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Growth Curves of Wild and Reintroduced Broad-Snouted Caimans (*Caiman latirostris*) and Their Management Implications

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Abstract. We describe body growth functions of broad-snouted caimans (*Caiman latirostris*) for wild and reintroduced individuals. Snout-vent length (SVL, cm) and age of young individuals and adult females were recorded for two different groups: (Py) animals born in the Proyecto Yacaré ranching program, from eggs collected in the wild; and (Wy) wild caimans Class I (< 25 cm SVL) whose age was determined by Size Frequency Analysis, plus females reintroduced by the Proyecto Yacaré and subsequently recaptured at reproductive age. To describe body growth, we adjusted five models through non-linear regression: Logistic, 4-Parameter Logistic (4-PL), Gompertz, 4-Parameter Gompertz (4-G), and von Bertalanffy. Each group was analyzed separately (Py and Wy), and we selected the most parsimonious model based on the Akaike criterion. We also analyzed the possible linear growth difference using ANCOVA. For Py, the Logistic model was best, whereas for Wy the most suitable was 4-PL, in which wild animals would arrive at the inflexion point 1.4 years later on average than in Py. Analyzing the stage at which their development was linear in shape, we detected that the wild animals had a similar growth rate to reintroduced individuals. As a result, although Py animals had experienced accelerated development whilst in captivity, it did not modify their subsequent growth in the wild. The likelihood of survival in this species increases with body size, thus it is important to emphasize that reintroduced animals are larger than wild animals of the same age and that previous farming conditions seem not to affect their growth in the wild. Therefore, we expect that reintroduced caimans will exhibit greater survivorship than natural animals of the same age. Consequently, an adjustment of the current ranching program should be considered, in the sense that population viability could be achieved by reintroducing a lower number of caimans each season.

Keywords. Growth models; Nonlinear regression; Ranching; Wild animals.

INTRODUCTION

Growth, survival, and reproduction are fundamental parameters in the life history of individuals and populations. Specifically in crocodylians, survival and reproduction are body-size dependent (Nichols et al., 1976; Hutton, 1987; Verdade, 2001; Larriera et al., 2004). Development in these animals is a complex process influenced by several factors, such as climatic conditions, resource availability within the habitat (food, shelter, sunbathing sites; Webb et al., 1978; Rootes et al., 1991; Tucker et al., 2006; Parachú Marcó et al., 2009; Silveira et al., 2013), sex (Webb et al., 1978; Hutton, 1987), genetics, incubation conditions (Piña et al., 2007), social factors (Lang, 1987), and even management practices (Piña and Larriera, 2002).

Growth patterns in reptiles can be adjusted by several theoretical models, like those presented by von Bertalanffy, Logistic, Gompertz and Richards, among others (Avery, 1994; Tucker et al., 2006; Rodríguez-Caro et al., 2013). In crocodylians, most studies use the von Bertalanffy model, building it with data from captures and recaptures, generally occurring at non-regular intervals (Campos et al., 2013; Silveira et al., 2013; Wilkinson et al., 2016). This procedure is commonly used as a consequence of both logistical difficulties in gathering the appropriate information and because individual crocodylians are long-lived, thus a considerable accumulation of data is required for the estimations to have acceptable precision (Abercrombie and Verdade, 1992).

Sustainable use has become a common component of crocodylian conservation and management plans. Some

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species are farm-raised, pursuing commercial or conservation objectives (Blake and Loveridge, 1975; Larriera and Imhof, 2006; Manolis and Webb, 2006). This strategy has proved to be successful in several cases (Dodd and Seigel, 1992), for example for *Alligator mississippiensis* (Daudin, 1802) (Elsey et al., 1992, 2000), *Crocodylus porosus* Schneider, 1801 (Webb et al., 2000) and *Crocodylus niloticus* Laurenti, 1786 (Blake and Loveridge, 1975). The stability of crocodylian populations in the medium and long-term under well-conducted commercial harvest programs is a clear indicator of the appropriateness of this approach (Hutton and Webb, 2002; Hutton et al., 2002; Larriera and Imhof, 2006). In farms, animals are maintained at controlled temperatures and fed efficiently in order to accelerate growth (Larriera et al., 1990; Piña and Larriera, 2002; Larriera et al., 2008). Wild broad-snouted caiman populations in Argentina are subjected to a reinforcing strategy through a ranching system. In this system, complete clutches of wild nests are harvested, artificially incubated and then hatched. Hatchlings are farmed for 9 months before being returned to nature during the warm months at the same place from where the eggs were collected (Larriera and Imhof, 2006). Once in nature, these individuals are subjected to the same environmental pressures endured by wild-born animals, although when released they are larger than wild individuals of the same cohort. Previous data indicate that wild and reintroduced females exhibit similar size at the reproductive age (Portelinha, 2016).

