SEASONAL VARIATION IN THE POPULATION PARAMETERS OF *Kinosternon scorpiodes* and *Trachemys Adiutrix*, and Their Association with Rainfall in Seasonally Flooded Lakes

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Abstract.—Seasonally flooded lakes in the northeast region of Brazil are important areas used for breeding and feeding by two species of turtle, *Kinosternon scorpioides*, the Scorpion Mud turtle, and *Trachemys adiutrix*, the Brazilian Slider Turtle. Over 6 y, we captured, marked, measured, and determined the sex of 183 *K. scorpioides* and 518 *T. adiutrix*. Over the study period as a whole, the sex ratio of *K. scorpioides* did not deviate significantly from 1:1, whereas there was a significant male bias in *T. adiutrix*. There was no significant relationship between relative abundance and mean monthly rainfall in either species, although we captured significantly smaller *K. scorpioides* females and larger *T. adiutrix* individuals (males and females) in the drier years. Seasonal residence times ranged from 14–90 d in *K. scorpioides* and 14–110 d in *T. adiutrix*. Residence time was not related significantly to mean monthly rainfall in either species. In *K. scorpioides*, the estimated annual female population size ranged from 14 to 78 individuals, while that of the males varied from 16 to 88 individuals, while in *T. adiutrix*, estimates of the female population size ranged from 71 to 444 individuals, and those of males, from 80 to 515 individuals. These findings indicate that both turtle species maintain resident populations in the study area, but present distinct patterns of annual variation in body size and the sex ratios, which points to distinct ecological requirements that may require differential conservation strategies.

Key Words.-freshwater turtles; mark-recapture; population size; seasonal rainfall; sex ratio; robust model

INTRODUCTION

Turtles are long-lived reptiles that inhabit many aquatic and terrestrial habitats (Close and Seigel 1999; Gibbons et al. 2000) and may present significant variation in population parameters (e.g., sex ratios and body and clutch sizes) over both spatial and temporal scales (Arshton et al. 2007; Beaudry et al. 2010; Iverson 2010; Eisemberg et al. 2015; Urban 2015). In more productive environments, for example, Gopherus polyphemus (Gopher Tortoise) had larger clutches, although clutch size was unrelated to temperature or seasonality (Arshton et al. 2007). By contrast, Eisemberg et al. (2015) found evidence that seasonal variation in rainfall and salinity influenced nesting patterns and female body size in Carettochelys insculpta (Pig-nosed Turtle) Close and Seigel (1999) observed populations. variation in the body size of adults in populations of Trachemys scripta elegans (Red-eared Slider) subject to different levels of harvesting, but no effects on

abundance. Beaudry et al. (2010) found that *Clemmys guttata* (Spotted Turtle) and *Emydoidea blandingii* (Blanding's Turtle) used a variety of widely scattered wetland habitats to satisfy their seasonally shifting ecological needs. Although geographic and temporal trends have been documented in population parameters in many populations of freshwater turtles (e.g., Roe and Georges 2008; Beaudry et al. 2010; Eisemberg et al. 2015), few data are available for Brazilian species.

Population studies of freshwater turtles in Brazil have focused mainly on the species that are either the most abundant and/or are subject to more intense hunting pressure for subsistence or illegal trafficking (Campos-Silva et al. 2017). Some of these studies have shown that hunting pressure leads to an imbalance in the sex ratio and age structure (Bernardes et al. 2014), while others have focused on seasonal patterns of population abundance (Bernardes et al. 2014; Portelinha et al. 2014; Brito et al. 2018). In the Rio Negro basin, Bernardes et. al (2014) observed population structuring

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in *Podocnemis erythrocephala* (Red-headed Amazon Side-necked Turtle), with mature individuals (males and females) being more common than immature ones. The low recruitment of juveniles in this population was associated with the collection of eggs from nests by local inhabitants. By contrast, most of the individuals captured in a *Podocnemis expansa* (South American River Turtle) population in a protected area on the Javaés River were juveniles (Portelinha et al. 2014). In both these studies, a considerable difference was found in the number of turtles captured between the breeding (low-water) and the non-breeding seasons, although a male-biased sex ratio was recorded only in *P. expansa*.

