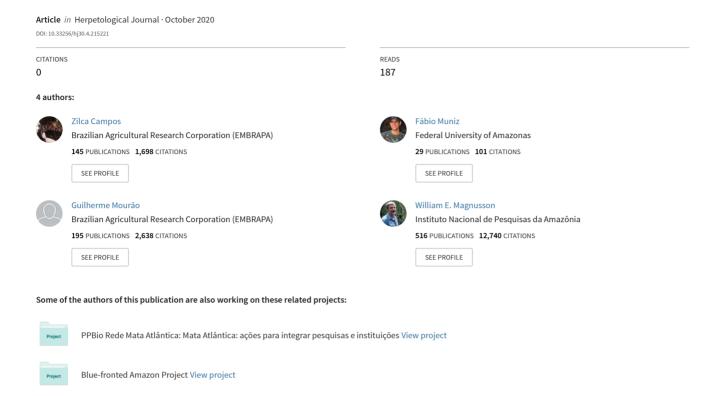
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Responses of crocodilians to construction of a hydroelectric dam on the Madeira River in the Brazilian Amazon

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The spillways of the Santo Antônio Hydro-electric Dam on the Madeira River in Brazilian Amazonia were closed in November 2011, inundating more than 100 km of river and reducing the annual fluctuations in water level. We surveyed the crocodilians in the affected area for two years before and for eight years after dam filling in order to evaluate the effects of the dam on the size structure of the population, the distribution of each species, and the detectability of individuals to interpret changes in apparent density. Our methodology was probably not appropriate to evaluate trends in population characteristics of *Paleosuchus palpebrosus* or *P. trigonatus*, but there was little evidence of an effect of the dam on the numbers of *Caiman crocodilus* and *Melanosuchus niger* in the area, and the distributions of all caiman species along the river changed only slightly after the dam was constructed. However, the proportions of small *C. crocodilus* and large *M. niger* detected in surveys increased eight years after dam filling. Despite having detectable effects on some population characteristics, the dam does not appear to represent a threat to the persistence of the species in the area if deforestation along the banks of the reservoir can be avoided.

Keywords: environmental impact, dam, crocodilians, Amazonia, conservation

INTRODUCTION

Large dams modify the aquatic environment (Agostinho Let al., 2005; Zeilhofer & Moura, 2009; Finer & Jenkins, 2012) and can have negative effects on the aquatic fauna (Mérona & Tejeriba, 2005; Sá-Oliveira et al., 2015), including crocodilians (Mourão & Campos, 1995; Botha et al., 2011). The Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis (IBAMA) requires studies of crocodilians as part of the monitoring activities in newly formed reservoirs in Brazil. Nevertheless, the changed abiotic conditions also affect the detectability of crocodilians, so simple counts may give misleading indications of species responses.

Surveys of crocodilians are strongly affected by water level (Da Silveira et al., 2008) and the principle effect of dams is to increase water levels, even in so-called runof-the-river dams, which do not form the large lentic reservoirs of conventional dams (Benchimol & Peres, 2015). Increased water levels and reduction in seasonal fluctuations in water level are likely to strongly impact crocodilian population dynamics due to changes in the availability of nesting areas (Mourão & Campos, 1995; Campos, 2019), foraging areas and facilitation of access by hunters (Campos, 2015). In some areas, the dams also affect pollution levels (Botha et al., 2011).

We studied the effects of the Santo Antônio

Hydroelectric dam on the Rio Madeira in south-eastern Amazonia, Brazil, on four species of crocodilians (Caiman crocodilus, Melanosuchus niger, Paleosuchus palpebrosus and P. trigonatus). This and other dams in the Brazilian Amazon have been strongly criticised for presumed negative environmental impacts (Lees et al., 2016). We surveyed the crocodilians in the affected area for two years before and for eight years after dam filling, in order to evaluate the impacts of the dam on the size structure of the population, the distribution of each species and the detectability of individuals to interpret changes in apparent density.

MATERIALS AND METHODS

Ethics Statement

The research project was approved by the Brazilian Environment Agency (IBAMA permit No. 017/02) and by the Chico Mendes Institute for Biodiversity Conservation (ICMBio permanent license No. 13048-1) for capture and marking caimans (Normative regulation N°.154/2007). All procedures followed ethical practices for animals approved by the Committee on the Ethics of Animal Research of the Brazilian Agricultural Research Organization (Embrapa No 009/2016). No biological material, such as blood or tissue, was collected in this study. These species are classified by the International

Union for Conservation of Nature (IUCN) as Lower Risk, least concern for conservation.

