ETHNOBIOLOGY AND CONSERVATION

RESEARCH ARTICLE

Ethnobiology and Conservation, 12:01 (21 January 2023)
doi:10.15451/ec2023-01-12.01-1-20
ISSN 2238-4782 **ethnobioconservation.com**

Stage-based model of population dynamics and harvest of Broad-snouted caiman (*Caiman latirostris*) under different management scenarios

Evangelina V. Viotto[1,2], Joaquín L. Navarro[3,4], Melina S. Simoncini[1,2,5] and Carlos I. Piña[1,2,5]

ABSTRACT

We created a matrix model structured by stages (divided into 5 stages) to evaluate the population dynamics of *Caiman latirostris* and the population behavior at different management intensities through ranching and hunting of adult individuals. We generated 5000 matrices by sampling the mean and variance values of survivals (p_i) and hatching for each stage. For each matrix, we obtained the growth rate λ and performed elasticity analyses. Modifying the mean matrix obtained from the previous analysis, we evaluated different scenarios of ranching, reintroduction, and hunting of adult females of the last two stages (E) raised here (class III animals, > 60 cm snout-vent length, divided into two: E4 and E5). We obtained a mean λ of 1.035 (range $0.88 - 1.12$), and 11.9% of the simulations had $\lambda < 1$. The vital rate with the highest elasticity and variance was that of the adult females of the last stage. Natural populations can tolerate a maximum of 5% adult female hunting, and ranching can extract 55% of nests from the wild without reintroduction or 80% of nest harvest, returning to the wild at least 3% of hatched animals in the ranching programs. Our model showed that hunting and ranching with reintroduction are feasible strategies to be applied without threatening natural populations. Increasing reintroduction makes it possible to extract more adult individuals and maintain the species' populations at sustainable levels.

Keywords: Crocodylia; LSA; Ranching; Hunting; Population simulation.

---

1 Centro de Investigación Científica y de Transferencia Tecnológica a la Producción - Consejo Nacional de Investigaciones Científicas y Técnicas - Provincia de Entre Ríos-Universidad Autónoma de Entre Ríos. España 149. CP 3105. Entre Ríos, Argentina.

2 Proyecto Yacaré-Laboratorio de Zoología Aplicada: Anexo Vertebrados Facultad de Humanidades y Ciencias, Universidad Nacional del Litoral, Av. Aristóbulo del Valle 8700, Santa Fe, Santa Fe, Argentina.

3 Instituto de Diversidad y Ecología Animal-Consejo Nacional de Investigaciones Científicas y Técnicas y Universidad Nacional de Córdoba - Rondeau 798, CP 5000, Córdoba, Argentina.

4 Cátedra de Problemática Ambiental. Departamento de Diversidad Biológica y Ecología Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Av. Vélez Sarsfield 299, CP 5000 Córdoba, Argentina.

5 Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Argentina. Tratado del Pilar 314, CP 3105. Entre Ríos, Argentina.

* Corresponding author ✉. E-mail address: EVV1 (evangelinaviotto@gmail.com), JLN (joaquin.navarrol@unc.edu.ar), MSS (melinasimoncini22@yahoo.com.ar), CIP (pina.carlos@uader.edu.ar)

Part of Special Issue:
Use, Management and Conservation of Wildlife in Latin America.
Edited by Hani R. El Bizri, Melina S. Simoncini, Jair H. Castro Romero, Alejandro Meléndez Herrada, Joaquín L. Navarro.

SIGNIFICANCE STATEMENT

This study presents the first model to analyze the population dynamics and harvest of the Broad-snouted caiman (*Caiman latirostris*). We use bibliographic information and analyze emerging parameters of the species. By employing Life Stage Analysis (LSA), we evaluate how the survival parameters of each stage affected the population dynamics and analyzed the matrix elasticity. Finally, by modifying the original model, we assess scenarios of hunting adult animals and egg ranching with different percentages of hatchling reintroduction, populations can be kept healthy, and what fixed extraction rate would lead to possible local extinction. This work provides a tool for analyzing the caiman population, useful for decision-makers, and generating new hypotheses to assess the ecology of the species.

INTRODUCTION

Population models structured by stages are widely used in conservation biology since they describe in a simple way the life cycle of the individuals in a population, incorporating fertility, mortality, and growth rates of each in a transition matrix stage (Caswell 2001; Crouse et al. 1987). They are part of a fundamental framework for decision-making in species where the ecology is poorly understood, funds for their research are scarce, or the impacts of management actions are unknown (Tucker 2001). Therefore, these tools are particularly suitable for demographic analyzes of crocodilian species (Fukuda et al. 2020; Nichols et al. 1976; Richards 2003; Tucker 2001).

Historical overexploitation of many crocodilian species, mainly by the leather industry, led to some of them becoming endangered (Larriera 2011). However, crocodilian populations have shown remarkable resilience if protected from overexploitation and when their wetland habitats remain intact. Remarkably, their recovery has been driven by the same commercial initiatives that caused the initial overexploitation (Larriera 2011; Wallace et al. 2013). Between 2011 and 2015, an average of 1.6 million crocodile and caiman skins were traded annually, all from legal, managed sources and, in many cases, based on the sustainable use of wild populations (Caldwell 2017). The most relevant management concern for recovered/recovering crocodilian populations is how they respond when regulated harvests are established on a specific age, size, or sex group (Tucker 1995).

The two most commonly employed sustainable use management strategies for crocodilians are ranching and hunting of adults. Ranching is considered the “safest” of them (Jenkins et al. 2004), as it involves “the rearing in a controlled environment of animals taken as eggs or juveniles from the wild, where they would otherwise have had a very low probability of surviving to adulthood” (CITES 2021). The obtained fully grown individuals are destined for commercial slaughter to get skins, meat, and other products (Larriera et al. 2008; Simoncini et al. 2020). Although ranching programs typically have provisions for reintroducing some of the raised individuals back into the wild, this has rarely been required.

The second strategy (hunting of adults) generated problems in the past because it was poorly controlled and carried out at unsustainable rates. However, there are currently successful programs of this type, i.e., *Caiman crocodilus fuscus* in Venezuela (since 1983, Velasco and Ayarzagüena 2010), and *Alligator mississippiensis* in the United States (since 1971, Elsey and Woodward 2010; Joanen et al. 2021). In both cases, hunting mainly males at low rates has maintained stable or increased populations. Although in Louisiana, harvest management is compensated by reintroducing individuals from ranching.

The Broad-snouted caiman (*Caiman latirostris*) is the southernmost species among crocodilians of the Neotropics (Borteiro et al. 2006). It is geographically distributed in southeastern Bolivia, southern Paraguay, northern Uruguay, and northeastern Argentina (Verdade et al. 2010). Environments with shallow water bodies, ravines, and estuaries, with abundant vegetation, are the preferred habitats by this species. It is considered a "keystone species" as it is a top predator in food chains and participates in nutrient cycling (Piña and Siroski 2004; Verdade et al. 2010). In the mid-twentieth century, hunting pressure seriously depleted their populations throughout their range (Larriera 2011), and since then, this practice has been banned. Although several of its populations showed signs of recovery, the effective number of breeders is still low today (Zucoloto et al. 2021).

In Argentina, the species has been recovering through management strategies and is currently classified as Least Concern (Siroski 2020; Prado et al. 2012). Since 1990, wild populations of the broad-snouted caiman in Santa Fe province have been managed through a conservation and commercial sustainable use program (Larriera and Imhof 2006; Simoncini et al. 2020). As a result, in 1997, the species was transferred from CITES Appendix I to Appendix II, allowing the commercialization of products and by-products when they come from ranching programs authorized by the Argentinean control agencies (Res 283/00, Secretariat of Environment and Sustainable Development of Argentina).

To date, various studies on the reproductive ecology of broad-snouted caimans have been carried out (Leiva et al. 2018, 2019; Simoncini et al. 2017, 2009), such as sexual determination by temperature (Parachú Marcó et al. 2017; Piña et al. 2003; Simoncini et al. 2014a, 2019), farm breeding (Piña and Larriera 2002; Poletta et al. 2008; Simoncini et al. 2020), and body growth (Moulton et al. 1999; Viotto et al. 2020). Nevertheless, the knowledge acquired has not yet been integrated into modeling techniques to evaluate how the different intervening variables are related and their implications on the species' population and harvest dynamics. It is necessary to know if the management practices carried out are the most appropriate and if it would be feasible to authorize the hunting of caimans under specific guidelines. Hunting adult *C. latirostris* without an adequate evaluation of how many individuals from different sizes or age categories can be extracted and whether it can be carried out in conjunction with ranching could once again endanger their populations.

Given the scarcity of data on the population densities of *C. latirostris*, and the need to understand how their population parameters are integrated, this paper uses simulation models. These models constitute a very convenient tool to analyze possible management strategies since they summarize the basic natural principles and a method to analyze the population's responses under study (Federico and Canziani 2005). Therefore, we developed a matrix model that allows us to understand the dynamics of wild populations by integrating the knowledge about the life cycle parameters of this species.

