See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/349717101

Science and conservation of Amazonian crocodilians: a historical review

Article *in* Aquatic Conservation Marine and Freshwater Ecosystems · March 2021 D0: 10.1002/aqc.3541

| TATION | | reads 181 | |
|-------------|--|--------------|---|
| authors, ir | ncluding: | | |
| Un Un | osé António Lemos Barão-Nóbrega niversity of Salford & Operation Wallacea | | Robinson Botero-Arias University of Florida |
| _ | PUBLICATIONS 35 CITATIONS SEE PROFILE | | 40 PUBLICATIONS 194 CITATIONS SEE PROFILE |
| | bio Muniz ederal University of Amazonas | | Zilca Campos Brazilian Agricultural Research Corporation (EMBRAPA) |
| _ | SEE PROFILE | | 149 PUBLICATIONS 1,919 CITATIONS SEE PROFILE |

Some of the authors of this publication are also working on these related projects:

Reestruturação do Programa de Pesquisa em Biodiversidade e Ecossistema View project

Ecology and conservation of the Paleosuchus View project

DOI: 10.1002/aqc.3541

SPECIAL ISSUE ARTICLE

WILEY

Science and conservation of Amazonian crocodilians: a historical review

Boris Marioni¹ | José António L. Barão-Nóbrega² | Robinson Botero-Arias³ | Fábio Muniz⁴ | Zilca Campos⁵ | Ronis Da Silveira⁶ | William E. Magnusson⁷ | Francisco Villamarín⁸

¹Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil

²School of Science, Engineering and Environment, University of Salford, Greater Manchester, UK

³Department of Wildlife Ecology and Conservation, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL, USA

⁴Laboratório de Evolução e Genética Animal, Universidade Federal do Amazonas, Manaus, AM, Brazil

⁵Laboratório de Vida Selvagem - Embrapa Pantanal, Corumbá, MS, Brazil

⁶Laboratório de Manejo de Faunas, Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Manaus, AM, Brazil

⁷Coordenação de Biodiversidade – Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil

⁸Grupo de Biogeografía y Ecología Espacial BioGeoE2, Universidad Regional Amazónica Ikiam, Tena, Napo, Ecuador

Correspondence

Boris Marioni, Instituto Nacional de Pesquisas da Amazónia, Av. Andre Araujo, Manaus 69067-375, AM, Brazil. Email: bmarioni@mac.com

Abstract

- Crocodilians represent one of the oldest extant vertebrate lineages. They have co-existed with humans throughout the Amazon basin for thousands of years, often having a strong cultural and economic influence on people's lives. Shifts in the socio-economic and political reality of the Amazon basin during the last century have led crocodilian populations to face large variations in their numbers according to different levels of exploitation and strategies for their conservation.
- 2. This article reviews the scientific knowledge obtained between 1945 and 2019 on the biology, conservation and management for the four Amazonian crocodilian (caiman) species (*Caiman crocodilus, Melanosuchus niger, Paleosuchus palpebrosus* and *Paleosuchus trigonatus*). It provides a general overview on past and current population status and research efforts involving caimans in the Amazon basin and discusses perspectives for the future.
- 3. The most significant studies on the ecology, genetics and management strategies are examined in more detail and this information is contextualized to provide an overview of the most relevant findings that might explain caiman population trends over the last 75 years.
- 4. Systems for sustainable management in the Amazon basin have been discussed for the past 20 years, but remain rarely applicable. It is necessary to develop new ways to maintain healthy caiman populations through innovative management programmes. Sustainable harvesting of wildlife has been shown to promote conservation targets, especially those initiatives based on community co-management. In this article, we propose some general guidelines for future management schemes, in the expectation that the information provided by the scientific community will be considered fully without political agendas determining the priorities.

KEYWORDS

fishing, floodplain, monitoring, protected area, reptiles, sustainability, wetlands

1 | INTRODUCTION

Caimans (Crocodylia: Alligatoridae) have co-existed with humans throughout the Amazon basin for more than 6,000 years, often having a strong influence on people's lives. Although river communities respect these large vertebrates, the opinion of the general public is generally negative towards caimans, especially those inhabiting areas in close proximity to human settlements. Despite low human population densities ($3-4 \text{ km}^{-2}$) in the Amazon region (FAO, 2016) and the relatively low incidence of attacks on people (Haddad & Fonseca, 2011; Pooley, 2018), conflicts have increased as caiman populations have steadily grown during the last four decades, especially in central Amazonia.

The Amazon basin covers approximately 700×10^6 ha (Venticinque et al., 2016), mostly belonging to Brazil (68%), but also in Peru (13%), Bolivia (10%), Colombia (4%), Ecuador (2%), Venezuela (1%), Guyana (1%) and Suriname (1%). The Amazon is mainly composed of non-flooded forests and several types of wetlands associated with highly dynamic hydrological systems influenced by annual flooding (Junk, Piedade, Wittmann, Schöngart, & Parolin, 2010). This heterogeneous spatial distribution of aquatic ecosystems sustains four sympatric crocodilian species (Figure 1): spectacled caiman (*Caiman crocodilus crocodilus*), black caiman (*Melanosuchus niger*), Cuvier's dwarf caiman (*Paleosuchus palpebrosus*) and Schneider's dwarf caiman (*Paleosuchus trigonatus*), as well as hybrids between *Caiman crocodilus crocodilus* and *Caiman crocodilus yacare* (Hrbek, Vasconcelos, Rebelo, & Farias, 2008). *Caiman C. yacare* is often considered a separate species (Busack & Sima, 2001; Roberto et al., 2020), but almost all the literature to date has considered all individuals of *Caiman* in the Amazon basin to belong to the species *C. crocodilus*, and in the absence of consistent characteristics to distinguish the two postulated species in the wild or in the literature, this review treats all Amazonian crocodilians in the genus *Caiman* as *C. crocodilus*. *Melanosuchus niger* and *C. crocodilus* are the largest species and are usually more abundant in floodplain areas where the majority of human settlements are located (Da Silveira, 2002; Da Silveira, Magnusson, & Thorbjarnarson, 2008).

Until the 1970s, most studies on South American crocodilians were still focused on morphology, nomenclature (Medem, 1958) and zoogeography (Sill, 1968), and the first attempts to speculate on ecological relationships between caimans and their environment were drafted by Fittkau (1970). As occurred with many crocodilian species worldwide, Amazonian caimans were hunted without constraints for their valuable skins. As a result, many wild populations experienced severe reductions, some becoming scarce with others considered nearly extinct (Grigg & Kirshner, 2015). The ban on hunting and commercialization of caiman products resulted in a progressive recovery of caiman populations (Thorbjarnarson, 1999). This was also a consequence of the creation of multiple protected areas in the region (Freitas et al., 2020). Current threats to crocodilians in the Amazon basin are mainly associated with habitat loss, increased pollution, dam construction, expansion of agriculture and uncontrolled urban growth (Campos, 2015; Campos, 2019). Today, Amazonian caimans are being killed to serve as bait to capture the scavenger fish Calophysus macropterus. Although local people in Brazil do not consume this catfish, its commercialization provides a source of



FIGURE 1 The four crocodilian species encountered in the Amazon basin: (a) Black caiman (*Melanosuchus niger*), (b) Spectacled caiman (*Caiman crocodilus*), (c) Schneider's dwarf caiman (*Paleosuchus trigonatus*) and (d) Cuvier's dwarf caiman (*Paleosuchus palpebrosus*)

Worldwide studies on natural history, ecology and the conservation status of crocodilians have resulted in a significant recent increase in available literature, with 25% of the studies being carried out after 2007 (Grigg & Kirshner, 2015). This information has contributed to the elaboration of conservation action plans and is the basis for designing management initiatives. The general aim of this review is to summarize scientific knowledge on the conservation and management of the four Amazonian crocodilian species within the Amazon basin. Based on this general overview of current research and perspectives for the future, we address five questions: (1) How has scientific knowledge on crocodilians evolved in the Amazon basin? (2) How were caiman populations affected by commercial exploitation? (3) What ecological attributes may explain caiman resilience to hunting? (4) Is there evidence on the viability of management of wild caiman populations in the Amazon? and (5) What are the main gaps that should be addressed for future research and conservation efforts?

2 | METHODS

A literature review was undertaken using the online search engine Web of Science (www.webofscience.com) up to December 2019 to evaluate the scientific literature on the four caiman species occurring in the Amazon basin. The decision to use this database was based on its clarity when returning results to the query, its detailed citation analysis tools (Falagas, Pitsouni, Malietzis, & Pappas, 2008) and the opportunity to exclude unpublished literature (summary reports, congress presentations and dissertations) when summarizing information. Undoubtedly, the latter category contains important information, but without peer review it is difficult to evaluate the scientific strengths and flaws of the literature. Furthermore, this information is not always readily available.

