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Density, Biomass, and Population Structure of Red-footed Tortoises (*Chelonoidis carbonarius*) and Yellow-footed Tortoises (*Chelonoidis denticulatus*) in the Northern Amazon, Brazil

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***Abstract.*—Red-footed Tortoises (*Chelonoidis carbonarius*) and Yellow-footed Tortoises (*C. denticulatus*) are of both ecological and socio-economic importance in South America as seed dispersers and important game species to rural and indigenous communities. Unfortunately, populations of both species are declining and yet we lack basic data on population structure and biology that can assist in developing management strategies for the conservation of these species. We used distance sampling along line transects and incidental captures to estimate density, biomass, and population structure of tortoise populations in the northwestern Amazon region of Brazil from January 2002 to July 2004. Estimated densities were 0.45 individuals/ha and 0.10 individuals/ha for *C. carbonarius* and *C. denticulatus*, respectively, with 4.38:1 *C. carbonarius*: *C. denticulatus* detected. Male: female sex ratios were 4.83:1 for *C. carbonarius* and 3.00:1 for *C. denticulatus* and biomass estimates were 2.87 kg/ha and 0.61 kg/ha, respectively. Juveniles comprised 8% of the *C. carbonarius* population, yet no juvenile *C. denticulatus* was found. At our study site, *C. carbonarius* were slightly larger whereas *C. denticulatus* were smaller than populations in the southern, core regions of the ranges of these species. Combined biomass estimates are greater than those reported for all other game species at the study site. These data provide baseline population data for non-hunted populations of these species in an area with a relatively undisturbed flora and fauna, an important element in developing management strategies to maintain viable populations of these threatened species elsewhere.**

Key Words.—size structure; Brazilian Amazon; distance sampling; population biology; sex ratio

Introduction

Both the Red-footed Tortoise (*Chelonoidis carbonarius*) and Yellow-footed Tortoise (*C. denticulatus*) are highly frugivorous and pass viable seeds in their feces, acting as important seed dispersers (Guzmán and Stevenson 2008; Jerozolimski et al. 2009; Lautenschlager et al. 2022; Strong et al. 2025). In addition, they are important components in the diets of rural peoples (Peres 2000; Morcatty and Valsecchi 2015). Therefore, maintaining viable populations of *C. carbonarius* and *C. denticulatus* is of both ecological and socio-economic importance; although both species have some protection because they are listed in Appendix II of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES; https://cites.org/sites/default/files/eng/app/2024/E-Appendices-2024-05-25.pdf) and *C. denticulatus* is listed as Vulnerable according to Red List of the International Union for the Conservation of Nature (IUCN) of Threatened Species (IUCN 2024). In the Red Book of Colombian Reptiles, *C. carbonarius* is also listed as Vulnerable whereas *C. denticulatus* is listed as Least Concern (Morales-Betancourt et al. 2016). Habitat destruction, harvesting for both subsistence and market economies, and, to a lesser degree, collecting for the pet trade, have all been cited as contributing factors leading to population declines (Pritchard and Trebbau 1984; Walker 1989a,b).

Chelonoidis carbonarius is found in southern Panama, Colombia, Venezuela, the Guianas, northern Brazil, Bolivia, Paraguay, and northern Argentina (Walker 1989a). It also occurs on several islands in the Caribbean, where it has been introduced as a food source (Pritchard and Trebbau 1984). *Chelonoidis*