The lack of information on the growth of either wild or reintroduced *Caiman latirostris* (Daudin, 1802) arouses interest in the development of these animals, particularly the fate of reintroduced individuals post-release (population reinforcement as defined by IUCN/SSC, 2013). The objective of this study was to describe and compare the growth of wild and reintroduced individuals of *C. latirostris*. From the obtained results, we aim to validate the assumption that ranching and release of reared individuals is an efficient strategy for fostering the population of this species. In this way, we hope to generate recommendations to ensure the viability of populations of this species in their natural habitat.

MATERIALS AND METHODS

We used data from captures obtained by Proyecto Yacaré from 1994–2016 in Santa Fe Province, Argentina. The study area includes floodplains and part of tributary rivers of the northwest of the province. It is characterized by numerous shallow lagoons, presents a gentle slope, and has slow drainage (Iriondo, 1985; Pautasso, 2003). Weather is temperate with marked seasonality and winter temperatures oscillating between 1–15°C, with an average of 9°C (Universidad Nacional del Litoral, 2018).

To create growth curves, we used snout–vent length (SVL, cm) and age (years) of individuals captured in warm months (October–March). Sex of broad-snouted caimans was determined through inspection of the cloaca for presence of a penis or clitoris (Piña et al., 2003, 2007). As this sexing method is only reliable beyond 35 cm SVL, depending on the species and observer experience (Ziegler and Olbort, 2007; Nuñez-Otaño et al., 2010; Combrink et al., 2012), individuals smaller than 35 cm were scored as “undetermined sex” (but see Ciocan et al. [2020] in this issue for sexing caimans). The data used for generating the model corresponded to immature individuals (Class I and II) and adult females. We eliminated male data because of their low frequency.

Data were classified into two groups, according to their origin. The group Py ($n = 61$) was composed of animals hatched from eggs collected in wildlife by the Ranching Program Proyecto Yacaré (Larriera and Imhof, 2006). For identification, these individuals were marked on their caudal scutes. They were raised in captivity, released into the sites where their nests were located, and later recaptured. In contrast, the group Wy ($n = 140$) was divided into three subgroups: wild-born Class I (CI; < 25 cm SVL, $n = 109$) individuals, Class II (CII; ≥ 25 cm SVL, $n = 1$) individuals, and the data of Py females at adult stage ($n = 30$). When a group of similar sized CI caimans were captured in the wild, we assumed they were from the same clutch and thus used their mean SVL as a single data point in our database. This prevented larger clutches having more leverage than single observations or clutches with fewer individuals. As such, we reduced 54 data points to 8 averages.

The age of Wy (those born in the wild) was estimated by the analysis of their size frequency using Gaussian Mixture Model from the “mixtools packages” (Benaglia et al., 2009; Fig. 1). We delimited three periods based on