MATERIAL AND METHODS

Initially, we generated a simple computational model to perform Life Stage Analysis (LSA, Wisdom et al. 2000). Then, we obtained the mean matrix that explains the population dynamics. Subsequently, we introduced modifications to simulate different hunting and ranching intensity scenarios, making it possible to estimate to which size and age categories these practices could be applied in wild populations of *C. latirostris* without putting them at risk.

Matrix population model and LSA

We used data from available literature to create the lifecycle diagram of the species (Figure 1). We then sketched a theoretical Lefkovitch matrix model, considering 5 life stages only for females (Caswell 2001), where the time intervals correspond to years. The general model is:

$$n_{t+1} = An_t$$

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t+\Delta t} = \begin{bmatrix} 0 & 0 & 0 & F_4 & F_5 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix} \text{x} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_t$$

The columns of the matrix represent the successive i stages, and the elements of each row indicate the parameters to which the stage corresponding to the column is making contributions. P_i is the probability of surviving and remaining in the same stage; G_i is the probability of surviving and growing into the next stage; and F_i is the i stage-specific reproductive output. To calculate these population parameters (P_i, G_i, F_i), we calculate the different vital rates as follows:

$$P_i = \left(\frac{1-pi^{di-1}}{1-pi^{di}}\right) pi \; ; G_i = \left(\frac{pi^{di}\,(1-pi)}{1-pi^{di}}\right)$$
$$F_i = cls_i * hatch_i * fem * bre_i$$

where p_i is the specific survival rate of each stage and d_i is the duration of that stage (Crouse et al. 1987). To obtain F_i: cls_i is the clutch size of each reproductive stage i; $hatch_i$ is the proportion of hatched eggs originated from each stage; fem is the proportion of females in the population; and bre_i is the proportion of females of each stage i that effectively reproduces that year, relative to the total number of females in the population.

We wanted the model to be as simple as possible and conservative in its estimates. Therefore, we assumed that the population is exclusively female, closed, and density-independent. The fact that it is not a population limited by the number of males allowed us to assess the dynamics accurately using a model including only females. This approach is possible because the broad-snouted caiman is a polygynous species with multipaternity within nests (Amavet et al. 2008). The high fidelity of females to the nesting site (Lance et al. 2009; Wilkinson 1983) and the marked population structure within each basin in Argentina justify the absence of migration. Both characteristics suggest that there would naturally be little movement of individuals between populations (Amavet et al. 2012). Finally, it is possible to assume density independence, given the low population densities reported and the gradual increase observed in the number of nests (Larriera and Imhof 2006).

We built and analyzed the model with R software (R Core Team 2019), using the Popbio package

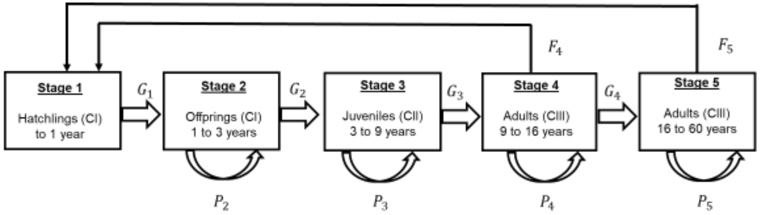


Figure 1. Simplified diagram of *C. latirostris* life history.

(Stubben and Milligan 2007). Once the matrix model was structured, we performed a Life Stage Analysis (LSA, Wisdom et al. 2000). We randomly extracted the vital rate values from a probability distribution based on its mean and variance. We modeled what we will call the survival rates from now on: p_i and $hatch_i$, limited to a scale from 0 to 1 by β distribution. We randomly selected $k = 5000$ matrix elements G_i, P_i, and F_i and thus generated k transition matrices with these distributions.

For each replication A_k from the matrix, we obtained the growth rate λ by the dominant eigenvalue of each matrix and the stable structure of the population (w_k). We identified the contribution to λ of each vital rate by calculating the respective elasticities (e_ij) of each element (G_i, P_i, and F_i) of each of the k matrices, as follows (e_{kij}):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial \log \lambda}{\partial \log a_{ij}}$$

where a_{ij} is each matrix component, according to i rows and j columns (Caswell 2001; De Kroon et al. 1986).

To assess how much each vital survival rate (p_i and $hatch_i$) affects λ, we calculated the coefficients of determination of the regressions between each variable and λ. We obtained the mean matrix (A_m) to calculate the elasticity (e_{mij}). To assess whether A_m is a decent predictor of populations, we extracted the difference between e_{mij} and each e_{kij}, and analyzed how they behaved around the value 0.

Parameter estimation

We defined the parameters using the literature on the target species and other crocodilians (see Table 1 for summary values included in each vital rate). We classified the individuals (females) into 5 stages based on the following biological parameters (Figure 1, Table 1):

- Stage 1 (E1): fraction of offspring belonging to Class I ($CI < 25$ cm snout-vent length-SVL) but which are in their first year of life (hatchlings). That is, animals of this class that are < 16.9 cm SVL, based on Viotto et al. (2020). Survival in this category is comparatively low;
- Stage 2 (E2): offspring also within Class I, but with more than one year of life until the end of CI (that is, from 1 to 3 years of age, with $17 < CI < 25$ cm SVL);
- Stage 3 (E3): Juveniles ($25.1 < CII < 68$ cm SVL) up to 9 years of age, not yet reproducing, but whose survival is higher than CI individuals.
- Stage 4 (E4): CIII adults, $68 < E4 < 79$ cm SVL, corresponding to animals up to 17 years of age. This class contributes to CI through F4.
- Stage 5 (E5): CIII adults of ≤ 79 cm SVL, corresponding to animals that would reach 60 years of age. This class contributes to CI through F5.

Crocodilians, as a rule, are divided into size classes. In this case, the classes are not homologous to the stages since we divide CI (E1 and E2) and CIII (E4 and E5) into two stages. The first class (CI) is divided due to the significant increase in survival after the first year of life (Smith and Webb 1985; Tucker 2001; Rootes and Chabreck 1992). In the case of CIII, its two stages have the same survival but differ substantially in terms of fertility.

We estimated the fertility of each stage according to the function F_i (Table 1); first, to estimate the cls_i, we considered the relationship between the size of females and their clutch size (Verdade 2001; Larriera et al. 2004). For this reason, we obtained the mean clutch size within each stage based on the function $cls_i = -6.77 + 0.5$ SVL (Leiva et al. 2018). We based the estimates of $hatch_i$ on Larriera et al. (2006), who reported that the hatching rate in the wild on average years varies between 40 and 50%, and on preliminary data from an ongoing study with camera traps that found that 30% of nests were successful in the 2018-2019 season, and 40% in 2019-2020 (Pierini, unpublished data). For bre_i, we considered that the smaller females must take more time between breeding attempts. Thus, we assumed that only a fraction of adult females would reproduce each year and that reproductive capacity varies according to their body size, assigning the values of 0.3 for E4 and 0.5 for E5; according to the minimum and maximum values reported by Portelinha et al. (2015). Concerning h, although Simoncini et al. (2014) found that 70% of individuals produced in average years were females, we used 50% because it was intended to be simple and as conservative as possible to maintain populations in the long-term.

The stage length (Table 1) for E1 and E2 were set as estimated by the body growth of *C. latirostris* (Viotto et al. 2020). In turn, E3 was bounded between the end of E2 and the time of first reproduction in the wild (approximately 9 years of age, with a stage duration of 6 years; Larriera et al. 2006). We assumed that d_i of E4 is 8 years (i.e., 17-year-old animals), and of E5, it is 43 years in length, thus completing a 60-year life cycle. In this way, each animal would live a maximum of 60 years. Considering that Wilkinson et al. (2016) found *Alligator mississippiensis* females still reproducing up to 83 years old (in South Carolina, United States), the maximum value considered here is more parsimonious and conservative.

As vital survival rate (pi), we used central values (mean and median), the standard deviation of different studies, and their maximums and minimums, depending on the data type entered. For E1, we limited survival between 0 and 0.11 (mean = 0.05), and for E2 from 0.4 to 0.8 (mean = 0.67) (Viotto et al. 2022). We used data from other crocodilians for the remaining stages due to the lack of data for broad-snouted caimans and the ecological similarity among species. In these cases, we extracted the means and deviations from data reported in the literature (Table 2), discarding those populations whose habitats freeze seasonally (Dunham et al. 2014). In this sense, information from ecologically and phylogenetically similar species is valid when gaps exist (Messerman et al. 2020).