The aquatic fauna of the seasonally flooded lakes of the central littoral zone of the Brazilian state of Maranhão includes the sympatric freshwater turtles Kinosternon scorpioides (Scorpion Mud Turtle), and Trachemys adiutrix (Brazilian Slider Turtle). Trachemys adiutrix is endemic to the northeastern region of Brazil (Vanzolini 1995; Fritz et al. 2012) and is listed as endangered by the International Union for Conservation of Nature (IUCN; van Dijk et al. 2014). Kinosternon scorpioides is much more widely distributed, ranging from southern Mexico to northern Argentina (Berry and Iverson 2011) and is not listed by IUCN, although is listed as least concern in a global assessment by the Tortoise and Freshwater Turtle Specialist Group (TFTSG) of the IUCN and by the Brazil Red Book of Threatened Species of Fauna (Rhodin, 2018; Instituto Chico Mendes de Conservação da Biodiversidade [ICMBio] 2018). Studies of K. scorpioides and T. adiutrix have recorded these turtles in both terrestrial (dunes and grassland) and aquatic habitats (temporary lakes) between the middle of the rainy season (March) and the middle of dry season (September), when these lakes are full of water (Barreto et al. 2009, 2010). Both species suffer from hunting pressure and illegal trapping, as well as exposure to garbage dumps, which often contain toxic materials, such as discarded batteries, located in close vicinity to the lakes in which these turtles are found (Barreto et al. 2009, 2010).

Despite the restricted distribution of *T. adiutrix* and the vulnerability of both turtles due to the fragmentation of the habitats they occupy, few data are available for either, apart from the observations of Barreto et al. (2009, 2010). There has also been no systematic monitoring of these species across their ranges to quantify the impact of the potential threats to population structure. From a conservation management perspective, it is essential to obtain data on population parameters to better estimate population trends and to develop adequate management strategies.

We studied the population biology of *K. scorpioides* and *T. adiutrix* in the seasonally flooded lakes of Curupu Island in Maranhão state, northeastern Brazil,

and obtained data for the development of local and regional conservation strategies, and the identification of population management priorities. Over 6 y, we surveyed the lakes on Curupu Island to determine the occurrence of both species, obtain capture-recapture data, and verify whether rainfall levels affect abundance and body size. We asked four principal questions of both species: (1) Is the sex ratio balanced? (2) What is the relationship between mean monthly rainfall and relative abundance, body size, and residence times? (3) Are recaptures and residence times related to sex? (4) How does population size vary between seasons?

MATERIALS AND METHODS

Study site.—We conducted the study on Curupu Island, in the coastal region of Maranhão state, in the northern littoral zone of Brazil (Fig. 1). The climate is controlled by seasonal shifts in the Intertropical Convergence Zone over the Atlantic Ocean and the prevailing winds, which combine to determine a 6-mo rainy season, from January to June-July, followed by a dry season during the second half of the year (Sena et al. 2013). The mean annual rainfall is 1,623 mm/y (Sena et al. 2013). The seasonal variation in rainfall has a direct influence on the characteristics of the local lakes, in particular through the inundation and later contraction of the seasonally flooded lakes, in addition to sudden changes in the depth of aquatic environments resulting from occasional heavy downpours. The principal lakes on the island are Jacaré, Duna, Grande, Olga, Tiché, Braço, and Urubu. Some of these sites are dominated by aquatic vegetation, including floating Water Hyacinth (Eichhornia crassipes) and emergent macrophytes (Eleocharis spp.). The vegetation surrounding the lakes is dominated by sedges, Cyperus spp. and Scirpus spp. (Cyperaceae), and Ipomoea spp. (Convolvulaceae). The lakes are relatively small in size, ranging in area from 0.1-3.14 ha (Appendix 1) with a mean depth of 0.5-1.5m, and they normally reach full capacity by the middle of the rainy season (March), while drying up completely by the middle of dry season (September). We obtained rainfall data for the study period from the São Luis meteorological station, located approximately 30 km west of the study site (www.inmet.gov.br).

Collection of biological data.—The number of lakes available for sampling in a given year varied during the study period, from March 2009 to July 2014, because some of the smaller lakes received an insufficient input of rainwater during the driest years (2010, 2012, 2013, and 2014). In the rainiest years (2009 and 2011), we monitored four and five lakes, respectively, between March and September, whereas in the driest years, we could only sample two or three lakes between May



FIGURE 1. (A) Brazil, showing the location of the state of Maranhão; (B) Maranhão, showing São Marcos Bay (highlighted), where Curupu Island is located; (C) Curupu Island, showing the study area (highlighted); (D) aerial photograph showing the study lakes. (Image from https://www.arcgis.com/home/user.html?user=esri basemaps).

and July. In each lake, we deployed a funnel trap for a 2-d sampling period every 14–15 d during the seasonal monitoring (Appendix 1), and we checked traps for turtles between 0500 and 1200. The traps were constructed of wooden slats with a funnel entrance (see Rocha et al. 1997; Barreto et al. 2009). We baited the traps with fresh fish and placed them 2–3 m from the lake shore.

