

Winter survivorship of hatchling broad-snouted caimans (*Caiman latirostris*) in Argentina

Evangelina V. Viotto^{1,2} , Melina S. Simoncini^{1,2,3} , Luciano M. Verdade⁴ ,
Joaquín L. Navarro^{5,6,7}  and Carlos I. Piña^{1,2,3*}

ABSTRACT

The first life stage of crocodylians is considered the most critical in terms of survival, particularly in regions that have well-defined cold seasons. To estimate this parameter for hatchling broad-snouted caimans, Class I (CI = snout-vent length < 25 cm), we released 36 caimans (18 in 2018, and 18 in 2019) born in captivity that were equipped with VHF radio-transmitters, and we monitored them during each first winter season. We actively searched for the animals during field trips and registered their status as alive, dead, lost transmitter (LT), or radio signal ceased (SC). Due to the occurrence of LT and SC, we proposed eight possible survival scenarios, assuming different combinations of "alive" and "dead" caimans. We analyzed each scenario and compared it between years. In 2018 we found 55.5% dead and 44.5% LT, resulting in survival estimates from 0 to 0.38 according to the scenario. In 2019 we found 50% alive, 33% LT, and 17% SC, with survival varying from 0.5 to 1. Survival in 2019 was higher than in 2018 in all scenarios. Assuming predation was the most plausible cause of LT, with the most likely scenarios estimated 0% survival in 2018 (although the minimum detectable by this methodology is 5%) and 67% in 2019. This information can be helpful for ranching with release programs, as it allows for a better adjustment of the reintroduction rate and opens up the possibility of earlier releases when resources to keep animals in enclosures are scarce.

Keywords: Crocodylia; Kaplan-Meier; Radio telemetry; Wildlife management.

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. Dr. Materi y España. CP 3105. Diamante, Entre Ríos, Argentina.

2 Proyecto Yacaré-Laboratorio de Zoología Aplicada: Anexo Vertebrados Facultad de Humanidades y Ciencias, Universidad Nacional del Litoral, Argentina.

3 Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Argentina.

4 Universidade de São Paulo, CENA / LE²Ave, Caixa Postal 09 Piracicaba, SP 13416-000 Brazil.

5 Centro de Zoología Aplicada, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Rondeau 798, CP 5000, Córdoba, Argentina.

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

7 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.

* Corresponding author ✉. E-mail address: FRS (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

Hatchling survivorship is still unknown for many crocodylian species, including *Caiman latirostris*, but it is suspected to be low. Knowing the parameters that govern the species' life history is important to generate proper management guidelines. We estimated the minimum and maximum survivorship of caimans in winter as 5% and 67%, respectively. This type of information can be useful for ranching programs that practice the release of animals in terms of conservation as a way of perpetuating the species. This allows for a better adjustment of the reintroduction rate and opens up the possibility of earlier releases when resources to keep animals in enclosures are scarce.

INTRODUCTION

In the life cycle of crocodylians, the first stage is the most critical, given the high mortality rate caused by predation (Somaweera *et al.* 2013) and by thermal stress during the winter of temperate climates (Larriera and Imhof 2006; Wood *et al.* 2017). The hatchling survival rate is still unknown for many crocodylian species, including *Caiman latirostris*, but it is suspected to be low. For example, in *Alligator mississippiensis*, the estimated survivorship was 16.4% in Louisiana (Carbonea 1987) and 10 to 25% in Florida (Temsiripong *et al.* 2006). One of the critical limitations for the survival of *C. latirostris* in Argentina is suspected to be the strong seasonality, with minimum temperatures below 0° C during winter (June–September) (Simoncini *et al.* 2009). Such low temperatures reduce crocodylian activity, which is limited to Sunbasking and staying in the water, and they do not feed (Diefenbach 1988; Larriera and Imhof 2006). Extreme climatic variations lead to mortality, especially in hatchlings or Class I (CI) animals (Brandt and Mazzotti 1990; Mazzotti *et al.* 2016), which corresponds to those with a snout-vent length (SVL) < 25 cm in *C. latirostris* (Leiva *et al.* 2018).

Knowing the parameters that govern a species' life history is important for generating effective management guidelines. Sustainable use of wild crocodile populations has shown that a depleted population can recover while a portion is commercially exploited (Larriera 2011). This has created economic incentives for conservation and sustainable use (Larriera 2011).

The conservation and sustainable use strategy chosen for caimans in Argentina has been ranching. This technique comprises collecting eggs in the wild, incubating them artificially, and rearing the hatchlings in captivity for a certain period (nine months, Larriera 2011; Larriera and Imhof 2006). In this system, hatchlings are kept under controlled conditions in heated greenhouses with food *ad libitum*. Approximately, 10% of the hatched individuals are released

at a size similar to a juvenile caiman ($25 \leq \text{CII} \leq 68$ cm SVL). The rest remain in captivity, destined for commercial production. The ranching technique was developed specifically to address the significant loss of eggs (around 40–50%; Larriera and Piña 2000; Larriera and Imhof 2006) and individuals during their first year of life in the wild. For *C. latirostris*, it is speculated that approximately 10% survive their first year of life (Larriera 2011).

Evidence shows that this conservation strategy has been effective for *C. latirostris*, as released caimans seem to have a relatively high survival rate (Larriera *et al.* 2006; Larriera and Imhof 2006). There are even reports of released animals reproducing in the wild (Larriera *et al.* 2006). In other species, such as the American alligator, it was found that when released at juvenile size (between 91–152 cm total length- TL) reported survival is 87% (Capelle 2017). On the other hand, hatchlings (< 30 cm TL) released at birth have the same survival rate as natural hatchlings (Temsiripong *et al.* 2006). For this reason, we can assume that reintroduced animals have a destiny similar to that of their wild counterparts, regardless of their size at the time of release (Larriera *et al.* 2006; Temsiripong *et al.* 2006; Viotto *et al.* 2020).