Management inclusion in the model

Using the mean Matrix (A_m), we created different management scenarios on natural populations by combining adult hunting and ranching by harvesting eggs and reintroducing animals to the wild. We included hunting in the basic model, determining the proportion of individuals within each stage that would be harvested (by time interval), assuming that extraction will occur after reproduction. We incorporated ranching as the proportion of eggs harvested from the wild; and reintroduction as the proportion of animals released at stage E3. We assumed that reintroduced animals have the same survival rate as wild-hatched animals. We included hunting and ranching with its corresponding reintroduction into the population matrix, as follows:

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & F_4 * (1 - Ranch) & F_5 * (1 - Ranch) \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & Rel_4 & Rel_5 \\ 0 & 0 & G_3 & P_4 * (1 - Harv) & 0 \\ 0 & 0 & 0 & G_4 * (1 - Harv) & P_5 * (1 - Harv) \end{bmatrix} * \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t}$$

$$Rel_i = cls_i * bre_i * Ranch * fem_g * hatch_g * Surv_g * Rein$$

Where *Harv* is the proportion of adult hunting on E4 and E5; *Ranch* is the proportion of eggs harvested, and Rel_i is the proportion of individuals reintroduced to the population, coming from nests of individuals at adult stages (E4 and E5). We estimated Rel_i considering the contribution of eggs by each reproductive stage ($cls_i * bre_i$), the egg harvest ratios ($Ranch$), farm hatching success $hatch_g$, survival of individuals in captivity $surv_g$, farm-hatched females fem_g, and proportion of offspring hatched in the production system to be reintroduced *Rein*.

With this model, we generated 5 scenarios: (1) hunting at stage E5 only, (2) hunting at E4 and E5, (3) ranching only, (4) ranching with hunting at E5, and, finally, (5) ranching with hunting at E4 and E5. Each scenario was evaluated with different extraction/return intensities, combining different adult hunting values. Harv (rank = 0 to 0.3), egg ranching *Ranch* (0 to 0.7) and return ratio *Rein* (0 to 1). In all the scenarios, we kept the rates of the proportion of females born at the farm (hig), hatching at the farm ($hatch_g$), and survival of animals at the farm ($surv_g$) fixed; these being 0.5, 0.75, and 0.75 (Siroski, personal comm.), respectively. Although these rates were invariable within the models, we generated scenarios combining different extraction and return rate intensities, evaluating the changes each simulated combination caused in λ. We analyzed the critical values of these rates, which can cause λ <1 and $\lambda < \lambda$m.

Table 1. Fixed and variable parameters with which the model on population dynamics of broad-snouted caiman (*Caiman latirostris*) was built.

Vital Parameter	Vital Rate	Meaning	Acronym	Value	Bibliography
Pi and Gi	Survival	Annual survival rate by stage	p_1	$\beta \sim(0.05, 0.02)$	Viotto et al. (2022)
			p_2	$\beta \sim(0.68, 0.02)$	Viotto et al. (2022)
			p_3	$\beta \sim(0.72, 0.06)$	Table 2
			p_4	$\beta \sim(0.85, 0.07)$	Table 2
			p_5	$\beta \sim(0.88, 0.02)$	Table 2
	Permanence	Time of permanence of individuals in each stage expressed in years.	d_1	1	Viotto et al. (2020)
			d_2	2	Viotto et al. (2020)
			d_3	6	
			d_4	8	
			d_5	44	
Fi	Hatching	Annual hatching rate of eggs laid for each reproductive stage	$hatch_4$	$\beta \sim(0.40, 0.07)$	Larriera et al. (2006); Pierini, unpublished data
			$hatch_5$	$\beta \sim(0.50, 0.07)$	Larriera et al. (2006); Pierini, unpublished data
	Reproductive females	Proportion of reproductive females of the pool of females available in the population	bre_4	0,3	Portelinha et al. (2015)
			bre_5	0,5	Portelinha et al. (2015)
	Females born	Proportion of females hatched each year.	fem	0.5	
	Clutch size	Number of eggs per nest that each reproductive stage lays	cls_4	29.98	Verdade (2001); Larriera et al. (2004); Leiva et al. (2018)
			cls_5	38.23	Verdade (2001); Larriera et al. (2004); Leiva et al. (2018)

Legend. Summary of parameters and vital rates used to generate the 5000 matrices. The name of the vital rates used to estimate the parameters (P_i, G_i, and F_i), their acronyms, biological meaning, the values they can take, and the bibliography from which they were extracted are shown. The vital survival and hatching rates come from a random sampling of mean β distribution and standard deviation in such a way that $\beta \backsim$ (*mean, standard deviation*).

RESULTS

Life Stage Analysis

From the random sampling of vital survival rates (p_i and $hatch_i$, Additional File 1) introduced in the stage-based model for *C. latirostris*, we obtained the eigenvectors λ_k, which ranged between 0.891 and 1.118; a mean matrix of $\lambda_m = 1.035$ (Figure 2). Out of 5000 combinations, 11.9% (595) had values of $\lambda < 1$, that is, in which there was a population decrease (Figure 2). The variability of λ better adjusted to the survival of E3, P_3 ($r^2 = 0.54$), followed by p_5 and p_4, ($r^2 = 0.20$ and $r^2 = 0.15$, respectively; Additional File 2).

The model predicted stable population structures composed of 62% ($S.D. = 3$) of individuals from E1, 11% ($S.D. = 1.5$) from E2, 12% ($S.D. = 1.5$) from E3, 7% ($S.D. = 1.7$) from E4, and 8% ($S.D. = 1.2$) from E5.

The vital rate with highest elasticity (and highest variance) was the permanence of animals at E5 (P_5), with mean $e_{m5} = 0.40$ ($S.D. = 0.11$, Figure 5), followed by P_4 (probability of permanence in stage 4), with mean $e_{m4} = 0.21$ ($S.D. = 0.04$), and then P_3 $e_{m3} = 0.13$ ($S.D. = 0.03$) (Figure 3). Both the transition and fertility probabilities had little or no effect on λ. We evaluated the difference between the mean matrix elasticity values and those of each k matrix for each parameter and found that A_m can be a good descriptor of the population (although P_3 and P_4 have a mean different from 0, they were very close to it; Additional File 3).

Management scenarios

The scenarios that included hunting always showed a slowdown in average population growth. According to these scenarios, hunting percentages higher than 10% at E5 females and 5% at E4 and E5 may endanger natural populations (Figure 4).

Regarding the ranching scenarios, we found that, as long as at least 3% (rate of 0.03) of the collected nests are reintroduced, the population would accelerate its population growth ($\lambda > 1.035$). This result was obtained in 96.5% of the analyzed scenarios. On the other hand, at 2.6%, there was projected a slowdown in population growth, related to combining egg collection rates ($Ranch$) of 10% onwards and return rates between (0-2%). Finally, 0.9% of scenarios corresponded to population decrease ($\lambda < 1$), generated by the extraction of more than 55% of nests without releases and/or $Ranch > 86\%$, with reintroducing up to 2%.

When integrating the scenarios of egg harvesting and extraction of adult E5 females only, 81.86% of the combinations generated an acceleration of population growth ($1.035 < \lambda$), 14.63% a deceleration ($1 < \lambda < 1.035$), and 3.51% a decrease ($1 < \lambda$, Figure 6). According to the model, at a rate of 0.15 for both hunting and ranching, when the reintroduction range of animals is greater than 30%, the populations will accelerate their growth (for more combinations, see Additional File 4). With the same hunting and ranching values mentioned above, populations slowed their growth when reintroduction was less than 10%. On the other hand, setting the quota at 15% hunting with 5% ranching and a return of less than 10% would cause population decline. Finally, supposing the objective was to hunt the maximum number of individuals (30%), at least 55% of the nests should be harvested, and reintroductions of at least 20% of the hatched animals should be conducted.

When integrating adult hunting at E4 and E5 with ranching, we found that 46% of the combinations of ranching, hunting, and return generate acceleration in population growth ($1,035 < \lambda$), 15% slowdown ($1 < \lambda < 1,035$), and 39% decrease ($\lambda < 1$, Figure 6). For example, in hunting and ranching scenarios equal to 15% ($Harv = 0.15$ and $Ranch = 0.15$) and a reintroduction range of animals higher than 80% ($Rein > 0.8$), the populations will accelerate their growth (for more combinations, check Additional File 5). The populations slow their growth with the same hunting and ranching values mentioned above but with lower than 20% reintroduction. The set of 15% hunting and 35% ranching, but returns lower than 20%, would make the combination of these practices unsustainable, causing the population to decline. Finally, if the aim was to hunt the maximum number of individuals (30%), harvest rates should be at least 55% of nests, and reintroduction should be at least 50% of the nests hatched.

