Copeia 2013, No. 1, 111–120

Middle Orinoco, Venezuela

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We quantified illegal and unmonitored harvest of three endangered sideneck turtles (*Podocnemis* spp.) by examining discarded turtle shells in 29 riverine communities both up- and down-river from the Arrau Turtle Wildlife Refuge in the Middle Orinoco, Venezuela. We compared harvested turtle sizes to those captured during in-water research surveys to determine harvest selectivity. We found fresh sideneck turtle shells in most communities visited; carapaces and plastrons from *P. expansa* were the most abundant despite their protected status. Turtle harvest was skewed toward females in all species, and toward juvenile *P. expansa* and adult *P. unifilis* and *P. vogli*. Considering historical accounts of widespread turtle husbandry in the area, *Podocnemis* spp. life history, and population recovery for these species in community-based conservation programs elsewhere in South America, we recommend community-managed captive breeding of faster-maturing *P. unifilis* and *P. vogli* to satisfy turtle consumption needs. These measures, along with improved nesting-beach protection, may allow recovery of populations of *P. expansa* and make possible their legal subsistence harvest in the future.

PROPER management of exploited wildlife for sustained harvest, maintenance, or recovery requires not only knowledge of the demography and life history of a species but also a detailed understanding of the type of harvest they are experiencing (Williams et al., 2002). Timing and selectivity of the harvest (Jensen, 2000; Freckleton et al., 2003), along with the life-history strategy of the harvested species (Heppell et al., 2000; Musick et al., 2000), determine whether the current harvest practice is sustainable. Traditionally, long-lived organisms like turtles have been thought of as being particularly susceptible to overharvesting (Congdon et al., 1993, 1994). Their life history strategy, characterized by delayed maturity, low egg and hatchling survival, and high juvenile, subadult, and adult survival (Crouse et al., 1987; Heppell, 1998; Chaloupka and Limpus, 2002), makes population growth sensitive to changes in subadult and adult survival (Doak et al., 1994; Cunnington and Brooks, 1996; Heppell et al., 1996) and in some cases, fertility (Chaloupka, 2002). In freshwater species, larger, older turtles are often selectively harvested (Escalona and Fa, 1998; Hernández and Espín, 2003; Fordham et al., 2006), and this can threaten population persistence because of the high reproductive value of these individuals (Congdon et al., 1993, 1994; Mogollones et al., 2010). Maintaining high adult survival may be crucial for the persistence of some long-lived organisms. However, fast-growing, early maturing, and highly fecund species, which similarly breed for many years after reaching maturity, can sustain a level of adult harvest while supporting viable populations (Stevens et al., 2000; Fordham et al., 2007, 2008, 2009).

Turtles have long been an important food resource for humans, but human population growth, enhanced harvest methods, and cultural merging have led to overexploitation of many turtle species (Klemens and Thorbjarnarson, 1995; Thorbjarnarson et al., 2000). Such is the case for the Arrau, *Podocnemis expansa*. Overexploitation of females and eggs reduced the population of nesting females in the Middle Orinoco, estimated at over 330,000 over 200 years ago (Humboldt, 1820), to less than 2000 by 1985 (MINAMB, 2008). With the decline of *P. expansa*, preferred for its size, gregarious nesting, and large clutches, hunting pressure has increased for congenerics like the Terecay, *Podocnemis unifilis*, and Galápago, *Podocnemis vogli* (Thorbjarnarson et al., 1993; Escalona and Fa, 1998). All three species are listed in Appendix II of CITES (UNEP-WCMC, 2009). In Venezuela, *P. expansa* is listed as critically endangered (Decreto No. 1486, Gaceta Oficial de la República de Venezuela, Lista oficial de especies en peligro de extinción de Venezuela. Vol. Número 36062, Caracas, 1996; Rodríguez and Rojas-Suárez, 2008), and lower risk/conservation dependent in the IUCN Red List (IUCN, 2009). *Podocnemis unifilis* is listed as threatened in Venezuela (Rodríguez and Rojas-Suárez, 2008) and vulnerable in the IUCN Red List (IUCN, 2009), and *P. vogli* is listed as threatened in Venezuela (Rodríguez and Rojas-Suárez, 2008).

Fordham et al. (2007, 2009) found that turtle species with relatively fast life histories may be able to sustain a level of subadult and adult harvest without affecting population viability. With an estimated age at maturity of 11–28 years (Hernández and Espín, 2006; Mogollones et al., 2010), *P. expansa* would be considered a late-maturing species, while informal estimates suggest *P. unifilis* and *P. vogli* should mature in 3–9 years (Ramo, 1982; Thorbjarnarson et al., 1993), suggesting the latter two species may be less vulnerable to overharvesting than *P. expansa*. However, *P. expansa* has persisted under continued harvest since pre-Colombian times, declining only after the influence of modern cultures had changed traditional harvest practices (baited hook lines and harpoons in the wet season) toward more efficient and less selective methods (trawl nets in the dry season) in order to satisfy both subsistence and commercial harvest demands (Thorbjarnarson et al., 1993; Perez A. et al., 1995; Thorbjarnarson et al., 2000; Escalona and Loiselle, 2003). Historically, indigenous communities

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Submitted: 6 October 2010. Accepted: 23 August 2012. Associate Editor: J. W. Snodgrass.

DOI: 10.1643/CE-10-158

along the Orinoco and Amazon rivers kept juvenile and adult turtles in flooded enclosures for aquaculture and directed wild harvest toward eggs on the nesting beaches (Carvajal, 1504–1584; Humboldt, 1820). Changing these practices toward nonselective mass harvests caused the demise of turtle populations and displaced traditional cultures as the main consumers of turtles (Thorbjarnarson et al., 2000).

