

Ecology of *Phrynops geoffroanus* and *Mesoclemmys tuberculata* (Testudines: Chelidae) in Climatically Distinct Areas of the Semi-Arid Caatinga and Atlantic Forest in Northeast Brazil

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ABSTRACT. – In general, chelonians are widely distributed, occupying areas with significant environmental variation, which may lead to great variations in their ecology such as morphological characteristics, sexual dimorphism, population structure, and reproductive aspects. In this context, our main objective was to characterize populations of *Phrynops geoffroanus* and *Mesoclemmys tuberculata* in areas of Caatinga and Atlantic Forest in Northeast Brazil to evaluate the relative importance of intraspecific factors and environmental differences in determining ecological parameters. Samples were collected in semiannual surveys (dry and rainy season) over a year. We measured morphometric variables and the mass of captured animals and correlated the reproductive pattern with the season and adults' reproductive condition. We did not find significant differences in size, maximum straight-line carapace length (SCL), or body mass of both species, regardless of sex, between the studied environments. We recorded reproductive males of both species throughout the year (dry and rainy seasons), and testicular volume was positively correlated with SCL. In contrast, eggs and oocytes were recorded exclusively in females collected during the rainy season. However, we found eggs and vitellogenic follicles simultaneously, indicative of multiple clutches in a reproductive season. In *P. geoffroanus*, we did not find a significant relationship between clutch size and female SCL, although egg volume was positively correlated with SCL. In *M. tuberculata*, we did not find a meaningful relationship between any of these parameters. Finally, the ecological parameters evaluated differed considerably between species and environments, presenting similar patterns in Caatinga and Atlantic Forest.

KEY WORDS. – Chelonian; freshwater turtles; morphology; sex ratio; size; reproduction

Turtles are animals with moderate investment in reproduction and reproductive parameters, which are generally influenced by environmental factors such as climate (Souza and Abe 2001; Vitt and Caldwell 2014). Especially for species with wide distributions, characteristics such as size at maturity, nesting period, clutch size, and frequency of reproductive events tend to vary according to temperature and precipitation gradients, reflecting genetic differences and/or resource availability in the environment (Gibbons et al. 1981; Gibbons and Greene 1990). Comparative data from different populations are essential to understanding plasticity in species reproduction. Population studies in areas with different climatic regimes are especially valuable because they can provide conditions to evaluate geographical ecology patterns (MacArthur 1972; Aresco 2004). Information regarding the population structure of freshwater turtles is needed for management and conservation purposes (Gibbons et al. 2000; Primack 2012; Stanford et al.

2020). However, such data are still scarce for the Neotropical region (Marques et al. 2013). In addition, these studies can also provide a powerful means of refining and testing models related to the life history theory and the influence of environmental variation on species (Dunham and Overall 1994). Characterization of the age structure, sex ratio, and morphological variations between sexes are important tools in interpreting the ecological processes that act on natural populations (Gibbons et al. 2001; Aponte et al. 2003; Silveira et al. 2012).

Species that occupy large areas with significant environmental variation may vary significantly in their autoecology (Clavijo-Baquet et al. 2010; Litzgus and Smith 2010). Morphological variation is commonly observed in turtle populations (Lucas et al. 2020). However, it is difficult to quantify and identify the evolutionary processes that have shaped such variation due to the complex interactions between the phenotype and the behavior of these animals (Delmas et al. 2007;

Litzgus and Smith 2010). This variation can be promoted by selective pressures or ecological factors, such as predation. In addition, the availability of food resources and reproductive behaviors may also influence the morphology of chelonians (Willemsen and Hailey 2003; Barros et al. 2012).