DISCUSSION

Our matrix model allowed us to describe the population dynamics of *C. latirostris* and advance in its knowledge. As with all models, the result is conditioned by the data quality, assumptions, and hypotheses (Dunham et al. 2014). In our case, the need for a primary evaluation of current and feasible management alternatives led us to compensate for the lack of data on *C. latirostris* by using some parameters from other species of crocodilians, assuming that this would not generate a relevant bias in the model. We base this assumption on crocodilians having similar life histories (Richards 2003; Tucker 2001). In this sense, robust estimates of vital rates from a subset of ecologically and phylogenetically similar species can be used to reveal key factors that may influence the viability of populations with poor demographic infor-

Table 2. Survival rates reported for other crocodilians

	Crocodylus johnstoni	*Crocodylus johnstoni*	*Crocodylus porosus*	*Crocodylus acutus*	*Alligator mississippiensis*	*Caiman crocodilus*	**Average**	**Standard Deviation**
	Southern Population	Northern Population			Florida			
	(a)	(a)	(a-b)	(a-c)	(d)	(a)		
CI	0.22	0.17	0.2	0.2	0.35	0.35	0.29	0.13
CII	0.66	0.72	0.65	0.65	0.6	0.6	0.45	0.10
CIII	0.93	0.89	0.79	0.79	0.79	0.79	0.72	0.06
CIV	0.92	0.98	0.9	0.9	0.88	0.88	0.85	0.07
CV	0.87	0.87	0.9	0.9	0.88	0.88	0.88	0.02

Legend. Published survival probability for different species of crocodilians and populations under similar ecological conditions to *C. latirostris*, which were extracted from: (a) Tucker (2001); (b) Webb and Manolis (1993); (c) Moler (1991); (d) Nichols et al. (1976); and (e) Dunham et al. (2014).

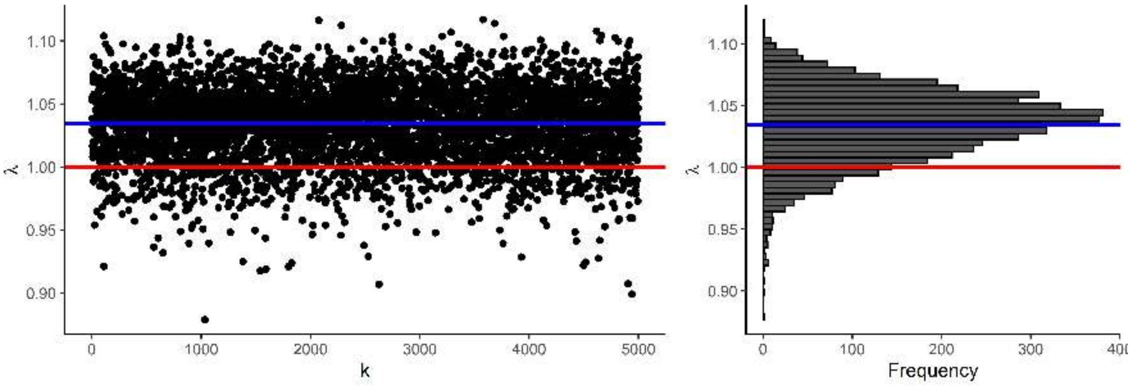


Figure 2. Distribution of λ in each of the 5000 simulations and the frequency of each value. Blue line: λ_m; red line: $\lambda = 1$

mation (Messerman et al. 2020). We always used only data that provided reasonably conservative management outcomes for the species in each case.

Estimation of the population growth rate (λ) is necessary to establish management levels (Caughley 1977), which is particularly true in the case of crocodilians (Fukuda et al. 2020; Smith and Webb 1985). The average growth rate predicted by our simulations is similar to those of other species, such as *C. niloticus* (1.04, Wallace et al. 2013), *C. acutus* (1.04, Briggs-Gonzalez et al. 2017), *Crocodylus johnstoni* (Range = 0.95 to 1.04, Tucker 2001), and *Alligator mississippiensis* in the southern United States (1.02, Dunham et al. 2014). Except for *A. mississippiensis* at the northern limit of its distribution (0.87, Dunham et al. 2014), all these studies report values of λ within the range found in our simulations.

Around 88% of the simulations generated values consistent with population growth. Even the mean of λ (λ_m) represents an annual increase of 3.7% (calculated as $\ln \lambda = r$). This value indicates that the wild populations of this species can increase without human intervention. In this regard, it is relevant to note that during the 1970s, caiman populations were severally declining, but after indiscriminate hunting was prohibited, they started to recover gradually. Although the ecology of *C. latirostris* has been studied during the last 30 years, systematized good quality data (i.e., with low error associated with the sample design) are still lacking. This situation prevents us from checking whether the λ_m obtained here is a reliable estimator of the actual parameter in natural populations.

It is necessary to highlight that Argentine caiman populations have been under management since 1990; thus, estimating population growth without human

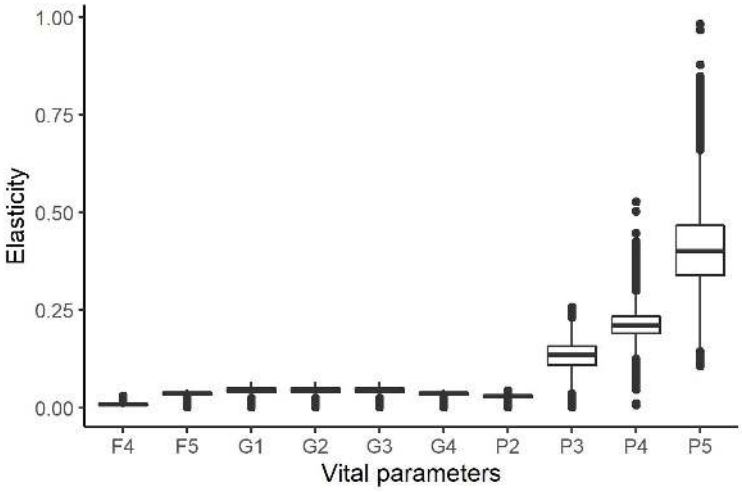


Figure 3. Estimated elasticity values for each vital rate of the transition matrix. The median (black line inside each box), the 95% confidence intervals (height of each box), and the extreme values of each element of the matrix (points) are represented.

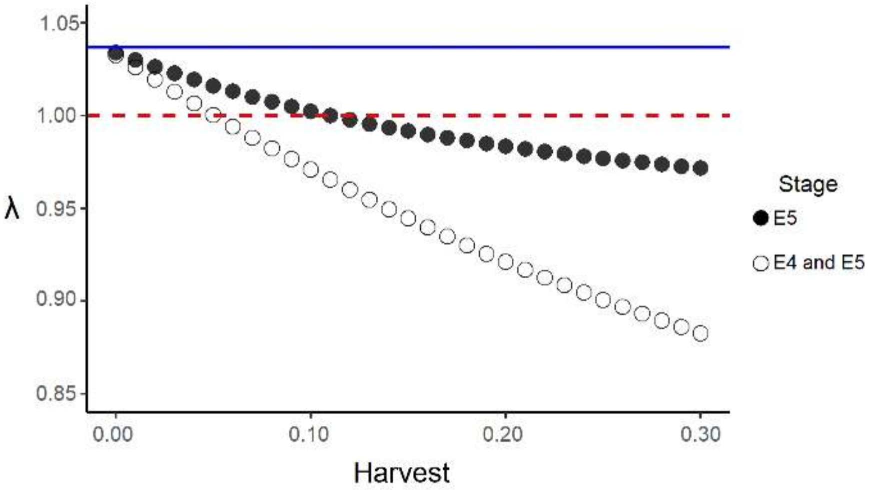


Figure 4. Expected values of λ under different hunting scenarios harvesting females of only stage E5 (black points) and E4 and E5 combined (empty points). Blue solid line: $\lambda_m = 1.035$; red dashed line: $\lambda = 1$.

intervention is virtually impossible. For example, since Proyecto Yacaré was launched in the 1990s, it has released animals close to E3 (Class II) (Larriera et al. 2008). This procedure has possibly accelerated the population growth rate of natural populations.

Elasticity analyses indicated that changes in the permanence of reproductive adult females cause the most remarkable variation in population growth ($e_{m5} = 0.41$, $e_{m4} = 0.22$; with a total of 0.63 between the two, Figure 5), followed to a lesser extent by the E3 juveniles ($e_{m3} = 0.13$). In other words, any strategy that increases adult females' retention rate will considerably increase the population growth rate. On the other hand, an increase of permanence in the rearing stage or in any of the vital rates that influence fertility will produce an insignificant impact on populations. These results agree with those obtained for long-lived species (Gaillard and Yoccoz 2003), whether of mammals (Freedman et al. 2003; Heppell et al. 2000), birds (Sæther and Bakke 2000), or reptiles, such as crocodilians (Briggs-Gonzalez et al. 2017; Dunham et al. 2014; Tucker 2001). In these species, population growth rates are more affected by changes in survival in the last stages of life (Briggs-Gonzalez et al. 2017; Dunham et al. 2014; Gaillard and Yoccoz 2003; Sæther and Bakke 2000;

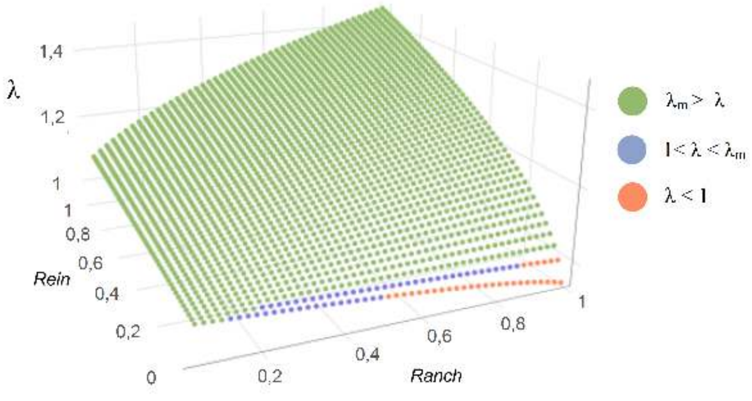


Figure 5. Representation of the λ values in each scenario, according to the combination of different harvest (*Ranch*) and return (*Rein*) rates. The pink points show $\lambda < 1$, causing population decrease; in blue are those λ that cause growth deceleration ($1 < \lambda < \lambda_m$, where $\lambda_m = 1.035$), and in green those that use the speed of population growth $\lambda_m < \lambda$.

