The Herpetological Bulletin 170, 2024: 7–13
RESEARCH ARTICLE

https://doi.org/10.33256/hb170.713

Reproduction and displacements of known-age caimans *Caiman yacare* in the Pantanal of Brazil

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ABSTRACT – We recaptured 26 female and 24 male Pantanal caimans *Caiman yacare* of known-age up to 36 years after marking. The relationship between clutch size and age for known-age females was highly variable although one female captured multiple times between 18 and 26 years of age showed little variation in clutch size. Captured known-age females attending nests varied from 73 cm to 89 cm snout-vent length and from 9 to 36 years old. These females continued to grow long after their first capture, so cessation of growth does not appear to be related to reproduction. Most known-age animals were recaptured within 10 km of where they hatched, but usually on a different ranch, so ranches cannot be used as autonomous management units. Our data indicate that the ratio of snout-vent length (SVL) at first reproduction (73 cm) to mean asymptotic SVL reported for this species (85.7 cm SVL) is much higher in female Pantanal caimans (0.85) than has been reported for most other reptiles (0.7).

INTRODUCTION

Many organisms can be placed on a continuum between species with short life spans combined with a large number of offspring (r selected) and long life spans with a small number of offspring (K selected) (Pianka, 1970). However, crocodilians are long-lived but also produce large numbers of relatively small offspring (Magnusson, 1986), raising the question as to whether they also differ in other life-history traits. Many reptiles start to reproduce at about 70% of maximum length, and these are often referred to as having indeterminate growth, i.e. growth continues throughout life (Andrews, 1982; Shine et al., 2016). Like other reptiles, crocodilians start reproducing long before they reach their maximum size, and are described as having indeterminate growth, though the evidence for this is controversial (Wilkinson et al., 2016). There have been no studies of the ratio of size at first reproduction and maximum size in crocodilians.

Generalities about the size at first reproduction are based on individual growth models (Charnov et al., 2001). However, data are usually not based on individuals, but are estimated from the smallest recorded size at reproduction and maximum asymptotic size in a large number of individuals. This assumes that individuals vary little in age at first reproduction and maximum size can be estimated from growth models (Shine & Iverson, 1995). However, frequently used sigmoidal models of growth are often imprecise (Campos et al., 2014), and data are not usually presented to indicate whether individuals follow the mean trajectory or remain parallel to it for most of their life (Magnusson, 2012).

Life-history data are essential for demographic studies and wildlife management, but long-term studies of individual crocodilians are rare due to the difficulty of marking large numbers of individuals and recapturing them (Bayliss, 1987). Demographic studies of most organisms suffer from the problem of defining the biological population being investigated (Magnusson, 2013), but this is even more difficult for crocodilians, which may make round-trip movements of over 1,800 km (Fukuda et al., 2019). On the other hand, the mean size of nesting female caimans may vary between areas within tens of km of each other (Campos & Magnusson, 1995). Such scale discrepancy indicates the importance of registering the movements of animals used in demographic studies to define the area in which the estimated population parameter may apply.

Individual crocodilians of the species for which long-term studies have been undertaken, such as *Crocodylus johnstoni* studied for 20 years (Tucker et al., 1997), *Caiman latirostris* studied for 22 years (Viotto et al., 2020) and *Alligator mississippiensis* studied for 46 years (Wilkinson et al., 2016), live long after reaching sexual maturity and have life spans that far exceed the duration of most studies. Indirect methods can be used to estimate mean age at first reproduction, displacement from natal areas and reproductive life spans, but these may have little precision, especially when derived from estimates of age based on size (Campos et al., 2014; Magnusson, 2012). Wilkinson et al. (2016) estimated that *A. mississippiensis* has a reproductive life span of 46 years, and individuals may live for more than 70 years in the wild. However, those intervals were based on estimates of age based on size. The longest period of nesting they recorded for an individual female was 31 years. Viotto et al. (2020) studied known-age *C. latirostris* individuals, or individuals captured at small sizes when age-size relationships are precise, and estimated first reproduction at about 8.1 years for females in the wild. Age at first reproduction based on known-age individuals is not known for other crocodilian species in the wild.