The search was linked to the 75-year period between 1945 and 2019 using the scientific names of the four target caiman species, and returned general information on the overall scientific production related to these.

3 | RESULTS AND DISCUSSION

3.1 | Scientific productivity on Amazonian caimans

The search query returned a total of 439 publications on the four Amazon species, excluding studies on *Caiman crocodilus* sub-species (*C. crocodilus fuscus* and *C. c. chiapascus*), which do not occur in the Amazon basin (Roberto et al., 2020). Of these, 65% corresponded to *C. crocodilus*, 20% to *M. niger* (84), 8% to *P. palpebrosus* (36) and 7% to *P. trigonatus* (33). Over the entire 75-year period, search results indicated 51 years with at least one publication on one of the Amazon caiman species, with annual numbers varying from 1 to 34

publications (mean = 9.2 ± 8.4). The most frequently studied species was *C. crocodilus* with a maximum of 20 studies per year (a mean of 5.6 studies per year for the 50 years with at least one publication on this species). For the other three species the mean publication rate was 3.2 studies per year for *M. niger* (26 years), a mean of 2.0 studies per year for *P. palpebrosus* (18 years) and a mean of 1.5 studies per year for *P. trigonatus* (21 years). More than 70% of publications on *M. niger* and *P. palpebrosus* were produced after 2010. Only 15% of scientific studies with *Paleosuchus* species were published before 2000. These results suggest that general scientific knowledge gathered on Amazonian crocodilians is growing consistently.

Brazil encompasses the largest portion of the Amazon basin. In consequence, the great majority of studies discussed here have been carried out in this country, which is also the origin of most of the scientists involved or the location of funding agencies responsible for such studies.

3.2 | Commercial exploitation of Amazonian crocodilians: from steady declines to thriving populations

During the first decades of the past century, the Amazon basin experienced a very prosperous but short period of rubber extraction. When this period ended abruptly, river communities turned to selling hides of local animals to supply North American and European markets (Antunes et al., 2016). Unfortunately, there is limited information on the status of caiman populations before the commercial exploitation of skins in the twentieth century. One of the first relevant studies noted that caiman eggs sold at very low prices might have had an adverse effect on population numbers, although caimans were still very abundant in the region (Reese, 1923). Between 1940 and 1950, different caiman products were legally commercialized by the cosmetic and leather industries (Pereira, 1944) and this period corresponded to the peak of skin commerce in the Amazon (Antunes et al., 2016). The widespread commercial exploitation of caimans that extended until the mid-1970s affected caiman populations throughout the entire basin.

Unregulated commerce took place for decades and no attempts were made to control harvesting areas, target species, body size of harvested individuals or hunting seasons. None of the supplier countries developed their own manufacturing industries or promoted internal markets. During most of the 20th century, both *M. niger* and *C. crocodilus* were heavily hunted for their skins, which resulted in sharp declines of wild populations throughout their distribution. There is no evidence that the two species of *Paleosuchus* were ever hunted sufficiently to drastically affect their densities (Da Silveira, 2003). Thus, subsequent discussion here of caiman hunting will only address *M. niger* and *C. crocodilus*.

In 1975, in response to increasing concerns that the unregulated trade could result in biological extinction, international agencies and individual countries regulated global commerce as a means to protect wild crocodilians by ratifying the Convention on International Trade in

Endangered Species (CITES). Amazonian countries (Brazil, Ecuador and Peru in 1975; Venezuela in 1977; Bolivia in 1979 and Colombia in 1981) ratified the CITES convention and put into place new defensive (for fauna) and restrictive (for humans) legislation. Complementary to the creation of several protected areas, killing or trade of wild species was now considered a crime in most countries and transgressors risked facing high fines or even jail sentences. Although international commerce was officially restricted, however, demand for skins was still high (Inskipp & Wells, 1979), and legal loopholes allowed trade of stockpiled skins acquired prior to the new legislation. This facilitated continuing illegal hunting for at least 10 years after the international ban (Antunes et al., 2016; Rebêlo & Magnusson, 1983), until the marbecame economically unviable and eventually ket faded (Da Silveira, 2002).

The first scientific studies documenting aspects of crocodilian commercial exploitation in the past were undertaken only after the ban on international commerce of wild fauna. Based on the number of skins traded, the wild stocks exploited commercially must have been massive at the beginning of the activity. Medem (1981) estimated that at least 11 million skins were exported from Colombia and reported species depletion in several parts of South America (Medem, 1983). More than 7 million caiman skins were legally exported from Amazonas State (Brazil) within a 15-year period. On the other hand, after the ban, the number of skins exported from Peru decreased greatly between 1960 and 1970 (Smith, 1981).

In the early 1980s, M. niger was thought to be on the brink of extinction throughout its range, mainly because of overhunting to supply the leather industry (Best, 1984; Plotkin, Medem, Mittermeier, & Constable, 1983; Vanzolini & Gomes, 1979). It was suggested that this large-bodied species is less resistant to hunting than the sympatric C. crocodilus, mainly because females need a longer period of time to attain sexual maturity (Magnusson & Rebêlo, 1983). Almost 30 years later, another study based on the numbers of exported skins confirmed that M. niger is one of the species least resilient to commercial exploitation among the many Amazonian vertebrates that were historically commercialized (Antunes et al., 2016). Apparently, differences in habitat use among caiman species influence their resilience to hunting pressure (Magnusson, 1986). Caimans occurring in lakes and rivers, such as some populations of M. niger, were more easily available and heavily affected by hunting than species living in swamps or savannahs where accessibility to the entire population was more challenging. Some initiatives to restore M. niger populations started during the 1990s. In Bolivia, the first reintroduction of M. niger was carried out in 1990, when 25 captive sub-adults (six males and 19 females) were released (Pacheco, Aparicio, & Thorbjarnarson, 1991). Subsequently, it was reported that 8-10 individuals of this group remained residents at the release location and later reproduced (Pacheco, 1995).

More than two decades after the ban on commercial hunting for skins, caiman populations were thriving in most of the Amazon basin. However, a new threat was reported in the 1990s in Brazil. Caimans were killed for their meat while their undervalued skins were discarded in the river. This was a result of a huge regional market of drysalted meat with more than 8,000 individuals killed annually in just one area, which represented approximately 100 t yr^{-1} sold illegally to markets in Colombia and the Brazilian State of Para (Da Silveira & Thorbjarnarson, 1999). There were no detailed studies on caiman population status as a function of meat commerce in other countries, although illegal traffic in caiman meat is still frequently found in some Peruvian and Colombian markets (Kirkland et al., 2018; van Vliet et al., 2014) despite wildlife trade being illegal in these countries since 1973 (Smith, 1981).

In spite of the continuing trade in meat, it has been suggested that where habitat loss was not a significant factor the reduction of commercial hunting for skins allowed many crocodilian populations to recover (Thorbjarnarson, 1999). Populations hunted for meat had very high densities in some regions (especially Brazil) and it was suggested that this new form of use based on a source-sink system could be sustainable because it targeted mainly sub-adult males away from reproduction areas (Da Silveira & Thorbjarnarson, 1999). Furthermore, since accessibility to some isolated water bodies is greatly reduced during the dry season in the Amazon, harvesting success is strongly affected by water level and hunting effort (Mendonça, Marioni, Thorbjarnarson, Magnusson, & Da Silveira, 2016). Lack of access to refrigeration combined with the high volume and mass of harvested meat hampers poachers from exploiting isolated areas, which are normally preferred nesting sites for M. niger (Thorbjarnarson & Da Silveira, 2000: Villamarín et al., 2011). Consequently, if well planned, meat harvesting of wild Amazonian crocodilian populations has been suggested to be both biologically and economically sustainable as it can target individuals of specific size/sex and has the potential to become a source of income for river communities (Da Silveira & Thorbiarnarson, 1999: Thorbiarnarson, 1999).

3.3 | Genetics and ecology of caiman populations

Scientific studies over the last 40 years have increased our knowledge on caiman biology. After decades of over-exploitation, studies on the genetic structure of populations showed that heavy commerce of skins during the past century had no detectable effect on the genetic diversity of the two most hunted species in the Amazon (Farias et al., 2004; Glenn et al., 2002; Vasconcelos et al., 2006).

These species suffered a similar decline in population densities as the American alligator (*Alligator mississippiensis*), considered today the most recovered crocodilian species in the world. It has been hypothesized that higher genetic diversity may confer resilience to species (Green et al., 2014; Souza-Filho et al., 2018; Willi & Hoffmann, 2009) and studies based on cytochrome b data have shown that *M. niger* and *C. crocodilus* are genetically more diverse than A. *mississippiensis* (Farias et al., 2004; Glenn et al., 2002; Muniz et al., 2018; Vasconcelos et al., 2006). This indicates that genetic diversity may provide some resilience to population declines for both Amazonian species.