Nocturnal Surveys

Surveys were carried out at night, generally between 19:30h and 23:30h, in the Madeira River and its main tributaries using a 7 m aluminum canoe with 15 hp outboard motor. Each survey period lasted 7 nights. Surveys extended from shortly above the Santo Antônio dam wall to just below the wall of the Jirau Dam (built after the Santo Antônio dam) (Fig. 1). Three surveys were undertaken before dam filling in July-August 2010 and 2011 (low water), and January-February 2011 (high water). Post-filling surveys were undertaken in July-August between 2012 and 2019 (7 surveys), and January-February in 2012 and 2013 (2 surveys). Water levels were as high in all post-filling surveys as they were during the highwater season before the dam was built. However, there was still variation in water level during this period and water levels were slightly lower during surveys in July and August than in January and February. Caiman were identified as Caiman crocodilus yacare (Ccy), Melanosuchus niger (Mn), Paleosuchus palpebrosus (Pp) or P. trigonatus (Pt). We use the subspecies definition for Ccy because its taxonomic status is unclear. There is a genetic and morphological cline between the Pantanal caiman (usually referred to as C. yacare) and the Amazonian spectacled caiman (usually referred to as C. crocodilus) and these two taxa cannot be reliably distinguished in a > 2000 km intergrade zone along the Madeira River (Farias et al., 2013a; Farias et al., 2013b). Individuals in the upper Madeira River are morphologically more similar to the Pantanal caiman than they are to the Amazonian spectacled caiman on the lower reaches of the Madeira River. As the definition of the species is arbitrary, we used the subspecific name to indicate probable relationships. Individuals that could not be approached sufficiently close for confident identification (eyes only - 16.7 % of individuals) were not included in analyses.

The location of each individual was recorded with a GPS (Garmin) and between 25 and 52 individuals per species were captured and their the snout-vent length (SVLM - cm) measured after visual estimation of the length (SVLE - cm). The relationship between SVLM and SVLE of each species was as follows: for Ccy SVLM = 4.03 + 0.956* SVLE (N = 30; r^2 = 0.951, P < 0.001), for Mn SVL $_{\rm M}$ = 9.358 + 0.819* SVL $_{\rm E}$ (N = 25; r^2 = 0.951, P < 0.001), for Pp SVL $_{\rm M}$ = 6.368 + 0.907* SVL $_{\rm E}$ (N = 52, r^2 = 0.931, P < 0.001), and for Pt SVL $_{\rm M}$ = 4.518 + 0.939* SVL $_{\rm E}$ (N = 64, r^2 = 0.93, P < 0.001).

Only one individual from each sib-group of recently-hatched caimans that we located (SVL < 24 cm) was included in analyses. Hatchling groups are difficult to locate and are comprised of individuals that cannot be considered independent samples, so including all group members would artificially inflate sample sizes for this size class. All statistical analyses were undertaken in SYSTAT® and the maps were created in QGIS 2.18.

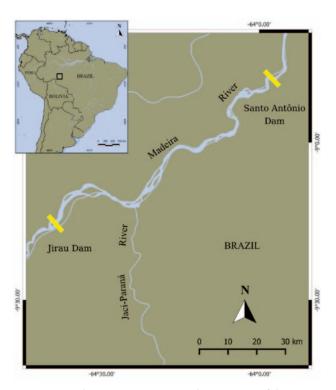


Figure 1. Study area encompassing the reservoir of the Santo Antônio Hydro-electric Dam to the wall of the Jirau Hydro-electric Dam (UHE Jirau) on the Madeira River, Brazilian Amazonia.

