Regional differences in growth rates of Orinoco crocodiles (Crocodylus intermedius) from the Venezuelan Llanos

Article *in* Herpetological Journal · October 2016

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Volume 26 (October 2016), 263–269

Herpetological Journal

FULL PAPER

Published by the British Herpetological Society

Regional differences in growth rates of Orinoco crocodiles (*Crocodylus intermedius*) from the Venezuelan Llanos

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Populations of the Orinoco crocodile (*Crocodylus intermedius*) have not recovered from past exploitation, and current abundances cannot be used for assessing the suitability of habitats they occupy. Growth constitutes an alternative way of assessing habitat quality. Since 1990, more than 9000 captive-reared Orinoco crocodiles have been released into the Venezuelan Llanos. In the present study, the growth rates of 127 recaptured crocodiles from different regions were compared. All individuals from Middle Cojedes and the Aeolian savannahs grew slower than expected by the von Bertalanffy model, whereas individuals from Caños in the Apure floodplains grew faster than expected. These inferences are corroborated with growth rate measurements for crocodiles under four years of age, which were lowest in Middle Cojedes (average of 14.1 cm/year) and highest at Caños (43.3 cm/year). Low growth rates can be explained by habitat deterioration due to human activities, and high growth rates in the Caños support that the lower reaches of whitewater rivers offer favourable conditions for the species. Crocodiles in high quality habitats may reach sexual maturity in six years, whereas more than a decade is required in poor-quality habitats.

Key words: growth models, habitat quality, Orinoco crocodile, reintroduction

INTRODUCTION

The Orinoco crocodile (*Crocodylus intermedius*) was commercially overexploited from 1929 to the early 1960s, and by the 1970s the species had disappeared from most of its historical distribution (Godshalk & Sosa, 1978; Medem, 1981, 1983). Anecdotal accounts and information from commercial exploitation activities indicate that the largest populations of *C. intermedius* were found in large rivers originating in the Andes (Whitney, 1912; Calzadilla-Valdés, 1948; Humboldt, 1975; Páez, 1980; Crevaux, 1988). Population size estimates of *C. intermedius* from the Venezuelan Llanos provide evidence that densities vary widely among localities (Godshalk & Sosa, 1978; Franz et al., 1985; Ramo & Busto, 1986; Thorbjarnarson & Hernández, 1992; Seijas & Chávez, 2000; Chávez 2000, Jiménez-Oráa, 2002; Llobet, 2002; Antelo, 2008). However, the influence of commercial exploitation precludes inferences between current densities and habitat quality. Since abundances of food resources and other habitat characteristics vary among localities, crocodilians are also characterised by corresponding differences in local growth rates to reflect the quality of habitats (Webb et al., 1978; Chabreck & Joanen, 1979; Hutton, 1987; Jacobsen & Kushlan, 1989; Brisbin, 1990; Brandt, 1991; Rootes et al., 1991; Bossert et al., 2000; Da Silveira et al., 2013; Campos et al., 2014). *Crocodylus intermedius* inhabits rivers and floodplain lagoons in the lowlands of the Orinoco river basin. Following Thorbjarnarson (1988) and Sarmiento (1983), the Orinoco tributaries can be divided into Category I (the Llanos), subdivided into Type A (the Andean/Coastal Range Drainage, including whitewater rivers characterised by high loads of sediments and nutrients) and Type B (the Internal Llanos, including clear or blackwater rivers of low sediment load); category II includes the Guayanan tributaries, which are clear or blackwater rivers considered as low quality habitat (Godshalk & Sosa, 1978; Thorbjarnarson, 1988). As part of a conservation program to restore *C. intermedius*, more than 9000 captive-reared Orinoco crocodiles have been released since 1990 in more than 70 locations in the Venezuelan Llanos (Babarro, 2014). The aim of the present study is to analyse and compare growth rates of Orinoco crocodiles within and between these categories, and discuss whether observed differences can be used to assess the quality of habitats.