Campos & Magnusson (1995) related clutch size to mass of female *Caiman yacare*, and Campos et al. (2006) reported the size-age relationship for the same species, but there has been no study of the direct relationship between age and clutch size. Wilkinson et al. (2016) did not find evidence of senility in *A. mississippiensis*, except for one emaciated individual. They reported determinate growth in the same species but growth ceased long after the estimated age at first reproduction.

Campos et al. (2014) concluded that age-size relationships based on the relationship between growth rate and size are biased for both males and females, because they differed from the age-size relationships of known-age animals. However, it is expected that an empirical relationship derived from direct observations could predict values for the dependent variable better than those modelled from a relationships between growth rate and size, and the bias would be opposite in direction for males and females. Therefore, it is important to obtain the independent data needed to test this relationship.

Adult *Crocodylus johnstoni* have home ranges that cover a linear distance of about 1 km (Tucker et al., 1997) and adult *Paleosuchus trigonatus* also have small home ranges that generally cover less than 1 km of stream (Magnusson & Lima, 1991), but juveniles of both species appear to wander over large distances. Small *C. c. yacare* cover much larger areas, but individuals with snout-vent lengths (SVL) >40 cm had generally moved less than 10 km when recaptured after 5 to 15 years (Campos et al., 2006). However, in that study, few of the caimans were recaptured after reaching sexual maturity.

Caiman yacare is one of the most intensively studied crocodilians (Campos et al., 2020). It is often considered a full species, even though its range extends well beyond the Pantanal and intergrades with the spectacled caiman, *Caiman crocodilus crocodilus*, over a wide area in the Amazon (Hrbek et al., 2008). While there is dissension about the number of species within the *C. crocodilus* clade, in the Amazon there is consensus that there is only one species in this clade in the Pantanal (Campos et al., 2020). There are no intensive studies of the species in the Amazon, so to avoid confusion we will refer to *Caiman yacare* in this study by its common name, the Pantanal caiman.

Here, we report data on growth, reproduction and long-term movement of known-age Pantanal caimans that were captured up to 36 years after hatching, in the same area investigated by Campos & Magnusson (1995), Campos et al. (2006) and Campos et al. (2014). Our working hypothesis was that analysis of this long-term data would confirm determinate growth in the species and show that individuals vary in their growth trajectories. These data would also allow us to assess whether the ratio between size at sexual maturity and maximum size for the Pantanal caiman is about 0.7, as in other reptiles.

MATERIALS & METHODS

Between 1987 and 2013, caimans were first captured at Nhumrim (18° 59´ S, 56° 39´ W), Campo Dora (18° 55´ S, 56° 40´ W), and Dom Valdir ranches (18° 55´ S, 56° 35´ W) (see Campos et al., 2020 for details). From 2014 to 2022, we continued to recapture caimans in the same areas. Recaptures were made during the day, mainly during the dry season (September to November), when caimans are concentrated in pools (Campos et al., 2011) or moving between pools and thermoregulation sites in the forest (Campos et al., 2006). During the high-water season most waterbodies are connected and forests and pastures are inundated. Few animals were recaptured under these conditions, so the movements reported is almost exclusively between dry-season refuges.

Between February 2004 and November 2010, we captured 1,272 new individuals, resulting in a total of 7,831 caimans marked in the study area since 1987. Only data for these new recaptures were used for this study. Hatchlings were marked by removal of tail scutes and/or application of a numbered aluminum tag (National Band & Tag™ 1005-1) attached to the interdigital membrane of the hind foot. Adults were marked by removal of tail scutes and with numbered plastic cattle ear tags fixed on the tail scutes or with a numbered aluminum tag (National Band & Tag™ 1005-3) attached to the interdigital membrane of the hind foot. Tail scutes were removed quickly with a surgical scalpel, and caimans showed no evidence of distress, such as struggling. These methods have been used on many species of crocodilians (e.g. Manolis & Webb, 2016), are regarded as effective, with no evidence of stress or infection. All procedures for capturing, manipulating and marking of caimans were approved by the EMBRAPA Ethics Committee (No. 009/2016) and authorised under SISBIO license (No. 13048-1) and IBAMA permits (No. 017/02).