The lack of information on the survival of *C. latirostris* offspring is due to the difficulty in determining population parameters that control the life history of crocodylians (Nichols 1987). Crocodylians are usually observed using night counts, mark-recapture, or aerial counts (Bayliss *et al.* 1986; Fujisaki *et al.* 2011; Piña *et al.* 2010; Portelinha *et al.* 2022). However, detecting hatchlings and youth crocodylians using these methods is difficult because of their small size (Fujisaki *et al.* 2011) and their tendency to stay hidden in aquatic vegetation or refuges (obs personal, Larriera and Imhof, 2006). In the few studies that include hatchling abundance, such data are generally treated separately from other size classes because of the high mortality exhibited by small individuals (Piña *et al.* 2010; Somaweera *et al.* 2013). Conse-

quently, the methods used for adult crocodylians tend to be relatively ineffective for hatchlings and young (Lang 1987).

For these reasons, we used radio-telemetry to track and locate Class I (CI) individuals (< 25 cm SVL) in the wild and to estimate their survival rate during their first cold season. Since this is one of the most vulnerable times for these crocodylians, it is necessary to know the proportion of hatchlings that stay alive after this critical period. We expected that, by estimating the survival of hatchlings after the period of most significant mortality, we would be able to detect the factors affecting this parameter. Such information might help determine the appropriate proportion of individuals that ranching programs should release for this species.

MATERIAL AND METHODS

Study Area

Fieldwork for this study was conducted from May to September (autumn-spring) in 2018 and June to January (autumn-summer) in 2019 in the largest lagoon at Reserva Natural Manejada El Fisco (RNMEF; 30°11'26" S, 61°0'27" W), located in the department of San Cristóbal, in the NW of Santa Fe province, Argentina (Figure 1) (Lorenzon and Leiva 2019). The primary objective of this reserve is the conservation and management of the broad-snouted caiman (Provincial Law No. 12.175 Art. 37). This region is one of the sites where eggs are collected for Ranching Program for "Proyecto Yacaré", a sustainable use program of the species (Larriera and Imhof 2006). The region's temperate climate has an annual average minimum temperature of 14.9° C (the average minimum temperature in winter is 7° C, and the maximum is 25.6° C), with average annual precipitation of approximately 1,380 mm. Although during winter there is a marked drop in temperature in this area, there is no ice or snow surface layer. The natural reserve is 2,000 ha and represents several landscapes such as upland and lowland areas, swamps, and ephemeral and permanent lagoons. The predominant vegetation is savanna forest (Larriera 1995; Montini *et al.* 2006), characterized by *Prosopis alba*, *Acacia caven*, *Celtis tala*, and *Geoffroea decorticans* (Lorenzon and Leiva 2019). The lagoon is approximately 300 ha, around 1.5 m deep, and is surrounded by dense aquatic vegetation such as *Typha* spp., *Juncus* spp., *Scirpus* spp., and *Ceratophyllum demersum* (De la Peña 1994). Because it is a managed reserve, controlled livestock activity is allowed, except in its core area, where the lagoon is located.

Transmitters

During 2018 and 2019, we released 18 *C. latirostris* each year with attached VHF radio transmitters in the lagoon at RNMEF. Animals were tracked in regular periods to evaluate survivorship. We selected caimans hatched in February at Proyecto Yacaré facilities in both years. We marked the hatchlings on caudal scutes (according to Larriera and Imhof, 2006) and attached transmitters ATS (Minnesota, USA; model A1080; 3.9 g, battery duration up to 441 days, 13 mm wide, 24 mm long) to all released animals.

The animals included in this study were selected based on their body mass, considering that each year's body size (SVL and TL) should be as similar as possible. At hatching, *C. latirostris* individuals measure 10 to 12.5 cm SVL (20.3–24.9 cm TL) and weigh 37.3 to 51.6 g (Simoncini *et al.* 2019). As the appropriate "transmitter mass/caiman mass" ratio required is less than 5% body weigh, we waited until the animals achieved 85 g before attaching transmitters. The caimans were previously kept in captivity (enclosures that have 50% natural light, 50% shade, 50% water, and 50% dry, Larriera *et al.* 2008), at 29° C to 31° C, and with food (70% chicken carcasses and 30% food specially designed for reptiles) provided *ad libitum*.

The transmitters were trapped between the subcutaneous tissue and the musculature with plastic thread. The procedure was as follows: 1) individuals were immobilized, and their eyes were covered; 2) local anesthesia was injected (lidocaine 10% - 10 mg/ml concentration -, diluted 0.1% in saline solution, injecting 2–3 mg/kg per live weight); 3) the area of intervention was disinfected with povidone-iodine, and a subcutaneous plastic thread was introduced; 4) before the final attachment, a thin layer of soft Epoxy glue was applied between the equipment and the nuchal zone to avoid friction; 5) using the threads (nylon 1mm thickness), each transmitter was fastened over the nuchal scales. A veterinarian performed all the surgical procedures at Proyecto Yacaré facilities in Santa Fe, Argentina. After the surgery to attach the transmitter, the animals were maintained for 7 days at 25°C to 26°C. During the following 15 days, the enclosure's temperature was gradually reduced to acclimate the animals to the natural environmental temperature to mitigate thermal stress after release.

