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

4

5

6 Rebecca J. Lakin<sup>1, 2\*</sup>, Paul M. Barrett<sup>2</sup>, Colin Stevenson<sup>3</sup>, Robert J. Thomas<sup>4</sup>  
7 & Matthew A. Wills<sup>1</sup>

8

9 <sup>1</sup>*Milner Centre for Evolution, University of Bath, Bath, UK BA2 7AY*, <sup>2</sup>*Department of*  
10 *Earth Sciences, Natural History Museum, Cromwell Rd, South Kensington, London SW7*

11 *5BD*, <sup>3</sup>*Crocodyles of the World, Burford Rd, Brize Norton, Carterton OX18 3NX*,

12 <sup>4</sup>*University of Cardiff, Cardiff, CF10 3AT*

13

14

15 Suggested RH – Crocodylian reproductive traits

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17 \*Corresponding author (r.j.lakin@bath.ac.uk)

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19

## Abstract

20

21

Relationships between distribution patterns and body size have been

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documented in many endothermic taxa. However, the evidence for these

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trends in ectotherms generally is equivocal, and there have been no studies

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of effects in crocodylians specifically. Here, we examine the relationship

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between latitudinal distribution and body mass in 20 extant species of

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crocodylians, as well as the relationships between seven important

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reproductive variables. Using phylogenetically independent contrasts to

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inform generalised linear models, we provide the first evidence of a

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latitudinal effect on adult female body mass in crocodylians. In addition,

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we explore the relationships between reproductive variables including egg

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mass, hatchling mass and clutch size. We report no correlation between

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egg mass and clutch size, upholding previously reported within-species

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trends. We also find no evidence of a correlation between measures of

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latitudinal range and incubation temperature, contrasting with the trends

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found in turtles..

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Keywords: *crocodylians; reproduction; generalised linear model; latitude; body size;*

38

*biogeography*

39

40 1 Introduction

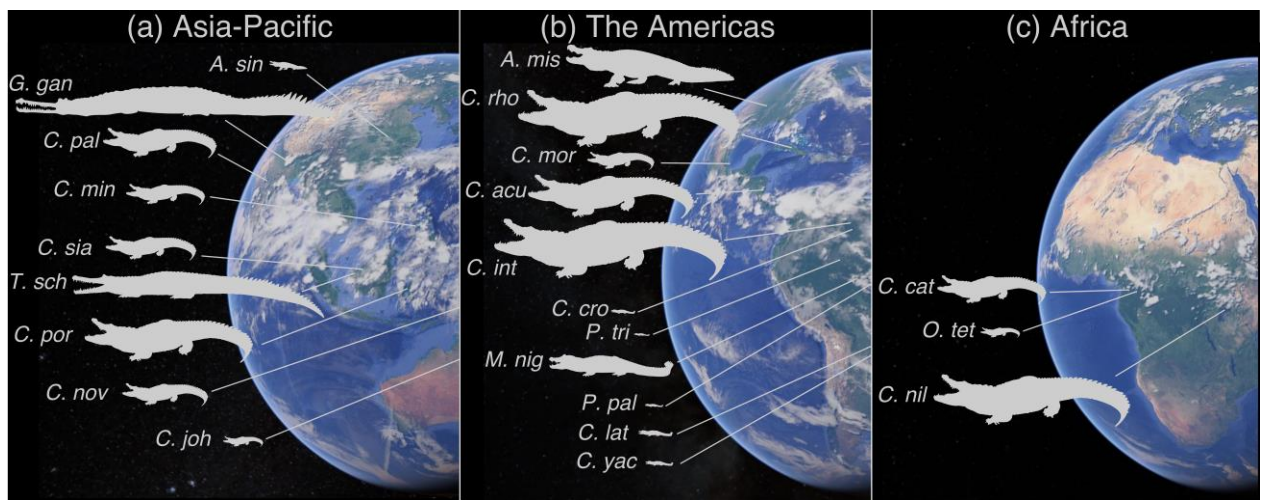
41

42 The broad impact of climate on the body size of numerous vertebrate and invertebrate  
43 groups has been demonstrated across latitudinal (Ray 1960; Wooller et al. 1985; Graves 1991;  
44 Kaspari and Vargo 1995; Saunders and Tarling 2018) and altitudinal (Bernadou et al. 2016; Davis  
45 and Burt Jr. 2019; Yu et al. 2019) gradients, insofar as these correlate with temperature gradients.  
46 While evidence of latitudinal size gradients is common in endotherms (Ashton 2002a; Blackburn  
47 and Hawkins 2004), the effect of latitude on ectotherm body sizes is more controversial (Ashton  
48 and Feldman 2003; Pincheira-Donoso et al. 2008). For example, amphibians (Ashton 2002b; Adams  
49 and Church 2008), lizards (Ashton and Feldman 2003; Cruz et al. 2005; Pincheira-Donoso et al.  
50 2008) and turtles (Ashton and Feldman 2003; Lindeman 2008; Angielczyk et al. 2015) have all  
51 been the subjects of studies with a diversity of findings. Strikingly, however, no previous studies  
52 have attempted to test whether this correlated variation applies to another major group of living  
53 reptiles, the crocodylians.