MATERIALS AND METHODS

Data on recaptured crocodiles were obtained from several sources (see Online Appendix 1), and individual identification, age, size, date and place of release were checked with a database maintained by the Venezuelan Crocodile Specialist Group (GECV). In case of discrepancies about reported sex between release and

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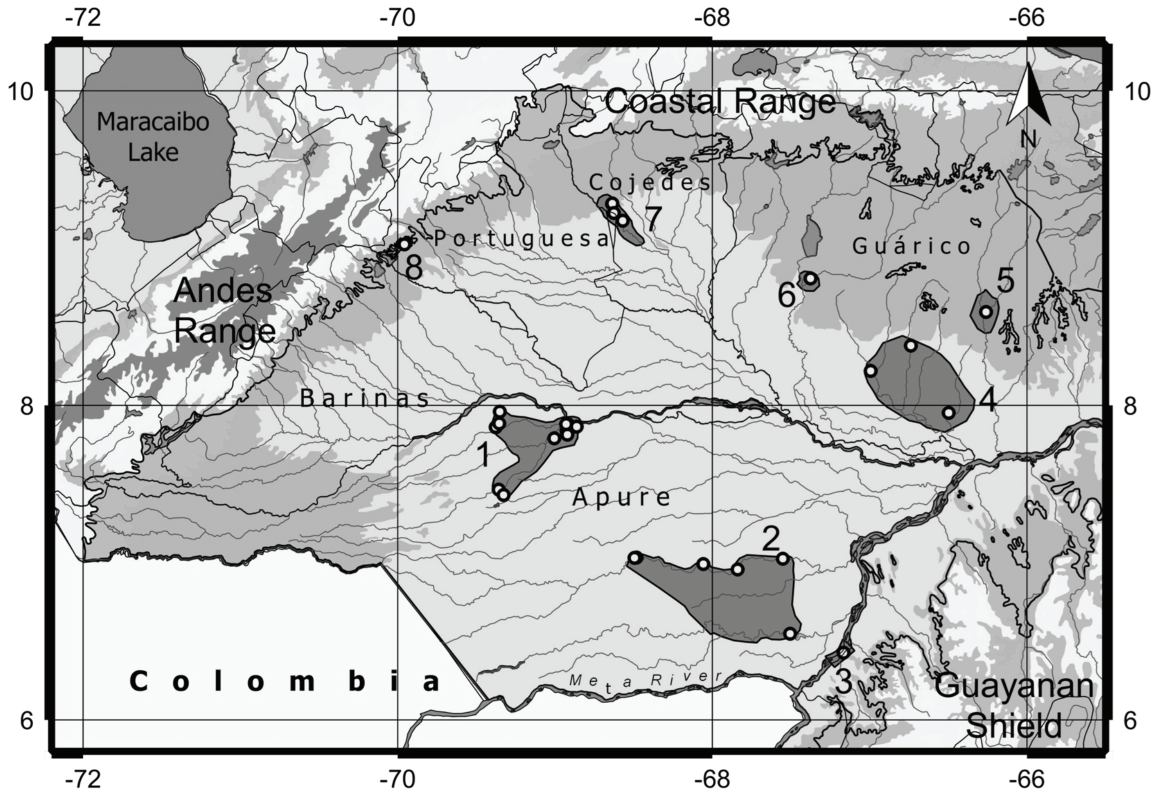

Fig. 1. Partial map of the Orinoco River basin in Venezuela. Dots represent locations where Orinoco Crocodiles (*Crocodylus intermedius*) have been recaptured. Darker areas (1 to 8) delimit the regions considered in this study: 1. Apure floodplains, 2. Aeolian savannahs, 3. Orinoco, 4. AGNP, 5. Middle Manapire, 6. Masaguaral, 7 Middle Cojedes, and 8. Tucupido.

recapture, the latter was used. The information obtained consisted of dates (hatching, release, recapture), place of release, and total length (TL) at release and during recapture. Crocodiles recaptured on more than one occasion were considered only once, using data from the last recapture. Considering geographical proximity and ecological characteristics, sites were grouped into eight regions (Table 1, Fig. 1). More information on their geographic, limnological and climatic characteristics is summarised in Online Appendix 2.