Locations of caimans were recorded with a GPS (Garmin GPSMAPS). Surveys were not undertaken in all areas in all years (see Supplementary Material, Table 1S), but all areas were surveyed on several occasions over the study period. Snout-vent length (SVL) of captured caimans was measured with a tape measure graduated in mm, and sex determined by inspection of the cliteropenis (Campos et al., 2006)

Using growth curves giving the size and growth-rate relationships for known-age caimans (see S1 Table 2 in Campos et al., 2014), we compared the size of newly captured known-age caimans to the values predicted by growth curves using t-tests. Multiple regression was used to investigate the independent effects of size and age on clutch size. This analysis was done using only the first data point for each of those females captured more than once and repeated with the data including recaptures. The relationship between distance from hatching site and age was nonlinear and we modeled it with a power curve, which was linearised by taking the logs of both dependent and independent variables. All statistical analyses were done in the R statistical environment (R Core Team, 2021), and we used the K means algorithm of Spring (2018) to classify the water bodies and map the study area based on a Sentinel 2 satellite image.

RESULTS

The permanent marking by scute-clipping (removal of a combination of single and double vertical tail scutes) made it possible to identify recaptures, which extended up to 36 years. We recaptured 26 females and 24 males that had been marked as hatchlings or at such small size (SVL < 24.2 cm) that we could estimate hatching year with confidence. The data for animals captured when more than 25-years-old

