REPTILES & AMPHIBIANS

Nesting Ecology of Black Caimans, *Melanosuchus niger* (Spix 1825) (Crocodylia: Alligatoridae), in the Lago do Cuniã Extractive Reserve, Amazon, Brazil

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Abstract.—The reproductive success of a population is the expression of life history traits such as fecundity and fertility, which are strongly affected by ecological factors. We investigated the use of nesting sites by female Black Caimans, *Melanosuchus niger* (Spix 1825) during three consecutive nesting seasons from 2019 to 2021 at Lago do Cuniã Extractive Reserve in the southwestern Brazilian Amazon. We examined factors influencing nesting ecology such as chamber temperature and applied multiple linear regressions to test hypotheses related to reproductive trade-offs between different variables, such as female, egg, and clutch sizes. We identified trade-offs between egg width, hatchling size, and clutch size, suggesting that larger clutches contain smaller eggs, resulting in smaller hatchlings. A better understanding of crocodilian reproductive strategies and trade-offs are essential to predict the viability of populations and to foster conservation initiatives at the Lago do Cuniã Reserve, where caimans are currently subjected to a sustainable harvesting management plan.

Resumo.—O sucesso reprodutivo de uma população abrange fatores ecológicos e biológicos, como fecundidade e fertilidade, história de vida e razão sexual. No presente estudo nós avaliamos o uso de áreas de nidificação por fêmeas de jacaré-açu (*Melanosuchus niger* Spix 1825) durante 2019-2021 na Reserva Extrativista Lago do Cuniã, os fatores que influenciam a ecologia de nidificação como a temperatura do ninho e os trade-offs reprodutivos que influenciam a biometria das ninhadas. Usamos regressões lineares, múltiplas e GLMM para testar as diferentes hipóteses. Trade-offs importantes foram encontrados entre largura dos ovos/ tamanho da ninhada e o tamanho dos filhotes, sugerindo que ninhadas maiores produziram ovos menores, porém com embriões maiores. Essas informações são essenciais para um melhor entendimento acerca das estratégias reprodutivas utilizadas pelas fêmeas reprodutivas e seus efeitos sobre a viabilidade da população na Reserva.

The nesting ecology of the order Crocodylia is influenced by several factors, including the choice of nesting habitats, nest chamber temperature, clutch size and mass, female size and egg biometry. Research on these factors has been conducted across a variety of crocodilian species (Murray et al. 2019). Nest temperature plays a crucial role in crocodilian reproduction, influencing both thermoregulation and sex determination of offspring.

Two main temperature-dependent sex determination (TSD) patterns have been documented: a unilateral one, where sex is defined under only one temperature range (e.g., males being produced at higher temperatures and females at lower temperatures); and a bilateral one, where sex can have more than one temperature range (e.g., females are produced under low and high temperatures, and males at the mean temperature) (Lang and Andrews 1994; González et al. 2019). Studies performed by Campos (2003), Escobedo-Galván (2006), and Villamarín-Jurado and Suarez (2007) described the effect of environmental sources such as insolation, humidity, and air temperature on crocodilian nest temperatures during the incubation period, thus influencing the sex ratio within clutches. Ultimately, together with survival rates, such patterns determine population sex ratios.

Extensive research has explored nesting ecology and habitat selection in various crocodilian species, including Morelet's Crocodile, *Crocodylus moreletii* (Duméril and Bibron 1851) (Villegas et al. 2017); American Crocodile, *Crocodylus acutus* (Cuvier 1807) (Casas-Andreu 2003); Yacare Caiman, *Caiman yacare* (Daudin 1801) (Campos 1993; Coutinho 2000); Broad-snouted Caiman, *Caiman latirostris* (Daudin 1801) (Montini et al. 2006); Freshwater Crocodile, *Crocodylus johnstoni* (Krefft 1873) (Somaweera and Shine 2012); Spectacled Caiman, *Caiman crocodilus* (Linnaeus 1758) (Da Silveira et al. 1997; Villamarín et al. 2011); Cuvier's Dwarf Caiman, *Paleosuchus palpebrosus* (Cuvier 1807) (Da Silva 2020); and Black Caiman, *Melanosuchus niger* (Spix 1825) (Thorbjarnarson and Da Silveira 2000; Villamarín-Jurado and Suárez 2007).