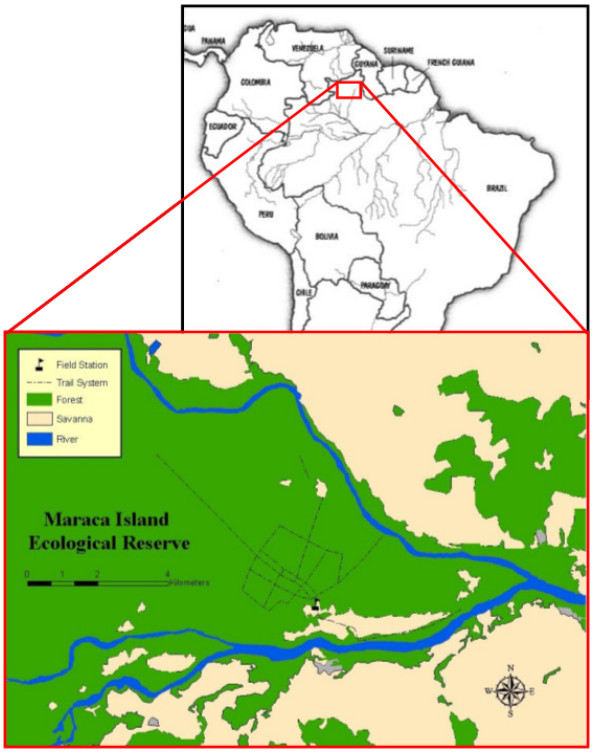

Figure 1. The study region and trail system at Maracá Ecological Station in Roraima, Brazil, where we studied Red-footed Tortoises (*Chelonoidis carbonarius*) and Yellow-footed Tortoises (*C. denticulatus*).

denticulatus has a somewhat smaller range, occurring in Amazonian Colombia, Ecuador, Peru, and Bolivia, southeastern Venezuela, the Guianas, and northern Brazil (Pritchard and Trebbau 1984). *Chelonoidis carbonarius* occurs more frequently along forest margins, gallery forests, and savannas, whereas *C. denticulatus* tends to be restricted to the moister forest interiors of the Amazon Basin (Pritchard and Trebbau 1984). The two species occur sympatrically in many areas, however, including northern Brazil (Balée 1985; Moskovits 1988; Moreira 1989, 1991; Souza-Mazurek et al. 2000), and Colombia (Castaño-Mora and Lugo-Rugeles 1981). Although there is some geographic variation in size, *C. carbonarius* tends to be smaller than *C. denticulatus*, with average linear carapace lengths (LCL) of 30 cm and 40 cm, respectively (Walker 1989a,b). Reported home ranges vary from 0.6 to 628.9 ha for *C. carbonarius* and 1.6 to 35.5 ha for *C. denticulatus* (Moskovits and Kiester 1987; Montaño et al. 2013; Tavares et al. 2019). Numerous indigenous and rural, non-indigenous groups have been documented to consume both species (Souza-Mazurek et al. 2000; Mena et al. 2000; Fachín-Terán et al. 2004; Morcatty and Valsecchi 2015; Fragoso et al. 2016).

To maintain viable populations and prevent further declines, management strategies that integrate biological and socio-ecological parameters of the species are needed (Klemens 1989; Heppell 1998; Iwamura et al. 2014). Studies that provide baseline data on natural populations are therefore important steps in meeting these management needs. To contribute to a better understanding of these species and to provide baseline data from populations that are not hunted, we studied *C. carbonarius* and *C. denticulatus* populations at the Maracá Ecological Station in northwestern Brazil, an intact old-growth forest and savanna region contiguous with the greater Amazon Forest. Our objectives were to: (1) estimate adult population density and based on captured individuals, determine; (2) species ratio; (3) sex ratio; (4) proportion of juveniles in the population; (5) size distribution of adults; and (6) estimate adult biomass based on density and adult mass for each species.

Materials and Methods

Study site.—Maracá Ecological Station is a 110,000-ha riverine island formed by the branching of the Rio Uraricoera, a tributary to the Rio Branco (Fig. 1). In 1978 it was designated an ecological reserve

and received protected status (Milliken and Ratter 1998). Situated in northwestern Brazil in the state of Roraima (3°20'N, 61°20'W), the island is located on the Guiana Shield region at the northeastern edge of the Amazon Basin where it meets the Rio Branco-Rupinuni Savanna (Moskovits 1985). Thus, the area consists of an ecological convergence of lowland Amazonian/Guiana Shield forest with Savanna vegetation. The study site is composed mainly of *terra firme*, Lowland Evergreen Rainforest, that borders Savanna vegetation (Milliken and Ratter 1998). Annual rainfall averages from 2,163 mm, with over 75% falling during the wet season between April and September (Couto-Santos et al. 2014). Due to its protected status as an ecological reserve and a history of minimal human habitation, Maracá supports a largely undisturbed ecosystem, including characteristic megafauna for this region (Moskovits 1985; Fragoso 1998). The study site is located at the eastern end of the island where a grid system of trails established by Moskovits (1985) and later expanded by J.M.V. Fragoso covers approximately 1,000 ha (Fig. 1).