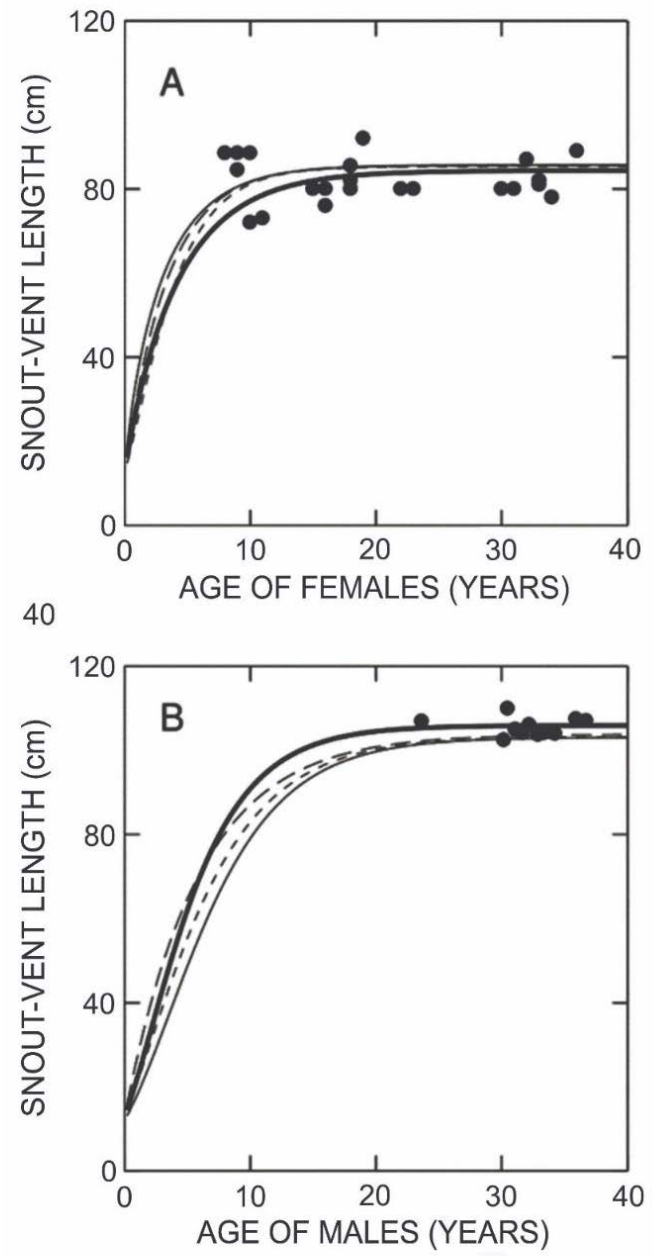

Figure 1. Relationship between size and age for known-age female **A.** and male **B.** Pantanal caimans based on the Richards curve (thick continuous line, from Campos et al., 2014), the filled dots are data from the current study indicating known-age caimans captured between 1987 and 2021. Models based on growth rate-size relationships for animals of unknown age are given by the thin continuous line (full Richards model), short dashes (von Bertalanffy, m = 0.667) and long dashes (monomolecular, m = 0) use the parameter values provided by Campos et al. (2014).

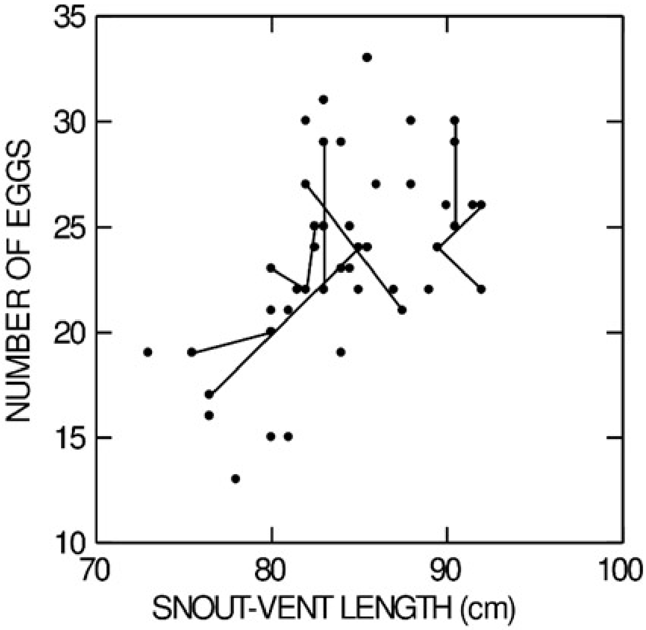

Figure 2. Clutch size in corresponding nests of female Pantanal caimans captured next to nests. Lines connect data points for individuals captured multiple times.

confirms negligible growth of older animals and that the empirical asymptote for known-age individuals from Campos et al. (2014) fits the data well for older animals (Fig. 1). T-tests comparing the observed SVL to that predicted by the model for animals captured subsequently were consistent with all models (P > 0.45 in all cases) given by Campos et al. (2014) for males (Fig. 1). Data from subsequent recaptures were not consistent with the model based on known-age animals for females (t_{48} = -3.1263, P = 0.0003), but the observed data were not significantly different from the other models (P > 0.11 in all cases). There was large scatter around the predicted values for all models (Fig. 1).

The number of eggs per clutch generally increased with female size, indicating that clutch size more than doubles over the lifespan of females (Fig. 2). However, individual females that were captured at nests did not necessarily show that relationship. Three females exhibited little or no growth between clutches (almost vertical lines on Figure 2), clutch size increased with SVL for three females, and it decreased with size for another three. The three females that did not grow had presumably reached their asymptotic sizes. The ratio of snout-vent length (SVL) of the smallest reproducing female in the study (73 cm) to mean asymptotic SVL 85.7 cm SVL), as estimated by Campos et al (2014), was 0.85.

There was a very weak relationship between age and SVL of known-age females (r^2 = 0.09, P = 0.233). The relationship between clutch size and age for known-age females showed large scatter, and one female captured multiple times between 18 and 26 years old showed little variation in clutch size (Fig. 3). Including only the first capture for the female captured three times, multiple regression indicated a positive effect (P = 0.012) of SVL on clutch size (CS), but a negative effect of age (P = 0.047) on clutch size (CS = -6.627 + 1.226*SVL – 0.581*AGE, N = 13, R^2 = 0.492, P = 0.034). Including all data for the female captured multiple times gave similar results (SVL, P = 0.011; AGE, P = 0.063).