The Arrau Turtle Wildlife Refuge (AWR), named after the common name for *P. expansa* in Venezuela, was created in 1989 to protect this species' main nesting beaches in the Middle Orinoco, Venezuela (Licata and Elguezabal, 1997). After more than 20 years of protecting nesting females, eggs, and hatchlings, and 15 years of reintroducing headstarted yearlings (>350,000 yearlings released), the number of nesting females has stabilized but has not increased (Hernández and Espín, 2003, 2006; Mogollones et al., 2010). Additionally, *P. expansa* scarcity, increasing human populations, and an ongoing economic crisis (Rodríguez, 2000; Salmerón, 2010) have led to increased harvest pressure on *P. unifilis* and *P. vogli* (Thorbjarnarson et al., 1993; Escalona and Fa, 1998). Harvest of *P. expansa* has been illegal since 1962 and *P. unifilis* and *P. vogli* have an unenforced quota of two turtles per person per year. Despite legal protection, harvest of these turtles is prevalent and goes unmonitored in the Middle Orinoco (Hernández and Espín, 2003), though local inhabitants report that for subsistence, turtles are only taken as bycatch and are not under directed harvest (C. L. Peñaloza, unpubl.). Continued harvest undermines conservation efforts of *P. expansa* carried out in the area by the Venezuelan Ministry of the Environment.

In other South American countries, adequate protection and involvement of local communities have increased the abundance of these turtles. In Bolivia, four years after the creation of a protected area that eliminated hunting pressure, the abundance of *P. unifilis* and *P. expansa* is higher in the protected area than in neighboring communities (Conway-Gómez, 2008). In Ecuador, a Cofán Indian community-based conservation program, which protects nests, hatchlings, and adults, has resulted in a two to three-fold increase in turtle abundance in only ten years (Townsend et al., 2005). In Venezuela, even though the AWR conservation program includes community outreach and environmental education programs aimed toward eliminating *P. expansa* consumption, there is still illegal commercial and subsistence harvest of this species (Hernández and Espín, 2003).

Podocnemis expansa is found in the large, slow moving rivers and main tributaries of the Amazon, Orinoco, and Esequibo basins. With the onset of the dry season and decreasing water level, turtles congregate in the main rivers to breed. Gregarious nesting occurs on seasonal sand-bank islands that emerge during the dry season when river waters are up to 20 m below high water. Turtles disperse into flooded forests to feed with rising waters during the wet season (Pritchard and Trebbau, 1984). *Podocnemis unifilis* and *P. expansa* frequently share the same habitat. However, *P. unifilis* is also found in smaller tributaries and during the dry season exhibits solitary nesting on river banks of main rivers and tributaries (Pritchard and Trebbau, 1984; Thorbjarnarson et al., 1993). *Podocnemis vogli* is restricted to the Venezuelan and Colombian flood plains of the Orinoco and its tributaries. This species is frequently found in small tributaries and lagoons and it nests during the dry season in the savanna. *Podocnemis vogli* is also known to burrow in the mud and estivate when lagoons dry out (Pritchard and Trebbau, 1984). Currently, these species are harvested during the dry season when they aggregate to breed in the main rivers. Members of local communities (ribereños) say they consume turtles (mostly *P. expansa*) taken as bycatch while trawling for fish with nets outside the AWR; they also harvest *P. unifilis* and *P. vogli* on land while female turtles nest, but not so *P. expansa*, because its nesting beaches are protected (Hernández and Espín, 2003; Peñaloza, unpubl.).

In order to make sound management decisions to ensure the ecological viability and sustained use of populations of *P. expansa*, *P. unifilis*, and *P. vogli*, we must fully understand current harvest pressure and link it to the life history traits of these species. In this study we describe and quantify the harvest of *P. expansa*, *P. unifilis*, and *P. vogli* turtles, and determine if there is selective harvest (by size or sex) when compared to in-water research surveys in the Middle Orinoco, Venezuela. We then suggest management actions based on harvest and life history characteristics.

MATERIALS AND METHODS

Study area.—The research site comprised a 120 km stretch of the Middle Orinoco River, Venezuela between the city of Puerto Páez, Apure (across from the Colombian border) and the town of La Urbana, Bolivar (Fig. 1). This stretch includes the AWR and 29 riverine communities located both up- (south) and down-river (north) from the wildlife refuge. From 19 April to 12 June 2008, we visited each community by river to search for turtle remains in open dumps and tracts of land adjacent to these communities, and we conducted in-water turtle surveys along a 25 km section of the Orinoco just north of the AWR.

Data collection: harvest.—We looked for turtle shells (carapaces and plastrons) discarded in the recent dry season (December 2007–March 2008) distinguished by the presence of epidermal scutes and overall structural integrity (as opposed to shells from the previous dry season that had disjointed bony plates or were too fragile to handle; Thorbjarnarson et al., 1993). We identified each shell to species according to its shape (Pritchard and Trebbau, 1984) and measured it to the nearest millimeter with a fiberglass tape measure (over-the-curve carapace length, CCL, and intergular to anal notch for plastrons, PL). We sexed plastrons by the shape of the anal notch or plastral length. Males have u-shaped anal notches while females and juveniles have v-shaped anal notches (Pritchard and Trebbau, 1984; Thorbjarnarson et al., 1993; Perez A. et al., 1995). Plastrons with an u-shaped anal notch were considered males. Plastrons with a v-shaped anal notch were considered females if they were larger than the geometric mean size for male turtles caught in the area since 1998 (Hernández and Espín, 2006; Mogollones et al., 2010; O. Hernández, unpubl.; see Table 1); smaller plastrons were considered as having come from juveniles. We define the population sex ratio as the sex ratio of all sexed individuals.