Tucker 2001).

Although the rate of permanence of adults (P_5) has higher elasticity than the permanence of subadults, the subadult category is the one that presents the highest correlation between the annual survival rate (P_3) and changes in λ. Despite these counterintuitive results, modeling studies and empirical data in long-lived species, such as *C. acutus* (Richards 2003) and sea turtles (Crouse et al. 1987; Crowder et al. 1994), are in agreement with our results. Models based on ages (not on stages, as in our work) applied to *C. niloticus* (Wallace et al. 2013) and *C. acutus* (Briggs-Gonzalez et al. 2017) showed that the annual survival of juveniles was the parameter of highest elasticity. When working with models based on stages and not ages, the estimated parameters per year should be grouped into a single population parameter according to the number of elapsed years in each stage. By doing so, the matrix element with the highest elasticity may end up being the adult classes. Richards (2003) mentions that, since survival is a parameter that can be affected by management, it is more appropriate to examine the elasticity of this parameter than of other matrix elements, which are functions of both annual survival and the duration of the stage. Therefore, our work indicates that a good population management practice would promote the passage of these animals from the juvenile to the adult stage and protect the adult females, ultimately, the reproducers in the system.

Management implications

Management simulations represent the first step to generating hypotheses about the likely impact of future harvest scenarios, thus passing a solid theoretical test before taking action in the field (Fukuda et al. 2020). As predicted by the sensitivity analyses, the viability of caiman populations is susceptible to eventual management actions that affect the later life stages. In contrast, the population is barely influenced by modifications occurring in the early life stages. These results indicate that it is possible to implement a low extraction rate of adult females in conjunction with a high rate of egg harvest.

The scenarios we generated allowed us to analyze the extraction rates that natural populations may tolerate. Our models suggested that caiman populations could support ranching or hunting, and both strategies together provided that extraction percentages are limited within specific ranges. For instance, it is possible to apply the ranching technique with an extraction intensity of up to 55% of the nests without reintroducing individuals (assigning all the produced specimens to commercial slaughter). However, to promote population growth, it would be necessary to reintroduce at least 3% of hatched animals, whether intended to harvest the resource to its maximum or even when it is impossible to know the actual percentage extracted from natural nests. When combining both management strategies (ranching plus hunting of adults), increasing the percentage of animals returned to the wild would be appropriate according to the rate of hunting implemented in the area. For example, our analyses indicated that for a hunting program pro-

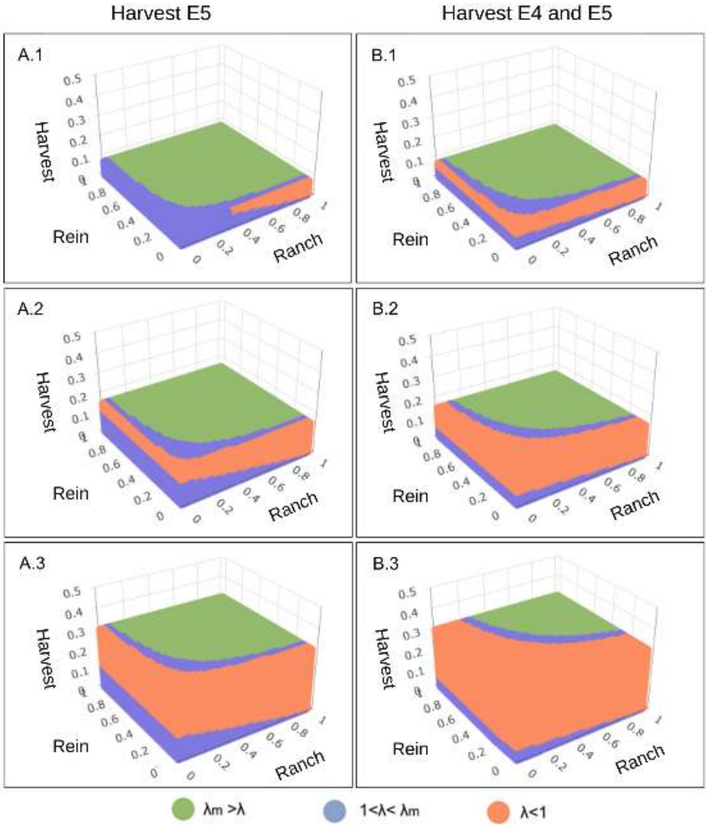


Figure 6. Relationship of λ according to the different combined percentages of adult hunting, collection, and return of individuals, both for block (A) Adult hunting of stage E5, and (B) Adult hunting of stages E4 and E5. Each row of graphs (numbered from 1 to 3) corresponds to visualizing the same cuts in different hunting stages. In this way: (1) represents the cut in 0.07 value of hunting; (2) cut at 0.20; and (3) cut to 0.30. The red dots show the scenarios where $\lambda < 1$, the green ones where $1 < \lambda < 1.035$, and the blue ones where $\lambda > 1.03$. *Harv*: proportion of adult hunting on E4 and E5; *Ranch*: proportion of eggs harvested, and *Rein*: proportion of offspring hatched in the production system to be reintroduced.

posed to extract up to 30% of E4 and E5 females, it should be harvested at least 55% of natural nests and reintroduced at least 45% of 9-month animals hatched and raised in captivity.

Although modeled adult females' hunting tolerance values were low (5% for E4 and E5 together and 10% for E5 only), this harvest quota is slightly higher than the one reported for other species of crocodilians. For example, a simulation model for *Crocodylus porosus* determined that it could support a harvest rate of only 1% of adults (Fukuda et al. 2020). Another similar analysis for *Alligator mississippiensis*, obtained a very similar value to that of our study: 4% of adult hunting (of both sexes) together with 4% of subadult hunting (Eversole et al. 2018). Adult hunting is usually implemented towards the extraction of large males only. This approach is chosen because, in a polygynous system (in which the maternal care of the litter is also added), females have more "value" for the population's viability, as they contribute the most to recruitment from year to year.

In crocodilians, it is considered that the capture of males is not harmful to the population (Joanen et al. 2021). Based on this, our model represents the tolerance of natural populations to occasional extractions of females. Therefore, we assume that the hunting of males should have a more negligible effect on population viability. Such a differential prey selection, however, requires a hunting method that confirms the sex of the animal before harvesting (e.g., spinel, and capture from a boat, instead of long-distance shooting). In addition, hunting sites can be established based on the different spatial distribution between males and females, allowing hunting mostly where it is known that there is a preponderance of males (Joanen et al. 2021). Therefore, our model provides a conservative value for any female- or male-focused management scenario. Suppose animals are categorized by size, and hunting caimans larger than 90 cm SVL is permitted. In that case, the most conservative hunting rate is possibly the 10% calculated here since this is the maximum error (hunting females mistaken as males) that adult E5 females would endure.

On the other hand, it is relevant to note that populations were stabilized below their potential (values consistently lower than λ_m) under all scenarios. We must emphasize that the sustainably harvested populations, i.e., those where removal is based on biological criteria, can remain stable (Velasco et al. 2002; Webb et al. 2004). Extraction of larger animals (males and females) can lead to competitive release, giving space for subordinates to grow and reach reproductive status faster. For example, Hines and Abercrombie (1987) conducted a study in which they extracted large females during three successive seasons and observed that the number of nests remained constant over time.

The population size imposes the most significant economic restriction on implementing sustainable hunting. The percentage to be extracted can represent a considerable and economically profitable number of individuals or an insignificant quantity. Consequently, hunting only adults, while feasible, might not be the most efficient strategy to obtain the best economic and conservation results. Such an option may be unprofitable unless the value of harvested individuals would be significantly increased by the market price of their products (Smith and Webb 1985). An acceptable conservation alternative may be to propose a mixed strategy, including adult hunting and ranching with the reintroduction of individuals. Thus, the release of juveniles may compensate for hunting older adults (Nichols et al. 1976). A clear example of this “mixed” strategy is the management of *Alligator missippiensis* in Louisiana. It comprises ranching of nests, reintroducing 12% of farm-hatched animals (1.2m long, Elsey and Woodward 2010), and hunting. The populations of this species have been stable in the last 30 years, with a hunting rate represented by approximately 3% of the population per year (Joanen et al. 2021).