RESULTS

Analysis of Variance (ANOVA) indicated that the number of individuals seen in surveys of Melanosuchus niger $(F_{1.10} = 12.48, P = 0.005)$ and Paleosuchus trigonatus $(F_{1.10} = 12.48, P = 0.005)$ = 5.45, P = 0.042) decreased after dam filling, though the numbers were similar before and after filling for P. palpebrosus ($F_{1.10} = 0.54$, P = 0.478) and Caiman crocodilus $(F_{1.10} = 1.89, P = 0.200)$. However, when water level (WL), which is a surrogate for detectability, was included as a covariate, Analysis of Covariance (ANCOVA) indicated no significant difference in the number of caiman seen before and after reservoir filling (BA) for M. niger (WL: $F_{1,9} = 13.268$, P = 0.005; BA: $F_{1,9} = 0.821$, P = 0.389), P = 0.005trigonatus (WL: $F_{1,9} = 5.485$, P = 0.044; BA: $F_{1,9} = 0.707$, P= 0.422), and *C. crocodilus* (WL: $F_{1,9}$ = 5.526, P = 0.043; BA: $F_{1,9} = 1.861$, P = 0.206). Only for $\widetilde{P.~palpebrosus}$ was there indication of a difference in number seen independent of water level (WL: $F_{1.9} = 6.676$, P = 0.030; BA: $F_{1.9} = 7.418$, P = 0.023). Fewer P. palpebrosus were seen than expected, even after taking into account the effect of water level on detectability. With the possible exception of M. niger, the numbers of caimans seen after reservoir filling were similar to those seen at comparable water levels before filling (Fig. 2).

A Kolmogorov-Smirnov test indicated that the size structure of individuals seen differed between high- and low-water seasons before dam filling for P. trigonatus (P = 0.011) and P. palpebrosus (P = 0.040), but not for M. niger (P = 0.986) or C. crocodilus (P = 0.455). Therefore, in comparisons between before and after filling, when water levels were high, we used only the data for the pre-

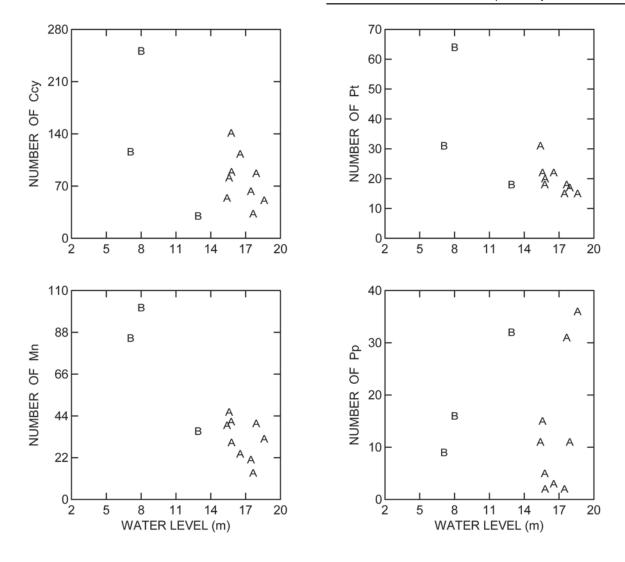


Figure 2. Number of caimans (Ccy = C. crocodilus yacare; Mn = M. niger; Pc = P. trigonatus; Pc = P. palpebrosus) in relation to water level (m), before (B) and after (A) filling of the Santo Antônio reservoir.

filling high-water season for the species of *Paleosuchus* and all data for the other two species. Given the large number of caimans seen, it is unlikely that the size of any one individual was estimated in more than one survey, so for the tests we combining years, assuming that all individuals were independent data points.

For *P. trigonatus*, Kolmogorov-Smirnov tests showed no significant differences in size structure between the pre-filling surveys and post-filling surveys until 2017 (P \geq 0.331 in all cases). There was evidence for a change in size structure in 2018 and 2019 (P = 0.016 and 0.068, respectively). Sufficient individuals of *P. palpebrosus* for yearly analyses (N \geq 42) were only seen until 2013. In 2012 and 2013 there was equivocal evidence of change in size structure (P = 0.153 and 0.063, respectively). Combining all post-filling surveys indicated a significant change in size structure for this species (P = 0.006).

Caiman crocodilus showed consistent differences between before and after reservoir filling ($P \ge 0.045$ in all cases), except for 2012 (P = 0.175). Combining all post-filling years indicated a significant overall change in size structure (P < 0.001). In contrast, the Kolmogorov-Smirnov tests for differences in size structure of M. niger

were inconsistent, showing no significant differences in most years (P \geq 0.192), but significant differences in 2012 and 2018 (P \leq 0.001). However, the pooled post-filling surveys (P = 0.019) indicated size-structure change.

The proportions of large individuals of *P. trigonatus* (SVL > 60 cm) and *P. palpebrosus* (SVL > 75 cm) declined (Fig. 3). Although statistically significant, the changes in size structure of individuals seen of the other species tended to be subtle. The proportion of individuals of *C. crocodilus* between 40 and 55 cm SVL tended to increase and the proportion between 55 and 70 cm SVL tended to decline. More large (SVL > 135 cm) *M. niger* were seen after reservoir filling. The proportions of other size classes were similar before and after filling.