Phrynops Geoffroanus has a wide geographic distribution in South America, from the Colombian Amazon to southern Brazil and northern Argentina (Rueda-Almonacid et al. 2007; Ferronato et al. 2009). It is found in the main hydrographic basins of the region and occurs in varied aquatic environments such as rivers, streams, and lakes (Costa et al. 2018; Pereira et al. 2018; Abrantes et al. 2021) and is even commonly found in urban environments (Martins et al. 2010; Andrade et al. 2020; Santana et al. 2020). Although it is a widely distributed species, there remain some questions about its taxonomy, regarding the occurrence of cryptic subspecies or species within the group, with some authors considering this freshwater turtle to be a “*Geoffroanus* complex” (McCord et al. 2001; Vogt 2008). Recently, Carvalho et al. (2022) tested taxonomic hypotheses using genomic data and were able to provide support for four species/lineages within the *P. Geoffroanus* species complex. According to the authors, these species/lineages are restricted to specific river basins and biomes but are morphologically cryptic, and specimens from the Northeast Brazil correspond to *P. Geoffroanus* lineage 3. *Phrynops Geoffroanus* is considered a medium-sized species (Rueda-Almonacid et al. 2007; Rodrigues et al. 2019), which nests in sandy or clay soil, usually covered by shrub vegetation, and preferably in places with good exposure to the sun (Medem 1960). In natural conditions (Souza and Abe 2001), clutches are laid in the driest period of the year while hatching occurs during the rainy season.

Mesoclemmys tuberculata is also a medium-sized species (Vanzolini et al. 1980; Ernst and Barbour 1989; Vetter 2005), and its neck is covered with conical tubercles, reflected in the name of this species (Ernst and Barbour 1989; Bonin et al. 2006). It is a freshwater turtle that is endemic to Brazil, occurring mainly in the semiarid region of the northeast (Vanzolini et al. 1980; Iverson 1992). It is generally associated with the Caatinga and Atlantic Forest, mainly in areas surrounding the São Francisco River basin (Batistella et al. 2008; Santos et al. 2008; Moura et al. 2014). However, it has also been recorded in the Caatinga-Cerrado ecotone of the São Francisco River basin, northwest Minas Gerais State (Silveira and Valinhas 2010). Most of the ecology of *M. tuberculata* remains unknown (Souza 2004; Santana et al. 2016, 2019). Reproductive parameters such as clutch size, egg parameters (size, volume, mass), average clutch mass, incubation time (days), reproductive season, and description of the nest location are unknown in natural environments (Santana et al. 2016).

In the present study, we tested the hypothesis that intraspecific factors are more important than differences in

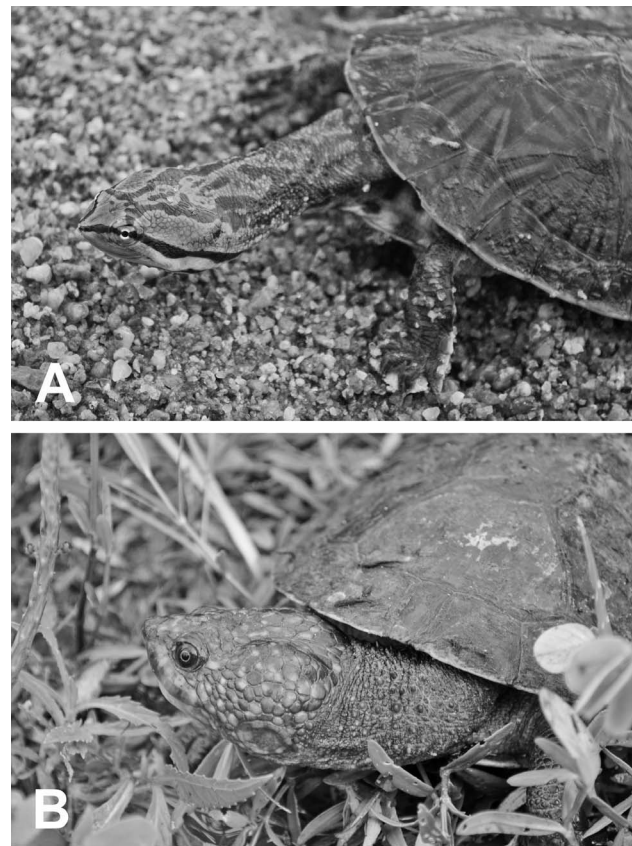


Figure 1. Individuals of (A) *Phrynops Geoffroanus* and (B) *Mesoclemmys tuberculata* from Sergipe, northeastern Brazil. Photos by D.O.S.

environments in determining the ecological parameters of *P. Geoffroanus* and *M. tuberculata* in areas of Caatinga and Atlantic Forest in northeast Brazil. More specifically, we evaluated the sex ratio and the presence of sexual dimorphism, and we described aspects of morphometry and reproduction of both species. Taking into account that most turtle species can be strongly influenced by climate, our prediction was that differences in the two environments are not sufficient to promote variations in ecological patterns.

