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Conservation and management implications of nest-site selection of the sympatric crocodylians *Melanosuchus niger* and *Caiman crocodilus* in Central Amazonia, Brazil

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ABSTRACT

Management of crocodylians is often based on source-sink dynamics, protecting breeding habitat and concentrating hunting in other areas. Nest distributions shed light on habitat use by breeding populations, which might be used as a basis for monitoring and management. The heterogeneous spatial distribution of *Melanosuchus niger* and *Caiman crocodilus* in Amazonia has been suggested to reflect past hunting pressure, often underestimating the natural ecological peculiarities of these species. Ground nest surveys combined with satellite imagery allowed us to evaluate whether nest-site use by *M. niger* and *C. crocodilus* reflects environmental constraints or is a result of hunting pressure. Our results indicate that there is little evidence that hunting pressure shapes nest-site use of these species in our study areas. *M. niger* nests mainly on the shores of stable, temporally impounded floodplain lakes isolated from the early stages of the annual rising water of main rivers. This behavior facilitates the identification of suitable nesting sites using moderate-resolution remote-sensing tools and should guide monitoring efforts and the protection of these areas. In contrast, *C. crocodilus* is a generalist species, able to nest hundreds of meters inside the forest far from permanent water. This makes the occurrence and distribution of nesting-sites unpredictable using Landsat images. Although nests of this species can be found around lakes where nests of *M. niger* also occur, the protection of these sites might help to preserve only a small portion of *C. crocodilus* nesting females. Thus, conservation strategies for *C. crocodilus* should probably be based on different approaches.

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1. Introduction

Because crocodylians are polygamous (Lang, 1987), the protection of reproductive females is an effective mechanism to sustain wild populations subject to harvesting (Magnusson, 1986; Thorbjarnarson, 1991). Management of these species is often based on source-sink dynamics by protecting breeding habitat and concentrating hunting in other areas (Campos et al., 2006; Da Silveira and Thorbjarnarson, 1999). In source areas, keeping death rates of reproductive individuals low should enhance recruitment by maintaining birth and emigration rates high (Pulliam, 1988). This is the conservation relevance of identifying such areas. However,

in diverse areas such as the Amazon basin, which holds four sympatric crocodylians, delineation of conservation strategies might be more complicated than in areas that hold only one commercially valuable species.

The black caiman (*Melanosuchus niger*) reaches high densities only in restricted areas (Da Silveira, 2002), specially on floodplains of nutrient-rich, silt-laden Amazonian rivers (locally known as várzea floodplains). The spectacled caiman (*Caiman crocodilus*) is common in a variety of habitats, including vast areas outside Amazonia (Ross, 1998). The heterogeneous spatial distribution of these two crocodylians is suggested to be the result of past hunting pressure. *M. niger* populations were depleted until the mid-1970s, and this provided the opportunity for the smaller and more resilient *C. crocodilus* to colonize areas formerly occupied by *M. niger*. Supposedly, as hunting pressure is reduced, *M. niger* populations would recover and progressively displace the smaller *C. crocodilus* (Magnusson, 1985). This is probably occurring already in several

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¹ In memoriam.

areas after more than four decades of trade prohibition. However, these observations are generally based on data from accessible places occupied mainly by non-reproductive individuals (Da Silveira and Thorbjarnarson, 1999).

Distributions of the reproductive portion of the population are poorly known. Since each nest represents one nesting female, spatial patterns of nesting sites shed light on habitat use by this segment of the population. Hydrology is one of the most important factors influencing the nesting ecology of many species of crocodilians (Ayarzagüena and Castroviejo, 2008; Campos and Magnusson, 1995; Joanen and McNease, 1989; Thorbjarnarson, 1994; Villamarín-Jurado and Suárez, 2007). Thorbjarnarson and Da Silveira (2000) suggested that *M. niger* mainly nests around lakes with stable water levels during the low-water season, and that this behavior might reduce the chances of nest flooding. However, várzea floodplains cover an enormous and heterogeneous area, and logistical inaccessibility makes it difficult to evaluate hydrological regimes and identify nesting areas only by in situ surveys. Ground nest surveys combined with satellite imagery allowed us to evaluate whether nest-site use by *M. niger* and *C. crocodilus* reflects environmental constraints or is a result of hunting pressure. This information should be useful to evaluate the applicability of source-sink dynamics for the management of these sympatric species. Specifically, we were interested in answering the following questions: (a) Are there species-specific differences in nest-site use? (b) How does hydrology influence nest-site use and hatching success? (c) Can existing remote-sensing tools predict nesting areas?