We defined harvest as the number of turtle remains found in each community. Total harvest ranged from the largest total of either carapaces or plastrons (minimum harvest) up to the sum of both carapaces and plastrons (maximum harvest) for a particular community. This allows us to account for carapaces and plastrons that may have come from the same turtle without having to discard information

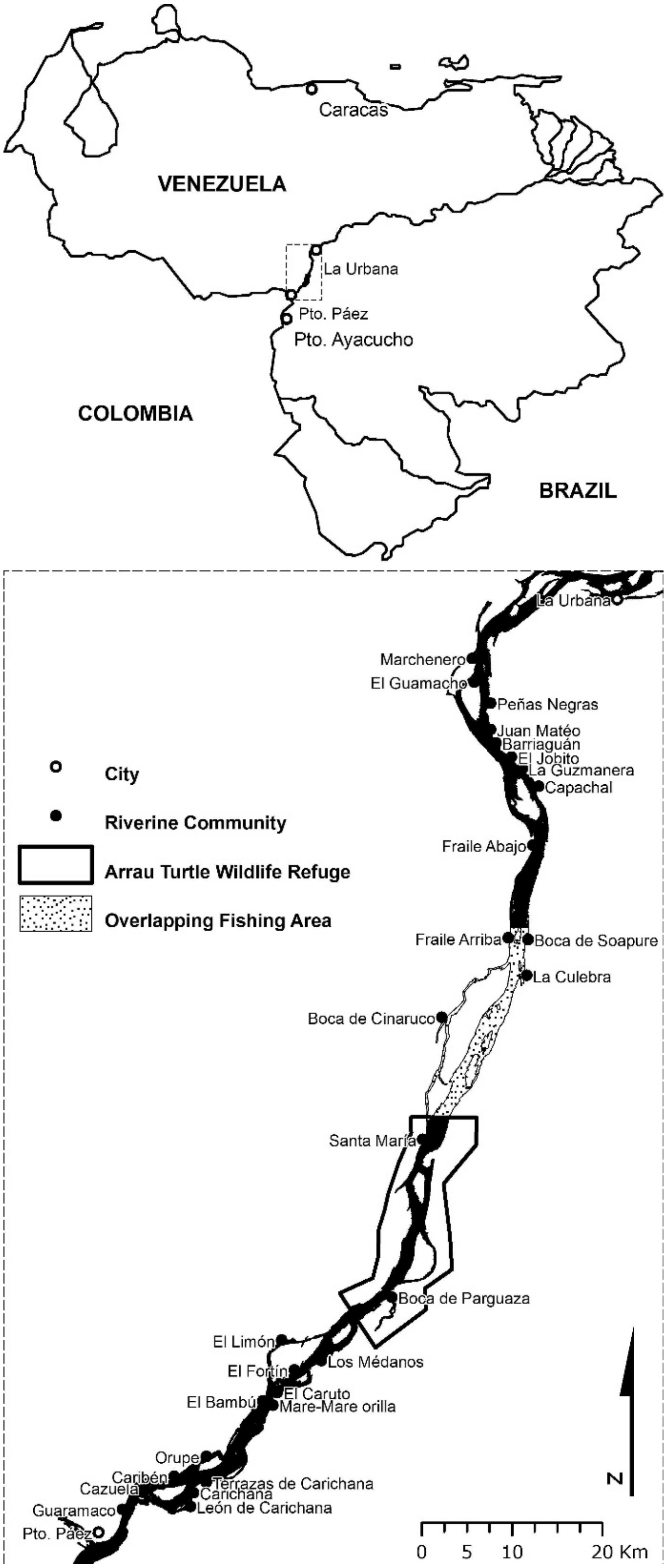

Fig. 1. Map of study area displaying name and location of riverine communities, the Arrau Turtle Wildlife Refuge, and the overlapping fishing area (just north of the refuge) in the Middle Orinoco, Venezuela.

about sex ratios or harvest numbers from communities where mostly plastrons where found (turtle meat is sometimes cooked in the carapace on an open fire; this cooking method does not leave carapace remains). We defined per capita harvest as total harvest per person in each community divided by percentage of community-land surveyed. This method underestimates actual turtle harvest because it does not account for turtles transported to other communities for consumption, turtle remains discarded into the river by ribereños who know consumption of certain turtles is illegal, or remains damaged or relocated by scavengers such as dogs. We obtained community population size from interviews with community leaders and members by C. L. Peñaloza (unpubl.).

Data collection: capture.—We conducted in-water turtle surveys just north of the AWR along a 25 km stretch of the Orinoco River from the southernmost tip of Vapor Island to Fraile Arriba Island (Fig. 1) to overlap with part of the fishing area used by ribereños. We visited six locations one to five times from 19 to 29 April 2008. We surveyed turtles with a 5 cm mesh-size trawl net, using the same fishing method used by ribereños, beach-seining, where the net is pulled between two boats or one boat and a person on land. Once landed, we identified turtles to species, measured CCL and PL, sexed male turtles by secondary sexual characteristics, and individually marked turtles by shell notching (*sensu* Pérez-Emán, 1990) before release. As with harvested turtles, we distinguished between females and juveniles by size using the geometric mean male size for the area (Table 1); all turtles with v-shaped anal notches larger than the male mean were considered females, whereas those smaller than the mean were considered juveniles.

Analysis.—We compared the species composition and size distribution of turtles harvested by locals (harvested) and those captured in our surveys (captured). Ribereños say they consume turtles taken as bycatch while trawling for fish with nets (10 cm mesh-size) outside the AWR; they also harvest *P. unifilis* and *P. vogli* on land while female turtles nest (Peñaloza, unpubl.). We used a Chi-squared test for all proportion comparisons, i.e., population sex ratios, proportion of juveniles to adults, species distribution along the river, and comparison of species composition between harvested and captured turtles. A *P*-value was computed by Monte Carlo simulation (MC-*P*, $n = 2000$) for comparisons with low expected values (<2). We compared size distributions of harvested and captured turtles using normal (Gaussian) kernel density plots in R (Bowman and Azzalini, 2007; R Development Core Team, 2008). The test statistic is the integrated squared difference between the two density estimates. Under the null hypothesis, the distribution of this test statistic is calculated from datasets created by random permutation of group labels on the entire dataset. A reference band is used to illustrate the comparison between density curves; it is centered at the average of the two curves and is equal to the width of two standard errors at any given point (Bowman and Azzalini, 1997).

RESULTS

Harvest.—Turtle consumption was widespread throughout the Middle Orinoco. Most of the turtle remains found were of *P. expansa* (74% of carapaces and 78% of plastrons), followed by *P. unifilis* (16% of carapaces and 13% of plastrons), and *P. vogli* (10% of carapaces and plastrons). We found three Mata-mata (*Chelus fimbriatus*) shells (carapaces and plastrons still connected), though we consider these as natural mortality because cooking requires removing the plastron to disembowel and carve the turtle. We found mostly *P. expansa* remains up-river of the AWR

Table 1. Shell Size of Male Sideneck Turtles Caught in the Middle Orinoco from 1998–2008. Values are geometric mean (mm) and range. The appearance of secondary sexual characteristics (u-shaped anal notch and engrossed and elongated tail) allows external sex determination in males. We distinguished between females and juveniles by size using the geometric mean male size; we assume turtles larger than the mean with a v-shaped anal notch were females.