METHODS

Study Sites. — Populations of *P. Geoffroanus* and *M. tuberculata* (Fig. 1) were studied in six localities (three in the Caatinga and three in the Atlantic Forest) in the State of Sergipe, Brazil (Fig. 2). The locations selected in the Caatinga area were the Monumento Natural do Rio São Francisco (09°41.202'S, 037°42.963'W, 189 m elevation; municipality of Poço Redondo), Monumento Natural Grota do Angico (09°40.852'S, 037°41.408'W, 170 m elevation; municipality of Poço Redondo), and Bacia do Rio Real (11°10.730'S, 038°02.300'W, 158 m elevation; municipality of Tobias Barreto). The Atlantic Forest areas selected were the Parque Nacional Serra de Itabaiana (10°45.251'S, 037°20.511'W, 208 m elevation; municipality of Areia Branca), Reserva Biológica de Santa Isabel

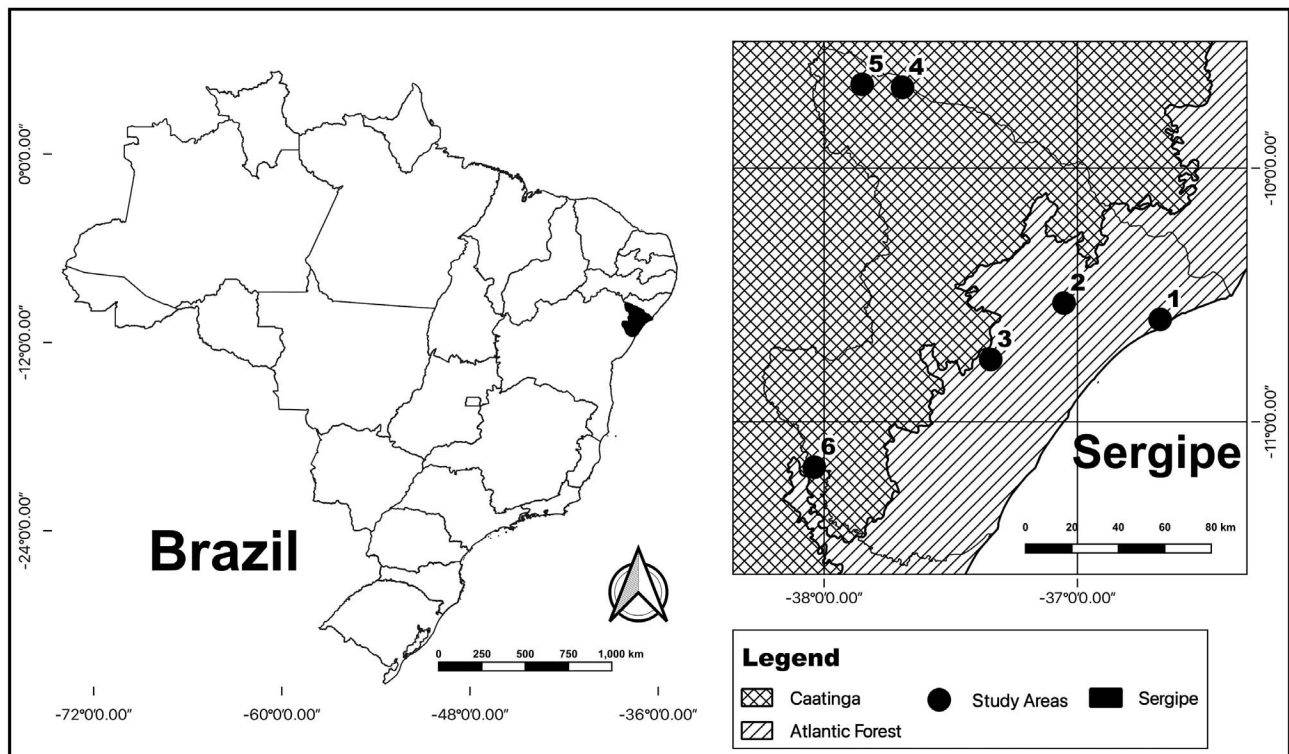


Figure 2. Selected locations for the development of the fieldwork: (1) Reserva Biológica de Santa Isabel (municipality of Pirambú); (2) Refúgio de Vida Silvestre Mata do Junco (municipality of Capela); (3) Parque Nacional Serra de Itabaiana (municipality of Areia Branca); (4) Monumento Natural do Rio São Francisco (municipality of Poço Redondo); (5) Monumento Natural Grota do Angico (municipality of Poço Redondo); and (6) Baía do Rio Real (municipality of Tobias Barreto).

(10°35.766'S, 036°40.366'W, 13 m elevation; municipality of Pirambú), and Refúgio de Vida Silvestre Mata do Junco (10°31.895'S, 037°03.142'W, 118 m elevation; municipality of Capela).

Turtle Collection. — Samples were obtained in semiannual surveys (dry and rainy season) over a year, lasting 10 consecutive days at each of the six sampling sites, with three in the Caatinga and three in the Atlantic Forest, totaling 120 d of sampling. The study was conducted in 2014, and we defined the rainy and dry seasons based on historical averages of the distribution of precipitation in these areas (Hijmans et al. 2005). The months from April to August were considered the rainy season, and the remaining months were assigned to the dry season.