Distance sampling.—We established 10 one-kilometer line transects to cover the entire study area. We spaced transects at least 1 km apart to avoid overlapping the same ranges of individual tortoises. We randomly located five transects within the grid and another five transects we randomly located along segments of the established trail system. Trails at the reserve were about 1-m wide, used only by a small group of researchers, and established independently of vegetation type, and thus should yield unbiased population estimates. We did not survey transects for at least two weeks after cutting to allow local wildlife to acclimate to the disturbance. A pair of observers (a Macuxi indigenous assistant and JNS or two Macuxi assistants) then walked the transects at a rate of 0.5–1.0 km/h every three weeks between 19 March and 5 July 2004. Transects were surveyed six times each for a total of 60 km walked during the study period. Surveyors measured the perpendicular distance of the tortoises to the transect using a 50 m fiberglass tape (to the nearest 10 cm). Surveyors also recorded the location along the transect with the aid of flags placed every 100 m along the transect. In addition, surveyors also recorded time of observation, species, sex, and body measurements for all tortoises, as described below. We generated density estimates of tortoises with the program DISTANCE 4.1 Release 2 (Thomas et al. 2004). Models that achieved the lowest Akaike's Information Criterion (AIC) and coefficients of variation were selected as the best fit. We also radio-tracked and/or thread-trailed 24 tortoises (19 *C. carbonarius* and five *C. denticulatus*) daily during the same period that the distance sampling was conducted to estimate the proportion of tortoises above ground or not completely concealed in debris piles. We used these proportions to calculate the correction factor (g_0) for each species, representing the proportion of tortoises visible for detection using distance sampling.

Additional captures and body measurements.—To increase rates of tortoise captures, we searched for tortoises along the trails in the study area daily, between 0700 and 1800 from 5–26 January 2002 and from 16 February to 16 July 2004, spanning both the wet and dry seasons of the study area. We also found tortoises opportunistically away from the trail system while tracking other tortoises fitted with radio transmitters or thread-trailing devices as part of another component of the study (Strong et al. 2025). Once a tortoise was found, surveyors recorded its location (± 10 m) with a Garmin GPS 315 (Garmin, Olathe, Kansas, USA). Surveyors marked individuals using a unique combination of notches filed into the marginal scutes of the tortoises after Moskovits (1985). Tortoises were either processed in the field and released immediately or taken back to the station and housed overnight to collect fecal samples (for another component of the study) before release at the capture point. Surveyors determined sex based on secondary sex characteristics specific to the species (Pritchard and Trebbau 1984). Male *C. carbonarius* have a dorso-lateral constriction at mid-carapace, a very pronounced concavity to the plastron, and a much smaller gap between the supracaudal and anal scutes compared to females. Male *C. denticulatus* have a slightly concave plastron and longer gular scutes compared to females, which have no concavity and shorter gulars. Sex of individuals of both species with a linear carapace length (LCL) < 20 cm could not be easily determined and we considered them juveniles (Pritchard and Trebbau 1984). For each tortoise, the following was measured: (1) LCL; (2) curved carapace length (CCL); (3) linear carapace width (LCW); (4) curved carapace width (CCW); (5) linear plastron length (LPL); (6) curved plastron length (CPL); (7) curved plastron width (CPW); (8) anal gap (measured as the distance between the midpoint of the supracaudal and anal scutes); (9) height; and (10) mass. We used tree calipers to

Table 1. Estimated strip half-width (ESW), encounter rate (n/L), and tortoise density (D) estimates generated from DISTANCE 4.1 Release 2 for Red-footed Tortoises (*Chelonoidis carbonarius*) and Yellow-footed Tortoises (*C. denticulatus*) at Maracá Island Ecological Reserve in northwestern Brazil from March to July 2004. Abbreviations are CV = coefficient of variation and CI = confidence interval.

Parameter	Point Estimate	Standard Error	% CV	Lower 95% CI	Upper 95% CI
		C. carbonaria			
ESW (m)	10.83	0.97	8.96	9.03	12.99
n/L (tortoises/km)	0.58	0.10	17.69	0.39	0.87
D (tortoises/ha)	0.45	0.11	23.96	0.27	0.75
		C. denticulata			
ESW (m)	9.00	0.82	9.08	7.26	11.15
n/L (tortoises/km)	0.13	0.03	25.00	0.08	0.23
D (tortoises/ha)	0.10	0.03	35.70	0.05	0.22

measure linear lengths and height (to the nearest 0.1 cm) and a flexible measuring tape to measure curved lengths (to the nearest 0.1 cm). We weighed tortoises to the nearest 0.1 kg using 20 kg spring scales. We estimated adult biomass (kg/ha) for each species by multiplying the mean mass of adult males and females by their respective proportion of the population (based on the ratios calculated from distance sampling) and then the number of individuals per hectare.