Species	Plastrons	Carapaces
P. expansa (*n* = 51)	236	321
	145–293	184–425
P. unifilis (*n* = 91)	199	279
	156–251	225–360
P. vogli (*n* = 4)	170	216
	132–319	160–310

whereas down-river the proportion of *P. unifilis* and *P. vogli* increased (58.59, df = 2, $P < 0.0001$; Fig. 2A).

The total harvest per turtle species in the Middle Orinoco is shown in Table 2. Within each species, we found mostly carapaces (63–70%) and female plastrons (45–65%). The plastron sex ratio of harvested turtles was skewed toward females for *P. expansa* (3:1, 23.75, df = 1, $P < 0.0001$) and *P. vogli* (13:1, 10.28, df = 1, $P < 0.005$) and balanced for *P. unifilis* (3:1, 3.55, df = 1, $P > 0.05$). Assuming females of *P. expansa* reach sexual maturity at the minimum nesting female size of 465 mm CCL (367 mm PL) and males do so at the geometric mean male size of 321 mm CCL (236 mm PL), 3–23% (female maturity size–male maturity size) of carapaces and 19% of plastrons were from adult turtles (18 males, 11 females). For *P. unifilis*, 59% of carapaces and 68% of plastrons were from adult turtles (4 males, 13 females) and for *P. vogli*, 71% of carapaces and 65% of plastrons were from adult turtles (0 males, 13 females).

The size distribution of turtle shells of *P. expansa* scaled to per capita harvest for each riverine community is shown in Figure 2B. We found turtle remains in 69% of the communities visited. Total turtle harvest in communities varied widely ($\bar{x}$ = 13–19, 0–101 shells), though this variation decreased once harvest was adjusted by community size. The average per capita consumption rate was 0.57 (range = 0–3.56, SD = 0.78) turtles per person for the 2007–2008 dry season, though two communities, Boca de Suapure II and La Culebra, had higher per capita consumption rates, 1.8 and 2.0 turtles per person per season (>1.58 and 1.79 SD above the mean, respectively), and one community had a significantly higher consumption rate of 3.6 turtles per capita for the season (Caribén, >3.84 SD above the mean). We did not find turtle remains in communities within the AWR, though we were informed that Ministry of the Environment officials had confiscated a 721 mm CCL carapace of *P. expansa* from a member of the Santa María community earlier in the season.

Comparison of harvest and capture.—The proportion of *P. expansa*, *P. unifilis*, and *P. vogli* was different between harvested and captured turtles (18.87, df = 2, $P < 0.0001$). There were more harvested *P. expansa* and *P. vogli* and fewer harvested *P. unifilis* than captured during in-water surveys (for sample sizes see legend Fig. 3). The sex ratio of *P. expansa* was female biased for harvested (3:1, 9.52, df = 1, $P < 0.005$) and captured turtles (6:1, 10.71, df = 1, $P < 0.005$), though these are not significantly different from each other (0.23, df = 1, $P > 0.1$). Captured *P. unifilis* were male biased (1:4, 18.28, df = 1, $P < 0.0001$) and *P. vogli* sex ratio was balanced (1:2, 0.33, df = 1, $P > 0.5$); sex ratios of harvested and captured *P. unifilis* and *P. vogli* were significantly different (189.80, MC-$P < 0.0005$ and 8.53, MC-$P < 0.03$, respectively). We did not find harvested male *P. unifilis* or *P. vogli* in the overlapping fishing area.

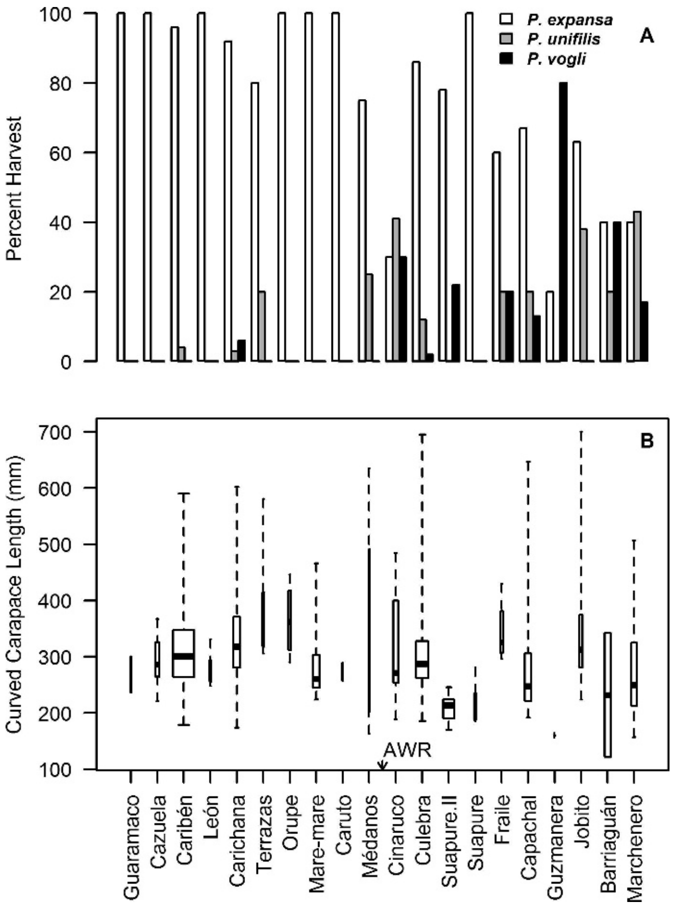

Fig. 2. (A) Percent harvest of *Podocnemis* spp. turtles by community in the Middle Orinoco, Venezuela. (B) Size of harvested *P. expansa* turtles in each riverine community scaled to per capita harvest (box width). Each box contains the lower data extreme, first quartile, median, third quartile, and upper data extreme (outliers are included in whiskers). Communities are listed in south (up-river) to north (down-river) order with the Arrau Turtle Wildlife Refuge approximately in the middle.