54

55 Crocodylians are a vital component of their ecosystems, often acting as keystone species  
56 in tropical regions (Ashton 2010). They represent the last surviving pseudosuchian archosaurs, a  
57 clade that once inhabited every continent and that has persisted for at least 230 Ma (Irmis et al.  
58 2013; Turner et al. 2017). Having survived the devastating Cretaceous-Paleogene (K-Pg) mass  
59 extinction (Bronzati et al. 2015; Puértolas-Pascual et al. 2016), as well as a number of other,

60 smaller or more protracted major extinction events (Hutchison 1982; Markwick 1993; Toljagić  
 61 and Butler 2013; Mannion et al. 2015), crocodylians have demonstrated remarkable resilience to  
 62 cataclysmic climate change and habitat loss (Toljagić and Butler 2013). Despite this, half of all  
 63 extant crocodylian species are currently threatened with extinction and, at the current rate,  
 64 vertebrate species loss will soon equal or even exceed that of the K-Pg event (Barnosky et al.  
 65 2011; Pievani 2014; Lécuyer 2018). To understand possible future trends in crocodylian diversity  
 66 more fully, it is important that their current diversity, ecology and distribution are fully  
 67 characterized (Figure 1). Despite previous work in this area (Martin 2007; Pierce et al. 2008;  
 68 Nicolaï and Matzke 2019), the nature of the relationship between geographical distribution and  
 69 the reproductive biology of living crocodylians is unclear.



70  
 71 *Figure 1. A representation of the relationship between the mean adult female body masses of 23*  
 72 *species of crocodylian and their latitudinal midpoint. Silhouette th scaled to body mass. (a) Asia-Pacific,*  
 73 *(b) The Americas, (c) Africa. Abbreviations (Asia-Pacific): Alligator sinensis, Gavialis gangeticus,*  
 74 *Crocodylus palustris, Crocodylus mindorensis, Crocodylus siamensis, Tomistoma schlegelii, Crocodylus*  
 75 *porosus, Crocodylus novaeguineae, Crocodylus johnstoni. (Americas): Alligator mississippiensis,*

76 Crocodylus rhombifer, Crocodylus moreletii, Crocodylus acutus, Crocodylus intermedius, Caiman  
77 crocodilus, Paleosuchus trigonatus, Melanosuchus niger, Paleosuchus palpebrosus, Caiman latirostris,  
78 Caiman yacare (*Africa*): Crocodylus cataphractus, Osteolaemus tetraspis, Crocodylus niloticus. Mesticops  
79 leptorhynchus, Crocodylus suchus and Osteolaemus osborni were excluded due to lack of reliable female  
80 mass data.

81

82 The resilience of crocodylians to historic mass extinctions is also much debated. Previous  
83 work has implicated many different factors in their survival, including diet (Sheehan and Hansen  
84 1986), aquaticism (Robertson et al. 2013), famine resistance (Robertson et al. 2013), induction  
85 of torpor at low air or water temperatures (Almandariz 1975; Brisbin Jr. et al. 1982; Sun et al.  
86 2019) and their propensity to burrow in order to take refuge from harsh environmental conditions  
87 (Thorbjarnarson 1989; Mobaraki et al. 2015). Another hypothesis concerns their unique  
88 reproductive biology (Charreau et al. 2017). Crocodylians have no sex chromosomes and hatchling  
89 sex is thought to be fully controlled by incubation temperature. Temperature dependent sex  
90 determination (TSD) systems have a threshold that yields an approximately 1:1 ratio of males  
91 and females at equilibrium (Escobedo-Galván et al 2016). Higher temperatures produce a greater  
92 proportion of males, whereas lower temperatures produce more females (Deeming and Ferguson  
93 1989; González et al. 2019). Counter-intuitively, the highest tolerable incubation temperatures  
94 produce mostly females, although these frequently fail to thrive (Marco et al. 2017). TSD was  
95 proposed as a possible buffer to extinction by Woodward and Murray (1993). Harsh  
96 environmental conditions are usually associated with a fall in ambient temperatures, and in  
97 species that utilise TSD these can result in a female-biased primary sex ratio (Tomillo et al. 2014;

98 2015; Carter et al. 2018). While lower temperatures may be consistent with the initial ‘nuclear  
99 winter’ effect of the end-Cretaceous bolide impact (Vellekoop et al. 2014; 2016), the longer-term  
100 warming resulting from increasing atmospheric greenhouse gas concentrations (Harrington 2001;  
101 Turner 2018) would be expected to skew sex ratios in favour of males. The latter scenario has  
102 been hypothesised as the most likely outcome of current trends in global warming (Miller et al.  
103 2004). Although TSD has been well documented within crocodylian species (Ferguson and Joanen  
104 1982; Deeming 2004; Piña et al. 2007), no comparisons of the effects of threshold temperature on  
105 development have been attempted across species, and little is known concerning the  
106 interrelationships between crocodylian reproductive characters.