Most known-age animals were recaptured within 10 km of where they hatched (Fig. 4). Although this distance might be a reflection of the size of the study area, recaptures of some individuals over much larger distances indicates that it probably reflects individual movement patterns. The overall relationship between distance from hatching site (DIST) and age (AGE) could be modeled with a power curve [ln(DIST) = 3.04 - 0.41*ln(AGE), N = 51, r^2 = 0.17, P = 0.003]. Inclusion of sex did not significantly improve the fit of the model (P =

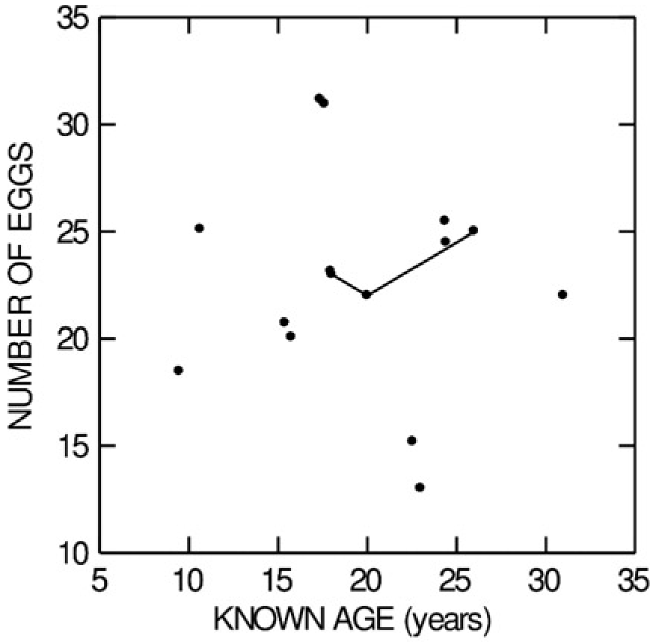

Figure 3. Relationship between the number of eggs in nests and the known ages of female Pantanal caimans. Lines connect data points for one female captured three times.

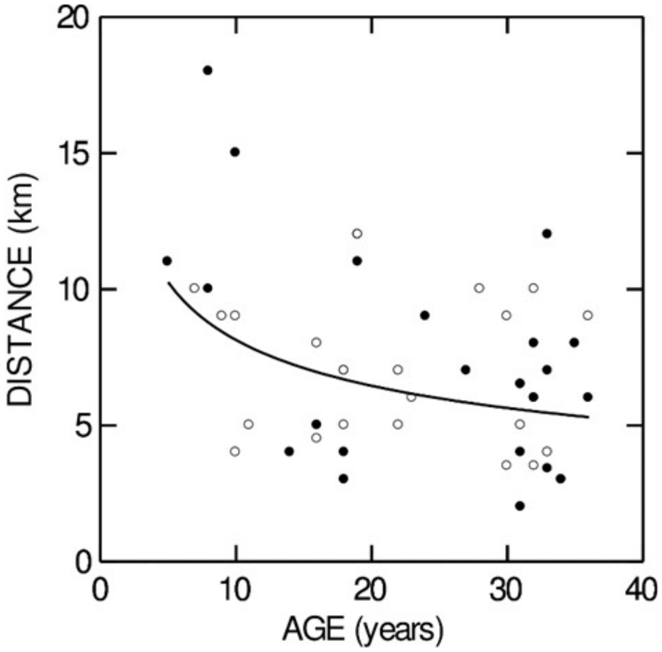

Figure 4. Distance from hatching site at which known-age female (open circles) and male (filled circles) Pantanal caimans were recaptured.