Results

We found 35 adult *C. carbonarius* and eight adult *C. denticulatus* along the transects. Based on simultaneously studied individuals with radio transmitters and those thread-tracked, we calculated correction factors (g_0) of 0.595 (standard error [SE] = 0.08) and 0.714 (SE = 0.17) for *C. carbonarius* and *C. denticulatus*, respectively. The data for *C. carbonarius* were grouped into 5-m intervals to generate a best fit using a uniform cosine model with one adjustment term (AIC = 86.34). The data for *C. denticulatus* were best modeled using a uniform key function with one cosine adjustment and grouped at 3-m intervals (AIC = 47.26). Both estimated density and encounter rate for *C. carbonarius* (0.45 tortoises/ha and 0.58 tortoises/km, respectively) were 4.5 times higher than those for *C. denticulatus* (0.10 tortoises/ha and 0.13 tortoises/km, respectively) and estimated strip half-widths were similar for both species (Table 1).

We detected a ratio of 4.38:1 *C. carbonarius*:*C. denticulatus*. The male:female sex ratio of 4.83:1 for *C. carbonarius* was significantly male-biased, while the sex ratio for *C. denticulatus* was not significantly different from parity (Table 2). No juveniles from either species were encountered along line transects. The estimated biomass for *C. carbonarius*, based on a male:female sex ratio of 4.83:1 is 2.87 kg/ha (95% Confidence Interval [CI] = 1.99–4.56 kg/ha) and that for *C. denticulatus*, based on a 3.00:1 sex ratio, is 0.61 kg/ha (95% CI = 0.14–1.14 kg/ha). Thus, the two species attain a combined biomass value of 3.48 kg/ha (95% CI = 2.13–5.70 kg/ha).

We incidentally captured an additional 159 *C. carbonarius* (83 males, 59 females, and 17 juveniles) and 41 *C. denticulatus* (34 males, seven females, and no juveniles) while searching trails and tracking other tortoises (Table 2). The resulting *C. carbonarius*:*C. denticulatus* species ratio of 3.87:1 is not different from the 4.38:1 from distance sampling (X^2 = 0.08, df = 1, P = 0.779). The pooled species ratio for all captures (204 *C. carbonarius* and 49 *C. denticulatus*) is 4.16:1. Juveniles detected represented 8% and 0% of the populations of *C. carbonarius* and *C. denticulatus*, respectively. The resulting male:female sex ratio of 1.41:1 for *C. carbonarius* was not significantly different from parity, but the sex ratio of

Table 2. Number of males (M), females (F), juveniles (J), resulting sex ratio (M:F), and Chi-square Test comparing sex ratio to 1:1 for Red-footed Tortoises (*Chelonoidis carbonarius*) and Yellow-footed Tortoises (*C. denticulatus*) captured during distance sampling surveys and incidentally at Maracá Island Ecological Reserve in northwestern Brazil between January 2002 and July 2004. For Chi-square results, df = 1 in all cases.

	C. carbonaria						*C. denticulata*					
Capture method	M	F	J	M:F	X^2	P-value	M	F	J	M:F	X^2	P-value
Distance sampling	29	6	0	4.83	8.47	0.004	6	2	0	3.00	1.06	0.302
Incidentals	83	59	17	1.41	2.04	0.153	34	7	0	4.86	9.97	0.002
Pooled	112	75	17	1.49	3.70	0.054	40	9	0	4.44	10.9	0.001

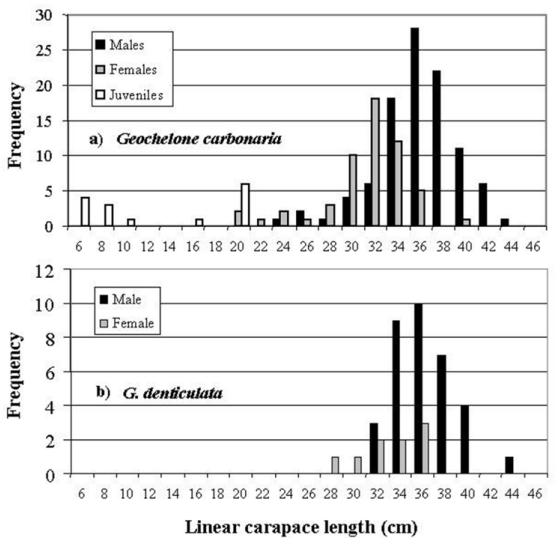

Figure 2. Size distribution of (Top) adult male, adult female, and juvenile Red-footed Tortoises (*Chelonoidis carbonarius*) and (Bottom) adult male and female Yellow-footed Tortoises (*C. denticulatus*) in northwestern Brazil between January 2002 and July 2004.