107  
108 The reproductive characters of crocodylians were first surveyed by Thorbjarnarson (1996). This  
109 work identified allometric relationships between egg mass, clutch size, clutch mass and female  
110 length: patterns that had previously been observed in other vertebrate groups (Rohwer 1988;  
111 Sinervo and Licht 1991; Shine 1992). However, the correlations and causal interactions between  
112 these reproductive variables were not the focus of this study.

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

119

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122

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

131

## 132 2 Methods

133

### 134 2.1 Data Collection

135

136 We compiled data from the literature for seven morphological, environmental and reproductive  
137 variables across 24 extant crocodylian species (Appendix I). We used the species list in Grigg and  
138 Kirschner (2015) (Figure 1) and included one recently described species (*Mecistops*  
139 *leptorhynchus*) (Shirley 2018). Recent taxonomic uncertainty makes the attribution of some  
140 reproductive data unclear, and two species (*Crocodylus suchus* and *Osteolaemus osborni*) were



141 therefore excluded (Shirley et al. 2014; Hallmann and Griebeller 2018; Isberg et al. 2019). The  
142 data compiled were:

- 143
- 144 i. Maximum latitudinal range (°)

145

  - 146 ii. Midpoint of latitudinal range (°)

147

  - 148 iii. Mean mass of breeding-age female (kg)

149

  - 150 iv. Mean fresh egg weight (g)

151

  - 152 v. Mean hatchling mass (g)

153

  - 154 vi. Threshold incubation temperature, or the temperature at which a clutch will produce  
155 approximately 50% males and 50% females (°C). The lower (female to male)  
156 threshold was selected in this case because females are often inviable at the higher  
157 (male to female) threshold.

158

  - 159 vii. Mean clutch size (number of eggs laid)

160

  - 161 viii. Mean duration of incubation (days)

162

163 We reviewed the literature in Google Scholar by searching for each species individually, coupled with  
164 appropriate terms (e.g. “*Crocodylus porosus* clutch size”, “*Caiman yacare* body mass”). Variations on  
165 these were used as necessary (e.g. “*Caiman yacare*”/ “*Caiman jacare*” + “body mass”/“female  
166 mass”/“weight”/“kg”). These were searched until pages returned only irrelevant results. Data were  
167 collated into a single spreadsheet (Appendix I). Continuous variables (female mass, egg mass,  
168 hatchling mass, clutch size and duration of incubation) were averaged to smooth over outlier results  
169 that be unrepresentative. The literature contains data from individual captive bred and wild caught  
170 specimens, as well as values that are themselves averages from various heterogeneous samples. This  
171 constrains the precision of our data, but we believe that there is a homogenous distribution of error. In  
172 addition, data on female mass were often derived from adults of different ages, and these were then  
173 averaged across multiple individuals and studies (Appendix I). Data on latitudinal range were taken  
174 from the IUCN Red List of threatened species (IUCN 2019).

175

176 For one species, *Tomistoma schlegelii*, there was insufficient information in the literature, and we  
177 therefore used data from our own observations. Hatchling mass data (see Appendix I) were  
178 averaged from a captive-born clutch laid at “Crocodiles of the World”, Oxfordshire, UK. This clutch  
179 consisted of 17 eggs, of which 14 successfully hatched (though one infant failed to thrive and died  
180 shortly after hatching). Eggs were laid on 16th April 2016 by an imported farm-raised female  
181 measuring 2.3 m (SVL). Eggs were separated and artificially incubated at 32.6° C (three eggs),  
182 32.0° C (five eggs), 31.5° C (five eggs) and 29.8° C (four eggs), and hatched after 92 days, 94

183 days, 95 days and 103 days, respectively. Hatchlings were weighed using a Marsden Super-SS B-  
184 100 waterproof electronic scale, accurate to 0.10 g.

185

186

187

## 188 2.2 Statistical analysis

189 For indicative purposes, non-phylogenetically controlled bivariate correlations between our seven  
190 variables are visualised in Figure 2. These were further tested using PGLS as sensitivity  
191 analyses. These results, and literature on archosaur reproduction generally and crocodylians  
192 specifically was used to frame five hypotheses:

193

194 i. Adult female mass is positively correlated with latitudinal midpoint, maximum  
195 latitudinal range, egg mass, hatchling mass and/ or clutch size, as in some species of  
196 crocodylians (Verdade 2001; Campos et al. 2008; Murray et al. 2013) and birds (Wendeln  
197 1997).

198 ii. Egg mass is positively correlated with female mass, hatchling mass and/or clutch size, as in  
199 some species of crocodylians (Verdade 2001; Murray et al., 2013), birds (Wiebe and  
200 Bortolotti 1995) and turtles (Wallace et al. 2006).