We used 20 hoop net traps placed in rivers, streams, and/or lagoons to capture individuals at each sampling point. In order to attract turtles, the traps were baited with beef placed in the water from 0600 to 1800 h and were checked every 3 h. There were occasional nocturnal collections. In environments with less-turbid waters, an active search (free diving with the aid of a mask, snorkel, and fins) was performed between 0700 and 1700 h.

Procedures. — We weighed the captured animals with a Pesola® scale (0.5-g precision) and performed 22 measurements with digital calipers (0.5 mm) and a tape measure (1 mm), the latter for curvilinear measurements: maximum straight-line carapace length (SCL), maximum

straight-line carapace width (SCW), length of third central scute (LC3), width of third central scute (WC3), curvilinear carapace length (CCL), curvilinear carapace width (CCW) between the union of the second and third vertebral scute to the carapace edge, maximum plastron length (MPL), maximum plastron width (MPW), anterior lobe plastron width (LBA), posterior lobe plastron width (LBP), opening between the distal ends of the anal scutes plastral (ASP), carapace and plastron terminal distance (CPD), cephalic width (CW) measured over the tympanic membrane, cephalic length (CL), mouth width (MW), right and left barb length (RBL, LBL), right and left barb width (RBW, LBW), total tail length (TTL), distance between cloacal opening and tail end (COT), and maximum carapace height (MCH) (Fig. 3). We selected these morphometric measurements following the methodology described by Bager et al. (2010) and Fagundes (2010a, 2010b) and adapted them to the present study.

We sexed each adult captured according to external morphological characteristics and secondary sexual characteristics, such as plastral concavity and tail length (Rueda-Almonacid et al. 2007; Brito et al. 2009; Molina et al. 2012).

We collected 5 individuals of each species, at each location, in each of the surveys, with the purpose of analyzing the reproductive cycle. Following measurements, the animals were partially anesthetized by being placed in a vessel containing water and ice at a temperature