According to the conservation objective to be achieved, the established rates of extraction and reintroduction can be adjusted. Unlike hunting, ranching allows a much higher percentage of extraction. Although we do not always know the proportion of nests collected from each population, some isolated data indicate that, in Argentina, this percentage is lower than the maximum achievable without reintroduction estimated in our study (55%). For example, at Cacique Ariacaiquin (Santa Fe province), drone images of the dam revealed that in 2018, 15% of the nests were collected (Scarpa et al. unpublished); while in Corrientes province, the harvest of nests ranges from 17 to 26% (Scarpa and Piña 2019). If the population is to be maintained, a recommended strategy would be to carry out releases when population density is low, that is, compensatory releases (Jenkins et al. 2004). This strategy is applied by the Zimbabwean ranching programs on *Crocodylus niloticus*.

On the other hand, if the growth of the *Caiman latirostris* population is to be accelerated, it would be advisable to return at least 3% of the animals born in captivity.

Whenever the number of animals released is increased, it should be taken into account that the environment’s carrying capacity can be a limiting factor for the survival of the offspring. Therefore, generating models that include density dependence would be advisable to evaluate the best release rate.

CONCLUSION

We have developed a deliberately simple simulation model that intends to accurately represent for the first time the most relevant aspects of the population dynamics and management of the broad-snouted caiman by using the currently available data. Based on this framework, we show that adult hunting, ranching, and a combination of both actions can be carried out sustainably as long as harvest rates in each life stage are adequately balanced. Here, we have not incorporated other factors that could affect the population dynamics of this species (Brandt et al. 2016; Simoncini 2011; Simoncini et al. 2014b), such as environmental changes, density-dependence, or sexual proportions in the model.

This model is theoretical; hence, it is necessary to collect systematic field data to validate and adjust it. As a first of its kind, this simulation model of the broad-snouted caiman population may provide better support to this species’ management and conservation and constitute an interesting tool to propose new hypotheses to be tested about its ecology and population dynamics. We advise that any management alternative implemented based on this model should be evaluated and monitored continuously to incorporate the proper adjustments.

ACKNOWLEDGMENT

We thank all the members of the Proyecto Yacaré for providing us with relevant information to generate the models. German González (IDEA; CONICET and UNC) also collaborated to prepare figures, and Daniel Aguilera and Darío Rocha in the programming. E. Viotto is a CONICET doctoral fellow at the CICyTTP (CONICET - Entre Ríos province - UAdER). This work was supported by the IUCN SSC Crocodile

Specialist Group Student Research Assistance Scheme (SRAS) and Fund for Scientific and Technological Research (FONCYT): Public Call for Scientific and Technological Research Projects - PICT 2019 N812 (to C. Piña). The Gordon and Betty Moore Foundation partly funds this publication through Grant No. GBMF9258.

DATA AVAILABILITY

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

CONTRIBUTION STATEMENT

Conceived of the presented idea: EVV, MSS, CIP, JLN. Carried out the experiment: EVV
Carried out the data analysis: EVV.
Wrote the first draft of the manuscript: EVV.
Review and final write of the manuscript: EVV, MSS, CIP, JLN.
Supervision: CIP, MSS, JLN.

REFERENCES

Amavet P, Rosso E, Markariani R, Piña CI (2008) **Microsatellite DNA markers applied to detection of multiple paternity in *Caiman latirostris* in Santa Fe, Argentina.** *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 309:637–642.

Amavet PS, Vilardi JC, Rueda EC, Larriera A, Saidman BO (2012) **Mating system and population analysis of the broad-snouted caiman (*Caiman latirostris*) using microsatellite markers.** *Amphibia Reptilia* 33:83–93.

Borteiro C, Prigioni C, García JE, Tedros M, Gutiérrez F, Kolenc F (2006) **Geographic distribution and conservation status of *Caiman latirostris* (Crocodylia, Alligatoridae) in Uruguay.** *Phyllomedusa* 5:97–108.

Brandt LA, Beauchamp JS, Jeffery BM, Cherkiss MS, Mazzotti FJ (2016) **Fluctuating water depths affect American alligator (*Alligator mississippiensis*) body condition in the Everglades, Florida, USA.** *Ecological Indicators* 67:441–450.

Briggs-Gonzalez V, Bonenfant C, Basille M, Cherkiss M, Beauchamp J, Mazzotti FJ (2017) **Life histories and conservation of long-lived reptiles, an illustration with the American crocodile (*Crocodylus acutus*).** *Journal of Animal Ecology* 86:1102–1113.

Caldwell J (2017) **World trade in crocodilian skins 2013-2015.** Cambridge, UK.

Caswell H (2001) **Matrix population models: construction, analysis, and interpretation.** Massachusetts, USA.

Caughley G (1977) **Analysis of vertebrate populations.** New York, USA.

Cedillo-Leal C, Simoncini M, Lang JW, Simoncini MS, Leiva PML, Piña CI (2017) **Eggshell structure in *Caiman latirostris* eggs improves embryo survival during nest inundation.** *Proceedings of the Royal Society B: Biological Sciences* 284: (1854), 20162675.

CITES (2021) **Ranching and trade in ranched specimens of species transferred from Appendix I to Appendix II** [`https://cites.org/sites/default/files/document/E-Res-11-16-R15.pdf`] Accessed 10 September 2022.

Crouse DT, Crowder LB, Caswell H (1987) **A stage-based population model for loggerhead sea turtles and implications for conservation.** *Ecological Society of America* 68:1412–1423.

Crowder LB, Crouse DT, Heppell SS, Martin TH (1994) **Predicting the impact of turtle excluder devices on loggerhead sea turtle populations.** *Ecological Applications* 4:437–445.

Dunham K, Dinkelacker S, Miller J (2014) **A stage-based population model for American alligators in northern latitudes.** *Journal of Wildlife Management* 78:440–447.

Elsey RM, Woodward AR (2010) **American Alligator *Alligator mississippiensis*.** In: S.C. M, Stevenson C (eds) Crocodiles. Status Survey and Conservation Action Plan. Third Edition, ed. Crocodile Specialist Group, Darwin, pp. 1–4.

Eversole CB, Henke SE, Turner BL, Glasscock SN, Powell RL, Wester DB, Ballard BM (2018) **A theoretical population and harvest model for american alligators (*Alligator mississippiensis*).** *Herpetological Monographs* 32:22–33.

Federico P, Canziani GA (2005) **Modeling the population dynamics of capybara *Hydrochaeris hydrochaeris*: A first step towards a management plan.** *Ecological Modelling* 186:111–121.

Freedman AH, Portier KM, Sunquist ME (2003) **Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape.** *Ecological Modelling* 167:47–64.

Fukuda Y, Webb GB, Edwards G, Saalfeld K, Whitehead P (2020) **Harvesting predators: Simulation of population recovery and controlled harvest of saltwater crocodiles *Crocodylus porosus*.** *Wildlife Research* 48:252–263.

Gaillard JM, Yoccoz NG (2003) **Temporal variation in survival of mammals: a case of environmental canalization?** *Ecology* 84:3294–3306.

Heppell SS, Caswell H, Crowder LB (2000) **Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data.** *Ecology* 81:654–664.

Hines T, Abercrombie CL (1987) **The management of alligators in Florida, USA.** In: Webb GJW, Manolis SC, Whitehead PJ (eds) Wildlife Management: Crocodiles and Alligators. Surrey Beatty and Sons, Chipping Norton, pp. 43–47.

Jenkins R, Jelden D, Webb G, Manolis S (2004) **Review of Crocodile Ranching Programs.** [`https://www.iucncsg.org/365_docs`].

Joanen T, Merchant M, Griffith R, Linscombe J, Guidry A (2021) **Evaluation of effects of harvest on Alligator populations in Louisiana.** *Journal of Wildlife Management* 85:696–705.

De Kroon H de, Plaisier A, Groenendael J van, Caswell H (1986) **Elasticity: the relative contribution of demographic parameters to population growth rate.** *Ecological Society of America Stable* 67:1427–1431.

Lance SL, Tuberville TD, Dueck L, Holz-Schietinger C, Trosclair PL, Elsey RM, Glenn TC (2009) **Multi-year multiple paternity and mate fidelity in the American alligator, *Alligator mississippiensis*.** *Molecular Ecology* 18:4508–4520.

Larriera A (2011) **Ranching the broad-snouted cayman (*Caiman latirostris*) in Argentina: An economic incentive for wetland conservation by local inhabitants.** In: Abensperg-Traun M, Roe D, O'Criodain C (eds) Proceedings of an international symposium on "The relevance of CBNRM to the conservation and sustainable use of CITES-listed species in exporting countries." Gland, Switzerland: IUCN and London, UK, pp. 86–92.

Larriera A, Imhof A (2006) **Proyecto Yacaré. Cosecha de huevos para cría en granjas del género Caiman en la Argentina.** In: D. MLB and, Ramadori (eds) Manejo de Fauna Silvestre en la Argentina Programas de uso Sustentable. Dirección de Fauna Silvestre, Secretaria de Ambiente y Desarrollo Sustentable, Buenos Aires., pp. 51–64.

