

Captive breeding of *Crocodylus intermedius* (Graves, 1819) under different stocking densities

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Abstract. *Crocodylus intermedius* is restricted to the Orinoco River basin in Colombia and Venezuela and one of the most endangered New World crocodile species. To determine optimal rearing density and to improve rearing conditions of *C. intermedius*, we worked with 228 captive-reared crocodiles housed in concrete enclosures and distributed into three densities. Crocodiles were fed five days per week and measured at one, six, and 11 months of age. These data were used to calculate a body condition index (BCI) as well as weight and length gain of each individual. Our results indicated that animals reared at a low density (1.82 m²/individual) were longer and heavier than animals reared at medium density (0.71 m²/individual) and high density (0.54 m²/individual). These data confirm that growth of *C. intermedius* is density-dependent, as in other crocodylian species. However, crocodiles reared at lowest density also attained the highest BCI. This confirms that the Orinoco Crocodile exhibits faster development at low densities. BCI estimates indicate that adding a second shelter was only beneficial at low stocking densities, whereas at high densities there were adverse effects on both weight and length gain. Use of a shelter and selecting a density that allowed rearing a maximum number of individuals while promoting a fast growth rate is beneficial for both conservation and commercial perspectives.

Keywords. Body condition, captive rearing, shelters, Orinoco Crocodile, stocking density.

Introduction

The Orinoco Crocodile (*Crocodylus intermedius*) is the largest crocodylian (Fig. 1A) in South America and one of the most endangered (Thorbjarnarson, 1988; Velasco et al., 2008). These large reptiles occupy a wide variety of habitats (Medem 1981, 1983), and commercial overexploitation of the species started at the end of the 1920s in both Colombia and Venezuela. Hunting was particularly intense from 1930–35 and continued in the following decades until the populations were severely reduced by the 1960s (Mondolfi, 1965; Medem 1981, 1983). Currently, *C. intermedius* is only found in a small

fraction of its original range, in small subpopulations and with some isolated individuals. In Venezuela the only relatively large and viable populations occur in the Capanaparo and Sarare-Cojedes River systems (Babarro, 2014; Velasco et al., 2020). In Colombia only a few individuals remain in the Arauca River (Ardila-Robayo et al., 2002; Balaguera-Reina et al., 2018).

Crocodylus intermedius is listed as Critically Endangered and legally protected in Colombia by Ministerial Resolution No. 383 (Ardila-Robayo et al., 1999) and in Venezuela by Presidential Decree No. 1486 (República de Venezuela, 1996). It is also listed in the *Red Book of Venezuelan Fauna* as Critically Endangered (Rodríguez et al., 2015). The International Union for Conservation of Nature lists the species as Critically Endangered (Balaguera-Reina et al., 2018), and it is also included on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2017). The Ministry of Environment (MARN) of Venezuela has developed an Action Plan for the conservation of *C. intermedius* (Velasco, 2003), consisting mainly of the captive breeding of animals, hatching their eggs in captivity, and rearing the resultant young crocodiles intended for reintroduction to the wild (Velasco et al., 2008). This effort has led to a significant increase in their population within their distribution range (Velasco et al., 2020).

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There are seven breeding/rearing facilities in Venezuela, although only three of them are currently devoted to the production of individuals to be released into the wild (Babarro, 2008; Hernández et al., 2010a; A. Velasco, pers. comm.). To date, Agropecuaria Puerto Miranda, Fundo Pecuario Masaguara (FPM), and the captive rearing centre of the Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora have their own adult breeding stock, and in cooperation with the Fundación para el Desarrollo de las Ciencias Físicas Matemáticas y Naturales (FUDECI), these facilities are also rearing hatchlings collected from the wild to produce most of the captive-reared individuals in the country (Babarro, 2008; O. Hernández, pers. comm.).

Efforts to aid in the recovery of natural populations use captive breeding as the main tool, because it reduces embryo and hatchling losses due to predation and other natural causes and allows for reintroduction of individuals with greater survival rates (Babarro and Hernández, 2013; Espinosa-Blanco and Vargas-Clavijo, 2014). However, captive breeding involves high costs and significant capital expenditure for maintenance, equipment, facilities, training of workers, and animal feed to guarantee a healthy individual with a high BCI (Body Condition Index) (Hernández et al., 2010a). The objective of this study was to determine the optimal density of individuals and number of shelters to improve rearing conditions and produce *Crocodylus intermedius* with good body condition and larger size when reintroduced into the wild. This would help the recovery of the populations and achieve the objectives of the Action Plan (Velasco, 2003) for conservation of this crocodile in Venezuela.