Considering that small crocodylians tend to stay in groups (Campos *et al.* 2012; Lang 1987), we released the individuals in three groups of six animals each, in different sites at the lagoon. The release sites were selected based on the presence of small animals on previous occasions (Figure 1), except for site 3 in 2018, which was randomly chosen because we found CI individuals in only two places. In 2019 we changed location 3 of 2018 to one where we had sighted hatch-



Figure 1. Location of "Reserva Natural Manejada el Fisco" (RNMEF) and image from SAS planet (software free) of the lagoon where caimans were released. Sites 1 and 2 were the same in both years. Site 3 (2018) is coloured in light yellow, and site 3* (2019) is blue.

lings (location 3* in Figure 1). To test the tracking method and monitor how the caimans adapted to the new habitat, we monitored them for three days "post-release" and repeated this procedure on days 7 and 14. After this initial period, individuals were tracked every 20 days. When temperatures decreased abruptly, we traveled to the field in the subsequent days to check for increased mortality since we suspected that mortality could be related to cold fronts. The animals were tracked for five months or until all were deceased. We tried to include the coldest (from May) and warmest periods (until December) in both years.

In 2018, we attached the transmitters on May 15, and caimans were released on June 4 (approximately three months of age). While in 2019, these procedures were performed on June 27 and July 16, respectively, when the caimans were 4 months old. In this way, we were looking to release larger animals in 2019 than in 2018, though still belonging to stage-class one ($CI \leq 25$ cm SVL, in 2018: SVL range = 14.5–16.5 cm, Body Mass range = 83–122 g; in 2019: SVL range = 16–19 cm, Body Mass range = 131–200 g), to find out whether the survival of the offspring varied due to this difference in size. We tested the difference in body size between years using the Kruskal-Wallis Test. Based on their release size, we estimate how old the animals would have been if they had been hatched and grown up in the wild, using the descriptive growth model of Viotto *et al.* (2020) and the SVL of each animal. On the other hand, the average ambient temperature on release day in 2018 was 15.49° C (range =

5.75 - 21.85° C, while in 2019 it was 11.55° C (range = 5.43 - 17.85), data from the webserver "Climate-Engine" (<http://climateengine.org>) (Huntington *et al.* 2017).

To determine the status of the animals (dead or alive), we actively searched for them using telemetry from 11 am to 5 pm during the winter (June to September) and from 5 pm through 11 pm during warmer periods. These schedules correspond to the times of greatest activity of caimans in each season. In this way, we took advantage of their basking behavior (in cold seasons) and foraging behavior (in warm seasons), which allowed us to visualize them with the lowest possible interference. Once a signal was detected, we located the individual or the transmitter. We also recorded the respective geographic coordinates and classified the status of each animal as alive, dead, unseen, or lost transmitter. We also recorded those cases where the transmission stopped (three in 2019). We captured and manipulated the radio-tracked individuals only at the end of the study when they were weighed and measured, and the transmitters were removed. We released the caimans at the same site of capture. To evaluate the climatic conditions to which the animals were exposed in the wild during the experiment, we obtained temperature data from the webserver "Climate-Engine" (<http://climateengine.org>) (Huntington *et al.* 2017). We counted the days with a maximum temperature $\leq 16^\circ$ C, since the release date to the end of the fieldwork in both years. This limitation was chosen because of

the reduced capacity for action of the immune system at lower temperatures in these animals (Reyes *et al.* 2018). We also report the minimum temperature to which individuals were exposed each year (<http://climateengine.org>).

Analysis

We performed all data analysis in R software version 3.6.2 (R Core Team 2019, www.r-project.org, accessed July 10, 2020). To analyze the survival rate, we used the non-parametric Kaplan-Meier test from the Survival package (Therneau 2019) at the end, compared years using the log-rank test. To build survival curves, we considered the time elapsed until we found either a dead animal, or a lost transmitter (LT), or when the radio signal ceased (SC).

Due to the occurrence of LT and SC animals, we proposed eight possible survival scenarios, assuming different combinations of "alive" and "dead" caimans in these two categories (Table 1). These scenarios ranged from the most optimistic (scenario 1), in which we considered all LTs and SCs to be alive, to the most pessimistic (scenario 8), in which we assumed that all the individuals that were not seen alive at the end of the study period were dead.

We formulated the different scenarios, considering where the transmitter was found (within or outside

the lagoon) and if the equipment surface showed damage. Only transmitters that were found unattached showed signs of damage (scratches/marks on the surface). Therefore, since it is unlikely that the caimans caused the damage themselves, those whose transmitters were found unattached were presumed to have been predated.

Skin Resistance Tests

To assess the probability of occurrence of LT, we evaluated the resistance of caiman skin to traction force applied to the stitches of the transmitter. For this purpose, we used 10 dead animals obtained from the Proyecto Yacaré of similar size to those selected for the survival assessment. To each of these corpses, we attached an epoxy transmitter model (of the same size and weight as the real device). While keeping the individual's body fixed, we secured a dynamometer to the model transmitter and pulled on until it was released. In addition, we investigated whether the caiman skin can reject and, after a time, remove the stitches holding the transmitter. With this aim, we attached epoxy transmitter models to 18 live animals (similar in size and weight to the 2019 group). We kept these caimans under observation at the Proyecto Yacaré facilities during the same period that the released animals were monitored in the field.

Table 1. Information of the evaluated models based on the presumed status of survival.