1.1. Study areas

This research was carried out in two Brazilian protected areas in central Amazonia. These reserves consist of várzea floodplains

influenced by the annual inundation of nutrient-rich, silt-laden waters. Water levels in both localities reach their annual peak between May and July, and the low-water period occurs between September and November (Ayres, 1993). Mean amplitude of water level is approximately 10 m (Junk, 1989).

The Mamirauá Sustainable Development Reserve (MSDR) is the largest protected reserve in the world entirely composed of várzea floodplains. It covers an area of 1124,000 ha, located approximately 600 km west of the city of Manaus (Fig. 1). The southeastern portion of this reserve is delimited by the confluence of the Amazon (Solimões) and Japura rivers. In this reserve, intensive hunting has been eliminated during the last 15 years and caiman populations have clearly grown; though illegal poaching occurs occasionally (Da Silveira and Thorbjarnarson, 1999; Da Silveira and Viana, 2003). An experimental legal harvesting program has been undertaken since 2004 (Botero-Arias et al., 2009).

The Piagaçu-Purus Sustainable Development Reserve (PP-SDR) covers 809,268 ha, of which only 50% consist of várzea floodplains. It is located between the Purus and Madeira rivers, approximately 350 km southwest of the city of Manaus (Fig. 1). There, intense illegal hunting currently occurs to supply the meat market in the neighboring State of Pará (Da Silveira, 2003; Marioni et al., 2006).

2. Materials and methods

2.1. Field data

In the Mamirauá-SDR, we carried out ground nest surveys up to 20 m landward of the water's edge. During the low-water seasons of 2007 and 2008 we searched for nests by walking along the shores of 67 water bodies. Ten of these water bodies were surveyed during both the years. In 2007, all the nests found were visited at