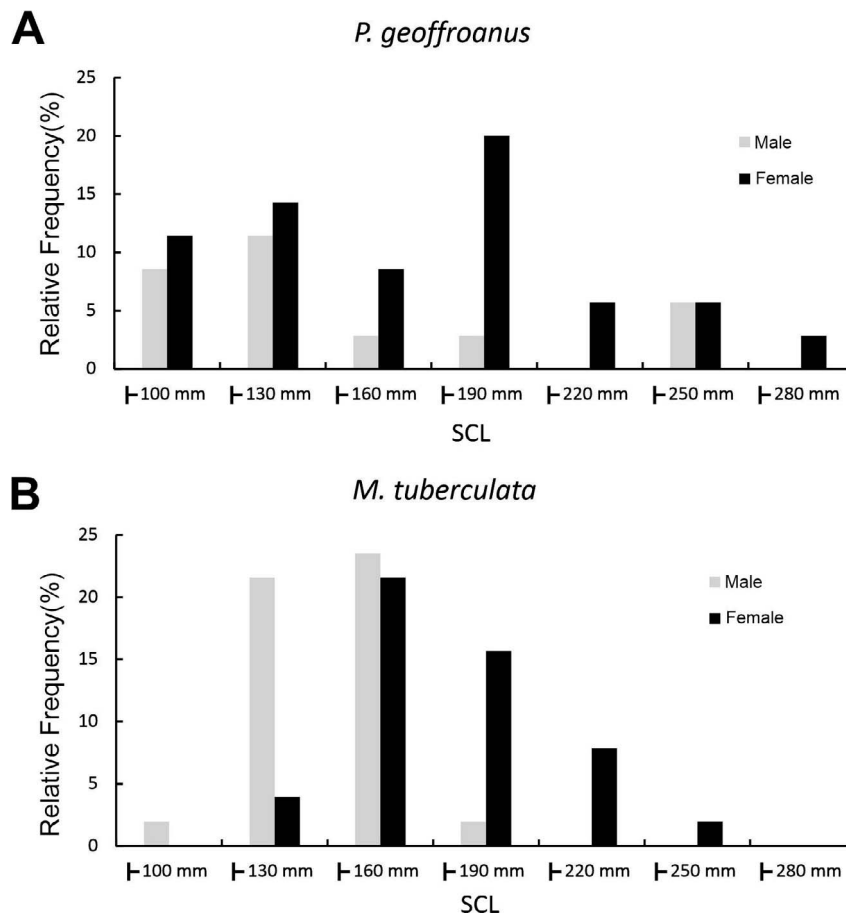


Figure 4. Relative frequency of maximum straight-line carapace length distribution (SCL) ($n = 85$) of adults of *Phrynops geoffroanus* and *Mesoclemmys tuberculata*, in the Atlantic Forest and Caatinga biomes, northeastern Brazil.

For the analysis of reproductive condition, we collected 61 turtles, 26 of which were *P. geoffroanus* (6 males, 12 females, and 8 juveniles) and 35 *M. tuberculata* (14 males, 17 females, and 4 juveniles). In *P. geoffroanus*, we found eggs in 41.7% ($n = 5$) of females from 224 to 285 mm in carapace length (mean = 254.8 ± 22.1 mm). (All values are presented as mean \pm SD.) In total, we collected 42 eggs, ranging from 7 to 9 per female (8.4 ± 0.9 eggs), with an average length of 27.8 ± 1.4 mm and a width of 26.0 ± 1.2 mm. We registered the presence of eggs and oocytes exclusively in females collected during the rainy season (June to August). All reproductive females simultaneously presented eggs and developed vitellogenic follicles, indicating the production of sequential clutches during the reproductive season. The females collected in the dry season were not reproductive.

In *M. tuberculata*, we found eggs in 41.2% ($n = 7$) of females of between 132.6 and 220.8 mm in carapace length (mean = 221.2 ± 25.8 mm). In total, we collected 46 eggs, ranging from 3 to 9 per female (6.6 ± 1.99 eggs), with an average length of 30.6 ± 2.4 mm and width of 24.9 ± 1.9 mm. As in *P. geoffroanus*, females of *M. tuberculata* had eggs exclusively during the rainy season, where all females with eggs also had vitellogenic follicles. Three females collected in the dry season showed only

vitellogenic follicles. Of the 9 females collected during the rainy season, only 2 had neither eggs nor vitellogenic follicles.

In *P. geoffroanus*, we did not find a significant relationship between clutch size (number of eggs) and SCL of females ($R = 0.368$, $F_{1,3} = 3.33$, $p = 0.165$), although egg volume was positively related to SCL ($R = 0.9669$, $F_{1,3} = 117.8$, $p < 0.01$). We also found no significant relationship in *M. tuberculata* between clutch size and female carapace length ($R = 0.179$, $F_{1,5} = 2.31$, $p = 0.189$) or egg volume ($R = 0.078$, $F_{1,5} = 1,508$, $p = 0.274$). With regard to the shape of the eggs, the degree of sphericity of *P. geoffroanus* eggs was 0.936 ($n = 35$) while that of *M. tuberculata* was 0.813 ($n = 42$).