Growth rates were calculated as the increase in TL (in cm) divided by the elapsed time (in years) between release and recapture. If only snout-vent length (SVL) was reported during recapture, TL was calculated as 1.84*SVL+2.7. By using a regression analysis with data of 215 wild crocodiles with different degree of tail mutilations (Seijas, 2011), the percentage of SVL represented in TL is calculated as 63.643–0.652*SCW, where SCW is the remaining number of single crest caudal whorls (for details see Seijas, 2011). Since %SVL can also be described as (SVL/TL)*100, SVL can be seen as (%SVL*TL)/100. Taken together, TL of crocodiles which miss a portion of the tail can be obtained as $TL(cm)_{Corrected}=TL(cm)_{Reported}(1.171-0.012SCW)+2.7$.

Table 1. Details of study sites.

Localities	Details
Apure floodplains	In the Apure state. According to type of water body, this region is divided into savannah lagoons Caños (rivers whose flow is interrupted in the dry season). See Lasso et al. (1999), Ayarzagüena & Castroviejo (2008) and Antelo (2008).
Aeolian savannahs	In the Santos Luzardo National Park, Apure state. See Sarmiento (1983), Schargel & Aymard (1993) and Jepsen & Winemiller (2007).
Orinoco	Located in the Tortuga Arrau Wildlife Refuge (TAWR), between Apure and Bolívar states.
The Aguaro-Guariquito National Park (AGNP)	Guárico state. See Jepsen & Winemiller (2002) and Marcano et al. (2007).
Masaguaral	In Guárico state, cattle ranch in the upper central llanos; only one record is available (Thorbjarnarson, 1988).
Middle Cojedes	Between Cojedes and Portuguesa states. See Seijas et al. (2001), Seijas & Chávez (2000), and Mendoza & Seijas (2007).
Tucupido	A reservoir near the Andes piedmont in Portuguesa state.

Table 2. Estimated values of parameters from non-linear fitting to von Bertalanffy growth model for recaptured Orinoco crocodiles (*Crocodylus intermedius*). S.E.: standard error. RSME: residuals mean square error. See meaning of parameters and detail of fitting methods in the text. "AF" refers to the region *Apure floodplains*.

	N	L_∞	S.E.	*b*	S.E.	*k*	S.E.	RMSE
Direct fitting								
All data	127	443.3	48.2	0.9211	0.0156	0.1042	0.022	29.7
All females	77	488.8	112.6	0.9335	0.0158	0.0942	0.037	27.4
All males	36	460.6	76.3	0.9090	0.0308	0.0930	0.03	32.7
Females AF	53	381.4	43.2	0.9439	0.0339	0.1601	0.041	23.7
Males AF	22	428.1	25.3	0.9778	0.0354	0.1474	0.022	19.4
Fabens method								
All data	127	483.8	46.2	0.9409	--	0.0944	0.016	24.7
All females	77	576.0	111.6	0.9503	--	0.0784	0.023	21.0
All males	36	507.5	90.1	0.9437	--	0.0809	0.026	29.8
Females AF	53	411.5	37.5	0.9305	--	0.1522	0.028	18.6
Males AF	22	441.8	29.2	0.9353	--	0.1387	0.021	19.9

To compare TL and age at time of recapture (in years) between release sites, a Bertalanffy growth model using least square methods and the non-linear fit command of the software JMP IN (2001, SAS Institute Inc.) was constructed. Fitting was performed with and without discriminating by sex. Given the large sample size, data from the Apure floodplains were also separately fitted to the model.