201 iii. Hatchling mass is positively correlated with adult female mass, latitudinal midpoint,  
202 maximum latitudinal range and/or egg mass, as in some species of crocodylians (Verdade

- 203           2001; Murray et al. 2013), birds (Ricklefs 1984; Smith et al. 1993) and turtles  
204           (Roosenburg and Kelley 1996; Wallace et al. 2006).
- 205    iv.    Clutch size is positively correlated with adult female mass, egg mass, latitudinal midpoint,  
206           maximum latitudinal range and/or duration of incubation, as in some species of  
207           crocodylians (Verdade 2001; Campos et al. 2008; Murray et al. 2013), birds (Erikstad et al.  
208           1993; Monaghan et al. 1995) and turtles (Roosenburg and Kelley 1996).
- 209    v.    Threshold incubation temperature is positively correlated with latitudinal midpoint,  
210           maximum latitudinal range and/or hatchling mass, as in turtles (Ewert et al. 2005).

211    The phylogeny of O'Brien et al. (2019) was used to produce phylogenetically-independent  
212    contrast (pic) values for each variable. These pic values (rather than our raw data) were used in the  
213    subsequent GLM analyses. This tree was constructed using multiple specimens representing  
214    each species and the tree was first pruned to remove duplicate specimens  
215    ('Alligator\_mississippiensis2', 'Alligator\_mississippiensis3', etc.). The first entry was kept by  
216    default in each case. Rooting and branch lengths were kept consistent with those published by  
217    O'Brien et al. (2019).

218    Before calculating the pic values, conspicuously non-normal continuous variables (female mass,  
219    egg mass and hatchling mass only) were log-transformed. Four species were excluded from our  
220    dataset because they were absent from the phylogeny of O'Brien et al. (2019) (*Crocodylus*  
221    *intermedius*, *Crocodylus moreletii*, *Caiman yacare* and *Masticops leptorhynchus*), leaving 20 species in  
222    the final analyses. We used the Akaike Information Criterion (AIC) to identify the minimum

223 adequate model by backward stepwise deletion of poorly fitting variables. All models used the  
 224 ‘Gaussian’ error family and ‘identity’ link function, and were implemented in the statistical  
 225 software environment R, using the *GGally*, *ape* and *phytools* packages (version 3.5.3) (R Core  
 226 Team 2013).

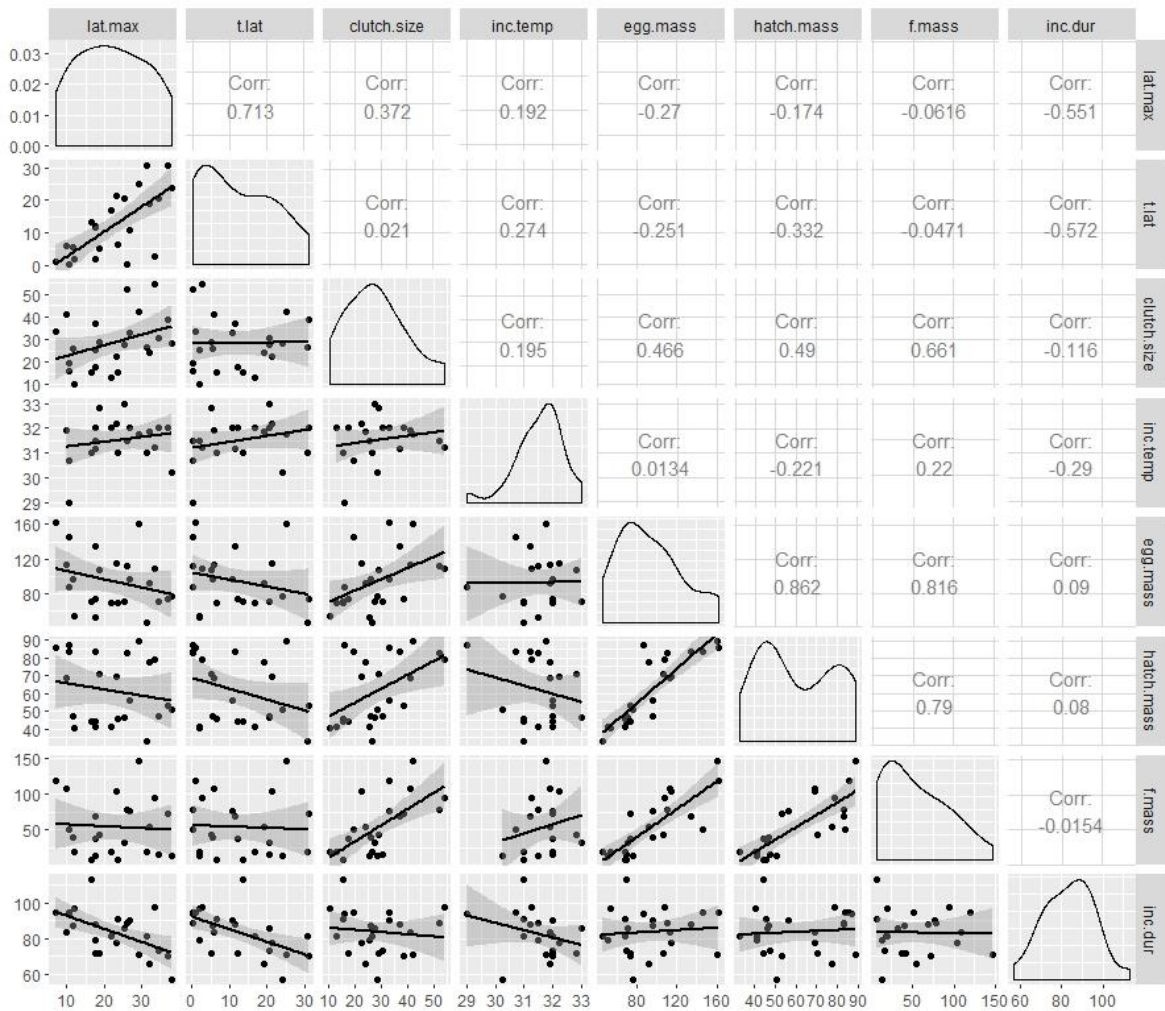
227 We constructed five GLMs based on the phylogenetically independent contrasts of all variables.  
 228 Models 3 and 5 were produced from a modified phylogeny of 17 species, excluding *Crocodylus*  
 229 *novaeguineae*, *Osteolaemus tetraspis* and *Tomistoma schlegelii*. This was because threshold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