We found reproductive males of both species throughout the study (dry and rainy seasons), comprising 50% of the *P. geoffroanus* collected, between 199.0 and 270.0 mm (mean = 244.7 ± 40.2 mm) and 86.7% of *M. tuberculata*, with carapace lengths between 139.5 and 187.0 mm (mean = 163.9 ± 14.4 mm). Testicular volume was positively correlated with SCL in males of both species: *P. geoffroanus* ($R = 0.735$, $F_{1,5} = 14.88$, $p < 0.001$) and *M. tuberculata* ($R = 0.339$, $F_{1,13} = 7.69$, $p = 0.017$).

Table 2. Descriptive statistics of the morphometric measurements of adult individuals of *Phrynops geoffroanus* from Atlantic Forest and Caatinga in northeastern Brazil. Linear measurements are in millimeters and mass in grams. Variables: Maximum straight-line carapace length (SCL), maximum straight-line carapace width (SCW), length of third central scute (LC3), width of third central scute (WC3), circular carapace length (CCL), circular carapace width (CCW), maximum plastron length (MPL), maximum plastron width (MPW), anterior lobe plastron width (LBA), posterior lobe plastron width (LBP), anal scutes plastral (ASP), carapace and plastron terminal distance (CPD), cephalic length (CL), mouth width (MW), right barb length (RBL), left barb length (LBL), right barb width (RBW), left barb width (LBW), total tail length (TTL), distance between cloacal opening and tail end (COT), and maximum carapace height (MCH).

Variables	Atlantic Forest				Caatinga			
	Males		Females		Males		Females	
	$\bar{x} \pm SD$	Min-Max	$\bar{x} \pm SD$	Min-Max	$\bar{x} \pm SD$	Min-Max	$\bar{x} \pm SD$	Min-Max
SCL	175.87 ± 86.04	120.6–275	198.00 ± 36.77	172–224	149.06 ± 26.52	124–199	190.02 ± 49.63	124.20–285.00
SCW	126.73 ± 50.65	93.2–185	148.45 ± 30.48	126.9–170	112.79 ± 16.59	97.4–144	144.90 ± 35.13	99.80–213.00
LC3	30.13 ± 13.28	21.3–45.4	34.60 ± 8.63	28.5–40.7	24.71 ± 4.47	20.4–33.2	30.24 ± 7.86	19.10–43.60
WC3	31.97 ± 5.51	26.7–37.7	36.40 ± 0.71	35.9–36.9	31.49 ± 3.61	26.3–36.6	33.61 ± 4.12	28.20–40.30
CCL	190.67 ± 94.88	130–300	218.50 ± 38.89	191–246	159.57 ± 26.83	133–211	197.94 ± 56.70	117.00–303.00
CCW	158.00 ± 65.18	115–233	184.00 ± 36.77	158–210	135.00 ± 20.05	116–173	169.44 ± 40.65	117.00–254.00
MPL	151.90 ± 67.76	108.7–230	181.00 ± 39.60	153–209	132.87 ± 23.42	109.5–179	168.35 ± 43.18	110.7–253.00
MPW	100.37 ± 42.32	71.9–149	117.65 ± 25.95	99.3–136	86.93 ± 14.14	74.8–113.7	112.38 ± 28.02	75.40–166.00
LBA	78.93 ± 32.72	57.6–116.6	93.65 ± 21.57	78.4–108.9	67.53 ± 10.83	57.6–87.5	88.19 ± 23.19	58.80–133.60
LBP	61.03 ± 24.89	44–89.6	71.75 ± 17.89	59.1–84.4	52.97 ± 8.78	45.6–70	69.96 ± 18.13	48.20–103.90
ASP	33.03 ± 12.96	24.1–47.9	39.90 ± 10.89	32.2–47.6	31.49 ± 4.55	26.9–39	38.28 ± 11.72	24.10–61.30
CPD	14.13 ± 7.54	8.5–22.7	12.75 ± 2.90	10.7–14.8	7.29 ± 1.77	5.1–10.7	8.84 ± 4.33	3.30–17.20
CW	33.73 ± 11.27	22.9–45.4	37.95 ± 8.27	32.1–43.8	27.16 ± 3.22	24.2–33.3	35.01 ± 8.15	25.00–51.30
CL	37.50 ± 13.55	27.4–52.9	43.35 ± 10.11	36.2–50.5	33.89 ± 4.79	28.8–43.3	42.61 ± 8.67	32.10–58.20
MW	24.47 ± 8.96	18–34.7	28.85 ± 5.73	24.8–32.9	20.20 ± 2.64	18.2–25.7	26.26 ± 6.41	19.00–39.60
RBL	3.73 ± 0.49	3.4–4.3	6.25 ± 1.91	4.9–7.6	4.34 ± 0.42	3.8–4.9	4.91 ± 1.74	2.90–8.30
LBL	3.93 ± 0.15	3.8–4.1	5.75 ± 1.63	4.6–6.9	4.23 ± 0.43	3.5–4.8	5.21 ± 1.50	3.00–9.00
RBW	1.50 ± 0.26	1.3–1.8	1.60 ± 0.71	1.1–2.1	1.19 ± 0.32	0.8–1.7	1.24 ± 0.40	0.30–2.10
LBW	1.43 ± 0.49	1.1–2	1.55 ± 0.64	1.1–2	1.16 ± 0.21	0.9–1.5	1.16 ± 0.42	0.30–1.80
TTL	51.13 ± 32.89	31.5–89.1	37.40 ± 12.02	28.9–45.9	39.16 ± 11.70	28.6–63	35.37 ± 12.09	22.7–62.5
COT	21.00 ± 10.84	11.7–32.9	18.15 ± 5.30	14.4–21.9	13.91 ± 3.62	10.4–20.2	16.51 ± 5.71	10.1–28.6
MCH	56.77 ± 22.76	42.3–83	68.00 ± 9.90	61–75	45.36 ± 5.67	38.9–54	56.71 ± 12.48	41.2–80
Mass	786.67 ± 956.35	195–1890	850.00 ± 452.55	530–11170	292.5 ± 188.6	190–675	661.36 ± 526.89	175–2070