The caimans were not uniformly distributed along the river before reservoir filling (Figs. 4 & 5). Most individuals of all species were in the upstream reaches and not near the proposed site of the dam wall, which was situated on a long series of rapids. However, the dam apparently did not have much effect on the distributions of P. trigonatus and M. niger. The correlation between densities in river segments before reservoir filling and 4-8 years after was high (r = 0.93, P < 0.001 for both species). The strength

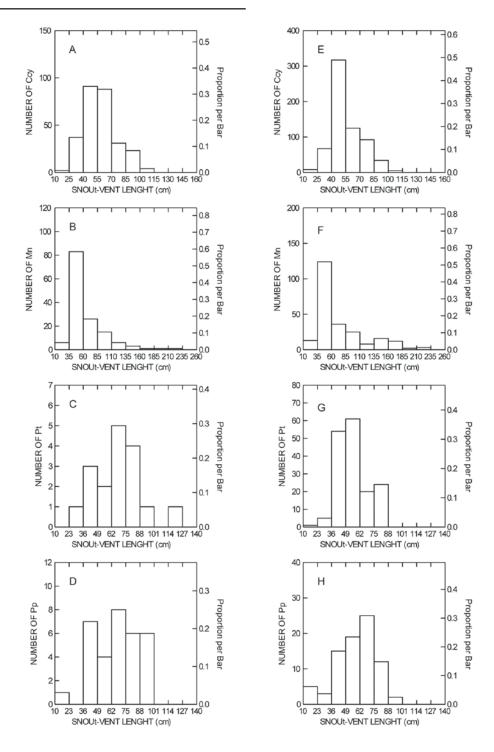


Figure 3. Size structure of caimans before (A, B, C, D) and after filling (E,F, G H) of the Santo Antônio reservoir. Ccy = *C. crocodilus* yacare, Mn = *M. niger*, Pt = *P. trigonatus*, Pp = *P. palpebrosus*.

of the correlation was less for *C. crocodilus* (r = 0.75, P = 0.001), indicating that the reservoir had a greater effect on the distribution of this species. Even so, after filling it was found in most areas that it had occupied before and the change was probably mainly due to the expansion of its distribution (Fig. 4). There was little relationship between the densities of *P. palpebrosus* (Fig. 5) in segments before and after dam filling (r = 0.31, P = 0.185).

DISCUSSION

The number of caimans of all species seen in surveys after reservoir filling tended to decline, but for three of the four species the decrease was not greater than expected given the higher water levels. For those species, the numbers seen after dam filling were similar to those recorded during high-water surveys before the dam was completed. This is consistent with numerous studies that have shown that water level is the principle determinant of the number of caimans seen in boat surveys (e.g.

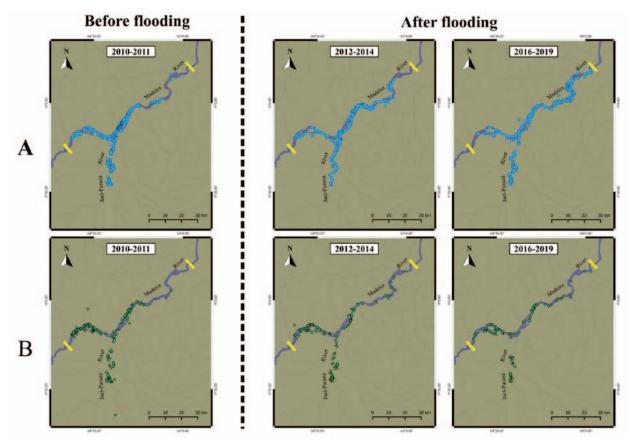


Figure 4. Spatial distribution of caiman before and after filling of the Santo Antônio reservoir. **A.** *C. crocodilus yacare*; **B.** *M. niger*. Data are for the pooled results of three pre-filling surveys (2010-2011), five early post-filling surveys (2012-2014) and four late post-filling surveys (2016-2019).