Scenario	LT	SC	Assumption	Survival rate (SE.)		Difference between years
				2018	2019	
1	-	-	All disappeared animals are alive, either LT or SC	0.38 -0.12	1	Chi: 15.3 P<0.001
2	-	All	Only the caimans that lost the transmitter are alive	0.38 -0.13	0.67 -0.12	Chi: 13.6 P<0.001
3	Out of water only	-	Of the disappeared animals, only the LTs found outside the lagoon are dead	0.35 -0.12	0.78 -0.1	Chi: 12.8 P<0.001
4	Out of water only	All	Of the disappeared animals, the LTs found outside the lagoon, and the SCs are dead	0.35 -0.12	0.5 -0.11	Chi: 11.7 P<0.001
5	Out of water + Marking		LT animals that had no mark on the transmitter and SC animals are alive	0.11 -0.07	0.67 -0.11	Chi: 23.2 P<0.001
6	Out of water + Marking	All	Only LT animals that had no mark on the transmitter are alive	0.11 -0.07	0.5 -0.12	Chi: 22.7 P<0.001
7	All		All LT animals are dead, but the SC is alive	0	0.67 -0.11	Chi: 30.5 P<0.001
8	All	All	All the animals that were not seen alive are dead	0	0.5 -0.1	Chi: 30.1 P<0.001

Legend. Information from the models evaluated based on the presumed status, alive or dead, of lost transmitters (LTs) and signal ceased (SCs) for each scenario, the final estimate of the probability of survival (P. Sup) according to the Kaplan-Meier model, the estimation of the difference between years according to the Log-Rank model, and the threshold of SVL at which the probability of mortality changes.

RESULTS

The caimans released in 2018 were smaller and lighter than those released in 2019 ($H_{SVL} = 22.8$, $df = 1$, $P < 0.001$; $H_{bodymass} = 26.8$, $df = 1$, $P < 0.001$; Figure 2). In 2018 the average SVL was 15.6 cm (SD = 0.68; range = 14.5–16.5 cm) and 102 g body mass (SD = 12.02; range = 83 – 122; Figure 2), whereas in 2019 the average SVL was 17.5 cm (SD = 0.98; range = 16–19) and 165 g (SD = 24.7, range = 130 – 200 g Figure 2). The transmitter weight/caiman body mass ratio was $3.9 \pm 0.5\%$ (range = 3.2–4.7) in 2018, and $2.4 \pm 0.5\%$ (range = 1.9 – 3) in 2019. We estimated that the animals released in 2018 were equivalent to wild animals of 0.9 ± 0.08 year-old (range = 0.78–1.02 year; equal to 11 ± 0.9 months old, range = 9.33–12.2 months; Figure 2), and those of 2019 to 1.1 ± 0.09 year-old animals (range = 0.96–1.25 year; equal to 13 ± 1.15 month-old, range = 11.5–15 months).

Individuals released in 2018 were exposed for longer periods to adverse conditions with a maximum temperature below 16°C (55 days in 2018 and 22 in 2019). The minimum temperature to which they were exposed in 2018 was -2.4°C and in 2019 = 0.85°C . None of the caimans kept as controls lost its epoxy transmitter model, although two died from undetermined causes in the first two weeks. Also, we did not observe necrosis of the attachment site in the released animals that were alive at the end of the study. The measured force required to pull out the sutures was 3.7 ± 1.5 kg.

Monitoring in 2018 lasted 106 days, in which we made six field trips to track the caimans until September 18, when the last loose transmitter appeared. We recovered the transmitters of all 18 released animals: ten were found on dead animals, and the rest were found loose (LT; nine presented marks in the resin, and one was found outside the lagoon). We recorded a death rate of 55.5% and 44.5% LT. At site 3, we did not register any LT (Table 2), while 100% of the animals were found dead, and at site 1, we registered the highest proportion of LT (83%) (Table 2). Even though we did not find any tagged caiman alive at the end of this period, our proposed scenarios estimated the survival rate could be between 0 and 0.38. This range was calculated according to the number of individuals considered dead or still alive because of lost transmitters or those that had stopped transmitting (Table 1, Figure 3).

In 2019, the monitoring period lasted 170 days, during which we carried out 10 field trips. On January 2, 2020, we completed the study, removed the transmitters from the animals, and subsequently released them. We recovered 83% of the transmitters (15/18; Table 2). We found six LT (five outside the

lagoon and one with damage to the transmitter's surface), nine live animals, and three transmitters were lost with no signal. In 2019 we found no dead caimans, so the estimated survival rate varied from 0.5 (Scenario 5) to 1 (Scenario 1). In all scenarios, survival was consistently higher in 2019 than in 2018 (Table 1, Figure 3).

DISCUSSION

Based on the animals found dead with the transmitter attached, assuming Scenario 1, the survival rate would be 0.38 for 2018 and 1 for 2019. However, this scenario does not consider data from animals that lost their transmitter. Therefore, if we assume that animals carrying LT transmitters were predated, we should include this type of mortality in our models. Thus, only scenario 7 would comprise all causes of death (i.e., cold stress and predation) of the eight proposed scenarios allowing us to estimate a more plausible natural survival rate.