Table 4. Descriptive statistics of the morphometric measurements of juvenile individuals of *Phrynops geoffroanus* and *Mesoclemmys tuberculata*. Linear measurements are in millimeters and mass in grams (see Table 2 for definition of abbreviations).

Variables	<i>P. geoffroannus</i>		<i>M. tuberculata</i>	
	$\bar{x} \pm SD$	Min–Max	$\bar{x} \pm SD$	Min–Max
SCL	76.78 ± 18.08	43–114.6	81.23 ± 30.08	46.5–99.1
SCW	63.35 ± 13.43	36.1–91.2	61.67 ± 23.07	35.2–77.5
LC3	12.15 ± 3.00	6.4–17.7	12.40 ± 4.56	7.3–16.1
WC3	22.28 ± 3.89	11.9–30	22.27 ± 5.41	16.1–26.2
CCL	83.15 ± 19.25	46–123	87.00 ± 32.92	49–107
CCW	74.28 ± 16.86	41–110	71.33 ± 28.01	39–88
MPL	66.61 ± 17.95	7.4–101.6	75.67 ± 28.56	42.7–92.8
MPW	47.23 ± 10.02	27.1–69.1	52.47 ± 19.92	29.6–66.1
LBA	35.05 ± 8.13	19.1–52.6	41.53 ± 16.90	22.1–52.8
LBP	27.78 ± 6.34	16.4–42.1	35.47 ± 14.51	18.9–45.9
ASP	14.35 ± 3.58	8.1–22.9	13.33 ± 4.71	8–16.9
CPD	4.92 ± 1.30	2.6–8.2	5.30 ± 3.06	2.1–8.2
CW	16.86 ± 2.58	11.4–23.1	21.77 ± 5.80	15.2–26.2
CL	43.08 ± 4.15	35.4–47.6	57.07 ± 9.44	47.2–68.6
MW	29.08 ± 3.52	23.3–33.8	38.07 ± 7.83	30.1–47.5
RBL	2.13 ± 0.45	1.5–2.7	2.63 ± 1.05	1.6–3.9
LBL	2.10 ± 0.41	1.4–2.5	2.55 ± 1.19	1.1–4.3
RBW	0.83 ± 0.25	0.5–1.2	0.95 ± 0.40	0.3–1.4
LBW	0.75 ± 0.27	0.4–1.2	0.93 ± 0.45	0.2–1.3
TTL	32.60 ± 9.40	14.2–38.1	32.10 ± 5.37	26.2–39.5
COT	11.58 ± 2.61	7–13.9	15.37 ± 2.76	12.1–20.5
MCH	53.18 ± 5.66	43.3–60	68.27 ± 8.61	59–80
Mass	478.33 ± 151.98	220–650	1010.00 ± 451.35	550–1680