Model No.	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

233  
 234 *Table 1: Initial structure of GLMs analysing relationships between phylogenetically independent contrasts in the*  
 235 *reproductive characters of extant Crocodylia. All models were conducted using the ‘gaussian’ error family and*  
 236 *‘identity’ link function. Abbreviations: clutch.size = mean clutch size; egg.mass = log mean fresh egg weight;*

237 *f.mass = log mean adult female body mass; hatch.mass = log mean hatchling mass; inc.dur = mean duration of*  
238 *incubation; inc.temp = threshold incubation temperature; lat.max = maximum latitudinal range; t.lat.=*  
239 *latitudinal* *midpoint.*

241 A Spearman's correlation matrix of our results is shown in Figure 2. The strongest positive  
242 correlations are between morphological reproductive characteristics (female mass vs egg mass ( $r_s =$   
243  $0.85$ ,  $p < 0.0001$ ), female mass vs hatchling mass ( $r_s = 0.79$ ,  $p < 0.0001$ ), and egg mass vs  
244 hatchling mass ( $r_s = 0.94$ ,  $p < 0.0001$ )). Other correlated traits are: (1) latitudinal midpoint vs  
245 duration of incubation ( $r_s = -0.60$ ,  $p = 0.005$ ); (2) female mass vs clutch size ( $r_s = 0.67$ ,  $p =$   
246  $0.002$ ); (3) egg mass vs clutch size ( $r_s = 0.56$ ,  $p = 0.01$ ); (4) hatchling mass vs clutch size ( $r_s =$   
247  $0.64$ ,  $p = 0.003$ ); (5) maximum latitudinal range vs clutch size ( $r_s = 0.045$ ,  $p = 0.046$ ) (6)  
248 latitudinal midpoint vs duration of incubation ( $r_s = -0.60$ ,  $p = 0.0055$ ). PGLS analyses  
249 supported the following significant relationships: (1) female mass vs egg mass ( $p = 0.0008$ ); (2)  
250 female mass vs hatchling mass ( $p = 0.0003$ ); (3) egg mass vs hatchling mass ( $p < 0.0001$ ); (4)  
251 latitudinal midpoint vs duration of incubation ( $p = 0.007$ ); (5) female mass vs clutch size ( $p =$   
252  $0.007$ ); (6) hatchling mass vs clutch size ( $p = 0.015$ ) and (7) latitudinal midpoint vs duration of  
253 incubation. Some relationships were not supported by PGLS analysis: (1) egg mass vs clutch  
254 size ( $p = 0.071$ ); (2) maximum latitudinal range vs clutch size ( $p = 0.121$ ).



255

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



262 3.1 Female Mass

263

264 Model 1 was constructed to account for the potential effects of latitudinal midpoint,  
 265 maximum latitudinal range, egg mass, hatchling mass, clutch size and duration of incubation on  
 266 female mass (Appendix II - initial and final models). The final model (Table 2) was the result of  
 267 backward stepwise deletion based on AIC value as a measure of model efficiency. This model  
 268 explained 85% of the deviance associated with adult female mass ( $D^2$ ). Mean clutch size ( $p =$   
 269  $0.0017$ ) was the most significant correlator to log mean female mass, followed by mean  
 270 latitudinal range ( $p = 0.026$ ), log mean hatchling mass ( $0.0027$ ) and maximum latitudinal range  
 271 ( $p = 0.0133$ ). Log mean egg mass and mean incubation duration both correlated poorly with log  
 272 mean female mass and were dropped from the model.