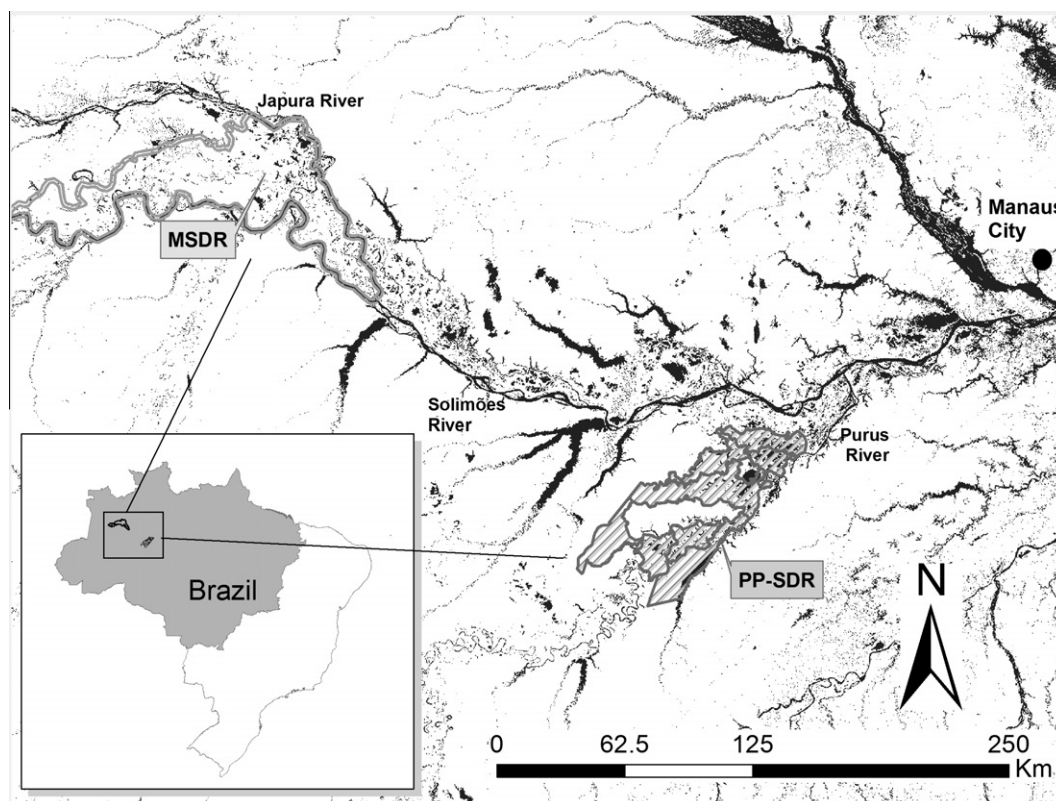


Fig. 1. Location of Mamirauá Sustainable Development Reserve (MSDR; open area with gray outline); and Piagaçu-Purus SDR (PP-SDR; hatched area with gray outline) in Brazilian Amazonia.

the beginning of the incubation period (September–October) and re-visited at the end (December–January) to document nest fate. We based identification of nest fate on the marks found on nest mounds and the state and location of eggshells (Da Silveira et al., 2010).

In the Piagaçu–Purus SDR, ground nest surveys began in 2005 as part of a long-term monitoring program and have been undertaken yearly since then. Data included in these analyses correspond to the period 2005–2008. We concentrated the search effort up to 400 m landward from the water's edge. We monitored 105 water bodies during the 4-year study; 72 water bodies were visited in one nesting season, 22 in two, and 11 in more than two nesting seasons. Although the survey effort was higher in this area, we believe that the conclusions drawn herein would only be reinforced if the survey effort was increased in MSDR.

As an estimate of annual nesting effort, we used the number of nests found near each lake as an index of relative abundance (nests/linear-km surveyed). For this, we quantified the distance surveyed (in most cases corresponding to the entire lake perimeter) joining manually the GPS track-points collected in the field and plotted on Landsat Thematic Mapper (TM) images (false-color composites of bands 5, 4 and 3), using Global Mapper v6.09 software.

Most of the surveyed water bodies were lakes ($n = 131$), although we also monitored some *ressacas* (a shallow water embayment that dries up during the low-water period; Castello, 2007), *canos* (canals connecting lakes with any other water body; Crampton, 1998), and *chavascal* sites (*várzea* scrub located in

topographical depressions, waterlogged throughout the whole year; Wittmann et al., 2002). All water bodies were located within the ~10 m amplitude annual-flood zone. Some of the lakes impounded water during the season of falling river levels and remained isolated from rising water during the early stages of floodplain inundation.

2.2. Hydrology

Water level variation was assessed on a daily basis through 2007–2008 in both localities. In the MSDR, we installed a water level gauge in the Jarauá river (one of the main canals in the area, 2°50'18" S, 64°59'45" W) and manually recorded the level twice a day between September 2007 and September 2008; in five other lakes, we used water level loggers (Onset Corporation) to obtain automatic daily measures. Water level from the Mamirauá canal (located approximately 20 km from the other sampled lakes, 3°02'20" S, 64°51'35" W) showed a high correlation with the Jarauá gauge ($R^2 = 0.99$, $P < 0.001$). We used available data since 1993 from the Mamirauá canal to estimate the mean annual period that the water of each of the five sampled lakes remained isolated from main river canals.

In the PP-SDR, we registered daily water level in the Caua canal (4°14'28" S, 61°45'36" W) since March 2007. Water level variation showed a high correlation ($R^2 = 0.98$, $P < 0.001$) with data from the nearby town of Beruri (about 80 km from the Caua level-gauge) provided by the Brazilian National Water Agency (ANA). Thus, data from Beruri were used in the analyses.