The Black Caiman is a mound nester, with nesting females typically choosing sites along the margins of partially dammed floodplains, which are isolated from the inundation of main rivers. This preference for areas with greater water stability serves to prevent nest flooding by the end of the nesting period, which coincides with the onset of the rainy season in the Amazon Rainforest (Thorbjarnarson and Da Silveira 2000; Banon et al. 2019). Depending on factors such as temperature and humidity, the incubation period can last from 80 to 90 days, a period during which females can be found displaying vigilant behavior close to their nests (Villamarín et al. 2011). Although ages and sizes of nesting females remain poorly known, females reach reproductive maturation at an estimated 185 cm total length (TL), with a mean reproductive size of 250 cm TL (Thorbjarnarson 1996; Ross 1998; Da Silveira 2001). The study conducted by Da Silveira et al. (1997) provided relevant information regarding nesting habitat selection by Black Caimans in the Amazonian Anavilhanas Archipelago. However, trade-offs and biometric aspects of both clutches and females, and effects of environmental factors on nesting ecology are still not fully understood, leaving important gaps in our understanding of the species' life history.

Life-history theory indicates that resources are allocated to growth and reproduction in certain optimal proportions, which are context-dependent. Since resources are likely to be limited, growth and reproduction-related traits cannot be simultaneously optimized, resulting in negative relationships between such traits that are known as trade-offs (Stearns 1989). Consistent patterns of trade-offs involving biological factors such as egg dimensions and clutch sizes are known in the Alligatoridae, where larger clutches with smaller eggs are characteristic of *Alligator* spp., whereas heavier clutches are associated with the production of larger eggs rather than the number of eggs in *Paleosuchus* spp. and *Melanosuchus niger* or larger clutches in *Caiman* spp. (Thorbjarnarson 1996). Previous studies have shown that egg biometry is related to offspring size (Piña et al. 1996; Larriera et al.

2004) and, consequently, to offspring survivorship (Campos 2003), suggesting that the trade-off between clutch size and egg size might be associated with reproductive success in crocodilian species. Additionally, the apparent influence of external conditions on the process of incubation and hatchling survival (e.g., higher nest temperatures affect offspring survival; Allsteadt and Lang 1995) indicates a need to study crocodilian life history trade-offs in the context of the environmental conditions affecting their nests.

The Lago do Cuniã Extractive Reserve is the only reserve in the Brazilian Amazon where natural populations of Black Caimans and Spectacled Caimans are currently subjected to a legal sustainable harvesting management plan (Coutinho et al. 2021). Management strategies for crocodilians often include sex- and size-specific quotas designed to protect breeding females. Therefore, understanding reproductive trade-offs of Black Caimans is imperative for the success of such strategies. Given that the Black Caiman harvesting quotas at Lago do Cuniã Extractive Reserve are male-size-selective, comprehending how environmental factors and reproductive trade-offs affect hatchling biology and population growth is needed to understand and monitor the dynamics of populations subjected to harvesting.

Hence, we investigated how nest temperature is related to air temperature, humidity, nest distance from the water, insolation, and clutch and nest sizes. We also hypothesized that (i) egg dimensions would be related to clutch size, (ii) egg mass would be negatively related to clutch size, and (iii) nest temperature and egg mass and size would be positively related to hatchling size.

Materials and Methods

We conducted this study in the Lago do Cuniã Extractive Reserve (Resex) located along the lower Madeira River in the State of Rondônia in the western Brazilian Amazon (Fig. 1). The Reserve encompasses 75,876.67 ha, 18,000 ha of which are characterized by the presence of water channels, locally known as igarapés, and lakes that may be interconnected from December to June/July, depending on the duration of the flood season.