Another of the mechanisms that facilitates the resilience of crocodilian populations to overhunting might be found in their mating system. Multiple paternity increases effective population size by

1060 WILEY-

maintaining genetic variation, and therefore acting as an important mechanism to preserve genetic diversity in isolated local populations (Chesser & Baker, 1996; Muniz et al., 2011; Rafajlović et al., 2013). Polyandry might be beneficial to females as it increases the genetic variability of their offspring (Yasui, 1998). Multiple paternity has been detected in both species subjected to heavy hunting in the Amazon basin (Muniz et al., 2011; Oliveira, Farias, Marioni, Campos, & Hrbek, 2010; Oliveira, Marioni, Farias, & Hrbek, 2014).

The population resilience of Amazonian caimans can further be associated with ecological strategies contributing to avoidance of competitive exclusion that have allowed the co-existence of the four species. Differences in diet among caiman species have been investigated (Da Silveira & Magnusson, 1999; Magnusson, da Silva, & Lima, 1987) and there is evidence suggesting that some species consume more terrestrial prey than others while occupying the same water body (Villamarín, Jardine, Bunn, Marioni, & Magnusson, 2017). Furthermore, larger species generally do not influence the feeding behaviour of smaller ones (Marioni, Da Silveira, Magnusson, & Thorbjarnarson, 2008).

Nesting ecology might also be an important factor influencing the persistence of caiman populations. Although reproduction in crocodilians is usually characterized by very high mortality rates at early stages (Somaweera, Brien, & Shine, 2013), parental care and nest-site selection might increase survival rates and facilitate population growth. Mortality of crocodilian eggs and hatchlings is generally caused by nest predation and flooding, and this applies to Amazonian species (Thorbiarnarson, 1996; Villamarín & Suárez, 2007). A relatively wide range of caiman nest predators has been identified in the Amazon basin (Barão-Nóbrega et al., 2014; Campos & Mourão, 2014; Campos, Muniz, Desbiez, & Magnusson, 2016; Villamarín & Suárez, 2007). However, there is evidence suggesting that in some species, the presence of attending females may reduce egg predation (Barão-Nóbrega et al., 2014; Campos & Sanaiotti, 2006; Torralvo, Botero-Arias, & Magnusson, 2017) and increase hatchling survival (Campos, Sanaiotti, Muniz, Farias, & Magnusson, 2012). Some studies indicate that nest-site selection may contribute to decreased egg mortality. Melanosuchus niger females seem to prefer water bodies isolated from the early annual rise of water level and thus the probability of nest flooding is greatly reduced (Thorbjarnarson & Da Silveira, 2000; Villamarín et al., 2011). A different nesting strategy is shown by females of the sympatric C. crocodilus, which often build their nests far from permanent water bodies where floods take longer to arrive (Thorbjarnarson & Da Silveira, 2000; Villamarín et al., 2011).

Crocodilian females have low mortality rates and relatively long life spans (Somaweera et al., 2013) and larger females lay more eggs (Campos, Magnusson, Sanaiotti, & Coutinho, 2008; Campos, Mourão, Coutinho, & Magnusson, 2014; Campos, Sanaiotti, Marques, & Magnusson, 2015) despite important metabolic costs (Barão-Nóbrega et al., 2017). Under ideal natural conditions, individual females may have many successful reproductive events throughout their lifespan (Gienger et al., 2017). All these biological and ecological features provide insights to explain the capacity of crocodilians to maintain numerous populations and recover from over-exploitation once commercial hunting ended.

3.4 | Drifting from total protection to sustainablemanagement initiatives of wild caiman populations

The information on genetics and ecology of Amazon caimans gathered during the last three decades suggests the feasibility of sciencebased sustainable-management programmes. Worldwide, crocodilian management programmes have been carried out in more than 40 countries since the late 1980s (Thorbjarnarson, 1992). Management programmes based entirely on the sale of wildlife skins have shown their limitations related to the instability of luxury markets (Thorbjarnarson, 1999). Thus, possibilities to diversify into meat production should be examined, adding value particularly in local markets where harvesting is taking place, as is the case in Venezuela (Thorbjarnarson & Velasco, 1999). In Louisiana, for example, the sale of alligator meat and skins reached 25 million USD per year in the early 1990s (Joanen, McNease, Elsey, & Staton, 1997).

Many successful management programmes are based on 'ranching' systems where wild-caught eggs or hatchlings are raised in captivity and a fraction of them are released back to the wild (Campos, Mourão, Coutinho, Magnusson, & Soriano, 2015; Thorbjarnarson, 1999). These programmes have provided evidence of the importance of stakeholder involvement in South America, especially in Argentina (Gelabert, Rositano, & González, 2017). Ranching systems are potentially important for conservation, and often involve release schemes (Hutton & Webb, 2003; Jenkins, Jelden, Webb, & Manolis, 2004), although the effectiveness of these has not been rigorously evaluated. Nevertheless, high costs associated with infrastructure, animal feeding and correct slaughter conditions make ranching economically unfeasible in most Amazonian localities. Only two ranching initiatives are known to have taken place in the Amazon basin, one near Manaus in Brazil and the other in Ecuador. Both were financially unsuccessful and collapsed (Thorbjarnarson, 1994; Velasco, 2008; Verdade, 2004).

Captive breeding programmes (farming) have proved to be biologically viable and economically effective in many countries worldwide (Adan, 2000; Tosun, 2013); however, as with ranching programmes, the amount of investment needed would be a limiting factor in the Amazon context, and local inhabitants would be excluded from such initiatives (Thorbjarnarson, 1999). It is important to emphasize, though, that legal management programmes may not be exempt from drawbacks and some have even been used as a way to launder illegal commerce (Miranda Montero, Khan, & Wright, 2019: van Uhm & Nijman, 2020). Between 2005 and 2010, illegal trade in *C. crocodilus* skins may have doubled the amount legally declared by countries, indicating a high frequency of poaching despite increasingly restrictive laws (Balaguera-Reina & Densmore, 2014; Da Silveira, Gordo, Marcon, & Silva, 1998; Webb & Jenkins, 2016).

Given the large extent of the Amazon basin and the high densities of caiman populations in some localities, extensive harvesting of wild individuals seems more appropriate, especially because of its lower operational costs and high conservation value for the environment (Da Silveira, 2011; Thorbjarnarson, 1999; Verdade, 2004). It has been proposed that protecting nesting sites (Da Silveira & Thorbjarnarson, 1999; Thorbjarnarson & Da Silveira, 2000; Villamarín et al., 2011) and establishing an upper size limit (Campos et al., 2008) would contribute to maintaining viable populations on a long-term management basis, avoiding females, which have a smaller size. To this end, geographical information systems and remote sensing coupled with nest surveys are useful tools to identify nesting sites at large scales and may guide management activities (Banon, Arraut, et al., 2019; Banon, Banon, et al., 2019; Da Silveira & Thorbjarnarson, 1999; Villamarín et al., 2011).

In general, Brazilian legislation prohibits harvesting and commercialization of wildlife, but it allows trade in a restricted number of species under strictly developed management plans within sustainable-development protected areas (Brazilian Government, 2011). This has permitted the commercialization of fish species that are protected in other areas, such as *Arapaima* spp., which has encouraged their population recovery and improved the income of local people (Campos-Silva & Peres, 2016). Such successful experiences (Castello, Stewart, & Arantes, 2011; Castello, Viana, Watkins, Pinedo-Vasquez, & Luzadis, 2009) could become working models to achieve sustainability in wild-harvest caiman-management programmes.

An experimental wild harvest and subsequent commercial initiative were carried out in the Brazilian mid-Solimões River (Brazilian upper Amazon) between 2004 and 2008. This was made possible by the downlisting of M. niger populations to CITES Appendix II, with the endorsement of the IUCN/SSC Crocodile Specialist Group in June 2007 (CITES, 2007). The main scope of this initiative was to generate technical procedures for the production of meat and skins in central Amazonian floodplains (Botero-Arias, Marmontel, & de Queiroz, 2009). After more than 550 adult M. niger were killed in three different experimental harvesting events, the main lesson learned was that the management of crocodilians in the Brazilian Amazon was, at that time, still economically unsustainable. Activities were planned under a government agenda, using unjustified extrapolations of population parameters and monitoring that violate basic principles of wildlife management (Da Silveira, 2011). Another important wild harvesting initiative in the Brazilian Amazon has been carried out in Rondonia State since 2010. No formally published information is available, however, except for an institutional technical report, which makes it difficult to evaluate its real success (Mendonça & Coutinho, 2010).

