that the only significant correlator to threshold incubation temperature in crocodylians is incubation duration (Model 5). This factor may help to explain the diversity of threshold incubation temperatures as, within species, eggs incubated at higher temperatures tend to hatch sooner than those incubated at lower temperatures (see section on *Tomistoma schlegelii*, Methods).

We identified no significant relationships between the threshold incubation temperature and either the mean or the maximum latitudinal range of crocodylians (Model 5). This suggests that the nest temperature of crocodylians is affected by factors other than latitudinal distribution. This stands in contrast to the relationship observed in turtles, in which latitude has a significant effect on reproductive traits and nest temperature (Iverson *et al.*, 1993; Ewert *et al.*, 2005). The clutch size of turtles correlates with latitude (Iverson *et al.*, 1993) and their sex ratio is affected by annual temperature fluctuations (Janzen, 1994). This supports observed differences in the nest functions and parental roles of turtles and crocodylians, and suggests that the presence of adult crocodylians at the nest plays a much greater

role in the temperature regulation of their nests than in turtles. Our results suggest that other factors (possibly the position, construction, location, shape or size of the nest) could contribute to the maintenance of an acceptable nest temperature (see also Grigg, 1987; Brazaitis & Wantanabe, 2011). In turtles, nest temperature is determined by ambient temperature and climate to a much higher degree (Hays *et al.*, 2010; Refsnider *et al.*, 2013; Santidrián *et al.*, 2015). Future research on the behaviour of nesting crocodylians may be necessary to shed further light on nest temperature regulation.

LIMITATIONS AND FUTURE WORK

We note that some sources in the literature measured female mass at first laying, while others measured older females. Because crocodylians grow consistently after sexual maturity (Seymour *et al.*, 2013), this could produce variable results. While our data were means from all of the published studies we were able to identify, we recognize the limitations of literature-based data collection, and acknowledge that the standardized collection of primary data would be preferable. This use of species mean values for mass, latitudinal distribution and clutch size also masks both population-level and biogeographical variation (Simoncini *et al.*, 2009). Gathering these additional data would offer greater power, and enable both within- and cross-species comparisons.

An extension of the present study could include additional parameters such as nest dimensions, nest humidity, geographical range and post-copulatory reproductive behaviours (nest defence, guarding of hatchlings, etc.) to test the influence of these on crocodylian distribution and behaviour.

Mortality rates among unguarded eggs and hatchlings have been suggested as factors that may promote selection for parental care (Klug & Bonsall, 2010; Klug *et al.*, 2012). Because there seems to be a wide within-species range of parenting behaviours in crocodylians (Hunt & Watanabe, 1982; Platt *et al.*, 2008), the group is a good model system for investigating the effects of different types of care. For example, do female crocodylians living in high-stress environments (at the edge of their range or in human-dominated landscapes) exhibit the same rates and types of parenting behaviour as those living in highly protected habitats? This represents an interesting subject for future research, especially as the habitats of crocodylians are increasingly subject to human encroachment and climatic stress (Langley, 2005; Amarasinghe *et al.*, 2015; Corvera *et al.*, 2017).

CONCLUSIONS

We present the first evidence for a latitudinal effect on the body size of extant crocodylian species and make the novel observation that major reproductive characteristics of extant crocodylians follow a consistent pattern of effect across the entire order.

We report no significant relationship between either latitudinal midpoint or maximum latitudinal range and threshold incubation temperature across sampled crocodylians. This contrasts markedly with the patterns seen in turtles and raises additional questions about the parental roles of crocodylians. Further work will be needed to clarify the possible responses of crocodylian reproduction and its impact on their resilience in relation to anthropogenic warming. This may have implications for future studies on the effects of climate, latitude and life history on ectothermic amniotes, and for conservationists and government departments responsible for legislating on wildlife protection and climate change mitigation strategies.

ACKNOWLEDGEMENTS

We thank Dr Daniel Field and Professor Tamas Szekely for their kind patience and support during the initial stages of this project. We would also like to thank Pedro L. Godroy for his balanced and helpful commentary on our paper, and four anonymous reviewers for their kind and thorough critiques. This study was conducted as part of the PhD project of R. Lakin, with funding

provided by the National Environmental Research Council [NE/L002434/1]. M.A.W. thanks the Natural Environment Research Council [NE/K014951/1] and John Templeton Foundation [61408].

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SUPPLEMENTARY INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Appendix S1. Data matrix with citations.

Appendix S2. R code for GLM models.

Appendix S3. Data matrix without citations - for use with S2.

Appendix S4. Crocodylian phylogeny from [O'Brien *et al.*, 2019](#).