We conducted surveys in a 3,450-ha area, encompassing two igarapés named Igarapé do Campo and Igarapé Grande, located adjacent to Cuniã and Arrozal Lakes. Igarapé Grande is characterized by its large size, dense vegetation, and high sinuosity to the north, where it connects with the Madeira River. Igarapé do Campo is a straighter body of water. Bushes grow between forest fragments along Igarapé do Campo, which ends in a large lake called Lago do Campo. In contrast to the uniformity of the igarapés, Arrozal Lake can be divided into two sections. The first section is narrow and almost completely filled with aquatic vegetation. The second section is a lake surrounded by both aquatic vegetation and dense forest.
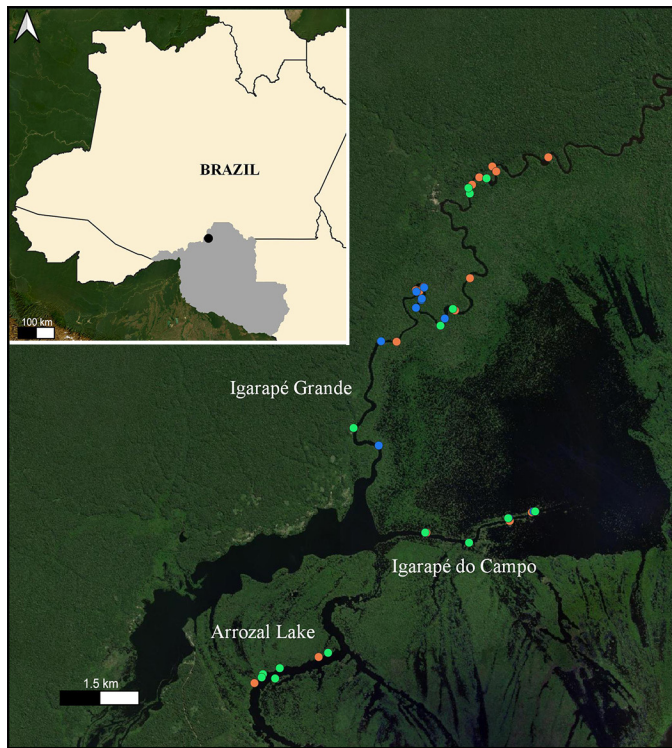
Figure 1. Georeferenced map of the Lago do Cuniã Extractive Reserve, Amazon (Datum: SIRGAS 2000), showing Black Caiman (*Melanosuchus niger*) nest distribution. Nests by year are indicated by orange dots (2019), blue dots (2020), and green dots (2021). Inset: Rondonia is shown in gray and the city of Porto Velho is indicated by the black dot. Map by Helena Gurjão Pinheiro do Val.

Field methods. *Nesting ecology.*—Experienced observers conducted nest surveys on foot alongside the bodies of water from September to November in 2019–2021. For every located nest (Fig. 2), the following data were recorded according to a standardized protocol defined by the Brazilian Federal Center for Research and Conservation of Reptiles and Amphibians (RAN) of the Chico Mendes Institute for Conservation of Biodiversity (ICMBio): air and nest chamber temperature using a thermistor (HI93510N; Hanna®, Barueri, Brazil) accurate to 0.01 °C; distance of the nest from water using a 50-m tape measure, insolation (i.e., exposure to sun or shade) defined as shaded, mixed shade, or sunny and exposed to the sun. To classify nests as 'large' or 'small,' we calculated the average size of nests (n = 27, mean length = 136 cm) and considered nests with lengths greater than 136 cm as large and those with lengths less than 136 cm as small.

Trade-offs.—Nests were considered intact when no sign of disturbance or predation were observed, including the presence of shells in the surrounding area. From each nest, all eggs were counted, and a random sample of six were weighed using a digital scale (accurate to 0.01g). We used these data to estimate clutch mass by multiplying the total number of eggs by the mean weight of the random sample. Egg length and width were measured using a caliper. All analyses encompassing clutch size and related variables (egg length, egg mass, egg width, and clutch mass) were performed only on intact nests. Nesting females are difficult to capture, both because they are rather wary but also because they can be dangerous. When the situation permitted a safe capture, we attracted the female by making noise close to the nest. Once the female was on land, we used a noose to capture and hold her, blindfolded her with tape, and tied her limbs with

Figure 2. A Black Caiman (*Melanosuchus niger*) female attending its nest (left) and a Black Caiman nest (right). Photographs by Joilson Barros and Helena Gurjão Pinheiro do Val.

Table 1. Statistical models used to test the hypothesis regarding Black Caiman (*Melanosuchus niger*) nesting ecology and reproductive trade-offs.

Hypothesis	Statistical Model	Dependent Variable	Independent Variables
1	GLM	Nest temperature	Air temperature, distance from water's edge, clutch size, insolation, nest length
2	Multiple regression	Clutch mass	Egg size, egg mass
3	Multiple regression	Hatchling size	Nest temperature, egg width, egg length

ropes before measuring her snout-vent length (SVL). When capture was not possible, female length was estimated using a graduated ruler made of a bamboo rod marked every 5 cm. During the nesting period, nesting females remain nearby in the river to protect their nests from predators. Therefore, we can assure that each measured female in the study was related to a particular nest.