For each animal captured, we recorded a standard set of data: the lake, date of capture/recapture, species, sex, and carapace length (CL). We measured CL to the nearest 0.1 cm using calipers. We determined the sex of the adult turtles by the relative length of the tail (in both species, the males have a considerably longer tail than the females) and the concavity of the plastron in *K. scorpioides* males (Pritchard and Trebbau 1984). We used CL as the measure of body size. We considered individuals of both species with a CL of at least 100.0 mm as adults, while smaller individuals were classified as juveniles (for details see Barreto et al. 2009). We marked turtles with a unique series of small notches made with a miniature hacksaw on the marginal scutes of the carapace (Cagle 1939). Once processed, we returned the animals immediately to the lake at the site of their capture. No turtles were euthanized or died accidentally during the study.

We used the mark-recapture data to estimate population size and the occupation of each lake by individuals of the two species. We estimated the use of the lakes by the residence times of the animals in the study area per season. We calculated residence time as the number of days between the first capture and last recapture.

Statistical analyses.-We tested for deviations from an expected (1:1) sex ratio of mature turtles of both species using a Proportions test, applied to the individuals captured between March 2009 and July 2014. This test verifies the null hypothesis that the proportions in different groups are the same. In each species, we used General Linear Models (GLM) with a Poisson distribution to model the relationship between relative abundance of individuals captured in each season and mean monthly rainfall during the 7 mo rainy season. Trapping effort varied from 24 d per season in 2012 to 72 d per season in 2011 (Appendix 1). As effort varied among seasons, we present turtle abundance as the number of individuals captured per unit effort, or CPUE (Fachín-Terán et al. 2003; Portelinha et al. 2014). We used Linear Regression to assess the relationship between CL and mean monthly rainfall recorded during the rainy season. As both species are sexually dimorphic (Pritchard and Trebbau 1984; Barreto et al. 2009), we analyzed females and males separately.

We evaluated differences in recapture rates between males and females for the whole study period using Pearson's Chi-square, and the variation in residence time (d) between males and females in each species using the Kruskal-Wallis rank sum test. We assessed the relationship between residence time (males and females combined) and mean monthly rainfall in the rainy season by Linear Regression in each species. We used a GLM with a binomial family and a logit link function to examine the potential effects of residence time (log transformation) on the movement pattern probabilities of individual turtles. We coded movement patterns as a binomial response variable, i.e., whether recapture occurred in the same lake or not.

In each turtle species, we applied a robust capturerecapture design to the data from the entire study period, with sex being considered as a group to estimate seasonal population size (Kendall et al. 1997). The robust design was defined by each primary sampling period (2009–2014) with multiple secondary sampling periods (seasons). The robust design method combines open (death and movements between seasons) and closed (no deaths or movement between days within a season) population assumptions to estimate demographic parameters (Steffensen et al. 2017). Each individual in an observable state is assumed to be subject to detection on one or more secondary sampling occasions (for details, see Kendall et al. 2019). We inspected a set of 10 models we believed to be biologically reasonable to investigate annual population changes. We used Akaike's Information Criterion (AIC) to compare models and conduct analyses in the RMark package (Laake 2013). We considered $P \le 0.05$ as the level for significance in all analyses, which we ran in the R program, version 3.3.1 (R Development Core Team 2016).

RESULTS

During the 6 y of our study, we collected 183 individual K. scorpioides (21 juveniles, 69 females and 93 males) and 518 T. adiutrix (29 juveniles, 202 females and 287 males). The adult sex ratio was male-biased in both species in all years except 2012, when it was femalebiased (Fig. 2). Considering the whole study period, however, the sex ratio was 1.3M:1.0F in K. scorpioides and 1.4M:1.0F in T. adiutrix, and the difference from a 1:1 sex ratio was significant in *T. adiutrix* ($\chi^2 = 14.69$, df = 5, P = 0.011) but not in K. scorpioides ($\chi^2 = 2.70$, df = 5, P = 0.740). Overall, the mean abundance of K. scorpioides was 0.66 individuals per trap-day, while that of T. adiutrix was 1.76 individuals per trap-day (Appendix 1). Relative abundance (CPUE) was not related systematically to mean monthly rainfall in the rainy season for either K. scorpioides ($F_{1,4} = 0.034$, P = 0.861) or *T. adiutrix* ($F_{1,4}$ = 0.036, P = 0.858). In *K*. scorpioides (Fig. 3A and B), we found a significantly positive relationship between CL and mean monthly rainfall in the rainy season in adult females (b = 0.03, r^2



FIGURE 2. Proportion of the females (gray) and males (white) of (A) *Kinosternon scorpoides* (Scorpion Mud turtle) and (B) *Trachemys adiutrix* (Brazilian Slider Turtle) captured per season (2009–2014) in the seasonally flooded lakes on Curupu Island, Maranhão, Brazil. The horizontal line crossing each plot indicates a sex ratio of 1:1. The total number of individuals captured in each season is shown within the respective bar.