One of the main reasons why wild harvesting of Amazonian caimans has not succeeded is that, unlike other countries with legal meat-harvesting programmes of crocodilian species, the federal Ministry of Agriculture in Brazil required caimans to be slaughtered under the same conditions as cattle, rather than like arapaima in Brazil or fish in general. This is especially problematic as most of the human population in the Amazon basin does not have access to electricity or even to clean water. Strong limitations on logistical conditions increase the time from capture to slaughter and most likely raise costs. These are all issues to be overcome to achieve sustainability in any management initiative with Amazonian caimans.

At the regional level, local legislation for wildlife management is different from country to country. Except for a community-based management programme in Bolivia (Aparicio & Rios, 2006), management activities of wild populations in the Amazon basin are still in their experimental phase and are being carried out only in Brazil (Table 1). Other management initiatives, such as captive-breeding farms in Colombia (Velasco, 2008; Webb, Brien, Manolis, & Medrano-Bitar, 2012) are focused on *C. c. fuscus*, a sub-species not occurring in the Amazon basin. In Venezuela, all successful harvesting activities carried out between 1990 and 2015 were conducted on *C. crocodilus* populations from the Orinoco river basin (Thorbjarnarson & Velasco, 1999; Velasco, 2008). Despite the wide extent of the Amazon basin and the occurrence of high-density caiman populations, we are not aware of any further management initiatives currently being undertaken.

3.5 | Perspectives for caiman conservation in the Amazon basin

At present, Amazonian caiman species exhibit stable populations throughout much of their distribution range (but see Ortiz, Dueñas, Villamarín, & Ron, 2020) and all four species are listed as Least Concern in IUCN Red Lists (Balaguera-Reina & Velasco, 2019; Campos, Magnusson, & Muniz, 2019; Magnusson, Campos, & Muniz, 2019; Ross, 2000). Populations of P. trigonatus and P. palpebrosus are generally not affected by commercial hunting, although they may be affected by dam construction, roads (Campos, Mourão, & Magnusson, 2017; Campos, Muniz, & Magnusson, 2012) and other local effects of human activities such as subsistence hunting, which is particularly heavy on these species in some places (Campos & Muniz, 2019; Da Silveira, 2003: Lugo, Lasso, Castro, & Morales-Betancourt, 2013). However, it is possible that some of the recently described evolutionary units (Muniz et al., 2018) have low effective population sizes, and in consequence lower resilience to long-term conservation threats. This indicates the importance of monitoring population genetic parameters of newly discovered lineages.

It is difficult to generalize about the Amazon basin, which covers an area similar to that of Australia or continental USA, but scientific research has revealed consistent trends. The first ecological information was generated for *M. niger* populations only at the end of the past century. In Brazil and Bolivia, some studies aimed at understanding how environmental variables (air/water temperature, water depth, percentage illumination by the moon and cloud cover) influence the number of caimans detected during night surveys (Da Silveira, Magnusson, & Campos, 1997; Pacheco, 1996). This information was useful for the standardization of long-term monitoring programmes and indicated that management decisions based on night surveys should be taken cautiously because the results obtained from one locality cannot be extrapolated to the entire Amazon basin (Da Silveira et al., 2008).

Sustainable harvesting of wildlife in the Amazon has been shown to promote conservation targets, especially those initiatives based on community co-management (Bodmer & Puertas, 2000;

¹⁰⁶² WILEY-

TABLE 1 Current conservation status of the four caiman species occurring in the Amazon basin according to IUCN Red List (https://www.iucnredlist.org) and CITES Appendix (https://www.cites.org), management actions, country, and main product issued from management action. LC = Least Concern, LR = Low Risk

| Species Name | Common Name | IUCN | CITES | Management type | Countries | Main product |
|-------------------------|-----------------------------------|------|--------------|--|-------------------------------------|---------------|
| Caiman crocodilus | Spectacled caiman | LC | II | Harvesting, ranching and captive breeding | Venezuela, Colombia ¹ | Skin and meat |
| Melanosuchus niger | Black caiman | LR | ² | Harvesting | Brazil | Skin and meat |
| Paleosuchus palpebrosus | Cuvier's smooth-fronted caiman | LC | II | - | | |
| Paleosuchus trigonatus | Schneider's smooth-fronted caiman | LC | П | - | | |

¹None of the management actions in these countries are carried out in the Amazon basin.

²Except for the populations of Brazil and Ecuador, included in Appendix II, subject to a zero annual export quota until an annual export quota is approved.

Campos-Silva & Peres, 2016; Castello et al., 2009; Mattos Vieira, von Muhlen, & Shepard, 2015) where all stakeholders are considered as part of the solution (Marioni, Botero-Arias, & Fonseca-Junior, 2013). After the ban on international commerce of crocodilian skins, total protection was the only reasonable choice of local governments to protect South American crocodilians. It was based on one basic rule: no hunting or commerce of any wildlife product anytime or anywhere; however, it is necessary to develop new ways to maintain healthy caiman populations while simultaneously alleviating poverty levels in local communities through innovative management programmes.

Systems of sustainable management have been discussed for the past 20 years but remain only a theoretical idea rarely applicable to the Amazonian reality. Fixed protocols and 'cookbook recipes' do not take into account the complexity of local environments and are often hard to implement in different regions or countries. We have developed some general guidelines, principally based on our experiences:

- i. Monitoring of caiman populations must be regularly carried out on a long-term basis by trained local people and under the guidance of independent scientists. The main aim will be to supervise population trends and eventually estimate annual quotas.
- ii. Strictly protected zones based on nest-site preferences within protected areas must be delineated with the involvement of local inhabitants, researchers and regional authorities. Reproduction areas have to be considered to build solid bases for a source-sink system (Brawn & Robinson, 1996; Da Silveira, 2011; Da Silveira & Thorbjarnarson, 1999) and a clear zonation is needed to avoid harvesting adult females.
- iii. Economic business plans must be elaborated to estimate the potential market of targeted products (meat, skins, etc.), as without a strong economic feasibility the management programme will not be viable. Consequently, community-based management projects must be designed to become economically independent over the mid-term. Financial dependence on regional politicians or private donors will most likely hinder management programmes in the long term. However, government funding as

initial economic support is very important to assess population status, to carry out early-stage population studies, to establish the first harvest quotas by surveying population trends, to train local people in the different phases of the project and to build the logistical infrastructure necessary to initiate the activity.

More than 10 years after the last attempt, a new harvesting programme for wild M. niger and C. crocodilus is being proposed for 2020 within a protected area in the central Brazilian Amazon. In this region. local communities have a broad experience in managing aquatic natural resources and it is also where some of the highest M. niger and C. crocodilus densities have been reported (Castello, Viana, & Pinedo-Vasquez, 2011). At least two distinct market plans will be proposed: meat, targeted towards regional and national consumers, and skins, which should be sold internationally. This new initiative was planned and strongly supported economically by local governments from the outset, which makes it difficult to replicate such experience in other localities without similar economic support, development time and expertise from everyone involved. There is great expectation that, contrary to previous endeavours, the information provided by the scientific community is considered in full and that political agendas do not determine the priorities. The past experience should be fundamental in implementing harvesting protocols already developed on a long-term and large-scale perspective in order to improve standard procedures for capture, slaughter and commercialization of caiman products.

For modern commercial exploitation of Amazonian crocodilians, an important challenge will be to develop markets for raw or manufactured products. Regional markets have not shown great demand for caiman meat, except in a few high-priced restaurants and supermarkets. Furthermore, although caiman skins have their place in the market, they are sold for lower prices (IUCN-SSC Crocodile Specialist Group, 2019; Louisiana Alligator Advisory Council, 2019), whereas alligator and crocodile skins are high-priced products considered 'classic' leathers owing to the scarcity of osteoderms (Fuchs & Schepp, 2006). Thus, the greatest challenge will be to maintain a sustainable production chain from local hunters to urban consumers.

Because management strategies need to be designed according to the characteristics of each region (Rodriguez-Cordero, Balaguera-Reina, & Densmore, 2019) and taking into consideration environmental conditions and land ownership, there is still a high demand for further scientific studies on caiman population trends across most of their range throughout the Amazon. Overall knowledge on the four Amazonian caiman species has increased significantly in Brazil during the last decade, but it is still incipient in many other countries, where few scientific studies are targeting these species. Although more research is necessary to understand the impacts of habitat loss and urban expansion, past experience has shown that science alone is not enough. Local communities and government agencies have to be involved to develop systems that are socially, economically and ecologically viable. Traditionally, when insufficient biological and social information is available, politicians tend to make uninformed decisions, yet the scientific community has gained a vast amount of knowledge that can provide valuable inputs to all the stages of the process. Effective actions towards sustainable management of wild caiman populations must then consider the best options to integrate economic return to local inhabitants, habitat preservation and species conservation.