In 2019, three intact nests were randomly selected and monitored throughout their incubation periods. We visited each nest every three to five days until the eggs hatched. Hatchling biometric data used in the present study referred to the 17 hatchlings found in their respective nests. Additionally, regarding the monitored nests, we set data loggers in two nests to measure maximum, minimum, and mean nest temperatures throughout the incubation period.

Data analysis. *Nesting Ecology.*—We used a generalized multilinear model to investigate whether abiotic (air temperature, distance from water, insolation) and biotic variables (clutch size) influenced the temperature of the nest chamber.

Trade-offs.—In order to select among the biometric variables, we performed a Principal Component Analysis (PCA), which showed a correlation between egg length, width, and volume. As egg width seemed to have a greater impact on other analyses than either length or volume, we focused on egg width as a measure of egg size. To test hypotheses related to life-history, we performed linear and multiple regressions using R software (Bates et al. 2022) (Table 1). All values were transformed to natural logarithms (Ln) to normalize data variation; significance level was defined as $p < 0.05$ for all tests.

Results

Nesting ecology.—The nesting season of Black Caimans at Lago do Cuniã begins in late August at the end of the dry season and hatchlings are seen at the beginning of the rainy season by the end of November. During three years, we examined 47 nests (17 in 2019, 15 in 2020, and 15 in 2021), 25 (53%) were at Igarapé Grande, 15 (32%) in Igarapé do Campo, and 7 (15%) at Arrozal Lake. Nests were under trees, such as the Three-leaf Piranhea (*Piranhea trifoliata*) in the Igarapé do Campo, whereas in the Igarapé Grande, nests were
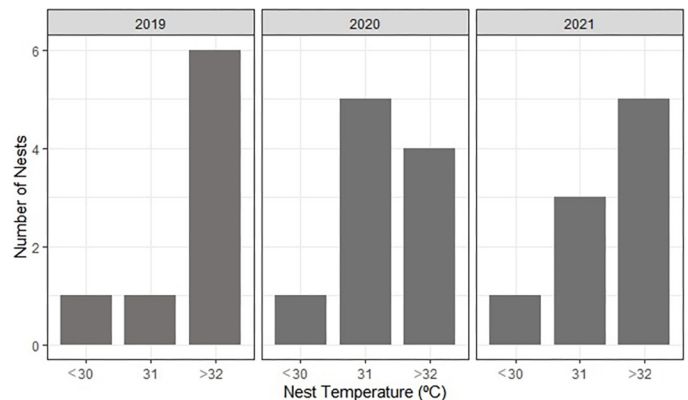
Figure 3. Black Caiman (*Melanosuchus niger*) nest temperature distribution from 2019 to 2021 at Lago do Cuniã Reserve, Brazilian Amazon.

constructed among bamboo groves and termite mounds. At Arrozal Lake, nests were located in steep forest terrain.

Most of the nests were intact (27 nests, 57%), whereas 4 (9%) were partially affected by predators, 14 (30%) were completely destroyed by predators, and 2 (4%) had already hatched. Both nests that had hatched previously were found in mid-November 2021, indicating that, on average, the incubation period is about 90 days. We observed females near 12 (25%) of the 47 nests.

Of the 27 intact nests, 25 had coverage levels recorded, 15 were covered by canopy (shaded), four were partially exposed to the sun (mixed cover), and six nests were completely exposed to sunlight. Air and nest temperatures (Fig. 3) were registered for the 27 intact nests and varied from 29.2 to 35.4 °C (n = 27; mean = 32.3 ± 1.3 °C) and 22.9 to 32.4 °C (n = 27; mean = 29.6 ± 2.2 °C), respectively, whereas distance from the water varied from 2 to 25 m (n = 27; mean = 7.18 ± 6.30 m). Maximum nest and air temperatures from the monitored nests were 30.5–32.8 °C (n = 8; mean = 31.20 ± 0.87 °C) and 32.8–34.2 °C (n = 9; mean = 33.60 ± 0.66 m), respectively; minimum nest temperatures were 28.5–30.5 °C (n = 8; mean = 29.50 ± 0.45 °C) and air temperature 29.8–32.7 °C (n = 9; mean = 31.80 ± 1.03 °C).

