Chelonian Conservation and Biology, 2020, 19(2): 165–185
doi:10.2744/CCB-1414.1

Population Status of the Megacephalic Map Turtles *Graptemys pearlensis* and *Graptemys gibbonsi* and Recommendations Regarding Their Listing Under the US Endangered Species Act

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Abstract. – The Pascagoula map turtle (*Graptemys gibbonsi*) and Pearl map turtle (*Graptemys pearlensis*) were first separated from the Alabama map turtle (*Graptemys pulchra*) in 1992 under the former name and subsequently recognized as 2 separate species in 2010. The possibility that they should be listed under the Endangered Species Act was raised 7 yrs after separation from *G. pulchra*, when basking surveys showed that at most sites they were considerably less abundant than 2 sympatric congeners listed as threatened: the Pearl River drainage's ringed sawback (*Graptemys oculifera*, listed in 1986) and the Pascagoula River drainage's yellow-blotched sawback (*Graptemys flavimaculata*, listed in 1991). Historical data also indicated that the sympatric species pairs may once have been more similar in abundance. Now, more than 2 decades later, *G. gibbonsi* and *G. pearlensis* are candidates for listing. From 2015 to 2018, we surveyed basking turtles in point counts and in jon boat and canoe surveys and conducted trapping at several sites to ascertain the status of the 2 candidate species. Data were also combined with similar data collected between 2006 and 2014. Despite their similarity morphologically and in their basic ecology, 3 important differences are pertinent to the question of whether the 2 candidate species should be federally protected. First, their river systems are geomorphically very different. The medium-size to large tributary streams that the 2 species inhabit are a considerably more prominent feature of the Pascagoula drainage than the Pearl drainage and may insulate populations from potential threats on the main stems. Second, *G. gibbonsi* inhabited 35% more stream reach, had 22% higher catch per unit effort, and were recorded at 44% higher numbers in point counts and 3% higher numbers in basking density surveys than *G. pearlensis*. Coarse-scale estimates of each species' global populations suggest that *G. gibbonsi* is $\sim$ 1.56 times as abundant as *G. pearlensis* overall. Third, the reasons for the listing of each species' sympatric sawback congener are very different: *G. oculifera* of the Pearl drainage was listed primarily due to existing and imminent but as-yet-unrealized habitat modification, while *G. flavimaculata* of the Pascagoula drainage was listed primarily due to perceived low populations, particularly in upper portions of the drainage, and concerns regarding water quality. We conclude that *G. pearlensis* warrants conservation protection via a listing as threatened, while *G. gibbonsi* should be listed either as threatened or as threatened by similarity of appearance. For *G. gibbonsi*, the former option would recognize a long-term historical decline in its relative abundance suggested by trapping data from the 1950s through 1970s, while the latter would recognize its less imperiled status and protect it from the pet trade while focusing recovery efforts on *G. pearlensis*.

Key Words. – Reptilia; Testudines; Emydidae; Pascagoula map turtle; Pearl map turtle; Pascagoula River; Pearl River; *Graptemys oculifera*; ringed sawback; *Graptemys flavimaculata*; yellow-blotched sawback; Mississippi; Louisiana; catch per unit effort; relative abundance; basking surveys

The US Endangered Species Act (ESA) of 1973 provides a framework for formal recognition of imperiled species and establishment of management guidelines to protect and recover populations. Terrestrial and freshwater species can become candidates for listing as endangered (E; in danger of extinction if not protected) or threatened (T; in danger of becoming endangered if not protected) by 1) direct action of the US Fish and Wildlife Service (USFWS) in the US Department of the Interior or 2) following petitioning by 1 or more individuals and organizations, a draft proposal to list the species followed by a period for public comment, and then a final ruling. While listing as E implies a more dire situation faced by the species, in most cases the level of federal protection and requirements for recovery planning under the ESA are equivalent for E and T species.