Materials and Methods

Animals and housing. In this study we worked with 228 hatchling (ca. 1 month old) *Crocodylus intermedius* (Fig. 1B). Out these, 114 hatched in the wild (Capanaparo, naturally incubated) while the remaining 114 hatched in captivity at FPM. Both groups were captive-reared at the latter's facilities in Guárico State, Venezuela. These animals had body weights (BW) of 60–130 g and total length (TL) of 300–350 mm and were labelled using numbered metal Monel tags and assigned to study groups with low, medium, and high stocking densities (space per individual of 1.82 m², 0.71 m², and 0.54 m², respectively; Table 1), which were determined based on the results of Hernández et al. (2010a).

They were housed in concrete enclosures with a living area of 20–40 m² divided into land (85%) and water

(15%; 40–50 cm deep) areas. Enclosures included one or two shelters that partially covered land and water areas (Fig. 1C), to determine how the presence of shelters affect the growth of the species. Air and water temperatures were consistent with ambient temperature (28–34°C). Enclosures were cleaned and refilled with clean water (24–27°C) two days per week before the animals were fed.

Diets and feeding schedules. Animals were fed *ad libitum* once a day, five days per week, with a diet consisting of 35% beef or cow liver, 35% sardines, and 30% dry pig feed pellets. Additionally, 5 ml of vitamins and 40 g of minerals were added for each kg of food (Boede and Sogbe, 2000).

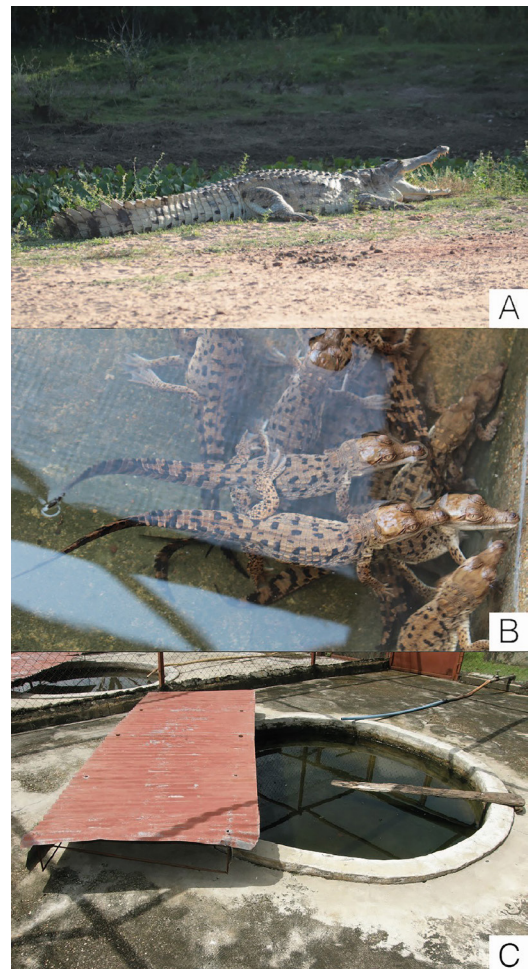


Figure 1. *Crocodylus intermedius* and their enclosures. (A) Adult *C. intermedius*. (B) Hatchlings of *C. intermedius*. (C) Enclosures for rearing *C. intermedius*. Photos by Alvaro Velasco.

Table 1. Treatment groups and housing conditions, including number of individuals, shelters, and living area, of *Crocodylus intermedius* during a series of rearing experiments under different stocking densities in Venezuela. The level of density is low (LD), medium (MD), or high density (HD).