The size distribution of harvested and captured turtles is shown in Figure 3. Harvested carapaces of *P. expansa*, and juvenile and male plastrons were larger than captured ones, whereas female plastrons were similar. Harvested shells and female plastrons of *P. unifilis* were smaller than captured ones. The size distribution of *P. vogli* was similar for harvested and captured turtle carapaces. We only captured one female *P. vogli* and we did not capture juvenile *P. unifilis* or *P. vogli*. Male *P. unifilis* and *P. vogli* were not harvested in this area. Harvested *P. expansa* were larger than those captured; 15% of harvested *P. expansa* were adults (6 males, 3 females) whereas only 6% of those captured were adults (3 males, 2 females), though this difference was not significant (2.28, df = 1, $P > 0.1$). Harvested *P. unifilis* were smaller than captured *P. unifilis* (6.173, df = 1, $P < 0.02$); 59% of harvested *P. unifilis* were adults (0 males, 5 females) while 88% of captured ones were adults (39 males, 12 females). A wide size range of *P. vogli* turtles were harvested, however, only one adult female was

Table 2. Sideneck Turtles Harvested in the Middle Orinoco during the 2007–2008 Dry Season. Values correspond to geometric mean curved length (curved carapace length and curved plastral length—intergular scute to anal notch), size range, and sample size in parentheses. Sex ratio in females:males; star indicates significantly skewed ratio (χ^2, $P < 0.005$). Total harvest ranges from the largest total of either plastrons or carapaces to the addition of both in an effort to account for shells coming from the same turtle.

Species	Carapaces (mm)	Plastrons (mm)			Sex ratio	Total
		Juvenile	Female	Male		Harvest
P. expansa	275 157–700 (261)	194 93–235 (62)	295 236–550 (70)	302 191–512 (23)	3:1*	n = 261–416
P. unifilis	302 190–438 (58)	148 100–173 (7)	261 212–313 (13)	251 190–325 (5)	3:1	n = 58–83
P. vogli	246 173–342 (34)	162 155–170 (6)	205 177–247 (13)	165 na (1)	13:1*	n = 34–54