The greater weight we give to scenario 7 is mainly due to the following evidence: (a) the transmitters had their attachment threads intact, and it takes about 3 kg of force to remove them from the caimans; (b) none of the animals in the 2019 control group kept in captivity with transmitter models rejected the attachment (due to thinning of the skin -suture rejection- which results in less resistance to the detachment of the device), which suggests that the same would occur in nature and therefore the transmitter would detach from the individual without any extra force being exerted; (c) some of the LT transmitters were found outside the lagoon, in a dry open area (one in 2018 and five in 2019), suggesting that the individuals had to leave the water and lost the transmitter there; however, this is not consistent with the behavior of caimans in this stage of their life cycle; (d) only the LT transmitters presented some damage, which suggests a possible predation event because the damage does not seem to have been caused by abrasion/friction with vegetation, which seems the most probable physical barrier where transmitters can be trapped in this area.

Under the assumption that the corpses we found were of those animals who died from natural causes and that the LTs resulted from predation, it is possible to differentiate both mortality causes. Scenario 1 represents the proportion of individuals that survived stress due to cold weather. Mortalities due to cold weather are recognized as one of the most critical factors in the caiman populations of Santa Fe (Argentina). It is strongly associated with the small size of the hatchlings during their first year of life (Larriera and Imhof 2006). Scenario 1 shows weak survival for 2018 (38%), while all caimans in the study survived

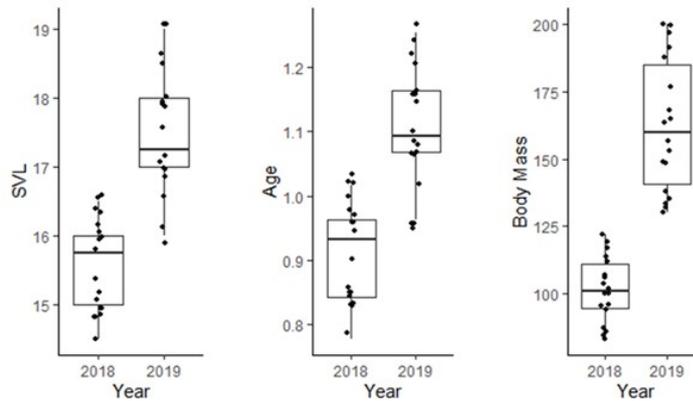


Figure 2. Box plot showing the median (black line inside each box), the 95% confidence interval (box width) and the extreme values of each morphometric trait of the caiman (dotted line length): SVL (cm), Age (year) and Body Mass (g). The points correspond to the values of each individual for each morphometric parameter evaluated.

Table 2. Final status of the released animals and their transmitters

	Site	LT	Dead (%)	Live (%)	BC (%)
2018	1	5 (83%)	1 (17%)		
	2	4 (67%)	2 (33%)		
	3	0 (0%)	6 (100%)		
2019	1	3 (50%)		3 (50%)	0 (0%)
	2	0 (0%)		5 (83%)	1 (17%)
	3	3 (50%)		1 (17%)	2 (33%)

Legend: Final status of the released animals and their transmitters, classified by site and by year. LT are the lost transmitters, and BC those that stopped to broadcast.

in 2019. This fact suggests that increasing the SVL by a few centimeters in a warmer year could decrease the mortality rate even when individuals are released in winter.

On the other hand, predation represents the other primary source of mortality in 2018 and the only source of mortality in 2019. Since predation in crocodylians depends on the individual’s size, young crocodiles are more vulnerable than those at other life stages (Somaweera *et al.* 2013). In general, hatchlings can be predated by large vertebrates, such as birds, mammals, fish, reptiles, and even some invertebrates (Somaweera *et al.* 2013). In our study area, herons, storks, foxes (*Lycalopex gymnocercus*), tegu lizards (*Salvator merianae*), and caracara (*Caracara plancus*) are possible predators of *C. latirostris* hatchlings (Larriera and Imhof 2006). However, it is not clear whether any of these animals produced damage

on the transmitters.

Scenario 7 reports 0% survival for 2018 and 67% for 2019. In 2018, the percentage of survivors reflect only the lower limit of natural variability. The relatively small sampling size may have influenced this result compared to the high number of individuals this species produces in a relatively short period. The R-selected reproductive strategy (Magnusson 1984, Chapman and Reiss 1998), typical of crocodylians from temperate climates (Larriera *et al.* 2004; Simoncini *et al.* 2009), is associated with high predation mortality in early life stages (Somaweera *et al.* 2013).

Also, if a population is small, a high hatchling mortality rate may result from stochastic processes, resembling the pattern of the entire small population (i.e., small population paradigm; Caughley 1994). For example, this process sometimes occurs in broad-