The emydid genus *Graptemys* consists of 14 recognized species of map turtles and sawbacks in eastern and central North America. The genus is distinguished by river drainage endemism (Lamb et al. 1994), the most extreme sexual size dimorphism known in the Tetrapoda (Gibbons and Lovich 1990; Stephens and Wiens 2009), and dietary diversity that is particularly strong among females, which vary greatly interspecifically in their trophic morphology (Lindeman 2000; Lindeman and Sharkey 2001). Five species make up a clade that is diagnosed by exceptional megacephaly in adult females and inhabit river drainages of the central Gulf Coast (Lamb et al. 1994; Lindeman 2013; Stephens and Wiens 2003; Praschag et al. 2017; Thomson et al. 2017). Large adult females of these 5 species subsist almost entirely on mollusks, while males eat primarily mollusks and aquatic insects (Sanderson 1974; Shealy 1976; Lindeman 2000, 2013, 2016; Selman and Lindeman 2015; J. Vučenović and P.V.L., unpubl. data, 2015–2018).

The species known today as the Pearl map turtle (*Graptemys pearlensis*) and the Pascagoula map turtle (*Graptemys gibbonsi*) spent almost a century and 4 decades, respectively, considered to be conspecific with other map turtles. The first 6 specimens of *G. pearlensis* were collected in the West Pearl River in 1891 and referenced in the description of *Graptemys pulchra* along with 2 additional syntype specimens collected in 1876 from the Mobile Bay river drainages (Baur 1893). A second species with megacephalic females, *Graptemys barbouri*, was described almost half a century later from the Apalachicola River drainage (Carr and Marchand 1942). Nothing new was published on *G. pulchra sensu lato* until Cagle (1952) and his students sampled in 2 river drainages, the Pearl and Escambia, and collected specimens that he placed under the name *G. pulchra*. Cagle's students collected the first 12 specimens of the species now known as *G. gibbonsi* in 1952 (Lindeman 2013), and these were also considered to be part of *G. pulchra* for the next 4 decades (e.g., Conant 1975; Mount 1975). Lovich and McCoy (1992) examined specimens of *G. pulchra* from all 4 river drainages. They designated 1 of the specimens from 1876 as lectotype and restricted the name *G. pulchra* to specimens from the Mobile Bay drainages, describing the Escambia Bay drainage specimens as *Graptemys ernsti* and the Pearl and Pascagoula river drainage specimens as *G. gibbonsi*; they also recognized some differences between specimens from the latter 2 rivers. Ennen et al. (2010) described the Pearl River drainage specimens as *G. pearlensis*, restricting *G. gibbonsi* to the Pascagoula River drainage specimens. Thomson et al. (2017) reported support for the monophyly of each of the 4 allopatrically distributed species formerly united as *G. pulchra sensu lato*.

As a consequence of the taxonomic situation, the conservation concern for the 4 species once lumped as *G. pulchra* has lagged behind that devoted to several congeners. The USFWS began review of 6 species of *Graptemys* in 1977 and added a seventh in 1982, but *G. pulchra sensu lato* was not among the species chosen for review (Lindeman 2013). Two of the species that were reviewed, the ringed sawback (*Graptemys oculifera*) of the Pearl River drainage and the yellow-blotched sawback (*Graptemys flavimaculata*) of the Pascagoula River drainage, were listed as T under the ESA 6 and 1 yrs prior, respectively, to the initial taxonomic splitting of *G. pulchra* in 1992 (USFWS 1986, 1991). In a subsequent series of basking surveys conducted in 1994 and 1995 throughout the geographic ranges of *G. oculifera* and *G. flavimaculata*, their predominance over *G. gibbonsi sensu lato*—which was outnumbered overall by the 2 sawbacks by $>$ 5:1—generated the initial concern for the possible need for listing of *G. gibbonsi sensu lato* (Lindeman 1998, 1999). Historical data suggested more equitable ratios of sawbacks to megacephalic species in past decades, although a tendency for more extensive upstream and tributary ranges in the megacephalic species was also noted (Lindeman 1999). Similarly, subsequent publications have also reported imbalances in the ratio of sawbacks to megacephalic species for both river drainages (Selman and Qualls 2009; Selman and Jones 2017) and suggested the possible need for the megacephalic species' federal listing. The need to determine the importance of tributary populations to overall population viability has been noted in all of these studies, and, indeed, numerous new upstream and tributary records documenting previously unknown populations were reported for various species of *Graptemys* between 1995 and 2012, including *G. pearlensis* and *G. gibbonsi* (Lindeman 2013, 2014a).

In 2010, *G. gibbonsi sensu lato* was included in a petition, submitted by the Center for Biological Diversity and associated nonprofit organizations, to list 404 species associated with freshwater habitats in the southeastern United States (Alexander 2018). It was subsequently announced to be among 374 of the petitioned species that would be reviewed for possible listing under the ESA (USFWS 2011).