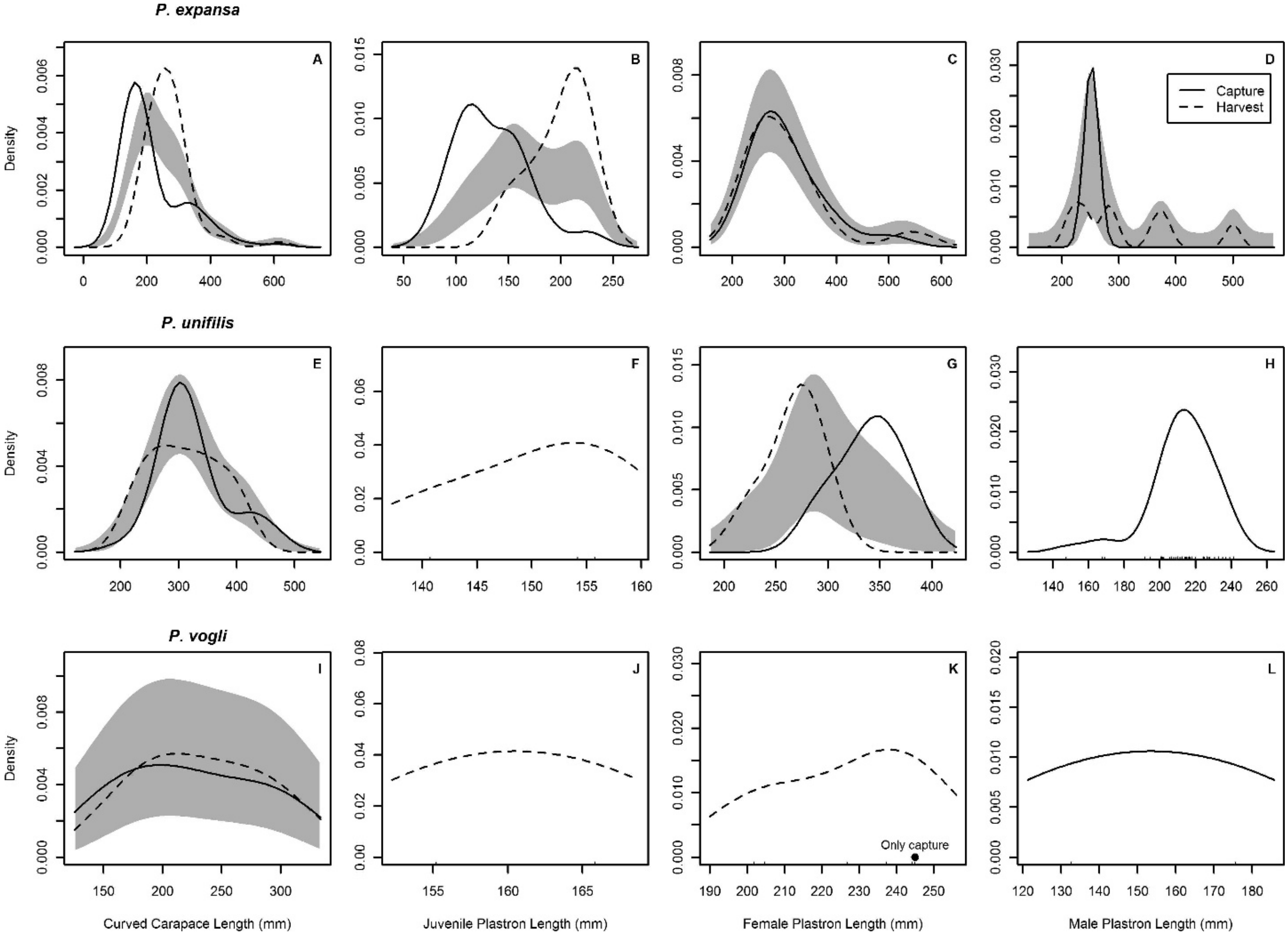

Fig. 3. Kernel density plot size comparison of captured and harvested *Podocnemis* spp. from the overlapping fishing area. The reference bands display differences between curves (equal to two standard errors). Captured and harvested shell size distributions were different for carapaces of *P. expansa* (A, $P = 0$, $n_{\text{harvest}} = 57$, $n_{\text{capture}} = 94$), juvenile (C, $P = 0$, $n_{\text{h}} = 57$, $n_{\text{c}} = 64$) and male plastrons (D, $P < 0.05$, $n_{\text{h}} = 8$, $n_{\text{c}} = 3$), and *P. unifilis* carapaces (E, $P < 0.01$, $n_{\text{h}} = 22$, $n_{\text{c}} = 56$) and female plastrons (G, $P = 0$, $n_{\text{h}} = 5$, $n_{\text{c}} = 12$). Size distribution of female *P. expansa* plastrons (B, $n_{\text{h}} = 26$, $n_{\text{c}} = 18$) and *P. vogli* carapaces (I, $n_{\text{h}} = 15$, $n_{\text{c}} = 3$) were not different. Male *P. unifilis* (H, $n_{\text{c}} = 44$) and *P. vogli* (L, $n_{\text{c}} = 2$) were not harvested, whereas juvenile *P. unifilis* (F, $n_{\text{h}} = 3$) and *P. vogli* (J, $n_{\text{h}} = 2$) were not captured. We captured only one female *P. vogli* (K, $n_{\text{c}} = 1$).

captured (245 mm PL); 53% of harvested *P. vogli* were adults (0 males, 5 females) and 67% of captured ones were adults (1 male, 1 female; 6.70, df = 1, $P < 0.01$).

DISCUSSION

Harvest.—There is widespread harvest of *Podocnemis* spp. in the Middle Orinoco. The most harvested species is *P. expansa* despite the fact that its consumption is illegal. Ribereños assure it is only taken as bycatch and only then for subsistence (Peñaloza, unpubl.). However, unusually high per capita harvest in some communities suggests there is also commercial harvest. Caribén had the highest per capita harvest of all riverine communities visited (3.6 turtles per person); its proximity to the city of Puerto Páez and the availability of several motor boats in the community would make it an ideal site for a seasonal ''turtle restaurant.'' Boca de Suapure II, a seasonal camp of non-local fishers, had the third highest per capita harvest rate (1.8 turtles per person) and some of the smallest turtles harvested (Fig. 2), which suggests larger turtles were sold along with the fish catch while small turtles provided sustenance for fishers. This was found for *P. unifilis* on the Nichare-Tuwadu rivers, tributaries of the Orinoco to the east (Escalona and Fa, 1998). Additionally, a comparison of our results with commercial harvest data from Hernández and Espín (2003) indicates larger turtles are channeled toward commerce (Fig. 4).

The difference in species composition of harvested turtles up- and down-river of the AWR (Fig. 2A) may be due to selective harvest or differences in species distribution along the river. If we consider *P. unifilis* and *P. vogli* are generally associated with smaller rivers (Pritchard and Trebbau, 1984), the presence of four Orinoco tributaries (Parguaza, Villacoa, Cinaruco, and Suapure rivers) within and down-river of the AWR could explain an increase in availability and therefore, harvest, of these species. Additionally, *P. unifilis* and *P. vogli* tend to prefer different nesting habitat (Pritchard and Trebbau, 1984) and they are smaller than *P. expansa*, which could allow for competitive displacement toward smaller, shallower rivers (Pluto and Bellis, 1986). Spillover effect from AWR protection could also contribute to increased *P. unifilis* and *P. vogli* abundance (e.g., McCullough, 1996).

Comparison of harvest and capture.—The difference between species composition of harvested and captured turtles suggests that ribereños from the Middle Orinoco prefer to consume *P. expansa* over *P. unifilis* and *P. vogli* turtles. This result supports findings by Hernández and Espín (2003). Even though only *P. expansa* plastrons are harvested in a larger proportion than they were captured, the proportion of carapaces is probably underestimated due to their destruction during cooking (roasted over an open fire).

Out of captured turtles, only *P. vogli* had a balanced sex ratio; *P. expansa* were skewed toward females and *P. unifilis* toward males. Even though Smith (1979) states that turtle sex ratio depends on capture method and reproductive status of the population, we believe the ratios we obtained reflect actual population sex ratios for these species. During the reproductive season for sidenecks (dry season), baited trot lines produced equal sex ratios for *P. unifilis* in two studies (Smith, 1979; Thorbjarnarson et al., 1993), whereas the same method produced a 2:1 female biased sex ratio in another study (Perez A. et al., 1995). Similarly, trawl and trammel nets have produced both female and male biased sex ratios during the reproductive season for sideneck turtles (Balensiefer and Vogt, 2006; Hernández and Espín, 2006; present study). In the case of *P. expansa*, historical commercial harvest may have left a relatively young nesting female population, with smaller females that build shallower and therefore hotter nests, which in turn produce a larger proportion of female hatchlings (Valenzuela, 2001). Preliminary studies of hatchling sex ratio confirm a strong female bias for this population (96% female, Peñaloza, unpubl.), and genetic studies show the population has low indices of multiple paternity for this species (Valenzuela, 2000; Pearse et al., 2006). Current harvest pressure on *P. unifilis* may be affecting sex ratios. Individual *P. expansa* and *P. unifilis* may distribute along the river according to their sex and, for females, by nesting preference. Female *P. expansa* are likely to be near island nesting beaches in the main river, whereas female *P. unifilis* prefer to be close to riverbanks in the main river and in smaller tributaries of the Orinoco. However, because most *P. expansa* we captured were not sexually mature, this may not be evident.