Study Group	Enclosure	Number of shelters	n	Pool		Living Area (m ²)	Density (m ² / Ind)
				Radius (m)	Depth (m)		
LD	1	1	22	1.5	0.48	40	1.82
	2	2	22	1.5	0.48	40	1.82
MD	3	1	55	1.5	0.48	39	0.71
	4	2	55	1.5	0.48	39	0.71
HD	5	1	37	1.5	0.48	20	0.54
	6	2	37	1.5	0.48	20	0.54

Analysis. The analysis was performed using Microsoft Excel. Measurements of BW and TL were taken at one, six, and 11 months of age. Body Condition Index (BCI) was estimated based on the equation of Leonart et al. (2000) and used as by Peig and Green (2009, 2010). The BCI is a method for evaluating the health and body condition of animals. It provides an estimate of an animal’s relative energy reserves. A higher BCI indicates better body condition, while a lower BCI indicates a poorer body condition.

$$M_i = P_i \left(\frac{L_0}{L_i} \right)^{b_{sma}} \text{ and } b_{sma} = \frac{b}{r}$$

where M_i is the BCI for the i^{th} individual, L_i the TL for the i^{th} individual, L_0 the mean of all L_i values, P_i the BW for the i^{th} individual, b_{sma} the allometric scale coefficient, b the slope of the curve $\ln BW/\ln TL$, and r the Pearson’s correlation index.

Data analyses. Shapiro-Wilk’s and Levene’s tests were used to determine normality and homogeneity of variance of the variables. After that, an ANOVA followed by Tukey’s test was used to detect differences in BCI between origin of individuals (wild vs. captivity) at the end of the experiment. A two-way repeated measures ANOVA was used to determine differences in growth of the animals (weight, length, and body condition index) between the three experimental densities and the presence of one or two shelters in the enclosure, through the experimental period (1, 6, and 11 months). These analyses were performed using SPSS software v25 (IBM Corporation, Armonk, New York, USA), and statistical significance was set to $\alpha < 0.05$.

Results

The optimum density of individuals for the captive-rearing of *C. intermedius* was determined by increases in BCI, BW, and TL during each interval between

measurements taken at the three experimental periods. Crocodiles showed a significant rise in BW ($p < 0.0001$) and TL ($p < 0.0001$) at the six- and 11-month assessments (Fig. 2A, B; Table 2). Differences in mean BW and mean TL between treatment groups were highly significant ($p < 0.0001$ and $p < 0.0001$, respectively). At the beginning of the study, there were no statistically significant differences between mean BW and mean TL between treatment groups. (Fig. 2A, B). However, at six and 11 months, mean BW of crocodiles reared at low density (LD-crocodiles) was significantly higher than for those reared at medium density (MD-crocodiles; 6 mo, $p = 0.003$; 11 mo, $p = 0.032$) and high density (HD-crocodiles; 6 and 11 mo, $p < 0.0001$). At the same time, mean BW of MD-crocodiles was higher than that of HD-crocodiles (6 mo, $p = 0.012$; 11 mo, $p = 0.036$; Fig. 2A; Table 2). Mean TL of LD-crocodiles at six and 11 months was similar to the mean TL of MD-crocodiles, and mean TL of crocodiles in both of those groups were longer than those reared at high density (6 mo, $p < 0.0001$; 11 mo, $p = 0.003$; Fig. 2B; Table 2).

The ANOVA revealed that there were differences in BCI between groups ($F = 418.1$, $p < 0.0001$; Fig. 2C). For example, the BCI of LD-crocodiles was greater than of MD-crocodiles ($p < 0.0001$) and HD-crocodiles ($p < 0.0001$). Similarly, the BCI of MD-crocodiles was greater than the BCI of HD-crocodiles ($p < 0.0001$). This result confirms the trend of BW and TL values, showing that *C. intermedius* have a higher growth rate at lower stocking densities. We also conducted an ANOVA to assess differences between BCI values of animals from Masagual farm, Capanaparo River, and Manapire River (Fig. 2D), but there were no statistical differences in BCI based on locality or origin (wild or captive born).

Mean BW and mean TL of crocodiles from different treatment groups were also evaluated according to the number of shelters present in the enclosure. Crocodiles