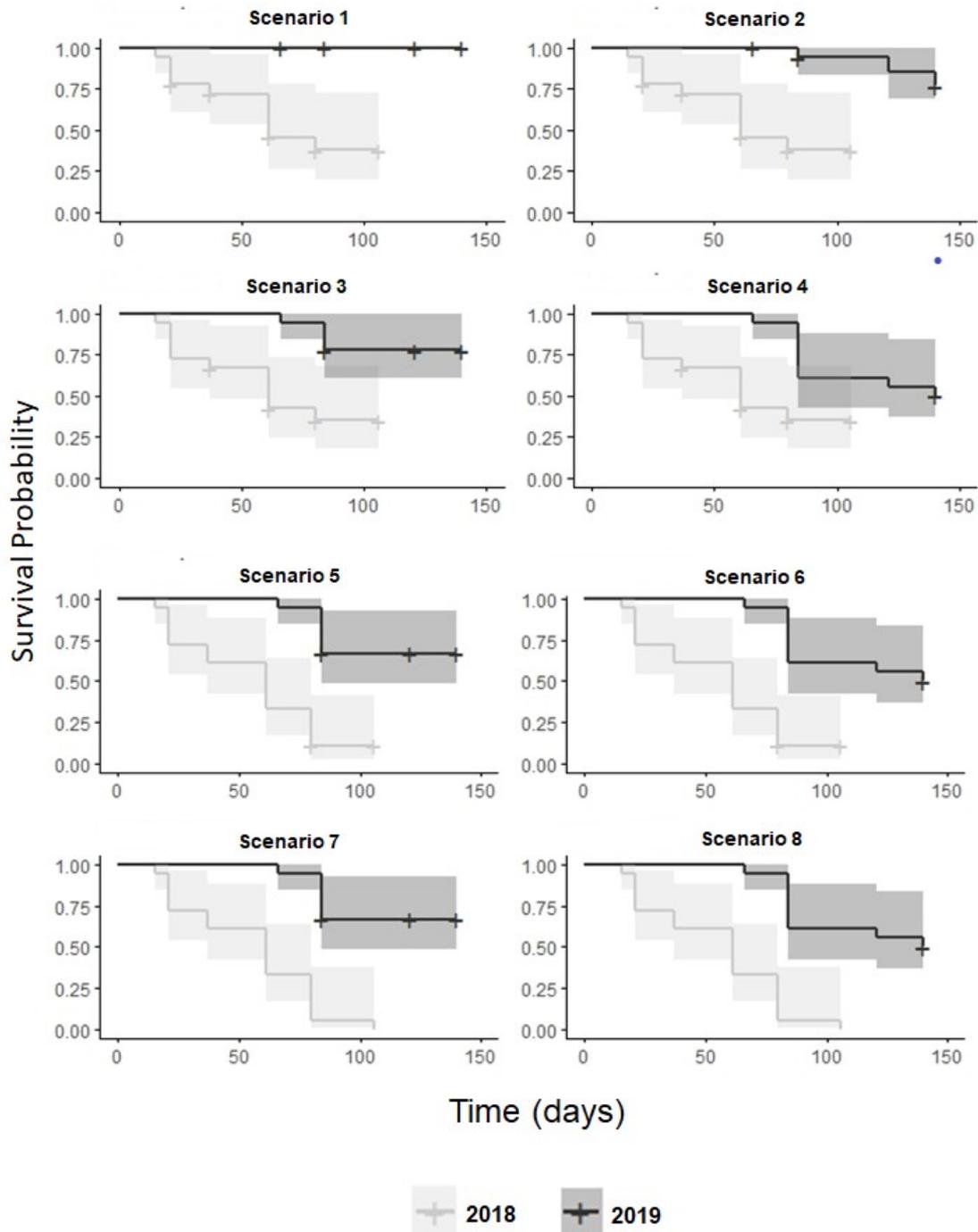


Figure 3. Survival curve estimated by the Kaplan-Meier Analysis, for the eight scenarios. A continuous line represents the probability of survival as a function of time. The respective confidence intervals are shown as a grey area (light grey for 2018 and dark grey for 2019). The survival curves for 2018 are drawn in grey and those for 2019 in black.

snouted caiman in Brazil (e.g., Verdade *et al.* 2002). Therefore, when using small sample sizes, one cannot completely rule out that observed mortality may be entirely the result of a random event. However, based

on the number of animals released with transmitters in this study, the survivorship rate of Scenario 7 was lower than the minimum detectable by this work (less than 5.5%; i.e., 1/18). The survival for the first year,

according to these scenarios (5.5%, Scenario 7), is consistent with the range obtained for animals within their first year of life from other species, such as *Gavialis gangeticus* in India, where survival ranges from 6.6 to 8.8% in the first year (Hussain 1999), or *A. mississippiensis* in Florida (between 1.9 and 17.9%, Mazzotti *et al.* 2009), and lower than that reported for the latter species in other studies (in Florida: 10 to 25%, Temsiripong *et al.* 2006; or Louisiana 16.4%, Carboneau 1987), or *Crocodylus johnstoni* in northern Australia (17% first-year survival, Smith and Webb 1985).

In all the scenarios analyzed, the survivorship rate was higher in 2019. Nevertheless, prevailing environmental conditions may influence the difference we detected between years. The highest survival rate occurred during the warmest year when the size of released animals was also larger. Consequently, our data reflects a combination of the effect of these two variables on survivorship. Furthermore, the difference between years may also be attributed to the natural variability in the offspring's survivorship, despite our effort to find the survival difference according to the size of the released animals.

One of the assumptions underlying this work is that the weight of the transmitters does not affect survival. It is generally accepted that the weight of the transmitter should not exceed 5% of the animal's body mass (O'Mara *et al.* 2014; White and Garrott 1990). In this study, the highest transmitter weight to body mass ratio was 4.6%. A survey conducted with iguana hatchlings (*Iguana iguana*; Knapp and Abarca 2009) evaluated this assumption and found that neither survival nor mobility was affected when the weight ratio was as high as 7.5%. As the weight of any object diminishes in the water, the equipment would have a more negligible burden effect on these aquatic animals than on terrestrial or flying ones. Therefore, transmitter weight is unlikely to have affected the survival estimates in this study.

One of the objectives of ranching programs that reintroduce animals is to maintain natural populations by reintroducing individuals that are more likely to survive the most critical life stages and reach sexual maturity (Larriera and Imhof 2006; Viotto *et al.* 2020). Temsiripong *et al.* (2006) propose that reintroductions should be based on the objectives of use or management. Based on the information reported in this work, out of every 100 eggs, 2 individuals would survive the first year (considering the 40% natural hatching rate - Larriera and Piña 2000; Montini *et al.* 2006) -, and the 5.5% survival rate reported in this work). Therefore, if the aim is to maintain the dynamics of the natural populations, at least 5% of the eggs collected should be reintroduced (we chose 5% instead of 2% considering a more parsimonious position

to avoid estimation errors). On the other hand, if the aim is to accelerate population growth, reintroduction should be greater than 5%. Based on this, Proyecto Yacaré in Santa Fe is accelerating population growth (reintroducing 7.5% of the eggs harvested or 10% of the hatched caimans, Siroski *pers.com.*).