Most of the *P. expansa* captured during in-water surveys were juveniles. Because this is a long-lived, late-maturing species (11–28 years, Hernández and Espín, 2006; Mogollones et al., 2010), this was expected. However, it is possible that nesting-beach protection and the reintroduction of captive-bred yearlings have increased the proportion of juvenile turtles (headstarted hatchlings account for 45% of captured turtles from 1998–2008, Hernández and Espín, 2006; present study), augmenting the size distribution skew toward juveniles. An increased skew toward juvenile turtles is evident when we compare the size distribution of *P. expansa* captured in the present study with those captured by Hernández and Espín (2003; Fig. 4A). The predominance of adult turtles in *P. unifilis* and *P. vogli* captures is expected for these species, which are thought to mature sooner than *P. expansa* (Ramo, 1982; Thorbjarnarson et al., 1993). We used the same fishing method as ribereños with a smaller net mesh-size (5 cm vs. 10 cm for ribereños). Barring selective harvest, we expect similar species composition and size distribution between harvested and captured turtles. Balensiefer and Vogt (2006) found sideneck turtles comparable in size to our captured *P. expansa* using 10 and 20 cm mesh-size nets (108–162 mm compared to 98–161 mm for the present study), suggesting that in our study, ribereños are selecting for *P. expansa* larger than 190 mm during harvest. In a re-analysis of Hernández and Espín (2003), using kernel density distributions to compare between harvested and captured turtles, we also found selective harvest of larger *P. expansa* (Fig. 4B); in fact, ribereños consistently harvest turtles in a certain size range (Fig. 4C). Because ribereños also harvest nesting female *P. unifilis* and *P. vogli*, differences between harvest and captured turtles may be caused by harvest method.

Podocnemis expansa.—Ribereños selectively harvested larger juveniles and males of *P. expansa* and, although the size of harvested and captured females of *P. expansa* is not significantly different, slightly more adult females were harvested than were found in the wild. If we assume size-selection for commercial harvest has not changed since Hernández and Espín (2003; Fig. 4D), large juveniles and adults are selected for commerce. Being a long-lived, late-maturing species, population growth in *P. expansa* is particularly sensitive to survival of large juveniles and adults (Heppell, 1998; Chaloupka and Limpus, 2002; Mogollones

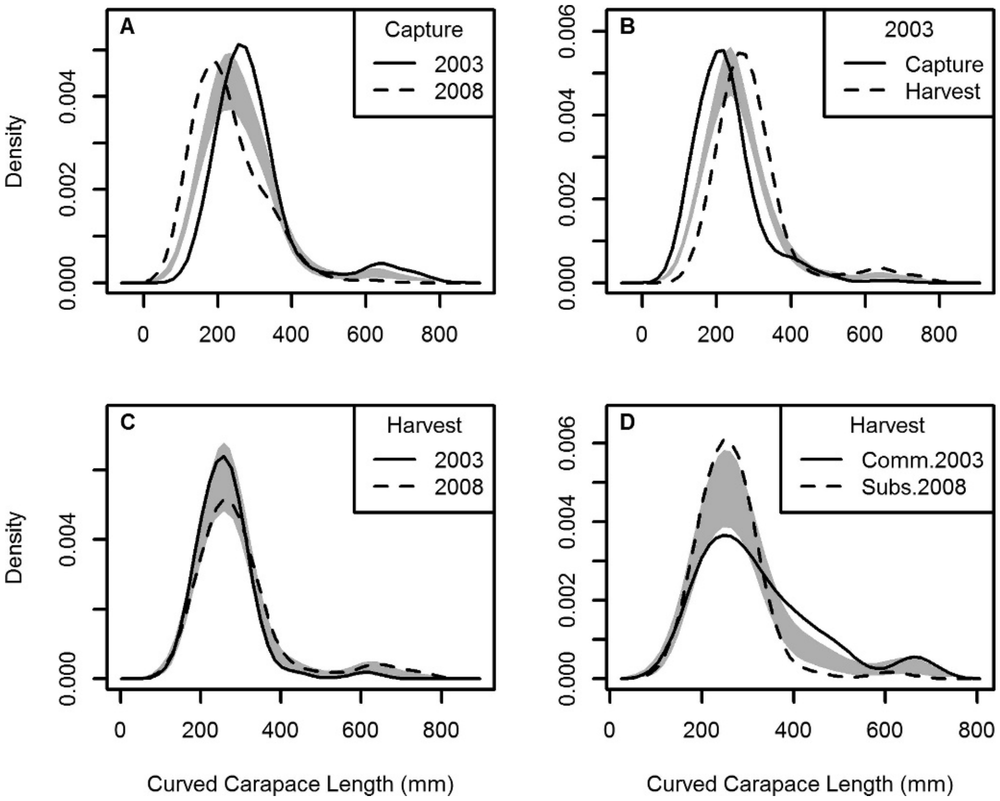

Fig. 4. Size comparison, using kernel density plots, of *P. expansa* harvested and captured in the present study with those captured, harvested for local consumption (subsistence), and commercially harvested (transported to cities) from Hernández and Espín (2003). (A) The proportion of smaller turtles in the wild has increased ($P = 0$). (B) Re-analysis of Hernández and Espín (2003) suggests larger *P. expansa* were also selected during harvest by ribereños ($P = 0$). (C) Ribereños are consistent in size selection of harvested *P. expansa* ($P = 0.09$). (D) Larger turtles are channeled toward commercial harvest ($P = 0$).

et al., 2010), which would make their selective harvest have a greater negative effect on population growth than, for example, harvesting *P. expansa* according to availability in the wild.

A necessary next step would be to determine the effect this type of harvest has on population structure, survival, and growth of *P. expansa* with population viability or mark–recapture studies (Jensen, 2000; Freckleton et al., 2003; Heppell et al., 2005; Fordham et al., 2009). It is possible current harvest, though illegal, is in fact sustainable due to density-dependent responses in the population, as found in Australia for another harvested long-lived species, the snake-necked turtle, *Chelodina rugosa* (Fordham et al., 2007, 2008, 2009). However, current levels of exploitation seem to be hindering recovery, and it may be necessary to control or eliminate harvest for some time, especially commercial harvest, to increase abundance of *P. expansa*. Depending on the life-history strategy of *P. expansa*, reinstating traditional harvest of eggs, a life stage with less influence on population growth, while eliminating harvest of wild juvenile and adult turtles, may be a long-term solution for population persistence. Once the nesting population starts to recover, harvesting eggs from the beginning of the season may be required to maintain high hatching success, as is the case for Olive Ridley sea turtles (*Lepidochelys olivacea*) in Costa Rica, where high nest density is related to a decrease in hatching success (Honarvar et al., 2008).