FIGURE 3. Relationship between the carapace lengths of *Kinosternon scorpioides* (Scorpion Mud Turtle; A: female, B: male) and *Trachemys adiutrix* (Brazilian Slider Turtle; C: female, D: male) captured in seasonally flooded lakes on Curupu Island, Maranhão, Brazil, and mean monthly rainfall in each of the six study years.

= 0.14, $F_{1,67}$ = 11.65, P < 0.001), but not in males ($F_{1,91}$ = 1.680, P = 0.198). In *T. adiutrix* (Fig. 3C and D), in contrast, we found a significantly negative relationship in both adult females (b = -0.083, $r^2 = 0.07$, $F_{1,200}$ = 16.57, P < 0.001) and males (b = -0.050, $r^2 = 0.09$, $F_{1,285}$ = 30.2, P < 0.001).

During the study, we recaptured 59 of the 162 marked K. scorpioides adults at least once (ranging from one recapture in 2014 to 25 in 2009), while we recaptured 58 of the 489 adult T. adiutrix at least once (ranging from zero in 2012 to 27 in 2014). We found no significant difference in the number of the turtles of either sex recaptured in either species (K. scorpioides: $\chi^2 = 0.61$, df = 1, P = 0.432; *T. adiutrix*: $\chi^2 = 0.13$, df = 1, P = 0.707) nor in seasonal residence times (K. scorpioides: H =0.27, df = 1, P = 0.603; T. adiutrix: H = 0.12, df = 1, P =0.723). Seasonal residence times ranged from 14 to 90 d (median = 38 d) in K. scorpioides and from 14 to 110 d (median = 33 d) in T. adiutrix. Seasonal residence time was not related significantly to mean monthly rainfall in either K. scorpioides ($F_{1,38} = 1.70$, P = 0.192) or T. adiutrix ($F_{137} = 0.420, P = 0.513$).

In each species, we recaptured 19 individuals at intervals of between one and five years. The interval between captures ranged from 301 to 1,805 d in *K. scorpioides* and from 272 to 1,867 d in *T. adiutrix.* Individuals with greater residence time in the study area had a higher probability of being recaptured in a lake different from that in which where they were first captured (*K. scorpioides:* Z = 2.91, df = 58, P < 0.001; *T. adiutrix:* Z = 2.01, df = 57, P = 0.041), reflecting the seasonal dynamics of lake use.

There was one best model generated to predict the population sizes of female and male K. scorpiodes with a WAICc = 0.57 (Table 1). The estimated annual population size of females varied from 14 ± 12.9 (standard error) individuals on occasion six to 78 ± 17.6 individuals on occasion three (Fig. 4A). The estimated annual population size of males varied from 16 ± 12.9 individuals on occasion six to 88 ± 17.6 individuals on occasion three (Fig. 4A). Similarly, there was one best model for *T. adiutrix* with a WAICc = 0.68 (Table 1). The estimated annual population size of females ranged from 71 \pm 33.9 individuals on occasion one to 444 \pm 101 individuals on occasion three. Once again, a similar pattern was observed in males, with population size ranging from 80 ± 33.9 individuals on occasion one to 515 ± 101 individuals on occasion three (Fig. 4B).



FIGURE 4. Estimated population size (\pm standard error) per year based on robust capture-recapture design formulation for *Kinosternon scorpioides* (Scorpion Mud Turtle; A) and *Trachemys adiutrix* (Brazilian Slider Turtle; B). In the case of *T. adiutrix*, the population estimate for 2012 was excluded due to an anomalously high estimate caused by the absence of recaptured individuals.