We report on our most recent (2015–2018) basking surveys and trapping aimed at determining the status of the megacephalic species *G. pearlensis* and *G. gibbonsi* throughout their respective ranges. We also combine these most recent data with data from earlier surveys in the 20th century (Selman and Qualls 2009; Selman and Jones 2017; P.V.L., unpubl. data, 2008–2013) to address the following objectives: 1) comparing the absolute and relative abundance of the 2 candidate species; 2) determining the status of the 2 species relative to their respective sympatric, federally listed sawback congeners, including how ratios of the sympatric pairs of congeners vary throughout the 2 river drainages; 3) determining as completely as possible the ranges of occurrence for the 2 candidate species with particular emphasis on critical examination of upstream range limits and occurrences in smaller tributaries of the river drainages; and 4) determining what percent of the estimated global population of each candidate species occurs in various main stem and tributary reaches. We then make recommendations regarding their status as candidates for federal listing.

METHODS

Description of Study Areas. — The Pearl River originates at the confluence of Tallahaga and Nanih Waiya creeks in northeastern Neshoba County, Mississippi. As it flows ~ 675 river km (rkm; all drainage distances herein were determined by detailed tracings using the path function in Google Earth) toward the Gulf of Mexico, southwesterly at first and then more southerly, 8 major tributaries join it, and it splits into 2 main channels near its delta, the larger West Pearl and the smaller East Pearl, with additional connecting channels in the delta. Primary drainage modifications date to the 1950s and 1960s and are in the regions of Mississippi's largest city, Jackson, with 1) impoundment of the Pearl River and lower Pelahatchie Creek in Madison and Rankin counties forming the Ross Barnett Reservoir (13,500 ha) and 2) channel modification in the Pearl for flood control downstream in Hinds and Rankin counties (Selman 2020) and, in the lower drainage, with 3) construction of a navigation canal in the early 1950s and diversion of flow into the West Pearl. Prior to canal construction, the West Pearl had been a smaller channel than the East Pearl (Piller et al. 2004; Tipton et al. 2004). Upper portions of the Yockanookany and Tuscolameta Creek have also been channelized, with straight artificial channels installed alongside sinuous natural channels (Selman and Jones 2017).

The Pascagoula River is a shorter river (~ 131 km) that originates in northern George County, Mississippi, at the confluence of 2 more extensive tributary systems: the Leaf River drainage to the west and the Chickasawhay River drainage to the east. The Leaf River originates in southern Scott County and flows ~ 306 km in a southerly/southeasterly route with several tributaries. The Chickasawhay River originates at the confluence of Okatibbee Creek and the Chunky River in northern Clarke County and flows ~ 259 km in a southerly/southwesterly route, joined by a smaller number of tributaries. The Pascagoula drainage has the distinction of being the largest river system within the ranges of the species of the genus *Graptemys* that is relatively unaffected by flow regulation via large main stem dams or other forms of water regulation (Dynesius and Nilsson 1994). Its largest impoundment is Okatibbee Reservoir (1420 ha) on upper Okatibbee Creek in northern Lauderdale County, Mississippi.

Sandy forested riverbanks and sandy river substrates dominate throughout both drainages, with a common feature being flat inner-bend sandbars opposite steep outer-bend cut banks, particularly along larger stream reaches. Deadwood used by *Graptemys* species for basking and underwater grazing is generally abundant in both drainages (Lindeman 1999). In-stream rock formations are prominent features of some portions of the Strong River (Pearl River drainage) and the Chunky River (Pascagoula River drainage). Current speed varies greatly with discharge, with frequent rainy periods that can temporarily raise water levels by several meters.

Point Counts. — Basking and surface-active turtles were counted from bridges, boat ramps, and other access points on sunny, warm days between early May and early July 2015–2018. Turtles were generally sighted and identified with 18× Canon image-stabilizing binoculars, but a spotting scope that magnified up to 60× was also used in some cases. Because point counts are often low, many of the sites were visited multiple times to increase sample size and increase the chances of detecting resident species. Voucher photographs were taken at several localities, in particular to document upstream extensions of the known ranges of *Graptemys* species.