4.86:1 for *C. denticulatus* was significant (Table 2). When distance sampling and incidentals are pooled, the sex ratios for both species are significantly different from unity (Table 2).

Male *C. carbonarius* were significantly larger than females for all body measurements except for anal gap (females significantly larger) and height (no difference). Male *C. denticulatus* were significantly larger than females only for linear carapace length (LCL), curved carapace length (CCL), and curved plastron length (CPL; Fig. 2, Table 3). Mean linear carapace length (LCL) for both male and female *C. carbonarius* is somewhat larger at Maracá than for two populations measured in Colombia and Venezuela (Table 4). For *C. denticulatus*, however, populations from the periphery of their range, such as the present study, French Guiana, and Venezuela, had smaller individuals than populations located in the central part of the range of the species, such as those from western Brazil, Peru, and Colombia (Table 4).

Discussion

Knowing how tortoise density and biomass compare to that of other vertebrates on Maracá allows us to better understand their potential ecological role in neotropical communities. Notably, while the density values for *C. carbonarius* (0.45 tortoises/ha) and *C. denticulatus* (0.10 tortoises/ha) are high with respect to other vertebrates found in the study area, biomass values (2.71 kg/ha for *C. carbonarius* and 0.61 kg/ha for *C. denticulatus*) were relatively low compared to mammals with larger bodies. For example, Pontes (2004) estimated the Red-rumped Agouti (*Dasyprocta leporina*) density and biomass values of 0.05–0.07 agoutis/ha and 0.20–0.30 kg/ha, respectively at Maracá. White-lipped Peccary (*Tayassu pecari*) density and biomass estimates were 0.21–0.67 peccaries/ha and 7.35–23.29 kg/ha, respectively, and Collared Peccary (*T. tajacu*) density and biomass estimates were 0.19–0.26 peccaries/ha and 4.91–6.77 kg/ha, respectively. Density and biomass estimates for Lowland Tapir (*Tapirus terrestris*) were 0.03–0.04 tapirs/ha and 7.87–8.82 kg/ha, respectively.

Compared to estimates of terrestrial chelonian biomass in other regions, *C. carbonarius* and *C. denticulatus* are not particularly high. Standing crop biomass estimates for terrestrial turtles reviewed by Iverson (1982) ranged from 2.05 kg/ha for Desert Tortoises (*Gopherus agasizzii*) to 583.5 kg/ha for Galápagos Tortoises (*Chelonoidis gigantea*), with a mean biomass of 103.8 kg/ha (n = 9). Because the data are strongly skewed left, however, the median value of 10.8 kg/ha is a better representation of the data. Also, estimates by Iverson (1982) were based on the maximum value of biomass whenever a range was given. When only the minimum values are used, the mean and median biomass values drop to 40.3 kg/ha and 3.1 kg/ha, respectively (range of values, 0.56–220 kg/ha), which compares more favorably to the estimated biomass of *C. carbonarius* and *C. denticulatus*. In another study of two sympatric species, Mason et al. (2000) estimated the biomass of Angulate Tortoises (*Chersina angulata*) was 0.06 kg/ha and for Leopard Tortoises (*Chelonoidis pardalis*) was 6.02 kg/ha.

The density estimates of 0.45 tortoises/ha for *C. carbonarius* and 0.10 tortoises/ha for *C. denticulatus* are approximately half of the estimates of 1.05 tortoises/ha (*C. carbonarius*) and 0.20 tortoises/ha (*C. denticulatus*) by Moskovits (1988). Her estimate of 570 ha for her study site were based on the Peterson Mark-recapture Method for estimating closed population sizes. Because the study spanned 20 mo, the closure assumption was most likely violated, resulting in an overestimate of population size (Lindeman 1990). Our distance sampling estimates could be underestimates, however, resulting from violating the key assumption that all detectable tortoises (those not in burrows or debris piles) are counted (Thomas et al. 2002). This proved

Table 3. Mean, standard deviation (SD), range of values, and sample size (n) of body measurements for male and female Red-footed Tortoises (*Chelonoidis carbonarius*) and Yellow-footed Tortoises (*C. denticulatus*) captured in northwestern Brazil between January 2002 and July 2004. Significant differences between means for males and females are indicated by one asterisk (*; $P \leq 0.050$) and two asterisks (**; $P \leq 0.001$) based on independent Two-sample *t*-test. The measurement Anal Gap is the distance between the midpoints of the anal and supracaudal scutes.