The von Bertalanffy model is expressed as $L=TL\infty$ $(1-be^{-kt})$, where *TL* is the predicted size at time *t*, TL_∞ is the maximum size attainable by the species, *b* relates both to the asymptotic size and the size at hatching, and *k* is an indication of the rate of proportional growth of the animal. Two procedures were employed to obtain the required parameters. In the first procedure (hereinafter called "direct fitting"), age and size were fitted to the model. In the second procedure (hereinafter called "Fabens method"), parameters were obtained following Fabens (1965). In a first step, data were fit to to $TL_{rec}=TL_{inic}+(TL_\infty-TL_{inic})*(1-e^{-kd})$, where TL_{rec} is the total length at recapture, TL_{inic} is the total length at releasing, and *d* is the time lapse between initial releasing and recapture. TL_∞ and *k* are as described above. Once TL_∞ was known, the parameter *b* was calculated solving the von Bertalanffy equation at *t*=0 as $b=1-28.6/TL_\infty$, as , where 28.6 is the total length (in cm) at hatching (Antelo, 2008). The Fabens method is independent of the age of recaptured individuals. When considering the whole data set, the number of values above or below the fitting curve (positive and negative residuals, respectively) should be roughly equal. Under the assumption of homogeneity of habitats, the number of positive and negative residuals for each region should not deviate significantly from random, and a bias can be used to reject the null hypothesis. Deviations were determined by means of a single-proportion test with the statistics software Past v. 3.06 (Hammer et al., 2001).

Growth rates of *C. intermedius* recaptured in different regions were compared using nonparametric tests (Kruskall-Wallis and Mann-Whitney U tests) using Past (Hammer et al., 2001).Only individuals up to four years of age were considered, assuming that growth rate does not decline significantly during the first years of age (Hutton, 1987; Ramo et al., 1992; Antelo, 2008).

Table 3. Descriptive statistics of annual growth in total length (TL) of *Crocodylus intermedius* up to four years of age, recaptured in different regions of the Venezuelan Llanos. Means with the same letter are no statistically different at the 0.05 alpha level (Mann-Whitney pairwise comparisons, corrected *p* values). Only samples with *n*>4 were considered.

		Growth rate (cm/year)				
Region	N	Mean	(min-max)	SD	Coeff. var	Mean comparisons
Lagoons	20	27.0	(12.1-55.3)	10.3	38.0	A
Caños	30	43.3	(0.4-81.5)	22.3	51.4	A
Aeolian savannahs	3	33.7	(32.3-34.8)	1.3	3.8	--
Orinoco	4	42.9	(22.8-57.5)	14.5	33.9	--
AGNP	4	47.5	(17.9-83.0)	34.3	7.2	--
Middle Manapire	21	30.7	(14.3-47.1)	8.5	27.6	A
Masaguaral	1	72.7	--	--	--	--
Middle Cojedes	9	14.1	(7.5-24.6)	6.3	44.4	B
Tucupido	2	15.7	(11.3-20.0)	--	--	--

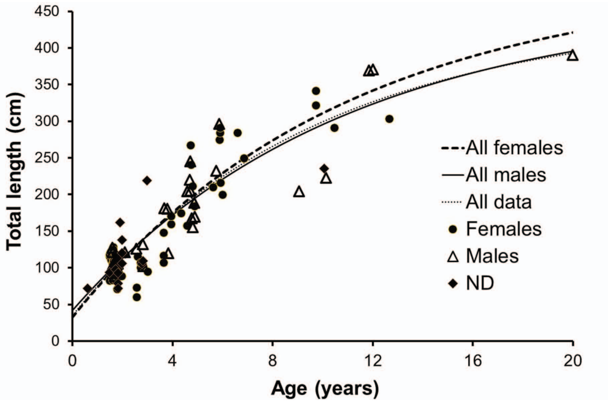

Fig. 2. Distribution of data points along *Crocodylus intermedius* growth curves obtained by direct fitting of data to the von Bertalanffy model. ND (no data) means that sex was unknown. For the sake of simplicity, only curves predicted with all the data by the direct fitting method are shown (i, ii, and iii in Table 3).

RESULTS

The TL of recaptured crocodiles ranged between 60 cm and 390 cm. The oldest recaptured crocodile was 20 years old, and the time between release and recapture ranged between 0.15 and 16.75 years. The parameters of the von Bertalanffy growth model are shown in Table 2. In all cases, the Fabens method produced higher asymptotic values than direct fitting and generally had lower residuals mean square error-RMSE. When the whole data set was considered, both methods predicted a larger asymptotic size for females than for males.