Boat Surveys. — Basking and surface-active turtles were counted from either a jon boat with an outboard motor or a canoe with a trolling motor, depending on stream width and depth, between 2015 and 2018. For these surveys, numbers of turtles recorded were divided by length of the survey, traced in Google Earth along the center of the stream, to generate basking densities (turtles/rkm). Turtles that could not be identified to species, either because they jumped into the water at the approach of the boat or were partially obscured by deadwood or other turtles, were also noted. Boat surveys generated much larger sample sizes than point counts; thus, most reaches sampled by boat were not revisited, with the exception of mark-resight efforts made on a stretch of the Pearl River near Jackson (Selman 2020) and at 6 sites on the Pascagoula drainage. For reaches where surveys were repeated, an average basking density was calculated, with averaging weighted by rkm if survey length was variable.

We corrected basking densities for unidentified turtles by assuming that they occurred at the same frequency as identified turtles in the survey, that is, that there was no interspecific difference in the probability of not being able to identify a turtle due to it either reentering the water or being partially hidden from view. Basking densities for each *Graptemys* species and for pooled non-*Graptemys* species that are reported herein are corrected for unidentified turtles.

We designated the Pearl and West Pearl rivers and the Leaf, Chickasawhay, and Pascagoula rivers as main stem habitats of their respective drainages based on relative channel width and depth. Tributaries were divided into large and small categories, with the large tributaries being the Yockanookany, Strong, Bogue Chitto, and East Pearl rivers for the Pearl River drainage and Tallahala, Buckatunna, Black, Red, and Big Black creeks for the Pascagoula River drainage.

Trapping. — At select sites during 2015–2018, we captured turtles using basking traps made from crawfish wire (Selman et al. 2012) or modified hoop nets (Lindeman 2014b), fyke nets (Vogt 1980), and opportunistic capture by hand or dip net. We recorded sex of turtles based on relative tail size and measured midline plastron length (PL) of each *Graptemys* specimen captured to the nearest 1 mm, determined body mass with spring scales, and notched marginal scutes in combinations of 2 or 3 that were unique within each species, following Cagle (1939). We categorized *G. pearlensis* and *G. gibbonsi* as hatchlings, older unsexed juveniles, adult males, juvenile females, or adult females based on whether individuals had growth annuli and enlarged tails as well as minimum recorded sizes for mature males (60 m PL) and mature females (180 mm PL). Turtles were released at their sites of capture.

Survey and Trapping Data. — We examined data from point counts in terms of numbers seen per point count, while we examined data from boat surveys in terms of densities (turtles/rkm). We computed catch per unit effort (CPUE) for each species as the number of turtles captured in each trap type per trap day (TTD; 1 day of checking basking traps) or per overnight set period for fyke nets (TTN); no CPUE was calculated for hand or dip net captures due to their irregular and opportunistic use. We also examined 2 indices of relative abundance for point counts, boat surveys, and trapping: 1) ratio of *Graptemys* seen or captured (expressed as sawbacks per sympatric megacephalic species) and 2) percent of all turtles seen or captured for each *Graptemys* species and combined non-*Graptemys* species.

We combined data from point counts, basking density surveys, and trapping from 2015 to 2018 with earlier data sets collected between 2006 and 2014 (Selman and Qualls 2009, all 3 types, Pascagoula River drainage; Selman and Jones 2017, basking density surveys and trapping, Pearl River drainage; P.V.L., unpubl. data, 2008–2013, point counts, both river drainages). Two of the earlier surveys on the lower Pascagoula's Escatawpa tributary and 1 on its Bluff Creek tributary were conducted upstream of the known range of *G. gibbonsi* and are not included here. In addition, during 6 Pascagoula drainage surveys within the range of *G. gibbonsi* in 2006–2007, unidentified turtles were not recorded (and in 3 of these, only *Graptemys* were counted); these surveys were withheld from calculations and summaries of corrected basking densities but were used for calculation and summation of relative abundance. At 5 sites on the Pearl River in 2008–2014, data on sex or size were recorded for only *G. oculifera* (Jones 2017; Selman and Jones 2017), so those trapping data could not be used in summarizing of population structure of *G. pearlensis*.