Another important piece of information based on our work that should be considered for caiman population management is that data from the 2019 fieldwork indicates that caimans with a SVL of 17.5 cm could survive the winter with a high survivorship rate (0.67, Figure 2). This result suggests that it is possible to reintroduce individuals earlier with a reasonable survivorship rate. Therefore, programs aiming to preserve populations could reduce costs by reintroducing caiman at the end of winter, not at the end of spring. This way, animals should have reached a size that reduces mortality, and although this is not the best weather season, extremely cold days are virtually over. It is necessary to remember that husbandry operations (including feedstuff and facilities) can be expensive (Hutton and Webb 2002). If a management program is not economically sustainable, it is unlikely to last long.

Finally, these alternative methods should first be tested experimentally, and if they are successful, their implementation should be accompanied by a population monitoring program. Additionally, we recommend evaluating the suitability of candidate release sites previously as the only site we chose at random presented the highest number of deceased animals in 2018. In this sense, our experience indicates that a good strategy may be to previously confirm the presence of small caimans at the candidate sites for release.

CONCLUSION

The winter survival rate of *Caiman latirostris* hatchlings is likely to be affected by environmental conditions and the size of the individual. Thus, reintroducing larger caimans in the wild during a warmer winter seems more effective than releasing smaller ones under lower environmental temperatures. This study also provided the basis to reduce to 5% the reintroduction of individuals carried out by the current management program. It is possible to reintroduce caimans hatched in captivity to their natural distribution area, in which they will present greater probabilities of survival from the beginning of spring onwards. Finally, it is desirable that individuals are released in sites where wild-born hatchlings are observed.

ACKNOWLEDGMENT

We thank all members of Proyecto Yacaré for providing the animals, the workspace, and assistance during fieldwork. D.G. Rocha (UNC-FCEfyN) for helping us with statistical survival models, L. J. Scarpa for their support to the field, Lonnie McCaskill for checking the English style and R. Ojeda-Adame and A. Vittori for attaching transmitters to caimans. E. Viotto is a doctoral fellow of CONICET at CICYTTP (CONICET-Prov. Entre Ríos-UAd-ER). This study was supported by Proyecto Yacaré, Yacarés Santafesinos (Gob. Prov. Santa Fe/MUPCN), PFIP 2008; PICT 2014 N2138 and 2019 N812 (to C. Piña), PICT 2014 N2212 (to M. Simoncini); IUCN-SSC Crocodile Specialist Group Student Research Assistance Scheme (SRAS); and Idea Wild Foundation. L. M. Verdade help a Productivity Fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Grant 312049/2015-3) and financial Support from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Grant 2017/01304-4). The Gordon and Betty Moore Foundation partially 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, CIP, MSS.

Carried out the data analysis: EVV, CIP.

Wrote the first draft of the manuscript: EVV.

Review and final write of the manuscript: EVV, MSS, LMV, CIP, JLN.

Supervision: CIP, MSS, LMV, JLN.

REFERENCES

Bayliss P, Webb GJW, Whitehead PJ, Dempsey K, Smith A (1986) **Estimating the abundance of saltwater crocodiles, *Crocodylus porosus* Schneider, in tidal wetlands of the Northern Territory: A mark-recapture experiment to correct spotlight counts to absolute numbers,**

and the calibration of helicopter and spotlight count. *Wildlife Research* 13:309–320.

Brandt LA, Mazzotti FJ (1990) **The Behavior of Juvenile *Alligator mississippiensis* and *Caiman crocodilus* Exposed to Low Temperature.** *Copeia* 3:867–871.

Campos Z, Sanaiotti T, Muniz F, Farias I, Magnusson WE (2012) **Parental care in the dwarf caiman, *Paleosuchus palpebrosus* Cuvier, 1807 (Reptilia: Crocodylia: Alligatoridae).** *Journal of Natural History* 46:2979–2984.

Capelle KD (2017) **Evaluating survival of released ranched American alligator in coastal Louisiana.** Louisiana State University and Agricultural and Mechanical College Follow.

Caughley G (1994) **Directions in Conservation Biology.** *The Journal of Animal Ecology* 63:215.

Chapman JL, Reiss MJ (1998) **Ecology: principles and Applications.** Segunda ed. Cambridge.

De la Peña P (1994) **Catálogo de nombres comunes de la flora Argentina.** Santa Fe.

Diefenbach COC (1988) **Thermal and feeding relations of *Caiman latirostris* (Crocodylia: Reptilia).** *Comparative Biochemistry and Physiology – Part A: Physiology* 89:149–155.

Fujisaki I, Mazzotti FJ, Dorazio RM, Rice KG, Cherkiss M, Jeffery B (2011) **Estimating trends in alligator populations from nightlight survey data.** *Wetlands* 31:147–155.

Huntington JL, Hegewisch KC, Daudert B, Morton CG, Abatzoglou JT, McEvoy DJ, Erickson T (2017) **Climate Engine: cloud computing of climate and remote sensing data for advanced natural resource monitoring and process understanding.** *Bulletin of the American Meteorological Society* 98:2397–2410.