ACKNOWLEDGEMENTS

The authors acknowledge all scientists, students and field assistants responsible for the research carried out on caimans in Amazon floodplains over the years. Without their effort, our knowledge of crocodilians would be much poorer. We also acknowledge all environmental enforcement authorities, financial agencies and communal councils responsible for issuing permits and providing financial and logistic support, which enabled the research continuing in different countries. There are no conflicts of interest for any authors of this manuscript. BM received a Ph.D. scholarship from the National Council for Scientific and Technological Development (CNPg -Brazil). WEM was supported by the CNPg and the Program for Biodiversity Research (PPBio-AmOc) and the National Institute for Amazonian Biodiversity (INCT-CENBAM). This study was financed in part by the Coordenação de Aperfeicoamento de Pessoal de Nível Superior - Brasil (CAPES) -Finance Code 001. We thank Leandro Castello for providing useful recommendations on preliminary versions and Dr Perran Ross (University of Florida) and Dr Matthew Shirley (Florida International University) for their critical suggestions on a previous version of the manuscript. We are immensely grateful to John Thorbjarnarson (in memoriam) for all his huge expertise, precious advice and dedication to crocodilian science, especially in relation to Amazonian caimans.

ORCID

Boris Marioni D https://orcid.org/0000-0002-5518-1895

José António L. Barão-Nóbrega D https://orcid.org/0000-0002-4814-2871

Robinson Botero-Arias D https://orcid.org/0000-0003-4032-2525 Fábio Muniz D https://orcid.org/0000-0001-8404-2686 Zilca Campos D https://orcid.org/0000-0003-0386-1618 Francisco Villamarín D https://orcid.org/0000-0001-9038-3516

REFERENCES

- Adan, R. I. Y. (2000). Crocodile farming: A multi-million dollar industry. SEAFDEC Asian Aquaculture, 22, 22–28.
- Antunes, A. P., Fewster, R. M., Venticinque, E. M., Peres, C. A., Levi, T., Rohe, F., & Shepard, G. H. (2016). Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Science Advances*, 2, e1600936. https://doi.org/10.1126/sciadv.1600936
- Aparicio, J., & Rios, J. (2006). Experiencias de manejo en el proceso de aprovechamiento sostenible del lagarto (*Caiman yacare*) en Bolivia (1995–2004). Revista Electrónica de Manejo de Fauna Silvestre en Latinoamérica, 1, 1–11.
- Balaguera-Reina, S. A., & Densmore, L. D. (2014). Legislation and conservation efforts concerning crocodiles in Colombia: A historical review. *Herpetological Review*, 45, 638–642.
- Balaguera-Reina, S. A., & Velasco, A. (2019). Caiman crocodilus. The IUCN Red List of Threatened Species, e.T46584A11062106.
- Banon, G. P. R., Arraut, E. M., Villamarín, F., Marioni, B., Moulatlet, G. M., Rennó, C. D., ... Novo, E. (2019). A review on crocodilian nesting habitats and their characterisation via remote sensing. *Amphibia-Reptilia*, 40, 1–21. https://doi.org/10.1163/15685381-20191159
- Banon, G. P. R., Banon, G. J. F., Villamarín, F., Arraut, E. M., Moulatlet, G. M., Rennó, C. D., ... Novo, E. M. L. D. M. (2019). Predicting suitable nesting sites for the Black caiman (*Melanosuchus niger* Spix 1825) in the Central Amazon basin. *Neotropical Biodiversity*, 5, 47–59. https://doi.org/10.1080/23766808.2019.1646066
- Barão-Nóbrega, J. A. L., Marioni, B., Botero-Arias, R., Nogueira, A. J. A., Lima, E. S., Magnusson, W. E., ... Marcon, J. L. (2017). The metabolic cost of nesting: Body condition and blood parameters of *Caiman crocodilus* and *Melanosuchus niger* in Central Amazonia. *Journal of Comparative* Physiology B, 188, 127–140. https://doi.org/10.1007/ s00360-017-1103-8
- Barão-Nóbrega, J. A. L., Marioni, B., Villamarín, F., Soares, A. M. V. M., Magnusson, W. E., & Da Silveira, R. (2014). Researcher disturbance has minimal impact on natural predation of caiman nests in Central Amazonia. *Journal of Herpetology*, 48, 338–342. https://doi.org/10. 1670/13-081
- Best, R. C. (1984). The aquatic mammals and reptiles of the Amazon. In H. Sioli (Ed.), *The Amazon. Monographiae Biologicae* (pp. 371–412). Dordrecht: Springer.
- Bodmer, R. E., & Puertas, P. E. (2000). Community-based comanagement of wildlife in the Peruvian Amazon. In J. G. Robinson & E. L. Bennett (Eds.), *Hunting for sustainability in tropical forests* (pp. 395–409). New York: Columbia University Press.
- Botero-Arias, R., Franco, D. L., & Marmontel, M. (2014). A mortalidade de jacarés e botos associada à pesca da piracatinga na região do Médio Solimões-Amazonas, Brasil. Tefé - Amazonas, Brasil: Instituto de Desenvolvimento Sustentável Mamirauá.
- Botero-Arias, R., Marmontel, M., & de Queiroz, H. L. (2009). Projeto de manejo experimental de jacarés no Estado do Amazonas: Abate de jacarés no setor Jarauá-Reserva de Desenvolvimento Sustentável Mamirauá, Dezembro de 2008. UAKARI, 5, 49–57. https://doi.org/10. 31420/uakari.v5i2.66
- Brawn, J. D., & Robinson, S. K. (1996). Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology*, 77, 3–12. https://doi.org/10.2307/2265649
- Brazilian Government. (2011). Lei n° 9.985, de 18 de julho de 2000; Decreto n° 4.340, de 22 de agosto de 2002; Decreto n° 5.746, de 5 de abril de 2006. Plano Estratégico Nacional de Áreas Protegidas: Decreto n° 5.758, de 13 de abril de 2006. Brasilia: Ministério do Meio Ambiente - Sistema Nacional de Unidades de Conservação da Natureza (SNUC).
- Brum, S. M., da Silva, V. M. F., Rossoni, F., & Castello, L. (2015). Use of dolphins and caimans as bait for *Calophysus macropterus* (Lichtenstein, 1819) (Siluriforme: Pimelodidae) in the Amazon. *Journal of Applied Ichthyology*, 31, 675–680. https://doi.org/10.1111/jai.12772