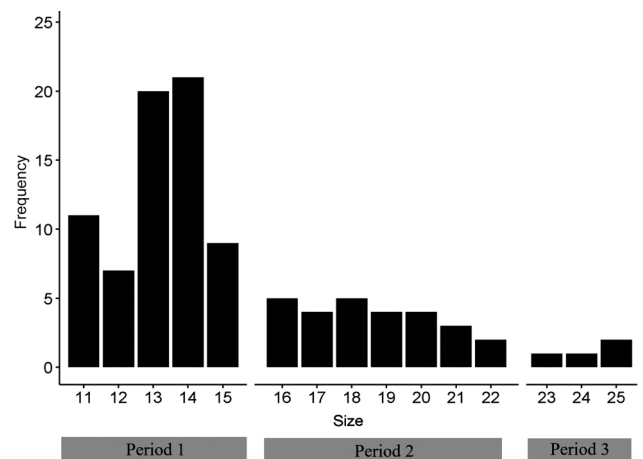


Figure 1. Histogram of the frequency distribution of snout–vent length (SVL, cm) of the captured wild caimans. The discontinuity in the graph shows the cut-off of the size that corresponds to each age in years, which was estimated through an analysis of size frequencies using Gaussian Mixture Model.

the intersection point between the Gaussian curves (Period 1 = 10–15.4 cm SVL; Period 2 = > 15.4–23 cm SVL; and Period 3 = > 23–25 cm SVL). Every Wy classified in those periods was analyzed on the basis of the capture date (after or before hatching time) to determine if they belonged to the assigned period (each period corresponds to 1 year; i.e., Period 2 represents a 2-year-old caiman). One Wy was captured and its age estimated to be 3.1; 0.9 years later it was recaptured, so we used this animal in the database only in the 2nd capture. In addition to these CI and CII specimens, we incorporated in the Wy group the data from 30 females raised and reintroduced by the Proyecto Yacaré (Py) that were recaptured 6–19 years later (thus of reproductive age). We included these adult females assuming that (a) any effect of captivity on their growth would have ceased due to the long period in the wild and (b) the asymptotic size would be the same between animals born in nature and the farm.

We tested five models of body growth by non-linear regression using the ‘nlslr’ package (Nash and Murdoch, 2017) in Rstudio (R Core Team, 2018), through an iterative process applying the Gauss-Newton algorithm. The models tested were Logistic, von Bertalanffy (VB), Gompertz (Dodd and Dreslik, 2008), 4-parameter Logistic (4-

$$PL, SVL = \frac{d}{(1 + b.e^{-k \cdot Year})} + \eta, \text{Logistics model plus constant),}$$

and 4-parameter Gompertz (4-GL, $SVL = d.e^{(b.e^{-k \cdot Year})} + \eta$, Gompertz models plus constant). For every model, we evaluated the ‘rate constant’ k (year^{-1}), which determines

the spread of the curve along the time axis ($\beta = \frac{\ln(b)}{k}$, years), where the maximum growth occurs. For 4-PL and 4-GL, the constant ($\eta = \text{cm}$) and the asymptotic size, such as ($\alpha = \eta + d$, cm), were obtained.

We selected the model that best described variations of our data based on the maximum likelihood principle using the Akaike information criterion adjusted for small samples (AIC_c). We calculated difference in AIC_c between

each model and the one with the lowest value. Later, we obtained AIC_c ’s normalized weight (w_i) of each model, which allowed us to compare them to each other and select the most plausible one for our data ($0.6 > w_i$). Data considered to be outliers (their values were beyond two standard deviations from the value predicted by the model) were eliminated, and the model was rerun to obtain a less biased estimation. We used the Jackknife technique to measure the effect of each data on the average value of each parameter and to estimate the bias for each predicted value.

To evaluate if there was a difference in the initial growth pattern between both groups, we built a linear regression model with interaction. In this case, to test their correlation, we used only data corresponding to the linear growth interval (up to 4 years in Wy and from 9 months to 5 years in Py individuals). Because the covariate model did not comply with the homoscedasticity assumption, we analyzed it with Generalized Least Squares in the ‘nlme’ package (Pinheiro et al., 2017), using the maximum likelihood method. For this purpose, we built the combined variance function $\text{varComb}(\text{varIdent}(\text{form}=\sim 1 | \text{Origin}), \text{varExp}(\text{form}=\sim \text{Time}))$ and used graphic analyses to evaluate model assumptions.