The growth trajectories predicted by the von Bertalanffy model are depicted in Fig. 2. In total, 59 out of 127 individuals (46.5%) had positive residuals. For Middle Cojedes and the Aeolian savannahs all residuals were negative (z=-2.80, p<0.01; and z=-2.95 ; p<0.01, respectively). For Caños, 21 out of 30 individuals with positive residuals also represented a significant deviation from random (z=2.58, p=0.01). Residuals for the other regions were more evenly distributed (p>0.05, detailed data not shown; Fig. 3).

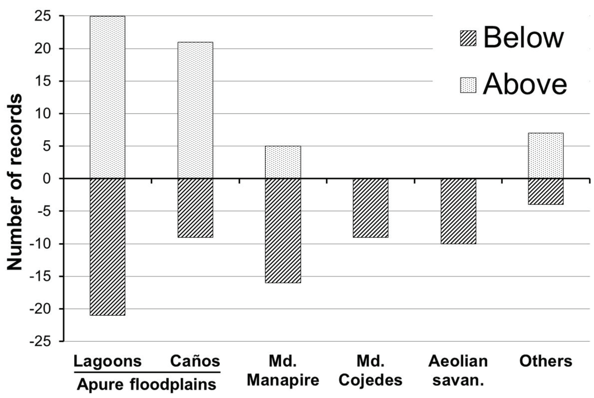

Fig. 3. Frequency distribution of data points above or below *Crocodylus intermedius* growth curves depicted in Fig. 2. "Others" include regions 3, 4 and 8, with less than four data points each.

When only records from Apure floodplains are taken into consideration, the asymptotic values were larger for males than for females, as is characteristic of all crocodilian species (Fig. 4). Regardless of the method used, growth curves for males and females do not markedly differ up to the fourth year. The models predict that around six years are required to reach a TL of 250 cm, the size at which the species is sexually mature (Antelo, 2008).

Growth rates for individuals under four years of age differed among regions (Table 3), particularly when considering the four data sets with the largest number of growth records (Kruskal-Wallis H=21.48; p<0.01). Crocodiles from the Cojedes River grew at the lowest rate (mean 14.1 cm/year), whereas those from Caños in the Apure floodplains grew fastest (mean 43.3 cm/year). Growth rates between Lagoons and Caños in the Apure floodplains were marginally significantly different (Mann-Whitney pairwise comparisons, U=171, p=0.066).

DISCUSSION

Growth rates of *C. intermedius* differed among regions. For individuals up to four years of age, growth rates ranged from low values in the Cojedes River to high values in the Apure and Guárico states. The unrealistic asymptotic size predicted by the von Bertalanffy growth model (particularly for females) is likely a consequence of pooling records from distinct ecological regions. Whitewater rivers are more productive than clearwater and blackwater rivers (Sioli, 1984), and a link between growth and productivity is supported by individuals from Caños growing faster than individuals from the Aeolian savannahs (see also Antelo, 2008). Although some rivers included in Caños might not be fully regarded as whitewater, they are in floodplains influenced by whitewater rivers such as the Apure and the Arauca (Sarmiento & Pinillos, 2001; Ayarzagüena & Castroviejo, 2008). Furthermore, Caños soils are richer and more productive than the Aeolian plains of the Capanaparo and Cinaruco (Jepsen et al., 1997). Muñoz & Thorbjarnarson (2000) reported that *C. intermedius* in the Capanaparo