	Males				Females			
Measurement (abbreviation)	Mean	SD	Range	n	Mean	SD	Range	n
				C. carbonaria				
Linear carapace length (LCL)**	35.1	3.5	22.3-42.2	100	30.4	3.7	20.0-38.7	55
Curved carapace length (CCL)**	48.4	5.0	33.0-58.4	112	40.2	4.8	25.7-54.3	75
Linear carapace width (LCW)*	19.6	1.7	15.0-23.5	100	18.1	1.8	13.4-21.3	55
Curved carapace width (CCW)**	37.4	3.5	28.7-44.3	110	35.8	3.9	24.7-48.6	74
Linear plastron length (LPL)**	28.0	2.6	20.0-33.0	100	23.9	2.3	17.7-28.7	55
Curved plastron length (CPL)**	30.6	4.2	3.4-45.7	111	25.4	2.5	18.3-35.3	75
Curved plastron width (CPW)**	19.4	2.0	14.1-27.5	112	17.2	2.0	12.2-24.9	75
Anal gap**	3.8	0.8	2.4-6.4	110	5.7	1.3	2.3-7.9	70
Height	13.5	1.2	9.5-16.5	96	13.4	1.4	9.4-16.5	50
Mass (kg)**	6.7	1.5	2.5-10.1	100	4.8	1.4	1.4-7.6	55
				C. denticulata				
Linear carapace length (LCL)*	35.2	2.6	30.8-42.6	34	32.6	3.1	26.6-36.0	9
Curved carapace length (CCL)**	44.4	3.0	38.7-50.7	40	40.2	3.2	32.6-43.0	9
Linear carapace width (LCW)	21.1	1.3	18.5-23.7	34	21.1	2.1	17.7-23.9	9
Curved carapace width (CCW)	38.4	3.0	32.4-48.4	40	39.6	4.1	31.3-43.7	9
Linear plastron length (LPL)	30.0	2.1	26.2-35.0	33	28.2	2.8	22.5-31.5	9
Curved plastron length (CPL)**	31.5	2.3	26.7-36.9	40	28.7	3.0	22.5-32.5	9
Curved plastron width (CPW)	21.5	1.8	18.0-26.2	40	19.8	2.3	15.2-22.2	9
Anal gap[1]	4.9	0.9	2.5-6.7	39	5.6	1.1	3.3-6.6	9
Height	14.5	1.0	12.9-16.4	26	14.6	1.3	12.1-15.7	9
Mass (kg)	6.2	1.1	4.4-9.1	34	5.9	1.8	2.3-7.9	9

problematic because juveniles and even adults on or near the transect can be overlooked in thick forest cover. Anderson et al. (2001) used *Gopherus agasizzii* to test distance sampling methods with known densities and found that survey teams missed 17% of subadult models (LCL = 18 cm) and 54% of juvenile models (LCL = 6.5 cm) on or near (± 5 m) the centerline. Thus, density estimates can be negatively biased using this method, particularly for smaller size classes and in thick vegetation where vision is obscured. While our correction factors (g_0) accounted for concealed tortoises, they did not account for differential detectability of juveniles. We met the other assumptions (Thomas et al. 2002) that

Table 4. Mean linear carapace length (LCL; cm) and sample size (n) for adult male (M) and female (F) Red-footed Tortoises (*Chelonoidis carbonarius*) and Yellow-footed Tortoises (*C. denticulatus*) in different regions of South America.