0.33), but few females less than 10 years old were captured. There was no statistically significant relationship between distance from hatching site and age for animals older than 10 years (P = 0.33).

There was a continuous displacement of animals away from nesting areas (Fig. 5), which resulted in a net movement from Nhumirim Ranch in the lake area to the other ranches near the rivers. However, animals showed two distinct displacement patterns; some moved within the ranches (lines parallel to the border between Nhumirim ranch and the other ranches on Figure 5) and others moved from Nhumirim to riverside areas on the other ranches (lines perpendicular to the Nhumirim ranch border on Figure 5). Displacement patterns were similar for males and females, with individuals of both sexes showing the two movement patterns.

DISCUSSION

Long-term data on growth and movement of crocodilians are difficult to obtain (Bayliss, 1987). In this study, we recaptured 50 individuals from a total of >6000 that were marked since 1987, but that required an intensive recapture program over 34 years. The data presented in Campos et al. (2014) suggested that all growth models fit the data well for females but seemed to underestimate growth of males. In contrast, the extended data for animals with ages up to 36 years show that for males all models appear to be unbiased, even if imprecise, but for females the empirical size-age relationship presented by Campos et al. (2014) is biased upward for females. Therefore, conclusions based on such relationships should be used with caution.

One of the major problems with the interpretation of size-age relationships is that there may be large individual variation, which cannot be accounted for without repeated recaptures of individuals (Magnusson, 2012). Growth of crocodilians tends to be deterministic, with negligible growth in large individuals (Wilkinson et al., 2016). This is reflected in the distinct asymptotes for the size-age relationships in Pantanal caimans. However, individual caimans differ greatly in their maximum potential sizes. Three females captured multiple times at nests varied imperceptibly in size among years, and two of those were captured three times, so it was not due to measurement error. Two of those females had snout-vent lengths (SVL) slightly larger than 80 cm, and one was slightly larger than 90 cm. Many females were captured at larger sizes, some of which had multiple recaptures at sizes that spanned the lengths of these three caimans. Therefore, asymptotic size is a characteristic of individuals rather than the species.

Females were found attending nests from 73 cm SVL and 9 years of age, but they continued to grow long after, so cessation of growth does not appear to be related to reproduction. One female was recorded breeding when 31 years old, so reproductive life span is greater than 20 years, and probably much longer, as it is in *A. mississippiensis* (Wilkinson et al., 2016). Larger nesting females tend to be older, and size has a positive effect on clutch mass, though this may be mediated through egg volume rather than clutch size (e.g. Larriera et al., 2004; Campos et al., 2008; 2015). Data on 13 known-age individuals indicates that age has a negative effect on clutch size independent of size, and the very weak relationship between age and size for those animals indicates that this is not because larger females tend to produce fewer larger eggs. This aspect needs further research, but the tendency may indicate the onset of reproductive senility.

Of the five individuals (four of which were male) that were recaptured when less than 8 years old, all had moved more than 10 km from their hatching site. In contrast,