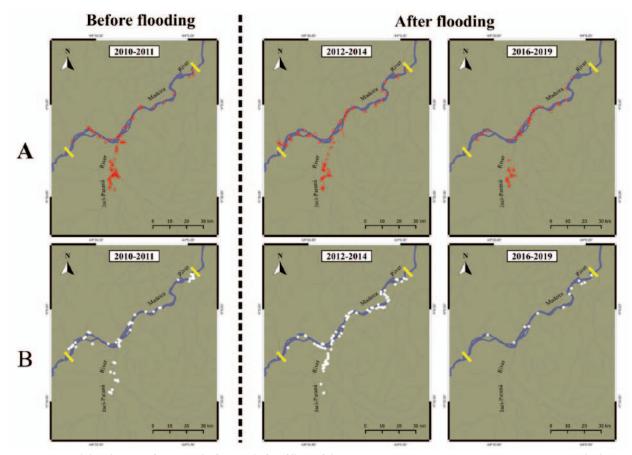


Figure 5. Spatial distribution of caimans before and after filling of the Santo Antonio reservoir. **A.** *P. trigonatus*; **B.** *P. palpebrosus*. Data are for the pooled results of three pre-filling surveys (2010-2011), five early post-filling surveys (2012-2014) and four late post-filling surveys (2016-2019).

Da Silveira et al., 2008; Fujisaki et al., 2011). Although the number of Paleosuchus palpebrosus seen declined more than expected due to increased water levels, we are hesitant to ascribe any biological significance to this because most individuals of P. palpebrosus live in habitats that are not appropriate for boat surveys (Campos et al., 2010; Campos & Magnusson, 2016; Campos et al., 2017). Most P. trigonatus individuals live in small streams, often far from large rivers, and individuals found around large rivers are probably vagrants (Magnusson & Lima, 1991). Although we did not register a decline for this species, the number of individuals near the banks of large rivers may not be a useful index of the abundance of the species in the region. In contrast, the margins of large water bodies are considered to constitute the principle habitat of Melanosuchus niger and Caiman crocodilus, so boat surveys probably provide reasonable indices of abundance for these species.

Hunting and other human activities affect the size structure of crocodilian populations (Mourão et al., 1996), so the distribution of sizes may be a more sensitive index of perturbation than attempts to estimate densities. For the reasons given above, we do not believe that boat surveys are appropriate to estimate densities of either species of *Paleosuchus*, and the reduction in the proportion of large individuals of these species seen may just be related to breeding adults moving further into the forest. However, the consistent finding of small individuals four to seven years after dam filling indicates that recruitment, and hence breeding, is occurring in the area.

The proportion of large individuals of *C. crocodilus* diminished after dam filling, with a concomitant increase in individuals of intermediate sizes. However, large individuals continued to be seen and the difference may simply have been a result of increased breeding after dam filling. *Caiman crocodilus* is the most widespread species of caiman and occupies a wide range of habitats (Velasco et al., 2010) including those that have been highly modified by humans. Studies should be continued, but there is presently little evidence that the change in size structure will negatively affect the species in the area in the long term.

The proportion of large individuals of *M. niger* increased after dam filling, with no concomitant reduction in the number of small individuals seven years after dam filling. It is possible that the increase in number of large individuals seen is a result of negative effects forcing the larger individuals into more exposed conditions, but it seems more likely that the dam increased the favorability of the river for this species, which is known to occur principally in lentic conditions (Marioni et al., 2013), with the change in size distribution indicating successful breeding and high survival of larger individuals.

The distributions of all species of caimans were originally higher in the upstream reaches away from the rapids where the dam wall was built. None of the species normally occur at high densities in highly turbulent water (Medem, 1981; Magnusson & Campos, 2010). This situation continued for some species after reservoir filling and the relative densities of *P. trigonatus*

and *M. niger* in segments along the river were similar to those before dam construction. The relative densities of *C. crocodilus* in different segments of river were less correlated with the densities before dam construction, but the pattern was similar and differences apparently arose from expansion rather than contraction of areas with higher relative densities. We attribute no biological significance to the lack of consistency of pre- and post-filling densities of *P. palpebrosus* because the major habitat of this species cannot be surveyed by boat.

Dam construction may cause hardship to some species (Sá-Oliveira et al, 2015; Campos, 2015). However, construction of the Santo Antônio dam does not appear to have eliminated any of the crocodilian species or reduced them to such low numbers that they are in imminent danger of extinction. However, there are still forested areas abutting much of the reservoir and increased deforestation rates associated with dam infrastructure could change that situation in the future. It is unfortunate that environmental legislation in Brazil only requires monitoring of the effects of dams for a few years after construction. There are many hydro-electric dams that were constructed in the last century that could be used to evaluate the long-term effects of dams on crocodilians if the funds were available to resurvey them.

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Author Contributions

ZC and FM collected the data; FM prepared maps; GM and WM made the statistical analyses; ZC and WM wrote the manuscript text.

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