1064 WILEY-

- Busack, S. D., & Sima, P. (2001). Geographic variation in *Caiman crocodilus* and *Caiman yacare* (Crocodylia: Alligatoridae): Systematic and legal implications. *Herpetologica*, 57, 294–312.
- Campos, Z. (2015). Size of caimans killed by humans at a hydroelectric dam in the Madeira River, Brazilian Amazon. *Herpetozoa*, *28*, 101–104.
- Campos, Z. (2019). Disruption of reproductive behaviour of black caiman, Melanosuchus niger in the Santo Antônio hydroeletric dam, Madeira River, Brazilian Amazon. The Herpetological Bulletin, 148, 26–28. https://doi.org/10.33256/hb148.2628
- Campos, Z., Magnusson, W. E., & Muniz, F. L. (2019). Paleosuchus trigonatus. The IUCN Red List of Threatened Species, e.T46588A3010035.
- Campos, Z., Magnusson, W. E., Sanaiotti, T. M., & Coutinho, M. (2008). Reproductive trade-offs in *Caiman crocodilus crocodilus* and *Caiman crocodilus yacare*: Implications for size-related management quotas. *Herpetological Journal*, 18, 91–96.
- Campos, Z., & Mourão, G. (2014). Camera traps capture images of predators of *Caiman crocodilus yacare* eggs (Reptilia: Crocodylia) in Brazil's Pantanal wetlands. *Journal of Natural History*, 49, 977–982. https:// doi.org/10.1080/00222933.2014.930757
- Campos, Z., Mourão, G., Coutinho, M., & Magnusson, W. E. (2014). Growth of *Caiman crocodilus yacare* in the Brazilian Pantanal. *PLoS* ONE, 9, e89363. https://doi.org/10.1371/journal.pone.0089363
- Campos, Z., Mourão, G., Coutinho, M., Magnusson, W. E., & Soriano, B. M. A. (2015). Spatial and temporal variation in reproduction of a generalist crocodilian, *Caiman crocodilus yacare*, in a seasonally flooded wetland. *PLoS ONE*, 10, e0129368.
- Campos, Z., Mourão, G., & Magnusson, W. E. (2017). The effect of dam construction on the movement of dwarf caimans, *Paleosuchus trigonatus* and *Paleosuchus palpebrosus*, in Brazilian Amazonia. *PLoS ONE*, 12, e0188508. https://doi.org/10.1371/journal.pone. 0129368
- Campos, Z., Muniz, F., & Magnusson, W. E. (2012). Dead Paleosuchus on roads in Brazil. IUCN/SSC Crocodile Specialist Group Newsletter, 31, 12–12.
- Campos, Z., & Muniz, F. L. (2019). Multiple uses of Cuvier's dwarf caimans, Paleosuchus palpebrosus, in the semi-arid region of northeastern Brazil. IUCN/SSC Crocodile Specialist Group Newsletter, 38, 5–8.
- Campos, Z., Muniz, F. L., Desbiez, A. L. J., & Magnusson, W. E. (2016). Predation on eggs of Schneider's dwarf caiman, *Paleosuchus trigonatus* (Schneider, 1807), by armadillos and other predators. *Journal of Natural History*, 50, 1543–1548. https://doi.org/10.1080/00222933.2016. 1155782
- Campos, Z., & Sanaiotti, T. (2006). Paleosuchus palpebrosus. Nesting. Herpetological Review, 37, 81–81.
- Campos, Z., Sanaiotti, T., Marques, V., & Magnusson, W. E. (2015). Geographic variation in clutch size and reproductive season of the dwarf caiman, *Paleosuchus palpebrosus*, in Brazil. *Journal of Herpetology*, 49, 95–98. https://doi.org/10.1670/11-224
- Campos, Z., Sanaiotti, T. M., Muniz, F. L., Farias, I., & Magnusson, W. E. (2012). Parental care in the dwarf caiman, *Paleosuchus palpebrosus* Cuvier, 1807 (Reptilia: Crocodilia: Alligatoridae). *Journal of Natural History*, 46, 2979–2984. https://doi.org/10.1080/00222933.2012. 724723
- Campos-Silva, J. V., & Peres, C. A. (2016). Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Scientific Reports*, 6, 34745. https://doi.org/10.1038/srep34745
- Castello, L., Stewart, D. J., & Arantes, C. C. (2011). Modeling population dynamics and conservation of arapaima in the Amazon. *Reviews in Fish Biology and Fisheries*, 21, 623–640. https://doi.org/10.1007/s11160-010-9197-z
- Castello, L., Viana, J. P., & Pinedo-Vasquez, M. (2011). Participatory conservation and local knowledge in the Amazon várzea: The pirarucu management scheme in Mamirauá. In M. Pinedo-Vasquez, M. Ruffino,

C. Padoch, & E. Brondízio (Eds.), *The Amazon Várzea* (pp. 259–273). Dordrecht: Springer.

- Castello, L., Viana, J. P., Watkins, G., Pinedo-Vasquez, M., & Luzadis, V. A. (2009). Lessons from integrating fishers of arapaima in small-scale fisheries management at the Mamirauá Reserve, Amazon. *Environmental Management*, 43, 197–209. https://doi.org/10.1007/s00267-008-9220-5
- Chesser, R. K., & Baker, R. J. (1996). Effective sizes and dynamics of uniparentally and diparentally inherited genes. *Genetics*, 144, 1225–1235.
- CITES. (2007). Convention on International Trade in Endangered Species of Wild Fauna and Flora. CoP14 Prop. 13. Considerations of Proposal for Amendment of Appendices I and II. *Conference of the Parties. The Hague* (Netherlands), 3-15 June 2007. Retrieved from http://www. cites.org/eng/cop/14/prop/E14-P13.pdf
- Da Silveira, R. (2002). Conservação e manejo do jacaré-açu (Melanosuchus niger) na Amazônia Brasileira. La Conservación Y el Manejo de Caimanes Y Cocodrilos de América Latina, 2, 61–78.
- Da Silveira, R. (2003). Avaliação preliminar da distribuição, abundância e da caça de jacarés no baixo Rio Purus. In C. Pereira de Deus, R. Da Silveira, & L. H. Rapp Py-Daniel (Eds.), Piagaçu-Purus: Bases científicas para a criação de uma Reserva de Desenvolvimento Sustentável (pp. 61–64). Manaus, Brazil: Instituto de Desenvolvimento Sustentável Mamirauá.
- Da Silveira, R. (2011). Management of wildlife in the floodplain: A critical look at threats, bottlenecks, and the future in Amazonia. In M. Pinedo-Vasquez, M. Ruffino, C. Padoch, & E. Brondízio (Eds.), *The Amazon Várzea* (pp. 137–144). Dordrecht: Springer.
- Da Silveira, R., Gordo, M., Marcon, J. L., & Silva, J. R. (1998). Skins from wild spectacled caiman confiscated in the Amazonia. *IUCN/SSC Crocodile Specialist Group Newsletter*, 17, 7–8.
- Da Silveira, R., & Magnusson, W. E. (1999). Diets of spectacled and black caiman in the Anavilhanas Archipelago, Central Amazonia, Brazil. *Journal of Herpetology*, 33, 181–192. https://doi.org/10.2307/ 1565713
- Da Silveira, R., Magnusson, W. E., & Campos, Z. (1997). Monitoring the distribution, abundance and breeding areas of *Caiman crocodilus crocodilus* and *Melanosuchus niger* in the Anavilhanas Archipelago, Central Amazonia, Brazil. *Journal of Herpetology*, 31, 514–520. https://doi. org/10.2307/1565603
- Da Silveira, R., Magnusson, W. E., & Thorbjarnarson, J. B. (2008). Factors affecting the number of caimans seen during spotlight surveys in the Mamirauá Reserve, Brazilian Amazonia. *Copeia*, 2008, 425–430. https://doi.org/10.1643/ce-06-035
- Da Silveira, R., & Thorbjarnarson, J. B. (1999). Conservation implications of commercial hunting of black and spectacled caiman in the Mamirauá Sustainable Development Reserve, Brazil. *Biological Conservation*, 88, 103–109. https://doi.org/10.1016/s0006-3207(98)00084-6
- Da Silveira, R., & Viana, J. P. (2003). Amazonian crocodilians: A keystone species for ecology and management... Or simply bait? IUCN/SSC Crocodile Specialist Group Newsletter, 22, 16–17.
- Falagas, M. E., Pitsouni, E. I., Malietzis, G. A., & Pappas, G. (2008). Comparison of PubMed, Scopus, Web of Science, and Google Scholar: Strengths and weaknesses. *The FASEB Journal*, 22, 338–342. https:// doi.org/10.1096/fj.07-9492lsf
- FAO. (2016). Amazon Basin. Food and Agriculture Organization of the United States (FAO). Retrieved from http://www.fao.org/nr/water/aquastat/ basins/amazon/index.stm
- Farias, I. P., Da Silveira, R., de Thoisy, B., Monjeló, L. A., Thorbjarnarson, J., & Hrbek, T. (2004). Genetic diversity and population structure of Amazonian crocodilians. *Animal Conservation*, 7, 265–272. https://doi.org/ 10.1017/s136794300400143x
- Fittkau, E. J. (1970). Role of caimans in the nutrient regime of mouth-lakes of Amazon affluents (an hypothesis). *Biotropica*, 2, 138–142. https:// doi.org/10.2307/2989771