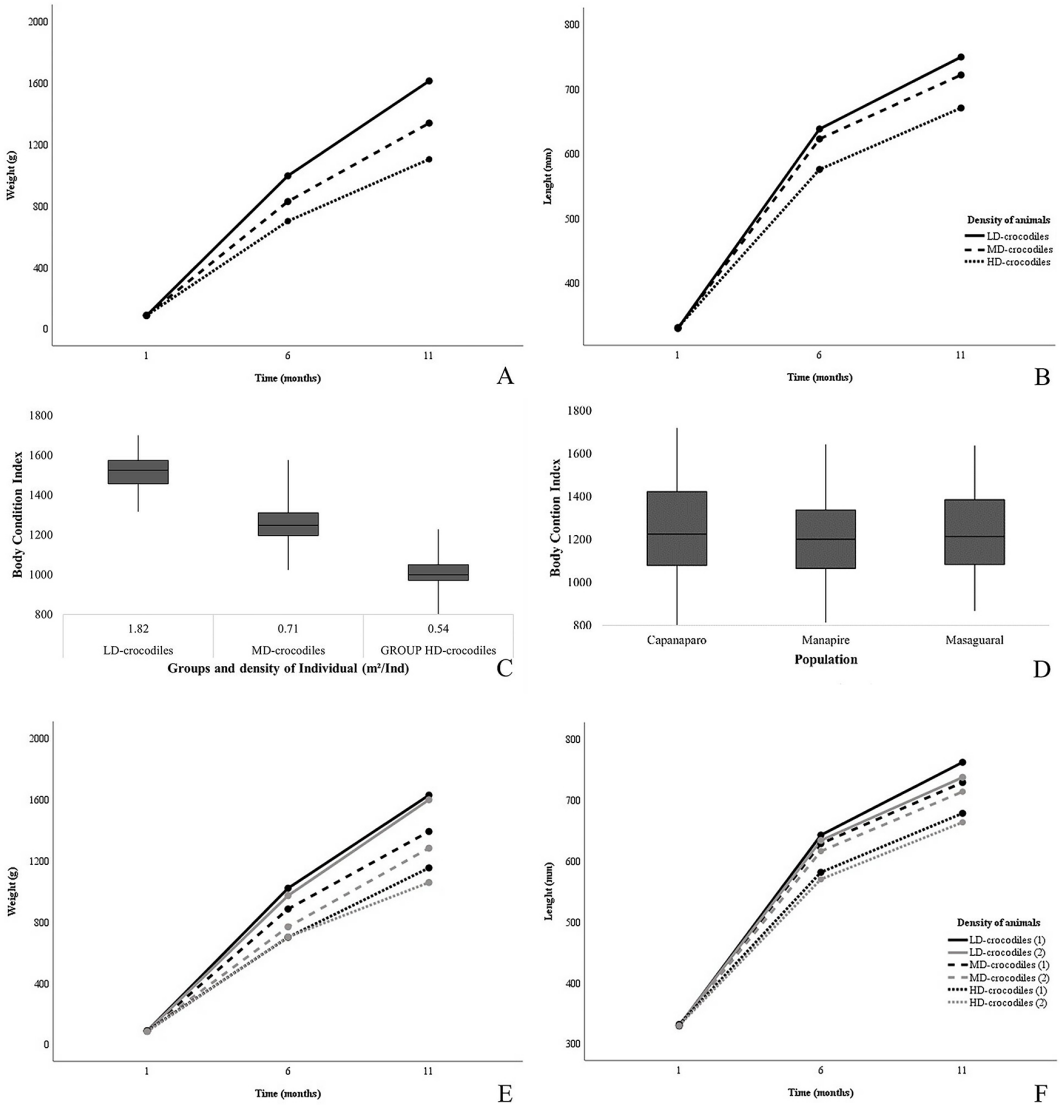


Figure 2. Growth of captive *Crocodylus intermedius* through the time under different stocking densities. (A) Body mass. (B) Total length. (C) Body condition. (D) Body condition by place of origin. (E) Body mass with varying shelter numbers. (F) Total length with varying shelter numbers. Numbers represent the shelter numbers for each group.

had a significant increase in BW ($p < 0.0001$) and TL ($p < 0.0001$) between the treatment group through the experimental period (Fig. 2E, F; Table 2).

Crocodiles in an enclosure with a single shelter after six months showed no significant differences in BW between LD-crocodiles and MD-crocodiles, or MD-crocodiles and HD-crocodiles. However, LD-crocodiles were heavier than HD-crocodiles ($p < 0.001$). When two shelters were provided, LD-crocodiles were heavier than HD-crocodiles ($p < 0.04$). Finally, the BW of MD-crocodiles and HD-crocodiles were similar to each other.