Hussain SA (1999) **Reproductive success, hatchling survival and rate of increase of gharial *Gavialis gangeticus* in National Chambal Sanctuary, India.** *Biological Conservation* 87:261–268.

Hutton JM, Webb GJW (2002) **Legal trade snaps back: using the experience of crocodylians to draw lessons on regulation of the wildlife trade.** In: IUCN CSG (ed) *Crocodyles*. Proceedings of the 16th Working Meeting of the IUCN-SSC Crocodile Specialist Group. Gland, pp. 1–10.

Knapp CR, Abarca JG (2009) **Effects of radio transmitter burdening on locomotor ability and survival of iguana hatchlings.** *Herpetologica*

65:363–372.

Lang JW (1987) **Crocodylian behavior: implications for management.** In: Weeb GJW, Manolis C, Whitehead PJ (eds) *Wildlife Management: Crocodile and Alligators.* pp. 273–294.

Larriera A (1995) **Áreas de nidificación y momento óptimo de cosecha de huevos de *Caiman latirostris* en Santa Fe, Argentina.** In: Larriera A, Verdade LM (eds) *La Conservación y el Manejo de Caimanes y Cocodrilos de América Latina.* Santo Tomé, pp. 221–232.

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.** Manejo de Fauna Silvestre en la Argentina Programas de uso Sustentable. Santa Fe, pp. 51–64.

Larriera A, Piña CI (2000) ***Caiman latirostris* (Broad-snouted caiman) nest predation: does low rainfall facilitate predator access?** *Herpetological Natural History* 7:73–77.

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.** Contribución al conocimiento de los caimanes del genero *Caiman* de Sudamerica. Santa Fe, Argentina, pp. 143–179.

Leiva PML, Simoncini MS, Portelinha TCG, Larriera A (2018) **Size of nesting female Broad-snouted Caimans (*Caiman latirostris* Daudin 1802).** *Brazilian Journal of Biology* 79:1–5.

Lorenzon R, Leiva L (2019) **Plan de manejo de la Reserva Natural Manejada “El Fisco”, Santa Fe, Argentina.** Período 2019-2024. Santa Fe.

Magnusson WE (1984) **The peculiarities of crocodylian population dynamics and their pos-**

sible importance for management strategies. In: IUCN C (ed) *Proceedings of the 7th working meeting of the Crocodile Specialist Group, Switzerland.* Gland, pp. 434–442.

Mazzotti FJ, Best GR, Brandt LA, Cherkiss MS, Jeffery BM, Rice KG (2009) **Alligators and crocodiles as indicators for restoration of Everglades ecosystems.** *Ecological Indicators* 9:137–149.

Mazzotti FJ, Cherkiss MS, Parry M, Beauchamp J, Rochford M, Smith B, Hart K, Brandt LA (2016) **Large reptiles and cold temperatures: Do extreme cold spells set distributional limits for tropical reptiles in Florida?** *Ecosphere* 7:1–9.

Montini JP, Piña CI, Larriera A, Siroski P, Verdade LM (2006) **The relationship between nesting habitat and hatching success in *Caiman latirostris* Crocodylia, Alligatoridae.** *Phyllomedusa* 5:91–96.

Nichols JD (1987) **Population models and crocodile management.** In: Webb GJW, Manolis SC, Whitehead PJ (eds) *Wildlife Management: Crocodiles and Alligators.* Chipping Norton, pp. 177–187.

O’Mara MTO, Wikelski M, Dechmann DKN (2014) **50 years of bat tracking: device attachment and future directions.** *Methods in Ecology and Evolution* 2014 5:311–319.

Piña CI, Siroski P, Príncipe G, Simoncini MS (2010) **Populations status of *Caiman yacare* and *Caiman latirostris* in North Argentina.** *Crocodylia* 1:1–5.

Portelinha TCG, Verdade LM, Piña CI (2022) **Detectability of *Caiman latirostris* (Crocodylia: Alligatoridae) in night count surveys.** *South American Journal of Herpetology* 23:25–31.

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

Reyes S, Moleón MS, Parachú Marcó, M. Virginia Pietrobon EO, Jahn GA, Siroski PA (2018) **Experimental consequences of low temperatures on *Caiman latirostris* immune and endocrine systems.** In: IUCN CSG (ed) *Proceedings of the 25th Working Meeting of the IUCN-SSC Crocodile Specialist Group.* IUCN: Gland, p. 183.

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 Integra-*

tive 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.

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

Somaweera R, Brien M, Shine R (2013) **The role of Predation in shaping crocodylian natural history.** *Herpetological Monographs* 27:23.

Temsiripong Y, Woodward AR, Ross JP, Kubilis PS, Percival HF (2006) **Survival and growth of American alligator (*Alligator mississippiensis*) hatchlings after artificial incubation and repatriation.** *Journal of Herpetology* 40:415–423.

Therneau T (2019) **A package for survival analysis in R.**

Verdade LM, Zucoloto RB, Coutinho LL (2002) **Mi-**

crogeographic variation in *Caiman latirostris*. *Journal of Experimental Zoology* 294:387–396.

Viotto E V., 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.

White GC, Garrott RA (1990) **Analysis of wildlife Radio-Tracking data.** San Diego.

Wood JP, Patton TM, Page RB (2017) **Movement and overwinter survival of released captive-raised juvenile American Alligators (*Alligator mississippiensis*) in Southeastern Oklahoma, USA.** *Herpetological Review* 48:293–299

Received: 10 February 2022

Accepted: 27 May 2022

Published: 29 August 2022