Larriera A, Piña CI, Siroski P, Verdade LM (2004) **Allometry of reproduction in wild Broad-snouted caimans (*Caiman latirostris*).** *Journal of Herpetology* 38:301–304.

Larriera A, Siroski P, Piña CI, Imhof A (2006) **Sexual maturity of farm-released *Caiman latirostris* (crocodylia: alligatoridae) in the wild.** *Herpetological Review* 37:26–28.

Larriera A, Imhof A, Siroski P (2008) **Estado actual de los programas de conservación y manejo del género Caiman en Argentina.** *Construccion al conocimiento de los caimanes del género Caiman de Sudamerica* 143–179.

Larriera A (2011) **Ranching the broad-snouted cayman (*Caiman latirostris*) in Argentina: An economic incentive for wetland conservation by local inhabitants.** In: Abensperg-Traun M, Roe D, O'Criodain C (eds) Proceedings of an international symposium on "The relevance of CBNRM to the conservation and sustainable use of CITES-listed species in exporting countries." Gland, Switzerland: IUCN and London, UK, pp. 86–92.

Leiva PML, Labaque MC, Fernandez ME, Piña CI, Simoncini MS (2018) **Physical and chemical characteristics of fertile and infertile eggs of wild *Caiman latirostris*.** Aquaculture 497:287–291.

Leiva PML, Simoncini TCG, Larriera A, Piña CI (2019) **Size of nesting female Broad-snouted Caimans (*Caiman latirostris* Daudin 1802).** *Brazilian Journal of Biology* 79:1–5.

Messerman AF, Semlitsch RD, Leal M (2020) **Estimating survival for elusive juvenile Pond-breeding salamanders.** *The Journal of Wildlife Management* 84:1–14.

Moler PE (1991) **American crocodile population dynamics.** Florida, USA.

Moulton TP, Magnusson WE, Melo MTQ (1999) **Growth of *Caiman latirostris* Inhabiting a Coastal Environment in Brazil.** *Journal of Herpetology* 33:479.

Nichols JD, Viehman L, Chabreck RH, Fenderson B (1976) **Simulation of a commercially harvested alligator population in Louisiana.** LSU Agricultural Experiment. Station Reports.470.

Parachú Marcó MV, Leiva PML, Iungman JL, Simoncini MS, Piña CI (2017) **New evidence characterizing temperature-dependent sex determination in Broad-snouted caiman, *Caiman***

latirostris. *Herpetological Conservation and Biology* 12:78–84.

Piña CI, Larriera A (2002) ***Caiman latirostris*** **growth: the effect of a management technique on the supplied temperature.** *Aquaculture* 211:387–392.

Piña CI, Larriera A, Cabrera MR (2003) **Effect of incubation temperature on incubation period, sex ratio, hatching success, and survivorship in *Caiman latirostris* (Crocodylia, Alligatoridae).** *Journal of Herpetology* 37:199–202.

Piña CI, Siroski PA (2004) **Cocodrilos en la Región Litoral: especies, distribución geográfica, modo de vida.** *INSUGEO, Miscelánea* 12:317–322.

Poletta GL, Larriera A, Siroski PA (2008) **Broad snouted caiman (*Caiman latirostris*) growth under different rearing densities.** *Aquaculture* 280:264–266.

Portelinha TCG, Jahn GA, Hapon MB, Verdade LM, Piña CI (2015) **Hormone levels and ultrasound evaluation of *Caiman latirostris* (Crocodylia, Alligatoridae) ovulation.** *South American Journal of Herpetology* 10:23–31.

Prado WS, Piña CI, Waller T (2012) **Yacares de la República Argentina.** *Cuaderno de herpetologia* 26:403–410.

R Core Team (2019) **R: A Language and environment for statistical computing.** [`https://www.r-project.org`].

Richards PM (2003) **Evaluating the relative effects of life history stages in the conservation of the American Crocodile (*Crocodylus acutus*) in Florida.** *Florida Scientist* 66:273–286.

Rootes WL, Chabreck RH (1992) **Sex ratios of American alligators live-captured and harvested by baited hooks.** *Wildlife Society Bulletin* 20:140–142.

Sæther BE, Bakke Ø (2000) **Avian life history variation and contribution of demographic traits to the population growth rate.** *Ecology* 81:642–653.

Scarpa LJ, Piña CI (2019) **The use of drones for conservation: A methodological tool to survey caimans nests density.** *Biological Conservation* 238:108235.

Simoncini MS (2011) **Influencia de las variables climáticas sobre la nidificación, éxito de eclosión y proporción de sexos de neonatos de *Caiman latirostris* (Crocodylia: Alligatoridae).** Universidad Nacional de Comahue, San Carlos de Bariloche, Argentina.

Simoncini MS, Cruz FB, Larriera A, Piña CI (2014a) **Effects of climatic conditions on sex ratios in nests of broad-snouted caiman.** *Journal of Zoology* 293:243–251.

Simoncini MS, Fernández MS, Iungman JL (2014b) **Cambios estructurales en cáscaras de huevos de *Caiman latirostris*.** *Revista Mexicana de Biodiversidad* 85:78–83.

Simoncini MS, Lábaque MC, Perlo F, Fernandez ME, Leiva PML, Paez AR, Teira G, Larriera A, Piña CI (2020) ***Caiman latirostris*** **meat characterization: Evaluation of the nutritional, physical and chemical properties of meat from sustainable ranching program in Argentina.** *Aquaculture* 515: [`https://doi.org/10.1016/j.aquaculture.2019.734570.`]

Simoncini MS, Leiva PML, Piña CI, Cruz FB (2019) **Influence of temperature variation on incubation period, hatching success, sex ratio, and phenotypes in *Caiman latirostris*.** *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 331:299–307.

Simoncini MS, Piña CI, Siroski PA (2009) **Clutch size of *Caiman latirostris* (Crocodylia: Alligatoridae) varies on a latitudinal gradient.** *North-Western Journal of Zoology* 5:191–196.

Siroski P, Bassetti LAB, Piña C, Larriera A. (2020). ***Caiman latirostris*.** (In: IUCN Red List of Threatened Species 2020). IUCN [`https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T46585A3009813.en`] 20 October 2021.

Smith AMA, Webb GJW (1985) ***Crocodylus johnstoni*** **in the McKinlay River area, N.T. VII. A population simulation model.** *Wildlife Research* 12:541–554.

Stubben C, Milligan B (2007) **Estimating and analyzing demographic models using the popbio Package in R.** *Journal of Statistical Software* 22:1–23.

Tucker AD (1995) **Are sustainable harvest models relevant to Johnstone's crocodile? The role of population simulations in adaptive management.** *Conservation through sustainable use of wildlife.* pp. 151–160.

Tucker AD (2001) **Sensitivity analysis of stage-structured demographic models for freshwater crocodiles (*Crocodylus johnstoni*).** In: Grigg GC, Seebacher F, Franklin CE (eds) Crocodilian Biology and Evolution. Surrey Beatty: Sydney, NSW, Australia, pp. 349–363.

Velasco A, Ayarzagüena J (2010) **Spectacled Caiman *Caiman crocodilus*.** In: Manolis C, Stevenson C (eds) Crocodiles. Status Survey and Conservation Action Plan. Third Edition, IUCN. Crocodile Specialist Group: Darwin, pp. 10–15.

Velasco A, Colomine G, De Sola R, Villarroel G (2002) **Effect of sustained cropping on wild population of *Caiman crocodilus* (Baba) in Venezuela.** Crocodiles. Proceedings of the 16th Working Meeting of the Crocodile Specialist Group of the Species Survival Commission of IUCN – The World Conservation Union. Gland, Switzerland and Cambridge UK, pp. 64–73.

Verdade LM (2001) **Allometry of reproduction in broad-snouted caiman (*Caiman latirostris*).** *Brazilian Journal of Biology* 61:431–435.

Verdade ML, Larriera A, Piña CI (2010) **Broad-snouted Caiman *Caiman latirostris*.** In: Manolis, S. C., Stevenson C (ed) Crocodiles. Status Survey and Conservation Action Plan Third Edition, IUCN. Crocodile Specialist Group: Darwin, pp. 18–20.

Viotto EV, Navarro JL, Piña CI (2020) **Growth curves of wild and reintroduced Broad-snouted Caimans (*Caiman latirostris*) and their management implications.** *South American Journal of Herpetology* 16:34–41.

Wallace K, Leslie A, Coulson T (2013) **Reevaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model.** *Journal of Animal Ecology* 82:155–165.

Webb GJW, Brook BW, Whitehead PJ, Manolis SC (2004) **Wildlife management principles and practices in crocodile conservation and sustainable use.** *Proceedings of the 17th Working Meeting of the IUCN-SSC Crocodile Specialist Group*, pp. 84–91.