273

Term	Coefficients	SE	F	p
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**

274 *Table 2: A Generalised Linear Model (Model 1) describing the effect of latitudinal midpoint, maximum*  
 275 *latitudinal range, hatchling mass and clutch size on the adult female mass of 20 species of crocodylian.  $D^2 =$*   
 276 *0.8510 SE = Standard error; F = F-value, p = p-value.*

277

278 3.2 Egg Mass

279 Model 2 was constructed to account for the potential effects of latitudinal midpoint,  
280 maximum latitudinal range, female mass and clutch size on egg mass (Appendix II). The final  
281 model (Table 3) explained 68% of the deviance associated with egg mass ( $D^2$ ). Log mean female  
282 mass ( $p < 0.0001$ ) was the only significant correlator to log mean egg mass. Latitudinal  
283 midpoint and mean clutch size correlated poorly with log mean egg mass and were dropped  
284 from the model.

285

Term	Coefficients	SE	F	p
max.lat	-0.0074	0.0049	1.9114	0.1858
log.f.mass	0.5117	0.0809	33.295	<0.0001***

286 *Table 3: A Generalised Linear Model (Model 2) describing the effect of maximum latitudinal range and adult*  
287 *female mass on the fresh egg weight of 20 species of crocodylian.  $D^2=0.6776$ . SE = Standard error; F = F-*  
288 *value, p = p-value.*

289 3.3 Hatchling Mass

290 Model 3 was constructed to account for the potential effects of latitudinal midpoint, maximum  
291 latitudinal range female mass, egg mass, clutch size, threshold incubation temperature and  
292 incubation duration on hatchling mass (Appendix II). The final model (Table 4) explained  
293 90% of the deviance associated with hatchling mass ( $D^2$ ). Log mean egg mass ( $p < 0.0001$ ) was  
294 the only significant correlator to hatchling mass. Log mean female mass, latitudinal midpoint,  
295 mean clutch size and mean incubation duration correlated poorly with hatchling mass and were

296 dropped from the model.

297

Term	Coefficients	SE	F	p
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

298 *Table 4: A Generalised Linear Model (Model 3) describing the effect of female body mass and fresh egg weight on*  
299 *the hatchling mass of 17 species of crocodylian.  $D^2 = 0.8997$ . SE = Standard error; F = F-value, p = p-value.*

300

### 301 3.4 Clutch Size

302 Model 4 was constructed to account for the potential effects of latitudinal midpoint,  
303 maximum latitudinal range, female mass, egg mass and hatchling mass (Appendix II). The final  
304 model (Table 5) explained 87% of the deviance associated with clutch size ( $D^2$ ). The most  
305 significant correlators to mean clutch size were log mean female mass ( $p < 0.0001$ ) and  
306 maximum latitudinal range ( $p < 0.0001$ ), followed by latitudinal midpoint ( $p = 0.0007$ ) and  
307 mean duration of incubation ( $p = 0.107$ ). Egg mass and hatchling mass were found to correlate  
308 poorly with clutch size, and were dropped from the model.

309

Term	Coefficients	SE	F	p
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 *

310 *Table 5: A Generalised Linear Model (Model 4) describing the effect of adult female mass, latitudinal midpoint,*  
311 *maximum latitudinal range and incubation duration on the clutch sizes of 20 species of crocodylian.  $D^2 =$*   
312 *0.8662. SE = Standard error; F = F-value, p = p-value.*

313

### 314 3.5 Threshold Incubation Temperature

315 Model 5 was constructed to account for the potential effects of latitudinal midpoint,  
316 maximum latitudinal range, female mass, egg mass, hatchling mass, clutch size and incubation  
317 duration on threshold incubation temperature (Appendix II). The final model (Table 6) explained  
318 42% of the deviance associated with threshold incubation temperature ( $D^2$ ). The only significant  
319 correlator to threshold incubation temperature was mean incubation duration ( $p = 0.0065$ ). Log  
320 mean female mass, log mean egg mass, log mean hatchling mass, mean clutch size, latitudinal  
321 midpoint and maximum latitudinal range all correlated poorly with threshold incubation  
322 temperature and were dropped from the model.