Nest temperature varied independently of air temperature and distance from water, but was negatively affected by clutch size ($p < 0.01$) and positively correlated with hatchlings size ($p < 0.01$) (Table 2). Additionally, nest size was negatively

Table 2. Statistical values from General Linear Model (GLM), ANOVA, and regression analysis of Black Caiman (*Melanosuchus niger*) nests in the Lago do Cuniã Extractive Reserve in 2019–2021.

| Variables	slope	R²	F/t	*P*-value
Nesting Ecology				
Nest Temperature				
Air temperature	-0.003	0.53	0.06	0.79
Distance from the water edge	0.000		3.14	0.07
Clutch size	-0.08		43.72	< 0.01
Insolation: nest length	0.03	0.53	12.07	< 0.01
Small + mixed	-1.63		-3.56	< 0.01
Small + shade	0.93		2.55	0.01
Trade-offs				
Clutch Mass				
Clutch size	1.05	0.90	1405.22	< 0.01
Egg width	1.71		78.00	< 0.01
Egg Width				
Clutch size	-0.01	0.027	6.14	0.01
Hatchlings Size				
Nest temperature	4.58	0.84	34.62	< 0.01
Egg width	1.55		9.45	0.008
Egg length	0.81		5.46	0.03
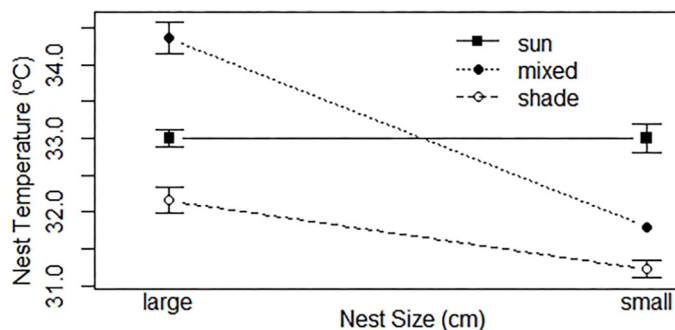
Figure 4. Mean and standard deviation of Black Caiman (*Melanosuchus niger*) nest temperatures according to nest size (large and small) and insolation levels (mixed, sun, and shadow).

related to nest temperature (p < 0.01), but the most significant result was the interaction between nest size and nest coverage (p < 0.01, see Table 2). These results indicate that small nests in mixed shaded areas had lower nest temperatures when compared to large nests also located in mixed shaded areas, and that small nests in shaded areas also had lower temperatures when compared with large nests with the same coverage. However, nest size did not affect nest temperature in nests without shade (Fig. 4).

Trade-offs.—Female total length was 180–340 cm (n = 16; mean = 252.2 ± 4.1 cm). Clutch mass was 2.0–5.3 kg (n = 27; mean = 4.1 ± 0.9 kg) and clutch size was 20–45 eggs (n = 31; mean = 29.9 ± 9.8). Egg width, length, and mass was 46–57 mm (n = 180; mean = 51. ± 21.8 mm), 76–100 mm (n = 180; mean = 84.4 ± 3.8 mm), and 104–165 g (n = 180; mean= 131.7. ± 12.8 g), respectively. Clutch mass was positively affected by both clutch size and egg width (n = 27, F = 566.35, r² = 0.915, df = 3, p < 0.001), mostly by egg width, as seen in the regression slope (see Table 2). Egg width showed a significant negative relationship with clutch size (n = 30, F = 6.14, r² = 0.027, df = 1, p = 0.014), supporting our hypothesis regarding constraints between clutch and egg sizes. Hatchling size was affected positively by both nest temperature and egg width (Table 2).

Discussion

Nesting ecology.—The abundance and density of Black Caiman nests found over the years at Lago do Cuniã Extractive Reserve is indicative of high environmental quality capable of providing both nesting and food resources to the crocodilian population. Also, the low variability in the number of nests among years appears to be an accurate indicator of the high population reproductive rate, probably with new reproductive females being recruited every year. In fact, nocturnal surveys conducted in 2004–2023 revealed a

robust crocodilian population and that, on average, the Black Caiman population has been increasing annually by 6% at Lago do Cuniã Extractive Reserve (RAN/ICMBio 2023).