	C. carbonaria		*C. denticulata*		
Region	M LCL (n)	F LCL (n)	M LCL (n)	F LCL (n)	Source
northwestern Brazil	35.1 (100)	30.4 (55)	35.2 (34)	32.6 (9)	This study
northwestern Brazil	33.5 (63)	30.5 (75)	35.1 (17)	33.5 (10)	Moskovits, 1985
western Brazil	–	–	44.4 (9)	42.3 (9)	Fachin-Teran et al., 2004
Peru	–	–	36.5 (10)	32.4 (9)	Fachin-Teran et al., 1996
Colombia	30.4 (15)	28.9 (15)	39.4 (15)	36.1 (15)	Castaño and Lugo, 1981
French Guiana	–	–	33.5 (8)	29.7 (8)	Fretey, 1977
Venzuela	29.8 (31)	29.1 (20)	32.4 (12)	31.0 (14)	Pritchard and Trebbau, 1984

tortoise distances were accurately measured from the centerline and tortoises were detected at their initial location prior to any movement in response to the observer(s). Thus, because distance sampling may provide negatively biased density estimates, the true tortoise densities in the study area most likely fall between the estimate of Moskovits (1988) and our distance sampling estimates.

Density estimates from Maracá are relatively low for *C. carbonarius* in relation to elsewhere in the range of the species. In an unpublished study comparing *C. carbonarius* populations in protected and unprotected sites in a savanna/forest mosaic in northwestern Venezuela, Tibisay Escalona used belt transects (10 m × 2 km bands) to estimate densities of 2.75–3.07 tortoises/ha ($\overline{x}$ = 2.91) for protected sites and 0.25–2.50 tortoises/ha ($\overline{x}$ = 1.13) for unprotected sites. In another Venezuelan study comparing a *C. carbonarius* population that was isolated by permanent flooding to a mainland population, Aponte et al. (2003) reported densities of 12.9 and 5.5 tortoises/ha for island and mainland populations, respectively. The island density of 12.9 tortoises/ha, based on the Schnabel Mark-recapture Method, is nearly 30 times larger than our estimate for Maracá. The island population was comprised of 50% of individuals younger than the island (16 y) and was likely a result of increased recruitment due to lack of egg and hatchling predators, rather than a lingering effect of tortoises forced on the island from flooding (Aponte et al. 2003). Therefore, changes in tortoise density could be attributed to changes in predator populations. Habitat quality may also play a role in determining tortoise densities or the possibility that in regions of sympatry, such as Maracá, interspecific competition between *C. carbonarius* and *C. denticulatus* could limit density.

The *C. carbonarius*:*C. denticulatus* species ratio of 4.16:1 was not significantly different from the estimate by Moskovits (1988) of 4.97:1 (189 *C. carbonarius*:38 *C. denticulatus*; X^2 = 0.028, df = 1, P = 0.840). One explanation for this skewed ratio at Maracá, suggested by Moskovits (1988), is that in the survey area, the *C. denticulatus* population represents a peripheral population to the main population located deeper in the forest where they competitively displace *C. carbonarius*, an edge/savanna species. Data presented on game species taken by the Waimiri Atroari Indigenous group, located closer to the center of the range of *C. denticulatus*, near Manaus, reported a species ratio of 0.31:1 (193 *C. carbonarius*:630 *C. denticulatus*; Souza-Mazurek 2001). The Waimiri Atroari do not favor one species over the other (pers. obs.), and thus, the ratio most likely reflects the natural population. Both species seem to be equally inconspicuous and use similar habitats in the study site (Moskovits 1985) and the bias is therefore not likely from different detection rates among species. These results suggest that *C. denticulatus* becomes relatively more abundant towards the center of its range, possibly as a function of distance from the forest-savanna ecotone.

All estimates of male:female sex ratios for *C. carbonarius* and *C. denticulatus* were biased toward males. Possible reasons for biased sex ratios include: (1) one sex moves more frequently and/or greater distances and is more likely to be observed than the other sex; (2) differential mortality between sexes, leading to bias towards the sex with lower mortality (Hailey 1990; Gibbs and Steen 2005); (3) different timing in maturity between sexes, with the sex ratio favoring the faster-maturing sex (Lovich and Gibbons 1990; Lovich 1996); and (4) skewed sex ratios of the hatchlings due to environmental sex determination (ESD; Janzen 1994; Mrosovsky 1994). Survival rates are not known for either species, let alone any differences between sexes, so the importance of differential mortality remains unknown. Sex ratios tend to be female biased in species in which males are larger than females (Lovich 1996); therefore, if there should be a bias in these populations, it would be expected to favor females because males are the larger sex for both species, which is not what we observed. Although ESD can cause short-term variation within cohorts (Janzen 1994), sex ratios tend to remain constant over the long term (Mrosovsky 1994) and are unlikely to cause the observed bias. The observed bias was likely due to a sampling methodology that favored detecting males, the more active sex. Radio- and thread-tracking results from a separate component of this study (Strong et al. 2025) and Moskovits and Kiester (1987) show that males tend to be more active in both *C. carbonarius* and *C. denticulatus* during the wet (mating) season, resulting in their higher detectability and subsequent numerical dominance in this study. The work by Moskovits (1988) spanned both the dry (non-breeding) season when females tend to be more active and the wet (breeding) season when males tend to be more active and thus, sampled when both sexes had higher detectabilities. The male:female sex ratios reported by Moskovits (1988) were 1.3:1 for *C. carbonarius* and 1.5:1 for *C. denticulatus*, neither of which was significantly different from parity. In