DISCUSSION

Variations in ecological aspects, such as morphological characteristics, often result from different seasonal regimes and have been described for several vertebrates (Leclair and Laurin 1996; Bitto and Egbunike 2006), including reptiles (Clavijo-Baquet et al. 2010; Lucas et al. 2020). With regard to turtles, seasonal differences can drive different ecological pressures that affect their size (Clavijo-Baquet et al. 2010; Litzgus and Smith 2010; Lucas and Bager 2017). However, these differences were not significant in *P. geoffroanus* and *M. tuberculata*; their size in the Caatinga, an environment with a more stochastic rain regime, was similar to that in the Atlantic Forest, an environment with a more predictable and seasonal pattern (Nimer 1989). This absence of morphological variation may be related to relatively short geographic distances between the studied populations (~ 150 km), despite drastically different environmental conditions, which may not restrict gene flow between them (Clavijo-Baquet et al. 2010), thus influencing the lack of morphological variation. These animals, which exhibit migratory behavior, can even disperse between different

watersheds (Milam and Melvin 2001; Clavijo-Baquet et al. 2010).

Female *Phrynops* and *Mesoclemmys* are, in general, larger than males (Cunha et al. 2019; Müller et al. 2019; Santana et al. 2019; Abrantes et al. 2021; Carvalho et al. 2022), so the lack of sex differences found in *P. geoffroanus* in this study may be related to the small sample size of adults. The sex ratio found, of 1:1, and the pattern of females being larger than males in *M. tuberculata*, agrees with Berry and Shine (1980), who suggested that species with smaller males are associated with the absence of disputed territories for female's access. In addition, larger females may increase reproductive potential in terms of the number and size of eggs produced and storage capacity (Lovich and Gibbons 1992; Bager et al. 2007; Kaddour et al. 2008). This pattern may be even more pronounced in species with multiple clutches per reproductive season, such as those recorded here (Bager et al. 2007, 2010). Similar patterns have been verified for several Chelidae species (Cann 1998; Garbin et al. 2016), including *P. geoffroanus* (Molina 1998). The length of the smallest adult *P. geoffroanus* and *M. tuberculata* individuals were similar to that described by Rodrigues and Silva

Table 5. Sex ratio verified for *Phrynops geoffroanus* and *Mesoclemmys tuberculata* in Atlantic Forest and Caatinga, in northeastern Brazil.

Species, location	Male	Female	Ratio	<i>n</i>	χ^2	<i>p</i> -value	Fisher's Exact
<i>P. geffroanus</i> , Atlantic Forest	60	40	1:1	5	0.09	0.7642	1
<i>P. geffroanus</i> , Caatinga	26.67	73.33	1:3	30	3.4548	0.0631	0.110
<i>M. tuberculata</i> , Atlantic Forest	54.55	45.45	1:1	11	0.0434	0.835	1
<i>M. tuberculata</i> , Caatinga	46.45	53.85	1:1	39	0.1141	0.7356	0.821

metric analysis is essential, as it can provide information on the degree of divergence between species and populations (Fernandez and Rivera 2001; Leary et al. 2003; Lindeman 2003; Yadollahvandmiandoab et al. 2018).

The main objective of turtle conservation is to ensure that viable populations exist in the long term; so to be successful, data on ecology, demography, habitat management, genetics, and husbandry need to be incorporated into management plans for each species (Stanford et al. 2020). Thus, other studies involving genetic analysis, habitat management, and husbandry could broaden the perspective of this study, leading to greater clarification of the patterns found and helping the conservation of the studied species.

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