Like those of most crocodilians, Black Caiman eggs in the Cuniã reserve are susceptible to predation by a number of predators, including Tegus (*Tupinambis* spp.), Jaguars (*Panthera onca*), Capuchin Monkeys (*Sapajus apella*), and Common Opossums (*Didelphis marsupialis*). Hatchlings could also be vulnerable to predators when leaving the nest and moving to water, suggesting that synchronizing hatching with the beginning of the rainy season and rise of the water level could have been an adaptive response to increase hatchling survival.

Nest temperatures showed a variation of 6.2 °C, whereas air temperature varied 9.7 °C. As observed in the field, some of this variation is attributable to rainy periods during the incubation period. We hypothesized that air temperature and distance from water would affect nest temperature. This was based on the assumption that short distance from water increased humidity within the nest and helped maintain a suitable environment for fermentation of nest materials, which would provide heat to keep nest temperature stable (López-Luna et al. 2020; Campos 2003; Escobedo-Galván 2006). However, such relationships were not statistically significant. On the other hand, we observed that an increase in clutch size caused nest temperature to decrease at a rate of -0.08 °C per unit increase in clutch size. This result, however, contradicts observations of American Crocodiles (Barragán Lara et al. 2021), in which mean clutch size and mean nest temperature were positively related.

Nest temperature, due to its role in determining clutch sex-ratio, has also been reported to affect hatchling size (Campos 2003). Hatchling size is believed to influence female fitness as larger hatchlings usually have higher growth rates, which in turn increases survival (Messel and Volicek 1989; Benabib 2009). Our results indicated that eggs incubated at < 31 °C and > 33 °C produced larger hatchlings when compared to eggs incubated at intermediate temperatures. Such a relationship was previously found for *Caiman latirostris,* in which larger hatchlings were recorded at an incubation temperature of 31 °C (Piña et al. 2007), and that altering temperatures to ~32 °C had a negative effect on hatchling size when compared to hatchlings maintained at constant temperatures between 32 °C and 33 °C (Simoncini et al. 2019). Likewise, hatchlings incubated at 31 °C were larger when compared to those incubated at 29 °C (Parachú Marcó et al. 2010). Moreover, studies also have described similar effects on hatchling growth and development under low (*Crocodylus porosus* and *C. johnstoni*; Webb et al. 1987), intermediate (*Crocodylus niloticus*; Hutton 1987; *Caiman latirostris*; Piña et al. 2007; and *Alligator mississippiensis*; Allsteadt and Lang 1995), and high temperatures (*Caiman yacare*; Campos 1993).

We observed that fully insolated nests, regardless of size, showed little variation in chamber temperatures when compared to nests located in shaded or mixed shaded areas. These results are congruent with those of Barragán Lara et al. (2021), who observed a negative correlation between direct solar radiation and nest temperature in American Crocodiles. When adding nest size as a covariate, our results agreed with those of López-Luna et al. (2020), in that smaller nests in shaded areas have cooler temperatures than larger nests in sunny areas. We also observed that nest size seems to play an important role in nest temperature, as large and small nests under the same environmental conditions (mixed and shaded areas), differed significantly in chamber temperature, confirming our hypothesis that nest size would affect nest temperature (Table 2).

Nest size in mixed areas is negatively correlated to nest temperature (Table 2), suggesting that variation in chamber temperature is more pronounced in nests that are exposed to both sun and shade periods, than those under a constant condition. Moreover, the type of material used to build the nest and the level of compaction can vary with nest size, which in turn could have an effect on nest temperature. This is in agreement with data in López-Luna et al. (2020).

Nest temperature influences crocodilian embryos in different stages of development, determining sex and influencing phenotypic characteristics during the embryonic period (Lance 2008; Miranda et al. 2012; Singh et al. 2020). According to previous experiments conducted with caimans, incubation temperatures ≥ 32 °C result mostly in males, whereas sex ratios vary at 31 °C, and temperatures < 31 °C result most in females (Gonzalez et al. 2019). *Melanosuchus* is a monotypic genus and, although the Broad-snouted Caiman is the closest relative of the Black Caiman, effects of temperature could differ. However, given the lack of studies on effects of temperature on sex ratios in Black Caiman clutches, we adopted the temperature ratio compiled by Gonzalez et al. (2019). Of 27 intact nests, 14 had chamber temperatures > 32 °C (male-biased sex ratio), nine had temperatures ~31 °C (mixed sex ratio), and four had temperatures < 31 °C (female-biased sex ratio) (Fig. 3). In fact, we did observe the same sex ratios in young and adult individuals at Lago do Cuniã Reserve (RAN/ICMBio 2023), which suggests that survival is not sex-biased within the population.