DISCUSSION

The individuals of both species captured in the study area were mostly adults. Fagundes et al. (2010) observed an equivalent population structure in *Trachemys dorbigni* (D'Orbigny's Slider Turtle) in southern Brazil, and similar patterns have been found in *K. scorpioides albogulare* in Colombia (Forero-Medina et al. 2007), and in *Emydoidea blandingii* (Blanding's Turtle) and *Chelydra serpentina* (Common Snapping Turtle) in Canada (Browne and Hecnar 2007). The latter authors found a reduced proportion of juveniles in

the populations of both *E. blandingii* and *C. serpentina* in 2001–2002 in comparison with 1972–1973, and concluded that the shift in age structure was likely related to a lack of juvenile recruitment, related to the intense predation of turtle nests by Raccoons (*Procyon cancrivorus*). Tesche and Hodges (2015), however, suggested that the use of only one sampling method, as in the present study, may lead to biases, such as the under-sampling of hatchling and juveniles. Because we found both hatchlings and juveniles, it seems likely that biases related to the use of the funnel traps contributed, at least in part, to the capture of a relatively large proportion of adult individuals.

During the study period as a whole, we recorded a male-biased sex ratio in T. adiutrix, while we found a balanced ratio in K. scorpioides. Some authors have suggested that a male bias, as observed here in T. adiutrix, may result from the cumulative differential mortality of females during overland movements to nesting migrations undertaken to move to favorable foraging sites, migrating to or from hibernacula, or to locating mates, which exposes female to more terrestrial predators, desiccation, overheating, and harvest by humans (Gibbons 1986; Buhlmann and Gibbons 2001; Sterrett et al. 2011; Steen et al. 2012). On Curupu Island, turtles were observed by Barreto (2009, 2010) crossing dunes to grassy areas where nests are usually found and observed also the turtles being harvested by humans from the local community.

Smaller *K. scorpioides* females and larger *T. adiutrix* individuals (both males and females) were captured in the drier years, indicating distinct responses of the two species to variation in climatic conditions. Some studies have shown that climatic changes influence resource availability (see Gibbons et al. 2000; Yom-Tov and Geffen 2011), and consequently, the abundance and

TABLE 1. Candidate models evaluated to estimate annual male and female population sizes of *Kinosternon scorpioides* (Scorpion Mud Turtle) and *Trachemys adiutrix* (Brazilian Slider Turtle) in the lakes of Curupu Island, Brazil. Models are ranked by Akaike's Information Criterion (AIC_c). We present the first five models (Δ AIC_c < 5) for each species. The S value is the probability of seasonal survival, p is the capture rate, and gamma' and gamma'' represent temporary emigration. The acronyms npar = the number of parameters in each model; DeltaAICc = the difference in each model's AIC_c values; W_{AICc} = the Akaike weight (sum of all weights: 1.00); ~1 = constant parameter; ~-1, which is allowed to vary by time, session, or session:time (capture-recapture parameters).

Model	npar	AIC _c	ΔAICc	WAICC
K. scorpioides				
S(~1)Gamma"(~-1 + time)Gamma'()p(~-1 + session:time)c()f0(~-1 + session)	52	609.36	0.00	0.57
$S(\sim 1 + time)Gamma'(\sim 1)Gamma'(\sim 1)p(\sim 1 + session:time)c()f0(\sim 1 + session)$	52	611.56	2.19	0.19
S(~-1 + time)Gamma"(~1)Gamma'()p(~-1 + session:time)c()f0(~-1 + session)	51	612.02	2.65	0.15
$S(\sim 1 + time)Gamma'(\sim 1)Gamma'(\sim 1)p(\sim 1 + session:time)c()f0(\sim 1 + session)$	53	613.79	4.43	0.06
T. adiutrix				
S(~1)Gamma"(~-1 + time)Gamma'()p(~-1 + session:time)c()f0(~-1 + session)	61	-539.10	0.00	0.71
$S(\sim-1 + time)Gamma'(\sim1)Gamma'(\sim1)p(\sim-1 + session:time)c()f0(\sim-1 + session)$	60	-535.86	3.24	0.14
S(~-1 + time)Gamma"(~1)Gamma'(~1)p(~-1 + session:time)c()f0(~-1 + session)	62	-534.10	4.99	0.05
$S(\sim 1)Gamma"(\sim -1 + time)Gamma'(\sim -1 + time)p(\sim -1 + session:time)c()f0(\sim -1 + session)$	65	-534.02	5.00	0.05

body sizes of reproductive individuals. During four of the six seasons in our study, annual rainfall was lower than the mean recorded over the preceding two decades, which probably reduced extremes in the hydrological cycle and the number of seasonal lakes present on Curupu Island. This reduction in the availability of lakes may have affected movement patterns and thus, the capture of individuals that disperse seasonally to these lakes to forage and breed. A number of studies have shown that larger individuals may be better able to respond to environmental stressors because they are more experienced at finding resources or because their larger size enables them to migrate through the nonaquatic matrix more easily (Brown and Shine 2008; Eckert et al. 2008). This would be consistent with the pattern we found in T. adiutrix and indicates that this species may be better able to respond to environmental stressors than K. scorpioides. In the dry season, the larger T. adiutrix individuals would be moving more frequently and would therefore be more likely to be caught than the smaller K. scorpiodes individuals.