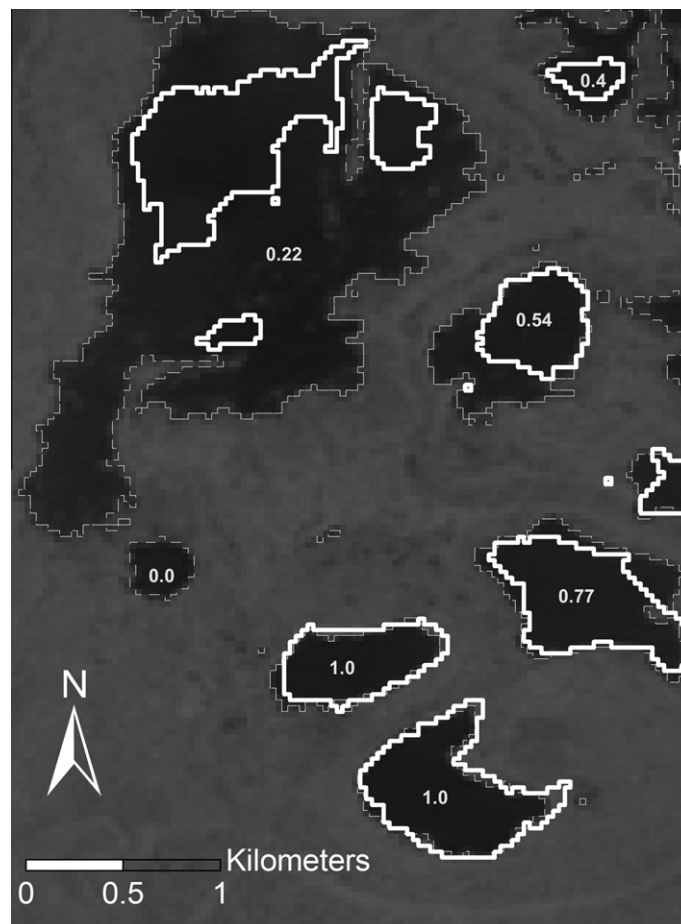


Fig. 2. Landsat Thematic Mapper image showing variation in open-water areas of floodplain lakes from low-water (thick solid white outline) to high-water period (thin dashed gray outline). Numbers within lakes represent open-water stability index (OWSI) values.

2.3. Remote sensing analyses

Seasonal hydrological differences between water bodies were assessed using the variation in their open-water area. In each study region, we used two Landsat TM images, one at high water and the other at low water, to delineate the surface area of each water body. These images were acquired on 24 July and 10 September 2007 for MSDR, and on 29 August 2008 and 19 September 1998 for PP-SDR. Differences in water levels between the two dates were 7.39 m and 7.95 m for MSDR and PP-SDR, respectively.

Using IDRISI Kilimanjaro software (Eastman, 2003) through unsupervised classifications, we extracted all objects classified as open water, and transformed the images into vector polygons. When the classifier did not separate lakes from adjacent water bodies due to the presence of a connecting canal, we performed manual cuts to close the polygons. The resulting polygons were used to calculate open-water areas of the lakes.

We created the open-water stability index (OWSI) as an indicator of the hydrological fluctuations of the lakes. This index is the ratio between areas at low-water (*LW area*) and at high-water periods (*HW area*):

$$\text{OWSI} = \text{LW area} / \text{HW area} \text{ (Fig. 2).}$$

The probability of caiman nests being present on the shores of a water body as a function of this index was assessed using logistic-regression analyses. Nest abundance (per km of surveyed shoreline) was related to this index using least-squares regressions in those water bodies with nests present. Statistical analyses were undertaken with the Systat 8.0 package (Wilkinson, 1998).

3. Results

We surveyed a total of 172 water bodies and found 1291 caiman nests distributed along their shores. *M. niger* nests were found in 48.8% of all surveyed water bodies (39 in MSDR and 45 in PP-SDR). Nests of *C. crocodilus* were found along the shores of 18% and 92% of surveyed water bodies in the Mamirauá and Piagaçu-Purus SDRs, respectively.