There is no relationship between the size of harvested turtles and the location along the Middle Orinoco (Figs. 2B), which discredits the assumption that the AWR will protect nesting females because they will remain close to nesting-beaches inside the refuge. This fact also substantiates the need for decentralized protection of sideneck turtles along the river. On the other hand, the AWR plays an instrumental role in protecting nests. The second most important breeding area for *P. expansa* in Venezuela, Brazo Casiquiare, is unprotected and 100% of nests are poached (Narbaiza et al., 1999; Hernández et al., 2007). Because of the continued widespread harvest of this species, there is a need to strengthen the conservation program to ensure its survival.

Podocnemis unifilis *and* P. vogli.—Harvest of these two species was selective in proportion, sex, and size. Proportionately fewer *P. unifilis* were harvested than found in the wild, whereas proportionately more *P. vogli* than available were harvested. This may result from ribereños harvesting the nesting females of these species. There may be more *P. unifilis* available in the water, but those were not taken because of the harvest method. Few *P. vogli* were available in the Orinoco because they prefer smaller rivers and lagoons (Pritchard and Trebbau, 1984; Pluto and Bellis, 1986), making harvest seem selective toward *P. vogli*. In addition to differences in species proportion, small female *P. unifilis* and *P. vogli* were selectively harvested. This is consistent with nesting female harvest method; whether or not smaller individuals indicate an earlier size at maturity than previously expected, requires more study. The absence of larger harvested females of *P. unifilis* suggests emigration of larger females to the main river, far away from riverine communities or, less likely, a self-imposed prohibition by ribereños against harvesting large females. Regardless, differences in harvest and capture method confound comparisons for *P. unifilis* and *P. vogli*.

Sex ratio differences between harvested and captured *P. unifilis* turtles are disturbing. Harvested *P. unifilis* were significantly biased toward females, while captured *P. unifilis* were so toward males. Selective harvest of females could be affecting population sex ratios both by decreasing the number of females in the population and by increasing the proportion of older larger females who build deeper cooler nests, which in turn produce a higher proportion of male hatchlings (Valenzuela, 2001). The absence of smaller females among captured *P. unifilis* may indicate intensive harvest of these individuals or size dependent distribution between the Orinoco and its tributaries, i.e., smaller females are found in smaller rivers whereas larger females are found in larger rivers (Pluto and Bellis, 1986). The persistence of this population may depend on determining and addressing the cause of these differences.

Results indicate that both *P. unifilis* and *P. vogli* undergo selective harvest of nesting females. Depending on the life-history strategy of each of these species and under the commonly held view regarding turtle harvest (Congdon et al., 1993; Congdon et al., 1994; Cunnington and Brooks, 1996; Heppell, 1998), this type of harvest may not be sustainable. However, if indeed *P. unifilis* and *P. vogli* are fast-growing, early-maturing, and highly fecund, their populations may be able to sustain a level of harvest (Fordham et al., 2008, 2009). These species are thought to have an earlier age at maturity than *P. expansa*—from three to nine years (Ramo, 1982; Thorbjarnarson et al., 1993)—but detailed demographic studies are lacking. *Podocnemis unifilis* is known to respond rapidly to protection; in Ecuador, a two to three-fold increase in population size of *P. unifilis* was recorded after five years of egg and ten years of adult protection (Townsend et al., 2005). An important next step would be not only to study the demography of these species but specifically the effect harvest has on wild populations.

After 21 years of protecting turtles in and around the AWR, it has become obvious that using force to eliminate consumption of this traditional staple is not an option in the Middle Orinoco. The consumption of *P. expansa*, *P. unifilis*, and *P. vogli* are deeply rooted in the lifestyle and economic reality of the ribereño. Locating, quantifying, and eliminating commercial harvest could be much more productive at this point. The reinstatement of long-forgotten traditional use practices like decentralized captive breeding of sideneck turtles, especially the smaller and faster-maturing *P. vogli*, should be promoted to decrease subsistence harvest of wild *P. expansa*, *P. unifilis*, and *P. vogli* turtles until populations have recovered. *Podocnemis vogli* is known to be prolific in artificial floodplain lagoons with minimal or no intervention (Ramo, 1982; Thorbjarnarson et al., 1993), making it ideal for aquaculture. Economic incentives or microloans to build ''backyard'' ponds of *P. vogli* can be a first step. The next, and most important, step would be to establish peer-to-peer monitoring between ribereños to ensure internal compliance as well as exclusion and prosecution of commercial harvesters. Ideally, we should work toward a future that resembles the past, where ''there is hardly a village containing fewer than a hundred corralled turtles and thus [ribereños] are ignorant of hunger'' (Acuña, 1641). Regardless of the program chosen for recovery, scarce funds for enforcement of regulations and the wide distribution and dependence of ribereños on turtles as a resource suggest that reestablishing the rights and responsibilities of ribereños in the stewardship and preservation of *Podocnemis* spp. will be fundamental for the persistence of these species.

ACKNOWLEDGMENTS

The Duke University Center for Marine Conservation, a Linnaeus Fund Award from the Chelonian Research Foundation, the Oak Foundation, Idea Wild, the Foundation for the development of Mathematical, Physical and Natural Sciences (FUDECI), and the Universidad Simón Bolívar Wildlife Management and Conservation Lab provided financial and logistic support for this project. We would also like to thank FONACIT for financing in-water turtle survey project Agenda Biodiversidad 2000001319. We are deeply indebted to R. Espín and FUDECI for invaluable logistic support without which this project would not have been possible. We would like to thank our field assistants E. Peñaloza, R. Chacín de Peñaloza, F. Peñaloza, and S. Black Peñaloza. We are also very grateful for the support of our two captains, P. Eduardo and R. Sosa; thank you for bridging the gap. We thank the contributions and suggestions of G. Pérez-Falcón Teague, which greatly improved the manuscript.

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