The movements among lakes and the residence times of the recaptured individuals of both species indicated that the study area is an open system, composed of both transient and resident individuals. Given this, not all the recaptured individuals were necessarily yearround residents, but rather, their behavior may have reflected breeding site fidelity in individuals nesting at sites distant from their resident lakes. In different years, seasonally flooded lakes may support either a healthy resident breeding population or may constitute sink populations that can only be sustained through recruitment from source populations (see Pulliam 1988). Regional persistence and population structure of many aquatic and semi-aquatic amphibians and reptiles are dependent on the availability of both aquatic and terrestrial habitats (Marsh et al. 1999). From a conservation perspective, the seasonal lakes of Curupu Island represent a significant biological component of the landscape. Roe and Georges (2008) observed that during the dry season, when a pond dried up, some individuals of Chelodina longicollis (Common Snake-Necked Turtle) moved to permanent wetlands, while others sought refuge in terrestrial habitats adjacent to these wetlands, for varying lengths of time.

The robust design modeling approach we used provided more robust values for *K. scorpioides* population estimates than for *T. adiutrix*. For female *K. scorpioides*, the model estimated an annual variation from 14 to 79 individuals, while to males was from 16 to 88 individuals. Whereas in *T. adiutrix*, the female population size ranged from 71 to 444 individuals, while of the males from 80 to 515 individuals. The lower recapture rate in *T. adiutrix* (11.8% versus 32.1% for *K. scorpioides*) resulted in considerable variation in seasonal estimates, including one estimate, from

occasion three, that was higher than the total number of individuals captured during the whole study period, which indicates a highly transient population. This contributed to the lack of precision in the abundance estimates, indicating that longer-term sampling will be required before the population trends can be defined more conclusively. Also, we can relate this fact with the efficiency of the traps to capture turtles like mentioned by Mali et al. (2014) that increasing mouth-opening size to increase captures without introducing biases caused by differential escape probabilities.

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LITERATURE CITED

- Arshton, K.G., R.L. Burke, and J.N. Layne. 2007. Geographic variation in body and clutch size of Gopher Tortoises. Copeia 2007:355–363.
- Barreto, L., L.C. Lima, and S.G. Barbosa. 2009. Observations on the ecology of *Trachemys adiutrix* and *Kinosternon scorpioides* on Curupu island, Brazil. Herpetological Review 40:283–286.
- Barreto L., L.E.S. Ribeiro, A.B.N. Ribeiro, R.R. Azevedo, D.L. Tavares, J.M.S Abreu, and N.P. Cutrim. 2010. Mapeamento de áreas de ocorrência e aspectos de conservação de tartarugas (Chelonia) de água doce no Estado do Maranhão, Brasil. Boletim do Laboratório de Hidrobiologia 23:49–56.
- Beaudry, F., P.G. Demaynadier, and M.L. Hunter, Jr. 2010. Nesting movements and the use of anthropogenic nesting sites by Spotted Turtles (*Clemmys guittata*) and Blanding's Turtles (*Emydoidea blandingii*). Herpetological Conservation and Biology 5:1–8.
- Bernardes, V.C.D, C.R. Ferrara, R.C. Vogt, and L. Schneider. 2014. Abundance and population structure of *Podocnemis erythrocephala* (Testudines,

Podocnemididae) in the Unini River, Amazonas. Chelonian Conservation and Biology 13:89–95.