M. niger nest abundance on the shorelines of those water bodies in which nests of the species were present, varied from 0.3 to 17.9 nests/km in MSDR (Mean = 3.2 ± 3.33), and from 0.1 to 12.0 nests/km in PP-SDR (Mean = 2.2 ± 2.46). In 2007, a sample of ten lakes in the MSDR showed mean abundances of *M. niger* nests (5.17 nests/km) slightly higher than in 2008 (2.86 nests/km) ($t = 2.039$, $df = 9$,

$P = 0.07$). In 90% of those lakes, nest presence was consistent during both the nesting seasons.

C. crocodilus nest abundance in PP-SDR ranged from 0.1 to 14.3 nests/km (Mean = 2.8 ± 2.96). In a sample of water bodies where *C. crocodilus* nests occurred, the mean abundance of nests was higher in *canos* than in lakes ($t = 2.6$, $df = 93$, $P = 0.01$). In the Mamirauá-SDR we found only 14 *C. crocodilus* nests, with relative abundances varying from 0.3 to 2.0 nests/km.

Hydrological regimes varied among water bodies studied in the MSDR. Water in the main canal started to rise during the first days of October 2007. The most hydrologically-isolated lakes were reached by rising water after 3 months (January 2008). By this date, the eggs of the monitored nests had already hatched (Fig. 3). Assuming that there was no significant physical change in those water bodies between 1993 and 2008, and that the sill level at which they lose connection with the main water flux was constant, we estimate that the mean annual period of hydrological isolation of our sampled lakes varied from 56 to 128 days. In our sample, *M. niger* nests occurred only on the shores of lakes that remained hydrologically isolated on average more than 81 days/year (Fig. 3).

Nest flooding was relatively low in the MSDR in 2007. Flooding killed eggs in 12.8% of the nests, all of which were located in only four of the 22 water bodies where nests were found in that season. Nesting success (percentage of nests that produced at least one live hatchling) was 14.2%. The eggs of 69.7% of nests were lost to predators (mainly humans, tegu lizards and jaguars). In PP-SDR we determined nest fates for only 26% of surveyed nests, representing 267 nests. Of these, the eggs of 4% were flooded, 54% were taken by predators and 21% hatched.

Moderate-resolution satellite imagery allowed us to evaluate remotely the hydrological characteristics of most water bodies. The unsupervised classifier used was able to identify 66.4% of the surveyed water bodies. OWSI values of these lakes varied between 0.06 and 1.0 (Mean = 0.66, $SD \pm 0.28$). Thus some floodplain lakes showed no change in their open-water area as local river levels dropped more than seven meters, while others shrunk to as little as 6% of their high-water area. Surveyed lakes in MSDR ranged between 0.27 and 49.1 ha, while in PP-SDR the size of lakes ranged from 0.09 to 222.75 ha. Despite these differences, almost 70% of all surveyed lakes in both areas were smaller than 10 ha during the low-water season.

Hydrological regimes, represented by the open-water-stability index (OWSI) strongly influenced the occurrence of *M. niger* nests