Crocodiles after all months in an enclosure with a single shelter showed no significant differences in BW between LD-crocodiles and MD-crocodiles, or MD-crocodiles and HD-crocodiles. However, LD-crocodiles were heavier than HD-crocodiles ($p < 0.009$). In enclosures with two shelters, LD-crocodiles were heavier than HD-crocodiles ($p < 0.014$). Finally, the BW of MD-crocodiles and HD-crocodiles were similar to each other (Fig. 2E; Table 2).

Regarding TL, after 6 mo. with a single shelter, LD-crocodiles and MD-crocodiles were not statistically

Table 2. Body mass and total length of captive *Crocodylus intermedius* during a series of rearing experiments under different stocking densities and shelter number in Venezuela. The abbreviations LD, MD, and HD correspond to the low, medium, and high stocking density groups, respectively (numbers represent the quantity of shelters per group). The mean and standard deviation are given for the specified group and time interval (months).

Measurement (mean ± SE)	Group	Time (months)		
		1	6	11
Body mass (g)	LD	86.05 ± 12.56	995.70 ± 267.01	1613.37 ± 669.74
	MD	87.31 ± 15.73	828.36 ± 278.92	1338.89 ± 561.96
	HD	86.38 ± 14.46	700.85 ± 278.960	1103.54 ± 566.73
Total length (mm)	LD	329.56 ± 9.65	638.05 ± 53.22	749.49 ± 94.88
	MD	329.30 ± 8.59	622.57 ± 53.38	721.71 ± 99.33
	HD	330.68 ± 7.78	575.42 ± 69.53	670.63 ± 99.81
Body mass (g)	LD1	86.19 ± 3.22	1020.24 ± 60.07	1628.81 ± 128.52
	LD2	85.91 ± 3.15	972.27 ± 58.69	1598.64 ± 125.57
	MD1	86.11 ± 2.01	884.44 ± 37.46	1391.20 ± 80.15
	MD2	88.60 ± 2.09	767.780 ± 38.93	1282.40 ± 83.29
	HD1	89.19 ± 2.65	699.84 ± 49.44	1153.55 ± 105.78
	HD2	83.82 ± 2.53	701.76 ± 47.21	1057.94 ± 101.01
Total length (mm)	LD1	329.10 ± 9.97	642.57 ± 47.83	762.14 ± 69.54
	LD2	330.00 ± 9.55	633.73 ± 58.71	737.41 ± 114.39
	MD1	329.54 ± 8.27	628.56 ± 56.94	729.02 ± 92.64
	MD2	329.04 ± 9.00	616.10 ± 46.68	713.82 ± 88.01
	HD1	331.52 ± 7.81	581.42 ± 67.12	678.35 ± 108.12
	HD2	329.91 ± 2.53	569.94 ± 72.22	663.59 ± 102.66

different. However, HD-crocodiles were shorter than LD-crocodiles ($p = 0.004$) and MD-crocodiles ($p = 0.006$). When reared with two shelters, HD-crocodiles were shorter than LD-crocodiles and MD-crocodiles ($p = 0.001$). After 11 months, with either one or two shelters, TL of crocodiles were not statistically different between LD-crocodiles, MD-crocodiles, and HD-crocodiles (Fig. 2F; Table 2).

Discussion

Many factors influence the growth rate of captive-reared crocodylian species, such as age, genetics, sex, metabolism, temperature, feeding, or if the animal was born in captivity or in the wild (Ardilla-Robayo et al., 1999b; Pérez-Talavera and Velasco, 2002; Pérez-Talavera, 2007, 2008; Hernández et al., 2010b; Serna-Lagunes et al., 2010; Espinosa-Blanco et al., 2017). In our study, crocodiles maintained at high density showed significantly lower growth and weight gain relative to the low and medium density groups (Fig. 2A, B). Elsey et al. (1990) reported that growth in juvenile American

Alligators, *Alligator mississippiensis* Daudin, 1801, was inversely proportional to stocking density, while Webb et al. (1983, 1992) reported a similar inverse relationship between growth rate and rearing density in Australian Freshwater Crocodiles, *C. johnstoni* Krefft, 1873, and Saltwater Crocodiles, *C. porosus* Schneider, 1801.