- Berry, J.F., and J.B. Iverson. 2011. Kinosternon scorpiodes (Linnaeus 1766) - Scorpion Mud Turtle. Pp. 063.1–063.15 In Conservation Biology of Fresh water Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Rhodin, A.G.J., P.C.H. Pritchard, P.P. van Dijk, R.A. Saumure, K.A. Buhlmann, J.B. Iverson, and R.A. Mittermeier (Eds.). Chelonian Research Monographs No. 5, doi: 10.3854/crm.5.063. scorpioides.v1.2011.
- Brito, E.S., R.C. Vogt, R.M. Valadão, L.F. França, J.Penha, and C. Strüssmann. 2018. Population ecology of the freshwater turtle *Mesoclemmys vanderhaegei* (Testudines: Chelidae). Herpetological Conservation and Biology 13:355–365.
- Browne, C.L., and S.J. Hecnar. 2007. Species loss and shifting population structure of freshwater turtles despite habitat protection. Biological Conservation 138:421–429.
- Brown, G.P., and R. Shine. 2008. Rain, prey and predators: climatically driven shifts in frog abundance modify reproductive allometry in a tropical snake. Oecologia 154:361–368.
- Buhlmann, K.A., and J.W. Gibbons. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. Chelonian Conservation Biology 4:115–127.
- Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.
- Campos-Silva, J.V., C.A. Peres, A.P..Antunes, J.V., and J. Pezzuti. 2017. Community-based population recovery of overexploited Amazonian wildlife. Perspectives in Ecology and Conservation 15:266–270.
- Close, L.M., and R. A. Seigel. 1997. Differences in body size among populations of Red-eared Sliders (*Trachemys scripta elegans*) subjected to different levels of harvesting. Chelonian Conservation and Biology 2:563–566.
- Eckert, S.A., J.E Moore, D.C. Dunn, R.S. Van Buiten, K.L. Eckert, and P.N. Halpin. 2008. Modeling Loggerhead Turtle movement in the Mediterranean: importance of body size and oceanography. Ecological Application 18:290–308.
- Eisemberg C.C., M. Rose, B. Yaru, Y. Amepoul, and A. Georges. 2015. Salinity of the coastal nesting environment and its association with body size in the estuarine Pig-nosed Turtle. Journal of Zoology 295:65–74.
- Fachín-Terán, A., R.C. Vogt, and J.B. Thorbjarnarson.
 2003. Estrutura populacional, razão sexual e abundância de *Podocnemis sextuberculata* (Testudines, Podocnemididae) na Reserva de Desenvolvimento Sustentável Mamirauá, Amazonas,

Brasil. Phyllomedusa 2:43-63.

- Fagundes, C.K., A. Bager, and S.T.Z. Cechin. 2010. *Trachemys dorbigni* in an anthropic environment in southern Brazil: I) Sexual size dimorphism and population estimates. Herpetological Journal 20:185– 193.
- Forero-Medina, G., O.V. Castaño-Mora, and O. Montenegro. 2007. Abundance, population structure, and conservation of *Kinosternon scorpioides albogulare* on the Caribbean island of San Andrés, Colombia. Chelonian Conservation and Biology 6:163–169.
- Fritz, U., H. Stuckas, M. Vargas-Ramirez, A.K. Hundsdorfer, J. Maran, and M. Packert. 2012. Molecular phylogeny of Central and South American slider turtles: implications for biogeography and systematics (Testudines: Emydidae: *Trachemys*). Journal of Zoological Systematics and Evolutionary Research 50:125–136.
- Gibbons, J.W. 1986. Movement patterns among turtle populations: applicability to management of the Desert Tortoise. Herpetologica 42:104–113.
- Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Mets, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:652–665.
- Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). 2018. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. ICMBio, Brasília, Brasil. 492 p.
- Iverson, J.B. 2010. Reproduction in the Red-cheeked Mud Turtle (*Kinosternon scorpioides cruentatum*) in southeastern Mexico and Belize, with comparisons across the species range. Chelonian Conservation and Biology 9:250–261.
- Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture– recapture data with Pollock's robust design. Ecology 78:563–578.
- Kendall, W.L., S. Stapleton, G.C. White, J.I. Richardson, K.N. Pearson, and P. Mason. 2019. A multistate open robust design: population dynamics, reproductive effort, and phenology of sea turtles from tagging data. Ecological Monographs 89:13–29.
- Laake, J.L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Center's (AFSC) Processed Report 2013-01, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service, Seattle, Washington, USA. 25 p.
- Mali, I., D.J. Brown, J.R. Ferrato, and M.R.J. Forstner. 2014. Sampling freshwater turtle populations using hoop nets: testing potential biases. Wildlife Society Bulletin 38:580–585.