RESULTS

The best model that described the growth of Py individuals was Logistic ($w_i = 0.6$, Table 1), defined by: maximum SVL (asymptote) $\alpha = 76.7 \pm 1.5$ cm (bias = 0.08), spread of the curve $k = 0.40 \pm 0.04 \text{ year}^{-1}$ (bias = 0.0007), and maximum growth at $\beta = 3.1 \pm 0.4$ years (bias = 0.03), with an SVL of 38.5 cm (Table 1). On the other hand, the best model for animals that completed their full development in nature (Wy) was the 4-PL ($w_i = 0.96$), with the following parameters: asymptote: $\alpha = 75.05 \pm 1.8$ cm, $k = 0.68 \pm 0.04 \text{ year}^{-1}$, maximum growth at $\beta = 4.5 \pm 0.4$ years with SVL of 41.4 cm, and constant $\eta = 9.5 \pm 0.9$ (Fig. 2). The inter-

Table 1. Output of the five analyzed models. The best model for each group based on the Akaike information criteria is highlighted in grey. AIC_c : Akaike value; ΔAIC_c : difference of the respective AIC_c with the lowest AIC_c value; w_i : normalized weight; α : asymptotic size (cm); β : inflexion point (years); k : rate constant (year^{-1}); and η : constant; ** Non-significant parameters.

	Selection criteria			Parameters			
	Model	ΔAIC_c	w_i	α	β	k	η
Py	Logistic	0	0.6	76.7 ± 1.5	3.1 ± 0.4	0.4 ± 0.04	-
	LC	2.3	0.2	73.7 ± 12	3.3 ± 1.5**	0.4 ± 0.08	-2.8 ± 11.1**
	Gompertz	2.8	0.1	78.3 ± 1.7	1.64 ± 0.3	0.3 ± 0.03	-
	GC	3.6	0.1	62.8 ± 8.1	3.3 ± 1.3	0.3 ± 0.06	14.3 ± 7
	VB	9.9	0	81.5 ± 2.6	0.9 ± 0.02	0.18 ± 0.02	-
Wy	LC	0	0.96	65.6 ± 1.4	4.5 ± 0.4	0.68 ± 0.04	9.45 ± 0.9
	GC	13.6	0.04	62.3 ± 1.3	3.8 ± 0.4	0.5 ± 0.04	14.1 ± 0.8
	Logistic	40.8	0	77.1 ± 0.9	4.0 ± 0.2	0.5 ± 0.02	-
	Gompertz	79.3	0	79.9 ± 1.3	2.9 ± 0.2	0.32 ± 0.01	-
	VB	110	0	89.2 ± 4.1	0	0.14 ± 0.02	-

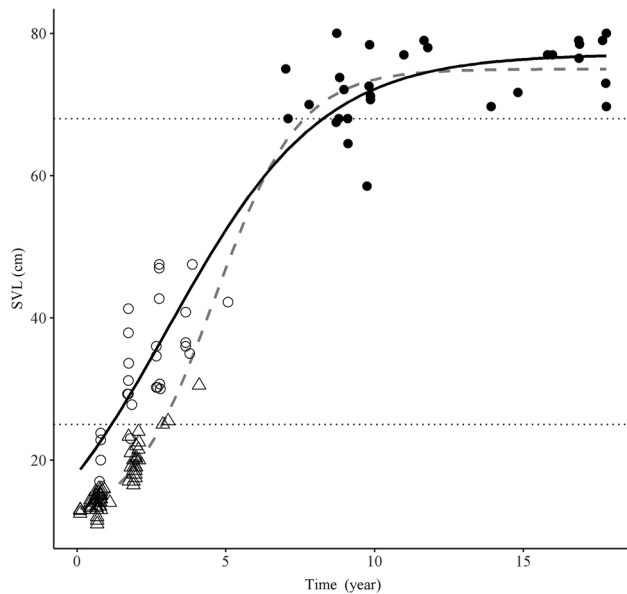


Figure 2. Non-linear models selected for each group of data of caimans. Dashed grey line: 4-PL Model, selected for Wy. Solid black line: Logistic Model selected for Py. Triangles: Wy Data; Circles: Py Data. Filled black circles: adult females of known age were used for curve fitting in both groups. The horizontal dotted lines depict the limits of the age class sizes as stated by Leiva et al. (2019).

section between the curves of both models occurred at 6.6 years old and 61.8 cm SVL. Thus, the start of Class III (CIII 68 cm SVL, Leiva et al., 2019) would be achieved for both groups at similar ages (about 7.9 years old).