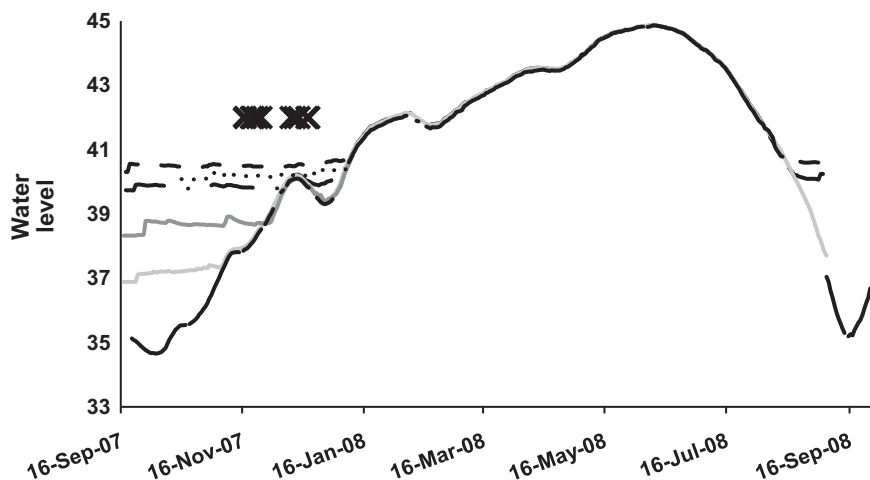


Fig. 3. Annual water level variation between September 2007 and September 2008 in six water bodies of the Mamirauá-SDR. Continuous black line is the Jarauá main canal. Gray lines are water bodies in which no nests were found. Black dashed lines are lakes isolated on average >81 days/year. Black crosses represent the estimated dates on which *M. niger* eggs hatched from a sample of 11 water bodies.

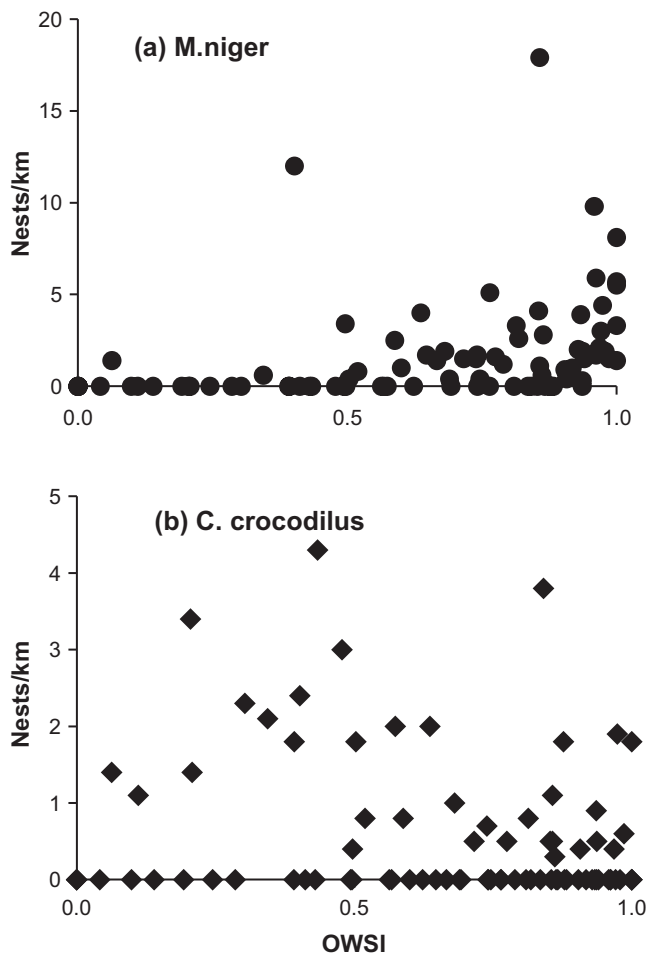


Fig. 4. (a) *Melanosuchus niger* and (b) *Caiman crocodilus* nest abundance (nests per km of shoreline) in relation to the open-water stability index (OWSI).

along the shores of lakes (Logistic regression: $P < 0.0001$; $N = 84$). In 93.6% of lakes where *M. niger* nests occurred, OWSI was higher than 0.5; only three lakes with nests of this species had OWSI values lower than 0.5 (Fig. 4a). Occurrence of *C. crocodilus* nests was not influenced by this index ($P = 0.099$; $N = 85$). Nesting of this species takes place in lakes within the whole range of OWSI values (Fig. 4b).

Although the occurrence of *M. niger* nests was related to OWSI, abundance in lakes in which nesting occurred was not predicted by this index ($R^2 = 0.007$; $N = 47$; $P = 0.57$). However, when nests of both species were found in the same lakes, a multiple regression model ($R^2 = 25.5$; $N = 47$; $P = 0.002$) showed that *C. crocodilus* nest abundance was negatively influenced by OWSI ($P = 0.001$), but was not related to *M. niger* nest abundance ($P = 0.124$).