Trade-offs.—Female size at first reproduction has been studied in several crocodilian species (Thorbjarnarson 1996; Campos 2003; Kofron 2009; Leiva et al. 2019). According to Thorbjarnarson (1996), female *Melanosuchus niger* start to breed at approximately 180 cm TL, although Barão-Nóbrega et al. (2017) described a mean size of nesting females of 270 cm TL. At Lago do Cuniã Reserve, the size of females found in close proximity to nests ranged from 180 to 340 cm TL, which is in agreement with the literature. When compared

to other alligatorids, at 230 cm TL, female *M. niger* size at first reproduction approaches that of the American Alligator (*Alligator mississippiensis*) (Guillete et al. 1997), and is slightly larger when compared to other medium-sized crocodilians such as the Broad-snouted Caiman (*Caiman latirostris*) (136–196 cm TL) (Leiva et al. 2019) and Spectacled Caiman *Caiman crocodilus*) (147 cm TL) (Barão-Nóbrega et al. 2017).

A positive relationship between clutch size/mass and female size/mass has been described for a number of crocodilian species (reviewed in Thorbjarnarson 1996). Presumably, larger females would be able to allocate more space to eggs, generating larger (and heavier) clutches. However, we found no significant relationship between clutch size/mass and female size, possibly because clutch size and mass are more a factor of female body mass and condition than size.

Trade-offs are an important component of life-history theory. Trade-offs between clutch size, egg size/mass, and female size have been reported for *Alligator mississippiensis* (Deitz and Hines 1980), *Caiman yacare* (Coutinho 2000), and *Caiman crocodilus* (Campos et al. 2008). Contrary to most findings, Larriera et al. (2004) demonstrated that larger female *Caiman latirostris* produce relatively smaller clutches of larger eggs. For *M. niger* the relationship between clutch mass and clutch size is statistically stronger than that of clutch mass and egg dimensions, which indicates that heavier clutches are mainly attributable to a greater number of eggs rather than fewer larger eggs. Crocodilian fertility depends not only on clutch size, but also on hatchling size and survival mainly through the first year of life, when hatchlings are most vulnerable to predators (Campos 2003) — and hatchling size is known to be affected by egg size (Piña et al. 1996).

In *M. niger*, egg width has a greater effect on hatchling size than egg length, which is in agreement with results obtained by Webb et al. (1983) and Brien et al. (2014) for *Crocodylus porosus* and by Larriera et al. (2004) for *Caiman latirostris*. Likewise, Lakin et al. (2020) also found a positive correlation between egg mass and hatchling mass for 23 crocodilian species distributed across the Asian-Pacific, the Americas, and Africa, among them the Black Caiman.

Relationships between hatchling size, clutch size, and egg dimensions provides new insights into *M. niger* nesting behavior. The negative effect of clutch size on egg width and the positive effect of egg width on hatchlings size indicate that larger clutches composed of smaller eggs produce smaller hatchlings, implying that females invest in litter quality (measured as hatchling size) at the expense of clutch size. As egg production demands energy allocation, females could produce few large eggs (improving quality) or several small eggs (favoring quantity). According to Mejíla-Reyes et al. (2023), this could be driven by selective pressures, where in a highly competitive environment females might produce

fewer competitive offspring rather than numerous smaller hatchlings. In contrast, in a less competitive condition, producing more eggs could improve female fitness.

The Lago do Cuniã Extractive Reserve supports a robust breeding population of *M. niger*, with females beginning to breed at 180 cm TL. The complex relationship between the material used to build nests, nest size, nest insolation, and clutch and egg dimensions ultimately results in a male-biased hatchling sex ratio. This supports the male size-specific harvest strategy currently applied in the reserve. Additionally, given that the sex ratio of the adult population is also male-biased, we conclude that the mortality rate is not sex-specific. As observed in other crocodilian species, trade-offs play an important role in *M. niger* reproductive behavior, the most important being the negative relationship between egg width and clutch size and the positive relationship between hatchling size and egg width, implying that hatchling quality (measured by hatchling size) depends on clutch size. Understanding how reproductive behavior and life-history traits reflect the adaptation of *M. niger* to an unstable habitat is essential to guide sustainable management of the species in the Brazilian Amazon forest.

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