- Marsh, D.M., E.H. Fegraus, and S. Harrison. 1999. Effects of breeding pond isolation on the spatial and temporal dynamics of pond use by the Tungara Frog, *Physalaemus pustulosus*. Journal of Animal Ecology 68:804–814.
- Portelinha, T.C.G., A. Malvasio, C.I. Piña, and J. Bertoluci. 2014. Population structure of *Podocnemis expansa* (Testudines: Podocnemididae) in southern Brazilian Amazon. Copeia 2014:707–715.
- Pritchard, P.H.C., and P. Trebbau. 1984. *Kinosternon* scorpioides scorpioides (Linnaeus, 1766). Pp. 239–248 *In* The Turtles of Venezuela. Pritchard, P.H.C., and P. Trebbau (Eds.). Contributions to Herpetology No. 2, Society for the Study of Amphibians and Reptiles (SSAR), Oxford, Ohio, USA.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132:653–661.
- R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http:// www.R-project.org.
- Rhodin, A.G.J. 2018. Global Conservation Status of Turtles and Tortoises (Order Testudines). Chelonian Conservation and Biology 17:135–161.
- Rocha, C.A., J.W. Franklin, W.P. Dantas, M.F. Farias, and A.M.E. Oliveira. 1997. Fauna e flora acompanhantes da pesca da lagosta no Nordeste do Brasil. Boletim Técnico-Científico Cepene 5:15–28.
- Roe, J.H., and A. Georges. 2008. Terrestrial activity, movements and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis* in a temporally dynamic wetland system. Austral Ecology 33:1045– 1056.
- Sena, A.C.S., P.R.S. Cavalcante, M.R.C. Silva, R. Barbieri, and F.A. Castillo. 2013. Limnological characterization of interdune ponds of Curupu Island, Raposa - MA, Brazil. Lakes and Reservoirs: Research and Management 18:356–365.

- Steen, D.A., J.P. Gibbs, K.A. Buhlmann, J.L. Carr, B.W. Compton, J.D. Congdon, J.S. Doody, J.C. Godwin, K.L. Holcomb, D.R. Jackson, et al. 2012. Terrestrial habitat requirements of nesting freshwater turtles. Biological Conservation 150:121–128.
- Steffensen, K.D., L.A. Powell, and M. A. Pegg. 2017. Using the robust design framework and relative abundance to predict the population size of Pallid Sturgeon *Scaphirhynchus albus* in the lower Missouri River. Journal of Fish Biology 91:1378–1391.
- Sterrett, S.C., L.L. Smith, S.W. Golladay, S.H. Schweitzer, and J.C. Maerz. 2011. The conservation implications of riparian land use on river turtles. Animal Conservation 14:38–46.
- Tesche, M.R., and K.E. Hodges. 2015. Unreliable population inferences from common trapping practices for freshwater turtles. Global Ecology and Conservation 3:802–813.
- Urban, M.C. 2015. Accelerating extinction risk from climate change. Science 358:571–573.
- Van Dijk, P.P., J.B. Iverson, A.G.J. Rhodin, H.B. Shaffer, and R. Bour. 2014. Turtles of the World. 7th Edition. Annotated checklist of taxonomy, synonymy, distribution with maps and conservation status. Pp. 329–479 *In* Conservation Biology of Fresh Water Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Rhodin, A.G.J., P.C.H. Pritchard, P.P. van Dijk, R.A. Saumure, K.A. Buhlmann, J.B. Iverson, and R.A. Mittermeier (Eds.). Chelonian Research Monographs No. 5, doi:10.3854/crm.5.000.checklist.v7.2014
- Vanzolini, P.E. 1995. A new species of turtle, genus *Trachemys*, from the state of Maranhão, Brazil (Testudines, Emydidae). Revista Brasileira de Biologia 55:111–125.
- Yom-Tov, Y., and E. Geffen. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. Biological Review 86:531–541.



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APPENDIX 1. Relative abundance of the individuals of *Kinosternon scorpioides* (Scorpion Mud Turtle; Ks) and *Trachemys adiutrix* (Brazilian Slider Turtle; Ta) marked during six years in each lake on Curupu Island, Maranhão State, Brazil. Catch per unit effort (CPUE) = the number of individuals divided by the number of trapping days per year (number in parentheses). Two dashes (--) means the lake was not sampled.

	2009 (64d)		54d) 2010 (31d)		2011 (72d)		2012 (24d)		2013 (40d)		2014 (48d)	
Lake - size	Ks	Та	Ks	Та	Ks	Та	Ks	Та	Ks	Та	Ks	Та
Duna - 0.2 ha	9	11	16	17	6	30	15	6				
Jacare - 0.1 ha	10	7	3	3	12	40						
Olga - 0.2 ha	17	11			8	2						
Tiche - 0.1 ha	5	7			5	13						
Grande - 3.2 ha					21	111	1	15	16	79	5	57
Braco - 0.8 ha									31	90	0	5
Urubu - 3.0 ha											3	14
Total catches	41	36	19	20	52	196	16	21	47	169	8	76
CPUE	0.64	0.56	0.61	0.64	0.72	2.72	0.67	0.87	1.17	4.22	0.17	1.58