4. Discussion

Our study demonstrates that hydrological regimes of open-water lakes influence nest-site choice of *M. niger*. Nests of this species occur mainly on the margins of partially impounded floodplain water bodies, isolated from the early stages of the annual rising water of main rivers as suggested by Thorbjarnarson and Da Silveira (2000). *C. crocodilus* uses a broader range of sites for nesting, where the hydrological regimes are much more variable. However, by placing nests far from permanent water bodies, they also remain isolated from early flooding.

The clear selection of *M. niger* females for hydrologically-stable conditions is probably a result of nest-guarding behavior. Females generally place their nests very close to the water's edge, and station themselves in the water nearby to guard them (Da Silveira et al., 2010; Thorbjarnarson and Da Silveira, 2000). In such situations, it is essential that water level remains stable during the incubation period in order to avoid nest flooding. Thus, lakes that remain isolated from the main water flux longer than other water bodies provide enough time for the eggs to hatch.

Incubation period in *M. niger* has not been reported; however, preliminary data under semi-controlled temperature conditions, suggest that it extends from 84 to 96 days (J.B. Thorbjarnarson, personal communication). In the closely related species, *Caiman latirostris* and *Alligator mississippiensis*, incubation period at constant temperatures varies from 69 to 81 and 63 to 84 days, respectively (Lang and Andrews, 1994; Piña et al., 2003). If *M. niger* has an incubation period in this range, it likely explains why nests of this species were found only on the shores of lakes that remain isolated on average more than 81 days per year.

Temporal hydrological isolation of *M. niger* nesting lakes is probably the result of low water flow through their canals caused by aquatic macrophytes. The presence of these plants leads to deposition of sediments that act as a sill, which causes the annual damming of the lake during low-water season, and retards the return of water to the lake during the rising-water period. However, the margins of open-water lakes are not the sole nesting sites used by *M. niger*. This species commonly nests on top of floating meadows present in water bodies varying from narrow stream canals to open lakes. Some of these water bodies show unstable hydrologic regimes during low water, and placing nests on floating macrophytes might reduce flooding risks.

C. crocodilus females are less dependent on permanent water from which to guard nests. They usually place their nests on elevated relict levees far from the margins of water bodies and guard hidden under leaf-litter (Da Silveira et al., 2010). In these places, hundreds of meters inside the forest, water takes longer to reach nesting sites, which reduces flooding risks. Crocodilian nest-site selection is generally considered to be an adaptation to reduce mortality due to nest flooding (Cintra, 1988; Crawshaw and Schaller, 1980; Kushlan and Jacobsen, 1990). Flooding of caiman nests in this study was much lower than that reported for other species in the wild (Allsteadt, 1994; Hall and Johnson, 1987; Platt et al., 2008; Webb et al., 1977, 1983). This suggests that the contrasting strategies used by these two sympatric crocodilians are effective to avoid nest flooding in hydrologically dynamic environments, such as várzea floodplains.

Amazonian floodplains within Brazilian territory cover an area of approximately 307,300 km², of which almost two-thirds represent Várzea (Ayres, 1993; Junk, 1997). Monitoring crocodilian populations in such a vast area demands the application of geo-processing tools which are presently the only option to gather biologically sound data cost-effectively. During this study, Landsat Thematic Mapper images were useful to estimate seasonal hydrological variation of almost two-thirds of all water bodies in the study areas. This amount of data is not likely to be gathered only by in situ surveys. However, an orbital sensor with 30 m spatial resolution operating in the optical portion of the spectrum has some limitations. Water under forest cover, narrow stream canals, and some water bodies covered almost totally by aquatic macrophytes, were not detected. Therefore, the scope of this research was restricted to open-water lakes, whose shores are common caiman nesting habitats. Other types of water bodies might be better studied in the future using higher spatial and temporal resolutions and microwave sensors.