- Freitas, C. T., Lopes, P. F. M., Campos-Silva, J. V., Noble, M. M., Dyball, R., & Peres, C. A. (2020). Co-management of culturally important species: A tool to promote biodiversity conservation and human well-being. *People and Nature*, 2, 61–81. https://doi.org/10.1002/pan3.10064
- Fuchs, K., & Schepp, U. (2006). The crocodile skin: Important characteristics in identifying crocodilian species. Frankfurt: Edition Chimaira.
- Gelabert, C., Rositano, F., & González, O. (2017). Sustainable use of caiman in Argentina: An analysis from the perspective of the stakeholders involved. *Biological Conservation*, 212, 357–365. https://doi.org/10. 1016/j.biocon.2017.06.012
- Gienger, C. M., Brien, M. L., Tracy, C. R., Manolis, S. C., Webb, G. J. W., Seymour, R. S., & Christian, K. A. (2017). Ontogenetic comparisons of standard metabolism in three species of crocodilians. *PLoS ONE*, 12, e0171082. https://doi.org/10.1371/journal.pone.0171082
- Glenn, T. C., Staton, J. L., Vu, A. T., Davis, L. M., Bremer, J. R. A., Rhodes, W. E., ... Sawyer, R. H. (2002). Low mitochondrial DNA variation among American alligators and a novel non-coding region in crocodilians. *Journal of Experimental Zoology*, 294, 312–324. https://doi. org/10.1002/jez.10206
- Green, R. E., Braun, E. L., Armstrong, J., Earl, D., Nguyen, N., Hickey, G., ... Castoe, T. A. (2014). Three crocodilian genomes reveal ancestral patterns of evolution among archosaurs. *Science*, 346, 1254449. https:// doi.org/10.1126/science.1254449
- Grigg, G., & Kirshner, D. (2015). Biology and evolution of crocodylians. Australia: CSIRO Publishing.
- Haddad, V., & Fonseca, W. C. (2011). A fatal attack on a child by a black caiman (Melanosuchus niger). Wilderness & Environmental Medicine, 22, 62–64. https://doi.org/10.1016/j.wem.2010.11.010
- Hrbek, T., Vasconcelos, W. R., Rebelo, G., & Farias, I. P. (2008). Phylogenetic relationships of South American Alligatorids and the Caiman of Madeira River. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, 309A, 588–599. https://doi.org/10.1002/ jez.430
- Hutton, J. M., & Webb, G. (2003). Crocodiles: Legal trade snaps back. In S. Oldfield (Ed.), The trade in wildlife: Regulation for conservation (pp. 108–114). London: Earthscan Publications Ltd.
- Inskipp, T., & Wells, S. (1979). *The international wildlife trade*. London: International Institute for Environment and Developent and the Fauna Preservation Society.
- IUCN-SSC Crocodile Specialist Group. (2019). Farming and the Crocodile Industry [Online]. Retrieved from http://www.iucncsg.org/pages/ Farming-and-the-Crocodile-Industry.html
- Jenkins, R. W., Jelden, D., Webb, G. J., & Manolis, S. C. (2004). Review of crocodile ranching programmes. Conducted for CITES by the Crocodile Specialist Group of IUCN/SSC.
- Joanen, T., McNease, L., Elsey, R., & Staton, M. (1997). The commercial consumptive use of the American alligator (*Alligator mississippiensis*) in Louisiana: Its effects on conservation. In C. H. Freese (Ed.), *Harvesting wild species* (pp. 465–506). Baltimore, Maryland: The John Hopkins University Press.
- Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J., & Parolin, P. (2010). Amazonian floodplain forests: Ecophysiology, Biodiversity and Sustainable Management. Heidelberg, Germany: Ecological Studies, Springer.
- Kirkland, M., Eisenberg, C., Bicerra, A., Bodmer, R. E., Mayor, P., & Axmacher, J. C. (2018). Sustainable wildlife extraction and the impacts of socio-economic change among the Kukama-Kukamilla people of the Pacaya-Samiria National Reserve, Peru. *Oryx*, *52*, 260–269. https:// doi.org/10.1017/s0030605317001922
- Louisiana Alligator Advisory Council. (2019). *Distinguishing features of crocodilian leathers* [Online]. Retrieved from https://www.louisianaalligators.com/crocodilian-leather-features.html
- Lugo, M., Lasso, C. A., Castro, A., & Morales-Betancourt, M. A. (2013). Paleosuchus trigonatus (Schneider 1801). In M. A. Morales-Betancourt,

C. A. Lasso, J. De La Ossa, & A. Fajardo-Patiño (Eds.), Biología y Conservación de los Crocodylia de Colombia - Serie Recursos Hidrobiolgógicos y Pesqueros Continentales de Colombia (pp. 201–210). Bogotá, D. C., Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH).

- Magnusson, W. E. (1986). The peculiarities of crocodilian population dynamics and their possible importance for management strategies. In 7th Working Meeting of the IUCN/SSC Crocodile Specialist Group. Quito, Ecuador: IUCN-The World Conservation Union, Gland, Switzerland.
- Magnusson, W. E., Campos, Z., & Muniz, F. L. (2019). *Paleosuchus palpebrosus*. The IUCN Red List of Threatened Species, e. T46587A3009946.
- Magnusson, W. E., da Silva, E. V., & Lima, A. P. (1987). Diets of Amazonian crocodilians. Journal of Herpetology, 21, 85–95. https://doi.org/10. 2307/1564468
- Magnusson, W. E., & Rebêlo, G. H. (1983). Brazilian crocodiles: Problems of conservation in a multi-species system. *Zimbabwe Science News*, 17, 56–57.
- Marioni, B., Botero-Arias, R., & Fonseca-Junior, S. F. (2013). Local community involvement as a basis for sustainable crocodilian management in protected areas of Central Amazonia: Problem or solution? *Tropical Conservation Science*, 6, 484–492. https://doi.org/10.1177/ 194008291300600403
- Marioni, B., Da Silveira, R., Magnusson, W. E., & Thorbjarnarson, J. (2008). Feeding behavior of two sympatric caiman species, *Melanosuchus niger* and *Caiman crocodilus*, in the Brazilian Amazon. *Journal of Herpetology*, 42, 768–773. https://doi.org/10.1670/07-306r1.1
- Mattos Vieira, M. A., von Muhlen, E. M., & Shepard, G. H. (2015). Participatory monitoring and management of subsistence hunting in the Piagaçu-Purus Reserve, Brazil. *Conservation and Society*, *15*, 254–264. https://doi.org/10.4103/0972-4923.170399
- Medem, F. (1958). The crocodilian genus Paleosuchus. Fieldiana: Zoology, 39, 227-247.
- Medem, F. (1981). Los Crocodylia de sur América. Bogotá, Colombia: Ministerio de Educación Nacional, Fondo Colombiano de Investigaciones Científicas y Proyectos Especiales.
- Medem, F. (1983). Los Crocodylia de sur América. Bogotá, Colombia: Colciencias.
- Mendonça, S., & Coutinho, M. (2010). Relatório Técnico sobre as atividades desenvolvidas na Reserva Extrativista do Lago do Cuniã e Estação Ecológica de Cuniã, Porto Velho, Rondônia. Brazil: Centro Nacional de Pesquisa e Conservação de Répteis e Anfíbios/RAN/ICMBio.
- Mendonça, W. C. D. S., Marioni, B., Thorbjarnarson, J. B., Magnusson, W. E., & Da Silveira, R. (2016). Caiman hunting in Central Amazonia, Brazil. *The Journal of Wildlife Management*, 80, 1497–1502. https://doi.org/10.1002/jwmg.21127
- Miranda Montero, J. J., Khan, M. N., & Wright, E. M. (2019). Illegal logging, fishing, and wildlife trade: The costs and how to combat it. Washington, D.C.: World Bank Group.
- Muniz, F. L., Campos, Z., Rangel, S. M. H., Martínez, J. G., Souza, B. C., De Thoisy, B., ... Farias, I. P. (2018). Delimitation of evolutionary units in Cuvier's dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807): Insights from conservation of a broadly distributed species. *Conservation Genetics*, 19, 599–610. https://doi.org/10.1007/ s10592-017-1035-6
- Muniz, F. L., Da Silveira, R., Campos, Z., Magnusson, W. E., Hrbek, T., & Farias, I. P. (2011). Multiple paternity in the black caiman (*Melanosuchus niger*) population in the Anavilhanas National Park, Brazilian Amazonia. *Amphibia-Reptilia*, 32, 428–434. https://doi.org/ 10.1163/017353711x587741
- Oliveira, D. P., Farias, I. P., Marioni, B., Campos, Z., & Hrbek, T. (2010). Microsatellite markers for mating system and population analyses of the spectacled caiman *Caiman crocodilus* (Linnaeus 1758). *Conservation*