Statistical Analyses. — We analyzed mean numbers of each *Graptemys* species recorded per point count and basking density in boat surveys in 2×3 analyses of variance (ANOVAs) with 2 time periods (2006–2014 vs. 2015–2018) and the 3 categories of river reaches (main stems and large and small tributaries). Due to large numbers of low values for point counts and basking density surveys, some of which were zeroes, each data point x was first transformed as $\ln(x + 1)$. Tukey's test was used post hoc to identify which reach categories differed in turtles/point count or basking density. We compared sympatric map turtle and sawback distributions across the 3 reach categories in totals recorded across point counts and across basking density surveys. Finally, drainage-wide population structures of *G. pearlensis* and *G. gibbonsi* were compared in a χ^2 test for independence with hatchling, older unsexed juvenile, adult male, juvenile female, and adult female categories.

Drainage-Wide Population Estimates. — To generate global population estimates for *G. pearlensis* and *G. gibbonsi*, we first traced the full extent of all occupied river reaches in the Pearl and Pascagoula river drainages using the path function in Google Earth. Because data at individual sites were not adequate for rigorous population estimation, we used a coarse-filter approach to estimate population density along river reaches. We first used combined basking survey data collected over series of sites on river main stems and tributaries to divide extended reaches from each drainage into 4 categories (high density, medium density, low density, and very low density). Based primarily on basking density survey data and secondarily on point count averages, we assigned a characteristic basking density to each of the 4 categories and assumed it represented the average density over the entire set of reaches so categorized. We then multiplied reach length in rkm by characteristic basking survey density and corrected for unobserved turtles by multiplying by 6.67, making an assumption based on previous mark-resight studies of *G. gibbonsi*, *G. flavimaculata*, and *G. oculifera* in which $\sim 85\%$ of paint-marked turtles were not detected in basking counts (Selman and Qualls 2009, 2011; Brown et al. 2016; Selman and Jones 2017; P.V.L., unpubl. data, 2016; see also Selman, in press). We then summed these estimates of total turtles for sets of reaches defining various portions of the drainage and for the total drainage. We used these population estimates to estimate percentage of the global population found in tributaries vs. main stem reaches for each species.

RESULTS

Point Counts. — From 2015 to 2018, we conducted 233 total point counts at 125 different sites on the Pearl River drainage. Of these, 174 counts at 82 sites were determined to be within the range of *G. pearlensis*, including 23 sites on the main stem Pearl and West Pearl rivers and 59 sites on 8 tributary stream networks (Lobutcha Creek, Tuscolameta Creek, Yockanookany River, Pelahatchie Creek, Strong River, Pushepatapa Creek, Hobolochitto Creek, and Bogue Chitto River) and 2 connected channels (East Pearl River and Pearl River Navigation Canal; Table 1). On the Pascagoula River drainage, we conducted 344 point counts at 210 sites. Of these, 248 counts at 136 sites were determined to be within the range of *G. gibbonsi*, including 27 sites on the main stem Pascagoula, Leaf, and Chickasawhay rivers and 109 sites on 15 tributary stream networks (West Tallahala Creek, Oakohay Creek, Bowie River, Tallahala Creek, Bogue Homa, Thompsons Creek, Gaines Creek, Atkinson Creek, Chunky River, Okatibbee Creek, Souinlovey Creek, Shubuta Creek, Buckatunna Creek, Black Creek, and Red Creek). To these point counts, we added 125 earlier counts for the Pearl River drainage (2008–2013) and 151 earlier counts for the Pascagoula River drainage (2006–2013), with most of the earlier counts taken at sites that were included in the more recent data (Table 1).

Generally, abundance of each *Graptemys* species declined with the size of the river reach surveyed. All 4 species averaged higher numbers seen per point count on main stem reaches than on tributary reaches in the most recent surveys, and all species but *G. flavimaculata* were more abundant in counts made on large tributaries than in counts made on small tributaries. In the larger data set, the main stem–tributary disparity was considerably greater for the 2 sawbacks ($\sim$ 10 times greater on main stem reaches for *G. oculifera* and 60 times greater for *G. flavimaculata*) than for the 2 megacephalic map turtles (approximately even for *G. pearlensis* and 4 times greater for *G. gibbonsi*). All other species pooled together likewise averaged higher at main stem sites than at tributary sites for the Pascagoula River drainage but averaged higher at tributary sites than main stem sites for the Pearl River drainage.