Although we might have underestimated the number of *C. crocodilus* nests in the MSDR, as we mostly surveyed areas close to the

water's edge, we found the same general patterns of nesting in both study areas, despite current differences in hunting pressure. The specialist *M. niger* nests mainly adjacent to the margins of hydrologically-stable water bodies, whereas the generalist *C. crocodilus* nests around most water bodies, often at greater distances from permanent water. The suggestion that *M. niger* will eventually proliferate as hunting pressure diminishes and will take over the places currently occupied by *C. crocodilus* (Magnusson, 1985), if true, is probably only applicable in non-breeding areas. If *M. niger* populations experience less hunting pressure, as is the case of MSDR (Da Silveira, 2002), they may grow and eventually displace *C. crocodilus*. However, nest-site selection by *M. niger* makes it improbable that all the available water bodies would be used for nesting, dislocating *C. crocodilus* females from their nesting sites. Spatial segregation, ecological differences in habitat selection and in resource use between *M. niger* and *C. crocodilus* have been reported for populations occurring in the most accessible sites (Da Silveira et al., 1997; Herron, 1994; Magnusson, 1985; Marioni et al., 2008), but these conclusions apply mostly to juveniles and non-reproductive adults.

Information on nest-site use by these two Amazonian crocodilians has important implications for conservation. The high nest-site selection showed by *M. niger* females, along with the feasibility of identifying source areas using readily accessible satellite images, might facilitate the implementation of zoning systems for sustainable use and monitoring. If nesting areas, such as isolated lakes and some narrow stream canals, are strictly preserved, the protection of reproductive females should be enhanced. This could guarantee the recruitment to the population, maintaining birth rates greater than death rates, as predicted by source-sink models (Pulliam, 1988). On the other hand, hydrologically unstable water bodies, such as main canals and connected lakes, might be subject to selective harvesting under controlled conditions if immigration rates are kept high. Besides being the most accessible for people, these water bodies are sink habitats occupied mainly by non-reproductive males (Da Silveira and Thorbjarnarson, 1999). Spatial segregation of breeding and non-breeding segments of the population facilitates conservation strategies for *M. niger* in várzea floodplains. However, it is also important to generate information about size structure and mobility of reproductive females in non-breeding areas and seasons, to evaluate their susceptibility to hunters. Furthermore, the establishment and enforcement of long-term monitoring programs of nesting areas and females, may facilitate the detection of trends in nesting populations in areas subject to controlled or uncontrolled harvesting, such as in MSDR and PP-SDR, respectively.

Since *C. crocodilus* does not show marked preferences for specific nesting sites, it is more difficult to identify source areas and the same zoning system applicable for *M. niger* might not be the best conservation strategy for this species. Although, the occurrence of sites with high nest abundances could indicate the most productive nesting sites to be protected, currently, these cannot be predicted using Landsat images. Alternatively, Campos et al. (2008) suggested that the most appropriate strategy to maintain viable *C. crocodilus* populations in the long term would be to set an upper size limit for harvesting in order to protect the largest reproductive females. However, given the great variation of size distributions of breeding females among populations, legal size limits should be based on the data from local populations (Campos et al., 2008). Thus, before implementing harvesting quotas, it is essential to generate information about size distributions of the reproductive population, specially nesting females of both species, from each area to be exploited. This is a task that local inhabitants are able to perform with basic training and support, and could be the starting point of community-based sustainable management programs.

4.1. Conclusions

M. niger nests occurred mainly associated with the margins of partially impounded floodplain lakes. This behavior probably reduces flooding risks, since the early rising of local rivers has little effect on water bodies where nesting of this species occurs. Using moderate-resolution remote-sensing tools, we could identify suitable nesting sites of this species in both reserves. This information should guide monitoring efforts and facilitate the protection of source areas. By prohibiting harvesting in these sites, reproductive females should be protected and recruitment rates might be sustained.

In contrast, *C. crocodilus* shows more plasticity for nesting and is less affected by water level variation. This makes the occurrence and distribution of nesting-sites unpredictable using Landsat images. Although nests of this species could be found around lakes where nests of *M. niger* also occur, the protection of these sites might help to preserve only a small portion of *C. crocodilus* nesting females. Since this study has shown that open-water impounded lakes make up only a small proportion of nesting habitats available for this species, conservation strategies for *C. crocodilus* should probably be based on different approaches, such as size-selective quotas. Monitoring efforts should give special attention to nesting sites.

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