Webb GJW, Manolis SC (1993) **Conserving Australia's crocodiles through commercial incentives.** *Herpetology in Australia: a diverse discipline* 250–256.

Wilkinson PM (1983) **Nesting ecology of the American alligator in coastal South Carolina. Columbia, USA.**

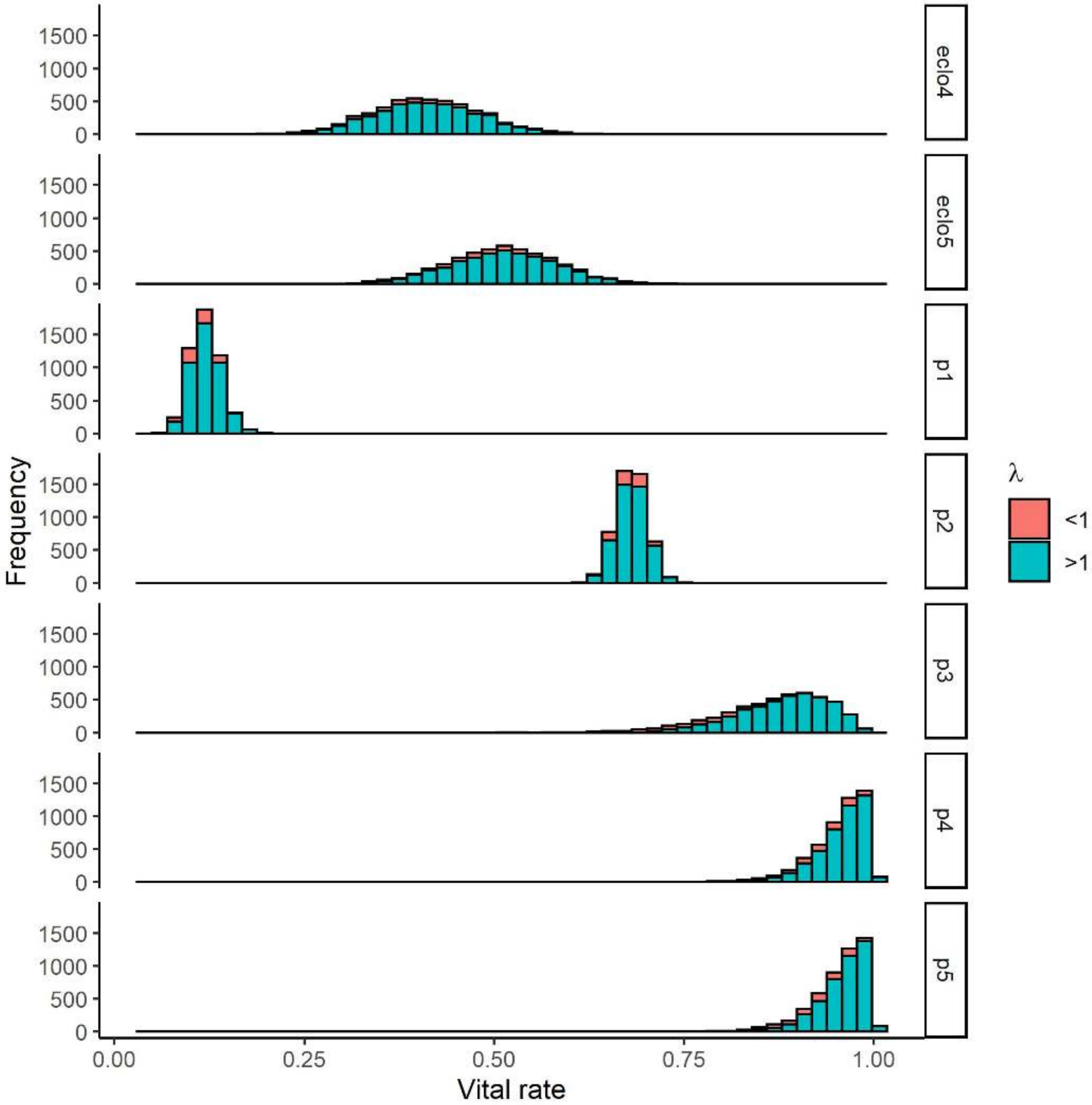
Wilkinson PM, Rainwater TR, Woodward AR, Leone EH, Carter C (2016) **Determinate growth and reproductive lifespan in the American Alligator (*Alligator mississippiensis*): Evidence from long-term recaptures.** *Copeia* 104:843–852.

Wisdom MJ, Mills LS, Doak DF, Ecology S, Mar N (2000) **Life stage simulation analysis: estimating vital-rate effects on population growth for conservation.** *Ecological Society of America Stable* 81:628–641.

Zucoloto RB, Bomfim GC, de Campos Fernandes FM, Schnadelbach AS, Piña CI, Verdade LM (2021) **Effective population size of broad-snouted caiman (*Caiman latirostris*) in Brazil: A historical and spatial perspective.** *Global Ecology and Conservation* 28:0–2

Received: 01 June 2022
Accepted: 29 July 2022
Published: 21 January 2023

Additional Files



Add File 1. Annex: Frequency distribution of vital survival and hatching rates, with which the 5000 matrices were generated. In pink is marked the frequency of cases in which each rate produces decrease values ($\lambda < 1$) and, in blue, when it leads to population growth values ($\lambda > 1$).

Add File 2. Adjustment of lambda to each survival rate.

Survival Rate	R^2
p_3	0.53
p_5	0.20
p_4	0.16
p_1	0.08
$hatch_5$	0.03
p_2	0.01
$hatch_4$	0.00

Legend: Coefficient of determination R^2, showing the adjustment of λ to each vital survival rate (p_i and $hatch_i$).

Add File 3. Differences between average matrix elasticity and each generated matrix.

		Difference eijm-eijk				
	Parameter	**Mean**	**SD**	**median**	**min**	**max.**
F_i	F_4	0	0	0	-0,01	0,02
	F_5	0	0,01	0	-0,04	0,01
G_i	G_1	0	0,01	0	-0,05	0,02
	G_2	0	0,01	0	-0,05	0,02
	G_3	0	0,01	0	-0,05	0,02
	G_4	0	0,01	0	-0,04	0,01
P_i	P_2	0	0	0	-0,03	0,01
	P_3	-0,01	0,04	0	-0,13	0,14
	P_4	-0,01	0,04	-0,01	-0,22	0,35
	P_5	0,02	0,11	0,01	-0,29	0,59

Add File 4. Effect on λ of different combinations of hunting individuals from E_5, with ranching, and return.

Harvest E5 + Ranch			
	Harv	**Ranch**	**Rein**
$\lambda < 1$	0.05	0.15-1	0
	0.15	0.05-1	0
		0.05	0.1
	0.3	0.05	0-0.5
		0.35	0-0.35
		0.45-1	0
$\lambda_m < \lambda < 1$	0.05	0.05	0
		0.05-0.45	0.05
		0.05	0.2-0.5
	0.15	0.05	0.2-0.7
		0.15	0.1
	0.3	0.05	0.6-0.1
		0.15	0.3-0.4
		0.45-1	0.1
$\lambda_m > \lambda$	0.05	0.05	0.6-1
		0.15-1	0.5-1
		0.25	0.2-1
	0.15	0.05	0.8-1
		0.15	0.3-1
		0.65	0.1-1
	0.3	0.15	0.5-1
		0.35	0.3-1
		0.55-1	0.2-1

Legend: Some combinations of the values of hunting of *Caiman latirostris* of stage E_5, Ranching and return, which cause population decrease ($\lambda < 1$), as well as deceleration ($\lambda m < \lambda$), for the Ranching scenarios and hunting of adult females corresponding to E_4 and E_5.

Add File 5: Effect on λ of the hunting combinations of individuals of E_4 and E_5, with ranching and return.

Harvest E4 and E5 + Ranch			
		Ranch	**Rein**
$\lambda < 1$	0.05	0.15-1	0
	0.15	0.05	0
		0.35	0.2
		0.45-1	0-1
	0.3	1-0.15	1
		0-0.35	0.5
		0-0.65	0.3
		0-1	0-0.02
$\lambda_m < \lambda < 1$	0.05	0.05	0-0.5
		0.15-0.45	0.01
		0.15	0.02
	0.15	0.15	0.3-0.7
		0.45-0.55	0.2
		0.75-1	0.1
	0.3	0.25	0.9
		0.45	0.5
		0.85	0.3
$\lambda_m > \lambda$	0.05	0.05	0.61-1
		0.15	0.3-1
		0.25	0.2-1
		0.55-1	0.1-1
	0.15	0.15	0.8-1
		0.25	0.5-1
		0.65-1	0.2-1
	0.3	0.25-1	1
		0.35-1	0.8-1
		0.55	0.5-1
		0.9	0.3-1

Legend: Combination of some *C. latirostris* hunting values ofE_4 and E_5, Ranching and return, which cause population decrease ($\lambda < 1$), as well as deceleration (λ m $<$ λ), for the ranching and adult female hunting scenarios corresponding to the E_4 and E_5.