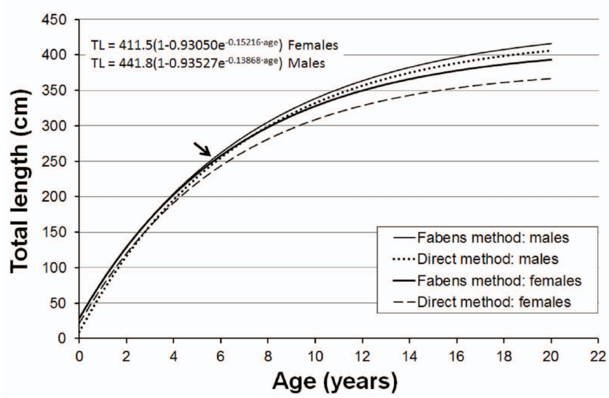

Fig. 4. Growth curves for Apure floodplains obtained by means of the direct fitting and Fabens methods. Only the equations by the Fabens method are shown. The arrow indicates the intersection of curves at 250 cm total length, the size at which most individuals reach sexual maturity.

grew at a rate of 35.1 cm TL/year, similarl to the values calculated in this study.

Growth rates were higher at lower elevations and declined upstream. According to Antelo (2008), captive *C. intermedius* slow their growth rates at water temperature below 28°C. In the upper llanos and the piedmont, the water temperature may frequently drop below this threshold (see Seijas et al. 2001). The slow growth rates of individuals in the Cojedes River are probably related to its location and to habitat deterioration. This water course is highly polluted, and has been affected by deforestation, channelisation, and damming (Seijas et al., 2001, Mendoza & Seijas, 2007). The growth rates presented herein corroborate previous findings by Seijas (1998) and Ávila (2008).

Although *C. intermedius* may occupy lentic water, rivers are its primary habitat (Medem, 1981; Thorbjarnarson, 1988; Seijas, 2011). This is supported by the present study, since individuals from the Apure floodplains grew slower than the ones from the neighbouring Caños (see also Chávez, 2000). Although based on only two individuals, the growth rates reached by *C. intermedius* from the Tucupido reservoir are remarkably low. Before this river was dammed, Thorbjarnarson (1988) estimated growth rates which are slightly above the ones found in the present study, suggesting a deterioration in habitat quality at the border of the species' range.

For both fitting procedures, the rather unrealistic asymptotic TL predicted for females is likely a consequence of the low sample size. The lower root mean square errors (RMSE) obtained with the Fabens method appears to a better fit to the data. Although the age of recaptured crocodiles was known, size at time of release into the wild may not be a good predictor of age. Released crocodiles come from several breeding facilities with different management strategies (Hernández, 2007; Hernández et al., 2010). As a consequence, released individuals of the same age may vary widely in size (Seijas, 2011; Babarro & Hernández, 2013). If growth after release depends more on size than on age, then the Fabens method is more adequate.

Although individuals from lagoons and Caños grew at different rates, data from these adjacent habitats in the Apure floodplains were combined to produce growth curves for both sexes. This is deemed to be justified since crocodiles move between these habitat types (Chávez, 2000).The inferred maximum lengths for the Apure floodplains are similar to previous record for the species (Medem, 1981; Antelo, 2008). The growth curves obtained for individuals form the Apure floodplains are within the range of the ones obtained by Antelo (2008).

The release of captive-reared crocodiles will continue. None of the areas where the species existed in the past should be discarded to restore populations, but optimal habitats should be prioritised. Individuals released in suboptimal and marginal habitats should be large (>150 cm TL) to shorten the time required to reach sexual maturity. In addition to water quality and productivity of habitat, availability of nesting substrate, abundance of predators or competitors, water temperature and human pressure may play an important role for growth and survival of *C. intermedius* (Thorbjarnarson, 1988). For example, despite its low productivity, the Cinaruco River with its sand beaches offers good substrates for nesting. On the other hand, the lagoons in El Frío, where many crocodiles have previously been released, lack sandy beaches but until recently were characterised by active conservation management (Antelo, 2008).

ACKNOWLEDGEMENTS

Some of the data analysed in this article were collected and kindly provided to the author by John Thorbjarnarson (†), Keila Matos, María Muñoz, Magdiel Jiménez-Oraá, Magddy Jiménez-Oraá, and Omar Hernández. Reviewers and the journal editor made important suggestions to improve the paper.

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Accepted: 3 November 2015

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