In two Venezuelan crocodile farms, Hernández et al. (2010a) reported rearing *Crocodylus intermedius* at 0.67, 0.8, 1.0, 1.33, and 2.0 m² / individual stocking densities. They reported a higher growth rate at low stocking densities, in a similar manner to the results presented in here (Fig. 2A, B). A low stocking density promotes better growth rates of captive *C. intermedius*, probably because this allows more living space for each individual and decreases the stress of food competition (Webb et al., 1983, 1992). These findings align with Webb et al. (2021), who determined an optimal stocking density of 1.24 m² / individual for Nile Crocodiles, *C. niloticus* Laurenti, 1768, and recommended avoiding higher stocking densities that could negatively impact growth, nutritional efficiency, and skin quality. These results and our study

indicate that the influence of stocking density on growth is consistent across various crocodylian species.

Generally, BCI is used to describe the health of animals and / or their energy reserves. Evaluating the BCI of the different stocking groups, with Orinoco Crocodiles at low density showing a good body condition, further confirming that they experience better development when raised at low densities (Fig. 2C). Joanen and McNease (1987) suggested an optimum rearing density of 0.1 m² / individuals during the first year of life, while Elsey et al. (1990) recommended a density not less than 0.18 m² / individuals for rearing juvenile alligators (7–10 mo old). Furthermore, Webb et al. (1983) suggested a density of 0.06–0.1 m² / individuals for *C. johnstoni* (3 mo old) increasing to 0.1–0.2 m² / individuals by the end of the first year. Alternatively, Webb et al. (1992) and Hernandez et al. (2010a) reported an optimum of 0.09 m² / animal for rearing *C. porosus* and *C. intermedius*, respectively. These variations in recommended densities highlight the species-specific requirements related to breeding conditions, including food quantity, nutritional demands, living area requirements, water depth, temperature, and stocking density (Ramo et al., 1992).

Hatchlings of different crocodylian species grow at different rates. Elsey et al. (1990) reported that alligators maintained under four different density treatments showed differences in growth, and that alligators maintained at the lowest stocking density were significantly heavier and grew significantly faster than at other densities, results similar to ours (Fig. 2A, B; Table 2). In contrast, *C. johnstoni* and *C. porosus* reared at high densities had lower growth rates, where some individuals failed to grow and lost weight, results similar to ours, where crocodiles reared at high stocking density grew more slowly than those at lower densities (Fig. 2A, B; Table 2; Webb et al., 1983, 1992). Social behaviour also plays a role in the relationship between stocking densities and growth in crocodylians. Higher densities that promote fast growth rates are also associated with a higher proportion of individuals that do not thrive (Webb et al., 1992). Conversely, lower densities are associated with higher food conversion rates (Webb et al., 1983). However, conversion of food to BW can be compromised if crocodiles are housed in small enclosures (Morgan and Tromborg, 2007).

In our study, growth between treatment groups was not influenced by either “clutch effect”, defined as the genetic influence of parent animals over the embryo (Bagatto et al., 2012), or by initial size of the animals (Table 2). However, in some cases the growth and

BCI of crocodylian hatchlings can be influenced by genotypic characteristics or age of the parents, which may translate into reduced growth or reduced hatchling fitness (Elsey et al. 1990; Martínez, 1996; Pearse, 2007; Sigler, 2007; Mendoza and Seijas, 2008; Serna-Lagunes et al., 2010; Lasso et al., 2011).

We expected that increasing the sheltering area within enclosures by adding a second shelter would increase growth rates by minimizing stress, but it may have decreased interactions between individuals and generated the opposite effect. The findings about the influence of shelter number were not conclusive and all results appeared to be attributable to stocking densities (Fig. 2E, F; Table 2). We observed that some crocodiles had difficulties to transit from water to the second shelter, making it difficult to use. In general, it has been reported that shelters are a necessary component of crocodylian enclosures to provide a sense of security and to minimize stress caused by any external disturbance, stimulating the growth rates of captive crocodylians (Antelo et al., 2008; Hernández et al., 2010a; Lasso et al., 2011; García-Grajales et al., 2016).

For *Crocodylus intermedius* and other endangered crocodylians, selecting optimal densities to allow a maximum number of individuals to be reared while promoting the fastest growth is beneficial for both conservation and commercial initiatives. Fast-growing individuals released into the wild can rapidly reach a size at which they are less vulnerable to predation, thereby enhancing their survival (Brandt, 1991; Elsey et al., 1992; Larriera et al., 2004; Larriera and Imhof, 2006). Additionally, increasing growth rates reduces the time crocodiles need to be maintained in captivity, lowering the feeding and maintenance costs.

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