In ANOVA comparisons, time period (2006–2013 vs. 2015–2018) was not a significant term for numbers of either *Graptemys* species seen per point count in the Pearl River drainage (*G. pearlensis*: $F_{1,295} = 0.21$, $p = 0.65$; *G. oculifera*: $F_{1,295} = 1.82$, $p = 0.18$), but both species differed in number seen among reach categories (*G. pearlensis*: $F_{2,295} = 3.44$, $p = 0.033$; *G. oculifera*: $F_{2,295} = 66.3$, $p < 0.0001$). In Tukey's post hoc tests, *G. pearlensis* counts were significantly higher on large tributaries than on small tributaries, with main stem reaches intermediate and not different from the other 2 categories. Densities of *G. oculifera* differed in all comparisons, with greatest counts on main stem reaches and lowest counts on small tributaries.

For the Pascagoula drainage, both *Graptemys* species were recorded in higher numbers in earlier surveys than in more recent surveys (*G. gibbonsi*: $F_{1,395} = 5.24$, $p = 0.023$; *G. flavimaculata*: $F_{1,395} = 5.44$, $p = 0.020$), and both had significant differences among reach categories (*G. gibbonsi*: $F_{2,395} = 21.77$, $p < 0.0001$; *G. flavimaculata*: $F_{2,395} = 68.97$, $p < 0.0001$). In Tukey's post hoc tests, *G. gibbonsi* densities were significantly greater on main stem reaches than on either category of tributary, while large tributaries had nonsignificantly greater densities than small tributaries. For *G. flavimaculata*, densities were significantly greater on main stem reaches than on either category of tributary, while small tributaries had nonsignificantly greater densities than large tributaries.

Density Surveys by Boat. — Between 2015 and 2018, we conducted 40 jon boat or canoe surveys on river reaches totaling 187.8 rkm on the Pearl River drainage and 31 surveys on river reaches totaling 135.3 rkm on the Pascagoula River drainage (Table 2). We could not identify 9% of all turtles observed during Pearl surveys and 7% of all turtles observed during Pascagoula surveys, with unidentified turtles occurring at $\sim$ 3 times greater frequencies on tributary reaches than on main stem reaches.

For *G. pearlensis*, basking density in 2015–2018 was 2.2 times higher on main stem reaches as on tributary reaches and 2.1 times higher on large tributaries than on small tributaries. For *G. gibbonsi*, basking density was 1.6 times higher on main stem reaches than on tributary reaches and 1.2 times higher on large tributaries than on small tributaries. In both river drainages, the main stem–large tributary–small tributary disparity was greater for the sympatric sawback species. For *G. oculifera*, we observed 9.0 times greater density on main stem Pearl and West Pearl reaches than on tributaries and 1.9 times higher density on small vs. large tributaries. For *G. flavimaculata*, we observed 12.0 times greater density of on main stem Pascagoula, Leaf, and Chickasawhay reaches than on tributaries and 2.8 times higher density on large vs. small tributaries.

Additional surveys conducted earlier include 1 2.7-rkm reach in the Pearl River surveyed in 2006 (Selman and Jones 2017) and 20 in-range reaches totaling 218.5 rkm in the Pascagoula River drainage surveyed in 2006–2008 (Selman and Qualls 2009). Combining data from the earlier surveys for the Pascagoula River drainage, density of *G. gibbonsi* rose by 26% on main stem reaches and declined by 5% on tributary reaches; that is, inclusion of the earlier surveys increased the disparity in density of *G. gibbonsi* between main stem and tributary reaches from a 1.6-fold difference to a 2.2-fold difference.

In ANOVA comparisons, all 4 *Graptemys* species exhibited significant differences in corrected basking density among main stem reaches, large tributaries, and small tributaries (*G. pearlensis*: $F_{2,38} = 5.84$, $p = 0.006$; *G. oculifera*: $F_{2,38} = 10.45$, $p = 0.0002$; *G. gibbonsi*:

Table 1. Point count results for sites within the known ranges of megacephalic map turtle species, broken down according to most recent data (2015–2018) and all data since 2006 (adding Selman and Qualls 2009 and P.V.L., unpubl. data, 2008–2013) as well as by main stem reaches, larger tributaries, and smaller tributaries, with total and average numbers and proportions of each *Graptemys* species and combined other species of turtles as well as the ratio of sawback to megacephalic *Graptemys* species. The Pearl River drainage is inhabited by *G. pearlensis* and *G. oculifera*, while the Pascagoula River drainage is inhabited by *G. gibbonsi* and *G. flavimaculata*.