In the period of linear growth, the covariate model showed that there was no interaction between the slopes according to the animals' origin ($P = 0.1145$). This shows that the linear growth rates of Py and Wy animals are the same, but individuals of Py are always larger (until the intersection of both curves). As a result, Py caimans are twice as large at the time of release (nine months of age) than those of Wy of the same age, and they reach 25 cm SVL (CII) 0.3 years after reintroduction. On the other hand, wild caimans need 2.6 years to reach CII.

DISCUSSION

Our analysis allowed us to select the models that best described the growth of reintroduced and wild caimans, revealing that the growth of these two groups was different. We found that the Logistic model best described the growth of Py, whereas the best model for Wy was 4-PL (Table 1). Different species or even populations of the same species can differ in their growth patterns, because the best model for one data set might not be the best model for another one (Tucker et al., 2006). These discrepancies might reflect the distinct influence of the underlying local processes on growth (such as temperature, seasonality, and the quality and availability of food).

The models selected here are consistent with the best model for *Alligator mississippiensis* in Louisiana (Elsey et al., 1992). That study used data from reintroduced and wild juveniles of known age, and we used animals of known age (individuals Py) or age estimated independently of the selected model (in our case using frequency analysis for Wy group). This approach differs from the one used in most works published previously (e.g., *Caiman latirostris*: Moulton et al., 1999; *A. mississippiensis*: Brisbin, 1988; Rootes et al., 1991; Wilkinson and Rhodes, 1997; Wilkinson et al., 2016; *Melanosuchus niger* [Spix, 1824]: Silveira et al., 2013; *Paleosuchus palpebrosus* [Cuvier, 1807]: Campos et al., 2013; *Crocodylus johnstoni* Krefft, 1873: Tucker et al., 2006; and *Crocodylus niloticus*: Hutton, 1987). Unlike those studies, the fact that the estimation of ages in our study was obtained independently from the model gives our approach an advantage at the time of decision making. Moulton et al. (1999) warned that ages obtained through models should be handled with caution when trying to predict certain specific characteristics of a population. This advantage is maintained despite the fact that in our data there is a gap in the intermediate zone of the curve, which can generate bias in the estimates of the model.

Another potential source of bias in this study could be the imbalance in the sample size of the components Wy data, and fundamentally the fact of the heterogeneous origin of our data as, on the one hand, Wy is composed of modeled data (from size frequency analysis; CI = 158, CII = 1) and, on the other, data from adult females of known age (CIII = 30 released from Py) are also used. In this sense, the modeled data show less dispersion than those of animals of known ages, so that the former might not represent all the variability of the species in that period of its life history. The reduced dispersion is present not only within Wy individuals of other classes, but also between Py and Wy of small size (Classes I and II; Fig. 2). Despite its weaknesses, using data from different origins to generate growth models has, as a counterpart, the advantage that it allows adding information that a single data source alone does not usually provide. In other words, when one set of data is somehow deficient, another can provide valuable complementary information (Eveson et al., 2004). Appealing to this alternative might be indispensable to obtain at least a first approximation to address a problem using an adaptive management scheme that, as new information is progressively generated, reduces the initial uncertainties in the decision making process.

Some authors state that asymptotic sizes obtained by growth models should not be interpreted as the maximum size that individuals could reach in the population but rather indicate the average value at which growth ceases in most individuals (Wilkinson and Rhodes, 1997; Tucker et al., 2006; Wilkinson et al., 2016). The com-

parison of the asymptotic value obtained in the Py model ($\alpha = 76.7 \pm 1.5$ cm) vs. that of wild reproductive females ($\bar{x} = 81.4 \pm 11.8$ cm, average calculated based on the years that only presented wildlife data reported by Leiva et al., 2019) suggests that the maximum size obtained by us with the Logistic model is similar to that of wild animals. Furthermore, the von Bertalanffy model reaches an asymptotic value of 94 ± 1.8 cm (Moulton et al., 1999) that is similar to what Bertalanffy predicts for Py (Table 1). However, this model, which exhibited the highest asymptotic value, is has the poorest fit to our data among all those tested here.