contrast, our study occurred primarily during the wet season, sampling the population when males were more active than females and were therefore likely to be over-represented in the sample. Sex ratios, as determined by searching method, indicate that distance sampling took place primarily during the wet season and resulted in a larger male bias for *C. carbonarius* than did the incidental captures, which took place over more of the dry season. These discrepancies in sex ratio demonstrate the need for long-term studies that accommodate the seasonal and annual variability in activity by sex and species to estimate vital rates and trends more accurately. Juveniles represented just 8% of the *C. carbonarius* population sampled and no juvenile *C. denticulatus* were found during the study period. These numbers are likely underestimates of the actual proportion of juveniles due to their cryptic nature (Anderson et al. 2001).

The frequency of adult LCL for *C. carbonarius* males and females is slightly skewed right, with a gradual increase in larger adults and a sharper drop-off of very large individuals. The sample size for *C. denticulatus* was too small to properly model the size structure. Males of both species were significantly larger than females, suggesting that males are territorial and engage in male-male combat to maintain their territories (Berry and Shine 1980). Although no combat was observed between *C. carbonarius* males, it was observed on two occasions between *C. denticulatus* males (pers. obs.), supporting this type of sexual dimorphism.

The mean LCL values for *C. carbonarius* and *C. denticulatus* were similar to those of Moskovits (1985), indicating a potentially stable population structure on Maracá over the past 20 y. Both male and female *C. carbonarius* are larger at Maracá than populations in Colombia and Venezuela, whereas *C. denticulatus* at Maracá and other northerly populations are somewhat smaller than populations located within the core range and non-ecotone forests of this species to the south. Differences in size between populations can be attributed to geographic variation (Pritchard and Trebbau 1984) or to the effects of hunters or collectors, who select for larger individuals, resulting in a greater proportion of smaller individuals in the population (Klemens and Moll 1995). It is more likely that hunting pressure is playing a role in the difference of LCL for *C. carbonarius* among the three sites, rather than geographic variation because the three sites are within the same contiguous range for the species in a relatively small geographic area (Pritchard and Trebbau 1984). Our study population is located in a region of very low human population density and no hunting takes place at Maracá, so the tortoise population is not affected by human pressures, whereas for the sites in Colombia and Venezuela, the extent of hunting and/or collecting is unknown. For *C. denticulatus* however, the difference in size between regions could be a cause of geographic variation, as sites located in the core of the range of this species, which are also areas of unbroken forest (i.e. Peru, Colombia, and western Brazil) show larger mean LCLs than do the regions located on the periphery of the range, which are near the forest-savanna ecotone (i.e. northwestern Brazil, French Guiana, and Venezuela), despite hunting pressure in the Peruvian and west Brazilian sites (Fachín-Terán et al. 1996; 2004). Larger sample sizes across more of the ranges of these species are needed, however, to properly assess the degree of geographic variation in size throughout their range. In addition, understanding how the degree of hunting and/or collecting pressure affects population density and structure is necessary to begin development of conservation strategies and management plans for these ecologically and socio-economically important species.

In conclusion, we found that although *C. carbonarius* and *C. denticulatus* achieve high densities and biomass values on Maracá compared to other vertebrate species, these values are low in comparison to estimates in other parts of their range. Data on population structure and density, from an area with little direct human impact, provides baseline data that is important in developing management strategies elsewhere in their ranges where populations may be threatened. Furthermore, we show the need for studies in other regions to better understand the geographic variation in size and population structure, as well as long-term studies that extend over both wet and dry seasons to capture the seasonal variability in tortoise activity levels.

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