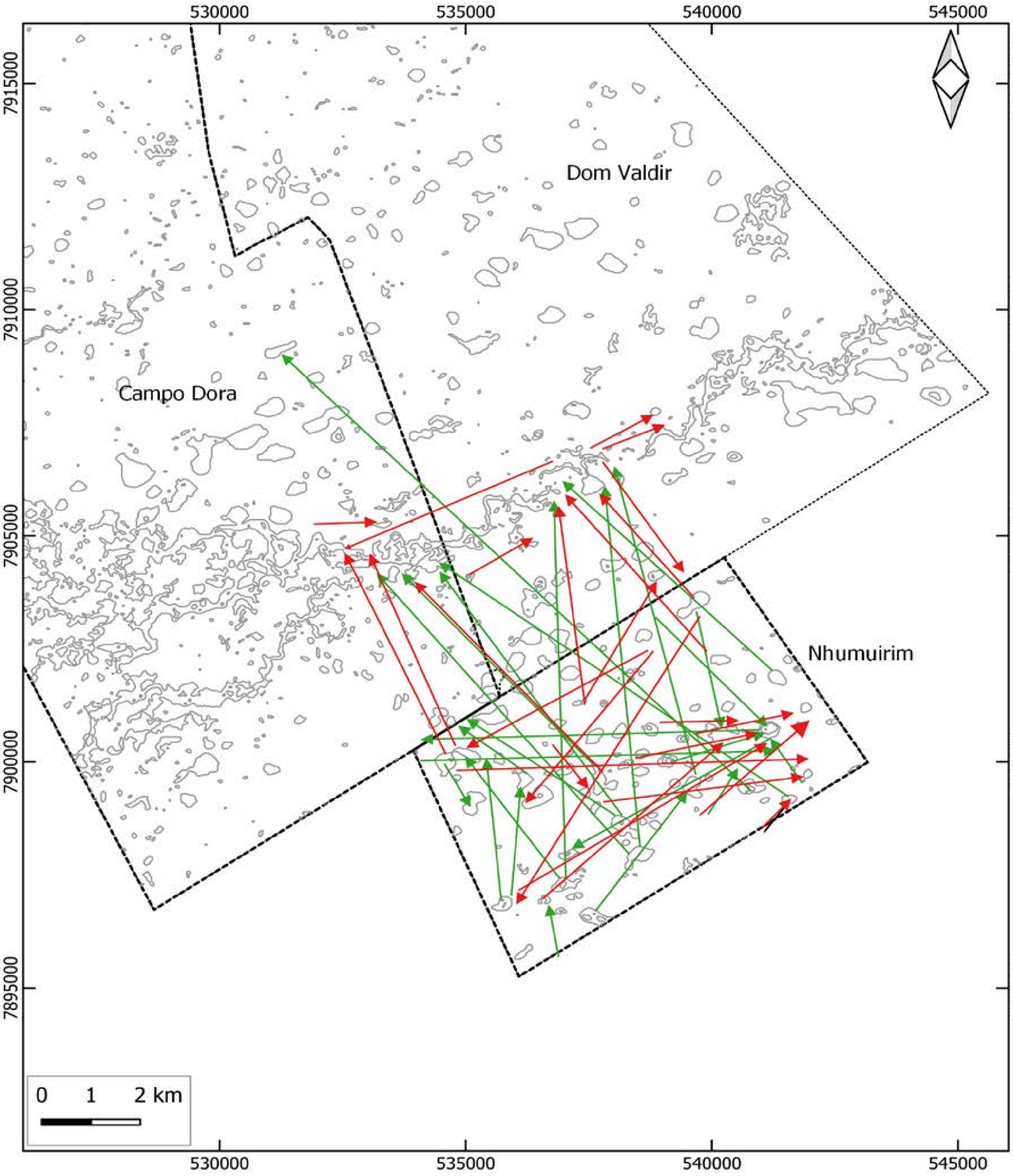

Figure 5. Map based on a Sentinel 2 satellite image of the study area (https://scihub.copernicus.eu/dhus/#/home). Polygons represent water bodies and the arrows indicate the capture and recapture sites from each caiman between 2007 and 2021. The displacements of male caimans are shown as green lines and the females as red lines.

most individuals recaptured when more than 10 years old had moved less than 10 km from the original nest site. This is consistent with the findings of Campos et al. (2006) that smaller animals move greater distances than larger individuals. The sharp cutoff in distances moved at about 10 km, especially for females, indicates that management units of these dimensions may be functionally autonomous, but movements of this order indicate that many or most individuals may not establish in the ranch in which they hatched, an important consideration for the definition of management units in the Pantanal (Campos et al., 2006).