323

Term	Coefficients	SE	F	p
inc.dur	-0.0260	0.0081	10.201	0.0065**

324

325 *Table 6: A Generalised Linear Model (Model 5) describing the effects of maximum latitudinal range, fresh egg*  
326 *weight, hatchling mass and duration of incubation on the threshold incubation temperature of 17 species of*  
327 *crocodylian.  $D^2 = 0.4215$  SE = Standard error; F = F-value, p = p-value.*

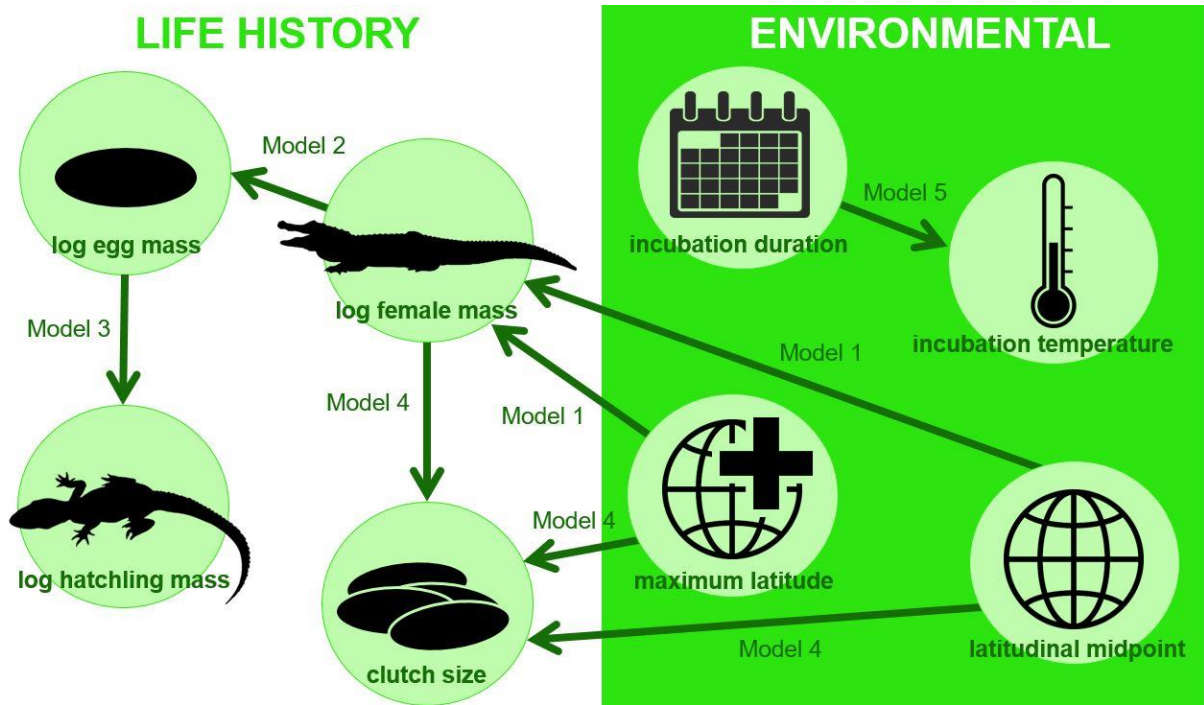
328 4 Discussion

329

330 4.1 General overview

331

332 A robust, positive correlation between latitude and body size has been well documented in  
333 endotherms (Gillman et al. 2009; Torres-Romero et al. 2016), but is much less compelling  
334 among ectotherms (Ashton and Feldman 2003; Lindeman 2008; Cruz et al. 2005), and has  
335 never been tested for in crocodylians. Here, we demonstrate that, despite low overall correlation  
336 coefficients, both latitudinal midpoint and maximum latitudinal range correlate significantly  
337 with adult female mass once the effects of phylogeny and other potentially confounding  
338 reproductive variables are controlled for ( $p = 0.0026$  and  $0.0133$  respectively, see Model 1,  
339 section 3.1). Furthermore, we describe significant relationships between some important  
340 morphological reproductive variables across crocodylians as a whole, a phenomenon that has  
341 previously been described only within species (Verdade 2001; Campos et al. 2008; Murray et al.  
342 2013). We demonstrate that these relationships are discrete with, for example, a significant effect  
343 of female mass on egg mass, and of egg mass on hatchling mass, but no direct effect of female  
344 mass on hatchling mass. Female mass is a significant predictor of clutch size in crocodylians, as  
345 well as both the latitudinal midpoint and maximum latitudinal range. We did not detect any  
346 significant relationship between threshold incubation temperature and either latitudinal  
347 midpoint or maximum latitudinal range (see Model 5, section 3.5). Some of the most  
348 biologically significant relationships described by our models are presented in Figure 3.