Growth dynamics of crocodylians are influenced more by the age at which first reproduction occurs than by the asymptotic size (Brisbin, 1988). Minimum reported reproductive size is 68 cm SVL for wild females (Portelinha et al., 2015) and 69 cm for reintroduced females (Larriera et al., 2006), the latter at 7.9 years old. Using our model, we can estimate the minimum reproductive age as 8.1 ± 1.8 years, similar to that found by Moulton et al. (1999) in Brazil, where caimans would begin to reproduce at 75 cm, age 8.6 years. Likewise, the minimum reported age of reproduction in captivity is 5 years (81 cm from SVL; Verdade et al., 2003), these females being larger than the reported wild ones. By achieving the necessary size earlier, females with more available resources could reproduce at a younger age. Therefore, females with more available resources could reproduce at a younger age because they grow faster and thus achieve the required size earlier. However, they might need to reach both a threshold size and age to be able to reproduce. Wilkinson et al. (2016) state that the optimal strategy for females might be to grow relatively rapidly to attain a size where chances of predation decrease and then shift substantial amounts of energy to reproduction and maintenance. In the studied populations, it looks like the growth of the females, rather than their age, would be the bottleneck to successfully achieve their first reproduction.

As the selected models are different, it is not possible to compare the growth change of Wy and Py. This parameter is strongly influenced by the asymptotic value and the minimum size used to build the models. Consequently, to avoid any bias of this type, it was necessary to analyze the phase of linear growth separately. In the linear phase of development (growth at Classes I and II), we detected that the absolute increase in SVL of wild animals did not differ significantly from that of reintroduced animals, but it started at a different initial size (Fig. 3). Similar conservation projects in other species have reported a similar growth or in some cases, a greater growth, for instance, in released *Alligator mississippiensis* in Louisiana (Elsey et al., 1992). In contrast, in *Crocodylus niloticus* the growth of reintroduced animals is lower than that of wild individuals (Blake and Loveridge, 1975).

Our analysis allows us to estimate that at the time of reintroduction (approximately 9 months of age), a Py animal achieves a size which is equivalent to that of a 2.6-year-old Wy and reaches the maximum growth point 1.4 years earlier. As the absolute growth of the Py caimans after their release is similar to that of Wy, we can conclude that their passage through captive conditions does not jeopardize their development in the wild. Furthermore, because survival in crocodylians is size dependent (Somaweera et al., 2013), remaining less time in the size Class I, which has the highest mortality, gives an advantage to the animals reintroduced by Proyecto Yacaré and, consequently, they should exhibit lower mortality than wild animals of the same age. Thus, we can affirm that the ranching program seems to be accomplishing its objective of fostering the caiman population.

Long-term studies of this species have shown that the release of captive-bred caimans is also a feasible management, and there is evidence that it is beneficial for the population's recovery. For example, since this approach was implemented in Argentina, the number of nests has progressively increased (Larriera and Imhof, 2006; Larriera et al., 2006; Leiva et al., 2019). Results obtained in this study support the idea that this method of ranching benefits wild populations of caimans. The benefit arises because the growth of ranched animals after being reintroduced is equal to that of wild animals of the same age,