Campos et al. (2006) reported a tendency for movement of animals away from nesting areas, which resulted in a net movement from Nhumirim Ranch in the lake area to the other ranches near the rivers. This tendency continued over the following 14 years, the animals showing two distinct movement patterns; some moved within the ranches and others moved from Nhumirim Ranch to riverside areas on the other ranches. This indicates a possible distinction between the principal areas used for nesting and areas where most growth of juveniles occurs. The area of isolated lakes may be less suitable for the maintenance of adults, as indicated by the smaller sizes of females captured near nests on Nhumirim Ranch than on other ranches (Campos et al., 2006). This is also reflected in smaller clutch sizes on Nhumirim Ranch (Campos & Magnusson, 1995). Despite a general tendency for juveniles to move away from the area, there was a much greater proportion of juveniles on Nhumirim Ranch than on the ranches in the river area (Campos et al., 2006). Perhaps nest success or survivorship of hatchlings compensates for the apparent lower productivity of the area.

It has been suggested that for female Pantanal caimans the minimum age at reproduction was 13 years (Campos et al., 2014), this was based on the size-age relationships and known size at reproduction. However, the long-term data clearly show first reproduction can occur at 9 years old. This reinforces the warning by Campos et al. (2014) that size-age relationships are unreliable and that care should be exercised when making extrapolations based on them, especially estimates of age based on size.

The short- and long-term studies of the Pantanal caiman all point to heterogeneity in individual life-history characteristics, such as growth, asymptotic size and clutch size, combined with large-scale heterogeneity in movement patterns associated with habitat selection. The long potential reproductive life span may reduce the effect of this heterogeneity on density variation, and most of the fluctuations in nesting effort between 1985 and 2015 were not related to environmental variables (Campos et al., 2015), but generic population models for the whole Pantanal will probably be unrealistic and modeling of local situations will be necessary to understand fluctuations in caiman numbers. This is especially important because the Pantanal appears to be moving from a relatively stable wet period that started in the 1970s and lasted until 2018, and is now returning to a more variable and dryer regime that was typical of most of the period of monitoring from 1900 (Marengo et al., 2016; 2021).

We will discuss the relationship between size at first reproduction and asymptotic size only for females, as males are probably physiologically capable of breeding long before they can get access the reproductive females to sire offspring (Coutinho et al., 2001). Based on the ratio of the size of the smallest reproductive female and asymptotic size, female Pantanal caimans first breed at about 86% of maximum size. However, that does not take into account the fact that many females stop growing long before reaching this size. For them, size at first breeding would be a much larger fraction of maximum size, especially if they started nesting at sizes larger than the smallest female we recorded.

The issue of how to estimate maximum size is not trivial. Use of mean asymptotic size and mean size at first reproduction (Shine & Iverson, 1985), would lead to estimates of the ratio of size at reproduction to maximum size in the Pantanal caiman much larger than that reported for other reptiles. Based on large samples of nesting females the ratio of maximum and minimum recorded size, which is a much more conservative index than that of Shine & Iverson (1985), the ratio differs between *C. yacare* (0.77) and *C. crocodilus* from central Amazonia (0.72) (Campos et al., 2008). To determine whether crocodilians in general have ratios of size at first reproduction to maximum size greater than 0.7 will require data on more species, all with population parameters estimated in the same manner.

ACKNOWLEDGEMENTS

We are grateful for the unconditional support of Embrapa Pantanal colleagues, Franscico Alves (in memoriam), Luís Espinoza (in memoriam), Procópio Ferreira (in memoriam), José Augusto Silva, Vandir Silva, Henrique de Jesus, Luís Alberto Rondon Denis Celin, Sandra Santos, Max Pinheiro and Marcos Coutinho. Also, we thank Luis Gomes da Silva (owner Campo Dora Ranch, in memoriam) and Vicente Gomes da Silva (owner Dom Valdir). The map was prepared by Luiz Alberto Pellegrin, Sensory Laboratory. WEM received a productivity grant from CNPq. Processo 3-7178/2021-8. Data were deposited in PPBio site https://search.dataone.org/view/PPBioAmOc.684.1; and data files hosted by Dryad and by Protocolis.io.

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Accepted: 12 May 2024

Please note that the Supplementary Material for this article is available online via the Herpetological Bulletin website: https://thebhs.org/publications/the-herpetological-bulletin/issue-number-170-winter-2024