1066 WILEY-

Genetics Resources, 2, 181-184. https://doi.org/10.1007/s12686-010-9221-6

- Oliveira, D. P., Marioni, B., Farias, I., & Hrbek, T. (2014). Genetic evidence for polygamy as a mating strategy in *Caiman crocodilus*. *Journal of Heredity*, 105, 485–492. https://doi.org/10.1093/jhered/esu020
- Ortiz, D. A., Dueñas, J. F., Villamarín, F., & Ron, S. R. (2020). Long-term monitoring reveals population decline of spectacled caimans (*Caiman crocodilus*) at a black-water lake in Ecuadorian Amazon. Journal of Herpetology, 54, 31–38. https://doi.org/10.1670/17-185
- Pacheco, L. F. (1995). Black caiman breeding in Normandia lagoon. IUCN/SSC Crocodile Specialist Group Newsletter, 14, 12–17.
- Pacheco, L. F. (1996). Effects of environmental variables on black caiman counts in Bolivia. Wildlife Society Bulletin, 24, 44–49.
- Pacheco, L. F., Aparicio, J., & Thorbjarnarson, J. B. (1991). The first reintroduction of black caiman, *Melanosuchus niger*, into the wild. *Herpetological Review*, 22, 90–91.
- Pereira, N. (1944). A utilização da carne do jacaré na Amazônia. Boletim Geográfico Rio de Janeiro, 2, 150–152.
- Plotkin, M. J., Medem, F., Mittermeier, R. A., & Constable, I. D. (1983). Distribution and conservation of the black caiman (*Melanosuchus niger*). Advances in Herpetology and Evolutionary Biology, 695–705.
- Pooley, S. (2018). Croc digest: A bibliography of human-crocodile conflict research and reports (2nd ed.). London: Simon Pooley.
- Rafajlović, M., Eriksson, A., Rimark, A., Hintz-Saltin, S., Charrier, G., Panova, M., ... Mehlig, B. (2013). The effect of multiple paternity on genetic diversity of small populations during and after colonisation. *PLoS ONE*, 8, e75587. https://doi.org/10.1371/journal.pone.0075587
- Rebêlo, G. H., & Magnusson, W. E. (1983). An analysis of the effect of hunting on *Caiman crocodilus* and *Melanosuchus niger* based on the sizes of confiscated skins. *Biological Conservation*, 26, 95–104. https:// doi.org/10.1016/0006-3207(83)90060-5
- Reese, A. M. (1923). The habitat of the Crocodilia of British Guiana. Ecology, 4, 141-146. https://doi.org/10.2307/1929488
- Roberto, I. J., Bittencourt, P. S., Muniz, F. L., Hernández-Rangel, S. M., Nóbrega, Y. C., Ávila, R. W., ... Hrbek, T. (2020). Unexpected but unsurprising lineage diversity within the most widespread Neotropical crocodilian genus *Caiman* (Crocodylia, Alligatoridae). *Systematics and Biodiversity*, 18, 377–395. https://doi.org/10.1080/14772000.2020. 1769222
- Rodriguez-Cordero, A. L., Balaguera-Reina, S. A., & Densmore, L. D. (2019). Regional conservation priorities for crocodylians in Bolivia. *Journal for Nature Conservation*, 52, 125753. https://doi.org/10.1016/ j.jnc.2019.125753
- Ross, J. P. (2000). *Melanosuchus niger*. The IUCN Red List of Threatened Species, e.T13053A3407604.
- Sill, W. D. (1968). The zoogeography of the Crocodilia. *Copeia*, 1968, 76–88. https://doi.org/10.2307/1441553
- Smith, N. J. H. (1981). Caimans, capybaras, otters, manatees, and man in Amazônia. Biological Conservation, 19, 177–187. https://doi.org/10. 1016/0006-3207(81)90033-1
- Somaweera, R., Brien, M., & Shine, R. (2013). The role of predation in shaping crocodilian natural history. *Herpetological Monographs*, 27, 23–51. https://doi.org/10.1655/herpmonographs-d-11-00001
- Souza-Filho, J. P., Souza, R. G., Hsiou, A. S., Riff, D., Guilherme, E., Negri, F. R., & Cidade, G. M. (2018). A new caimanine (Crocodylia, Alligatoroidea) species from the Solimões Formation of Brazil and the phylogeny of Caimaninae. *Journal of Vertebrate Paleontology*, 38, e1528450. https://doi.org/10.1080/02724634.2018.1528450
- Thorbjarnarson, J. (1994). Comments on the Ecuadorian proposal for the transfer of populations of *Melanosuchus niger* to appendix II under the ranching criteria. *Prepared for the IUCN/SSC CSG Steering Committee Meeting*.
- Thorbjarnarson, J., & Da Silveira, R. (2000). Secrets of the flooded forest. *Natural History*, 109, 70–79.

- Thorbjarnarson, J., & Velasco, A. (1999). Economic incentives for management of Venezuelan caiman. *Conservation Biology*, 13, 397–406. https://doi.org/10.1046/j.1523-1739.1999.013002397.x
- Thorbjarnarson, J. B. (1992). Crocodiles: An action plan for their conservation. Gland, Switzerland: IUCN - The World Conservation Union.
- Thorbjarnarson, J. B. (1996). Reproductive characteristics of the order Crocodylia. *Herpetologica*, 52, 8–24.
- Thorbjarnarson, J. B. (1999). Crocodile tears and skins: International trade, economic constraints, and limits to the sustainable use of crocodilians. *Conservation Biology*, 13, 465–470. https://doi.org/10.1046/j.1523-1739.1999.00011.x
- Torralvo, K., Botero-Arias, R., & Magnusson, W. E. (2017). Temporal variation in black-caiman-nest predation in varzea of central Brazilian amazonia. PLoS ONE, 12, e0183476.
- Tosun, D. D. (2013). Crocodile farming and its present state in global aquaculture. *Journal of FisheriesSciences.com*, 7, 43–57. https://doi.org/10. 1371/journal.pone.0183476
- van Uhm, D. P., & Nijman, R. C. C. (2020). The convergence of environmental crime with other serious crimes: Subtypes within the environmental crime continuum. *European Journal of Criminology*, 0, 1477370820904585. https://doi.org/10.1177/1477370820904585
- van Vliet, N., Mesa, M. P. Q., Cruz-Antia, D., de Aquino, L. J. N., Moreno, J., & Nasi, R. (2014). The uncovered volumes of bushmeat commercialized in the Amazonian trifrontier between Colombia, Peru & Brazil. *Ethnobiology and Conservation*, *3*, 7. https://doi.org/10. 15451/ec2014-11-3.7-1-11
- Vanzolini, P. E., & Gomes, N. (1979). Notes on the ecology and growth of Amazonian caimans (Crocodylia, Alligatoridae). *Papéis Avulsos de Zoologia*, 32, 205–216.
- Vasconcelos, W. R., Hrbek, T., Da Silveira, R., de Thoisy, B., Marioni, B., & Farias, I. P. (2006). Population genetic analysis of *Caiman crocodilus* (Linnaeus, 1758) from South America. *Genetics and Molecular Biology*, 29, 220–230. https://doi.org/10.1590/s1415-47572006000200006
- Velasco, A. (2008). Crocodile management, conservation and sustainable use in Latin America. In Crocodiles. Proceedings of the 19th Working Meeting of the Crocodile Specialist Group (pp. 72–88). Gland, Switzerland and Cambridge UK: IUCN - The World Conservation Union.
- Venticinque, E., Forsberg, B., Barthem, R., Petry, P., Hess, L., Mercado, A., ... Goulding, M. (2016). An explicit GIS-based river basin framework for aquatic ecosystem conservation in the Amazon. *Earth System Science Data*, 8, 651–661. https://doi.org/10.5194/essd-8-651-2016
- Verdade, L. M. (2004). A exploração da fauna silvestre no Brasil: Jacarés, sistemas e recursos humanos. *Biota Neotropica*, 4, 1–12. https://doi. org/10.1590/s1676-06032004000200002
- Villamarín, F., Jardine, T. D., Bunn, S. E., Marioni, B., & Magnusson, W. E. (2017). Opportunistic top predators partition food resources in a tropical freshwater ecosystem. *Freshwater Biology*, 62, 1389–1400. https:// doi.org/10.1111/fwb.12952
- Villamarín, F., Marioni, B., Thorbjarnarson, J. B., Nelson, B. W., Botero-Arias, R., & Magnusson, W. E. (2011). Conservation and management implications of nest-site selection of the sympatric crocodilians *Melanosuchus niger* and *Caiman crocodilus* in Central Amazonia, Brazil. *Biological Conservation*, 144, 913–919. https://doi.org/10.1016/j. biocon.2010.12.012
- Villamarín, F., & Suárez, E. (2007). Nesting of the black caiman (Melanosuchus niger) in Northeastern Ecuador. Journal of Herpetology, 41, 164–168. https://doi.org/10.1670/0022-1511(2007)41[164: notbcm]2.0.co;2
- Webb, G. J., Brien, M., Manolis, C., & Medrano-Bitar, S. (2012). Predicting total lengths of spectacled caiman (*Caiman crocodilus*) from skin measurements: A tool for managing the skin trade. *Herpetological Conservation and Biology*, 7, 16–26.
- Webb, G. J. W., & Jenkins, R. W. G. (2016). Concerns about the production and trade in brown caimans (*Caiman crocodilus fuscus*) from Colombia.

Information document SC66 Inf. 20 submitted by European Union at 66th meeting of the CITES Standing Committee, 11, 19.

- Willi, Y., & Hoffmann, A. A. (2009). Demographic factors and genetic variation influence population persistence under environmental change. *Journal of Evolutionary Biology*, 22, 124–133. https://doi.org/10.1111/ j.1420-9101.2008.01631.x
- Yasui, Y. (1998). The genetic benefits' of female multiple mating reconsidered. *Trends in Ecology & Evolution*, 13, 246–250. https://doi. org/10.1016/s0169-5347(98)01383-4

How to cite this article: Marioni B, Barão-Nóbrega JAL, Botero-Arias R, et al. Science and conservation of Amazonian crocodilians: a historical review. *Aquatic Conserv: Mar Freshw Ecosyst.* 2021;31:1056-1067. <u>https://doi.org/10.1002/</u> aqc.3541