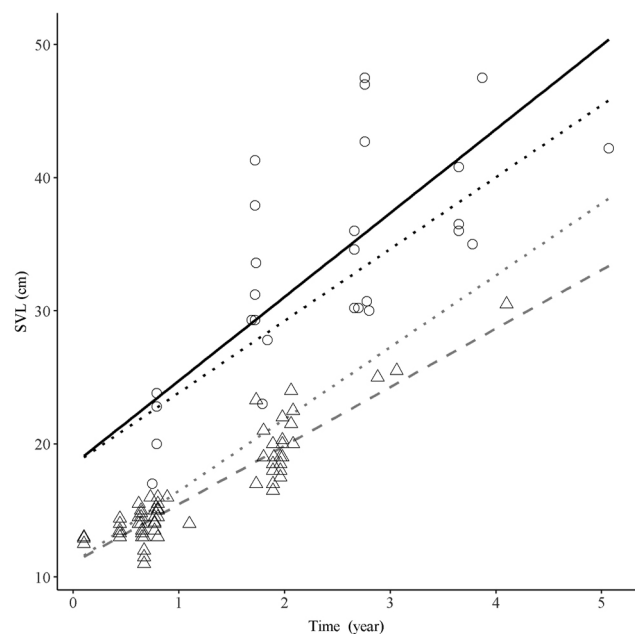


Figure 3. Growth during the first years in the wild of reintroduced caiman (grey) and wild caiman (black). Solid line represents linear function for reintroduced (Py) animals (snout-vent length [SVL]_{Py} = 6.3 years + 18.4 cm); gray dashed line represents linear function for wild (Wy) animals (SVL_{Wy} = 4.6 years + 10.9 cm). Slope of both lines are similar (slope: $T = -1.59$, $P = 0.1145$). Dotted lines represent those produced with the mean slope of the original functions (black for Py, SVL_{Py} = 5.4 years + 18.4 cm; grey for Wy, SVL_{Wy} = 5.4 years + 10.9 cm).

but they are larger than wild conspecifics of the same age. It takes Wy longer to reach the size of Py because they face a more rigorous environment during the first winter in wild conditions. Wy individuals also have higher predation risk during their early stages of development. Therefore, the reintroduced animals have a higher probability of survival than the wild animals of the same age.

Our data indicate that a Wy needs 2.6 years to reach CII (when mortality will be reduced), whereas a Py reintroduced caiman would need only 0.3 years in the wild to reach CII. If we consider that mortality during CI is independent of caiman size, released caimans will have higher chances to reach CII than Wy as it would take only 0.3 years to be 25 cm SVL. Our results could have implications for the necessary number of caimans to reintroduce for ensuring population viability. To estimate the number of animals to be released, we can think of a scenario in the wild in which 30 nests with an average clutch size of 35 eggs (Simoncini et al., 2009) would produce 1,050 eggs. During incubation, 35% of those nests could be lost, resulting in 682 hatchlings; but this estimation seems to be a conservative number based on: 50–62% of the nests predated (Deitz and Hines 1980), up to 41% in dry years (Larriera and Piña 2000), and 28.5% lost only by colony of red imported fire ants in nests of *C. latirostris* (Parachú Marcó et al., 2015). Data from Proyecto Yacaré indicate that approximately 10% of the hatchlings survive their first year (Viotto et al., unpublished results), and we can assume that 30% of the survivors would reach CII. This means that from the 682 hatchlings, 20 caimans would reach CII. On the basis of previous data (Nichols et al., 1976; Woodward et al., 1987; Wood et al., 2017), we consider that our scenario is conservative and that a lower percentage of caimans would reach CII.

In contrast, Proyecto Yacaré reintroduces 10% of the harvested nests (to be included in the reintroduction group, the nest must have at least 35 hatchlings). In the same scenario of 30 nests harvested from one place, the program selects three nests (at least 105 hatchlings) that will produce at least 70 animals for reintroduction (23 cm SVL on average), which is approximately three times more hatchlings than those produced from 30 nests reaching CII (25 cm SVL) in wild conditions. We estimate that a 5% reintroduction (instead of the 10% currently being released by Proyecto Yacaré) would be closer to natural survivorship.

Models are simplified approximations of a complex reality that contains many unknown factors, so they should always be interpreted with caution when bringing them to reality. For this reason, in order to avoid endangering the animal populations involved, it is necessary to implement adequate monitoring and control mechanisms. In the case of the broad-snouted caiman, if it were decided to reduce the number of released young, as we suggest, it would also be necessary to carry out studies over a longer term, in an experimental way, and accompanied by

systematic monitoring. This would enable researchers to evaluate whether or not the proposed and implemented release percentages are adequate for the maintenance of the structure and abundance of the caiman population under the existing environmental scenario and the permitted conditions of use.

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