350

351 *Figure 3: Map of the interactions between some important reproductive variables in Crocodylia. Positive*  
 352 *relationships shown are between latitudinal midpoint and log mean female mass ( $p = 0.0026$ ); maximum latitudinal*  
 353 *range and log mean female mass ( $p = 0.013$ ); log mean egg mass and log mean female mass ( $p < 0.0001$ ); log mean*  
 354 *egg mass and log mean hatchling mass ( $p < 0.0001$ ); log mean female mass and mean clutch size ( $p < 0.0001$ ;*  
 355 *maximum latitudinal range and mean clutch size ( $p < 0.0001$ ); latitudinal midpoint and mean clutch size ( $p =$*   
 356 *0.0007); and mean incubation duration and threshold incubation temperature ( $p = 0.0065$ ).*

357

## 358 4.2 Implications of results

359 The strongest associations in our study are between morphological reproductive variables (Models  
 360 1, 2 and 3). These include adult female mass, fresh egg weight, hatchling mass and clutch size  
 361 (Figure 3). Intraspecific relationships of this kind have previously been documented in the

362 American alligator (*Alligator mississippiensis*) (Murray et al. 2013) and in the broad-snouted,  
363 spectacled and Yacare caimans (*Caiman latirostris*, *C. crocodilus* and *C. yacare*) (Verdade 2001;  
364 Larriera et al. 2004; Campos et al. 2008). Here, we verify the same trends across extant  
365 crocodylians as a whole. We report a significant positive effect of female mass upon clutch size  
366 (Model 4), a result that contrasts with the findings of previous species-level studies (Verdade  
367 2001). We find no evidence for any correlation between egg mass and clutch size, which is a  
368 biological trade-off that has been described in many other taxa (Lack 1967; Sinervo and Licht 1991;  
369 Rowe 1994).

370  
371 We found no significant relationship between threshold incubation temperature and hatchling  
372 mass (Models 3 and 5), suggesting that the temperature required to produce an even sex ratio is  
373 not significantly different in crocodylian species that produce large hatchlings compared with  
374 those that produce small hatchlings. This result is consistent with previous studies that  
375 examined trends within species (Joanen and McNease 1989; Campos 1993). The effects of  
376 contemporary climatic warming on the reproductive biology of crocodylians has yet to be  
377 examined (Zhang et al. 2009; Simoncini et al. 2014), but based on deep-time associations  
378 between crocodylian distributions and climate change (Markwick 1998; Quintero and Wiens  
379 2013; Mannion et al. 2015), it is plausible that all crocodylians are vulnerable to rapid warming,  
380 and that this should be considered a threat to local populations (Dudgeon 2014).

381  
382 Our results suggest that the only significant correlator to threshold incubation temperature in

383 crocodylians is incubation duration (Model 5). This factor may help to explain the diversity of  
384 threshold incubation temperatures as, within species, eggs incubated at higher temperatures tend  
385 to hatch sooner than those incubated at cooler temperatures (see section 2.1 on *Tomistoma*  
386 *schlegelii*, Methods).

387  
388 We identified no significant relationships between the threshold incubation temperature and  
389 either the mean or the maximum latitudinal range of crocodylians (Model 5). This suggests that  
390 the nest temperature of crocodylians is affected by factors other than latitudinal distribution.  
391 This stands in contrast to the relationship observed in turtles, in which latitude has a significant  
392 effect on reproductive traits and nest temperature (Iverson et al. 1993; Ewert et al. 2005). The  
393 clutch size of turtles correlates with latitude (Iverson et al. 1993) and their sex ratio is affected  
394 by annual temperature fluctuations (Janzen 1994). This supports observed differences in the  
395 nest functions and parental roles of turtles and crocodylians, and suggests that the presence of  
396 adult crocodylians at the nest plays a much greater role in the temperature regulation of their  
397 nests than in turtles. Our results suggest that other factors (possibly the position, construction,  
398 location, shape or size of the nest) could contribute to the maintenance of an acceptable nest  
399 temperature (see also Grigg 1987, Brazaitis and Wantanabe 2011). In turtles, nest temperature is  
400 determined by ambient temperature and climate to a much higher degree (Hays et al. 2010;  
401 Refsnider et al. 2013; Santidrián et al. 2015). Future research on the behaviour of nesting  
402 crocodylians may be necessary to shed further light on nest temperature regulation.

403



404 4.3 Limitations and future work

405

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

415 An extension of the present study could include additional parameters such as nest dimensions,  
416 nest humidity, geographic range, and postcopulatory reproductive behaviours (nest defence,  
417 guarding of hatchlings, etc.) to test the influence of these on crocodylian distribution and  
418 behaviour.

419

420 Mortality rates among unguarded eggs and hatchlings have been suggested as factors that may  
421 promote selection for parental care (Klug and Bonsall 2010; Klug et al. 2012). Since there  
422 seems to be a wide within-species range of parenting behaviours in crocodylians (Hunt and  
423 Watanabe 1982; Platt et al. 2008), the group is a good model system for investigating the effects  
424 of different types of care. For example - do female crocodylians living in high-stress

425 environments (at the edge of their range or in human-dominated landscapes) exhibit the same rates  
426 and types of parenting behaviour as those living in highly protected habitats? This represents an  
427 interesting subject for future research, especially as the habitats of crocodylians are increasingly  
428 subject to human encroachment and climatic stress (Langley 2005; Amarasinghe et al. 2015;  
429 Corvera et al. 2017).

430

## 431 5 Conclusions

432

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

436

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

445

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459

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