River drainage	Reaches	No. of counts (no. of sites)	Megacephalic map turtle species: *Graptemys pearlensis/gibbonsi*			Sawback species: *Graptemys oculifera/flavimaculata*			Other turtles			*Graptemys* ratio
			n	*n*/count	Proportion	*n*	*n*/count	Proportion	*n*	*n*/count	Proportion	
2015–2018 surveys												
Pearl	Main stem reaches[a]	41 (23)	53	1.3	0.17	197	4.8	0.62	67	1.6	0.21	3.7
	Tributary reaches	133 (59)	100	0.8	0.19	40	0.3	0.08	382	2.9	0.73	0.4
	Larger tributaries[a]	73 (30)	72	1.0	0.18	35	0.5	0.09	295	4.0	0.73	0.5
	Smaller tributaries	60 (29)	28	0.5	0.24	5	0.1	0.04	86	1.4	0.72	0.2
	Total	174 (82)	153	0.9	0.18	237	1.4	0.28	449	2.6	0.54	1.5
Pascagoula	Main stem reaches[b]	51 (27)	100	2.0	0.16	318	6.2	0.52	196	3.8	0.32	3.2
	Tributary reaches	197 (109)	133	0.7	0.28	20	0.1	0.04	321	1.6	0.68	0.2
	Larger tributaries[b]	70 (46)	57	0.8	0.36	9	0.1	0.06	91	1.3	0.58	0.2
	Smaller tributaries	127 (63)	76	0.6	0.24	11	0.1	0.03	230	1.8	0.73	0.1
	Total	248 (136)	233	0.9	0.21	338	1.4	0.31	517	2.1	0.48	1.5
Combined data, 2006–2018												
Pearl	Main stem reaches	84 (27)	73	0.9	0.15	326	3.9	0.67	86	1.0	0.18	4.5
	Tributary reaches	215 (65)	198	0.9	0.24	82	0.4	0.10	559	2.6	0.67	0.4
	Larger tributaries	143 (36)	159	1.1	0.24	77	0.5	0.12	427	3.0	0.64	0.5
	Smaller tributaries	72 (29)	39	0.5	0.25	5	0.1	0.03	110	1.5	0.71	0.1
	Total	299 (92)	271	0.9	0.20	408	1.4	0.31	645	2.2	0.49	1.5
Pascagoula	Main stem reaches	95 (37)	287	3.0	0.21	622	6.5	0.46	446	4.7	0.33	2.2
	Tributary reaches	304 (125)	221	0.7	0.27	44	0.1	0.05	550	1.8	0.67	0.2
	Larger tributaries	110 (51)	95	0.9	0.33	11	0.1	0.04	179	1.6	0.63	0.1
	Smaller tributaries	194 (74)	126	0.7	0.24	33	0.2	0.06	371	1.9	0.70	0.3
	Total	399 (162)	508	1.3	0.23	666	1.7	0.31	996	2.5	0.46	1.3

[a] Pearl River drainage main stem reaches were the Pearl and West Pearl rivers, while tributaries categorized as large were the Yockanookany, Strong, Bogue Chitto, and East Pearl rivers.
[b] Pascagoula River drainage main stem reaches were the Pascagoula, Leaf, and Chickasawhay rivers, while tributaries categorized as large were Tallahala, Buckatunna, Big Black, Black, and Red creeks.

Table 2. Weighted averages of basking density (corrected for unidentified turtles; see text) and relative abundance of each *Graptemys* species and combined other turtle species from jon boat and canoe surveys. Data are broken down according to most recent surveys (2015–2018) and all surveys since 2006 (including data from Selman and Qualls 2009, Selman and Lindeman 2015, and Selman and Jones 2017) as well as by main stem reaches, larger tributaries, and smaller tributaries. The Pearl River drainage is inhabited by *G. pearlensis* and *G. oculifera*, while the Pascagoula River drainage is inhabited by *G. gibbonsi* and *G. flavimaculata*. No surveys were conducted on tributaries of the Pearl River drainage prior to 2015.

				Megacephalic map turtle species: *Graptemys pearlensis*/*gibbonsi*			Sawback species: *Graptemys oculifera*/*flavimaculata*			Other turtles			Unidentified turtles			
River drainage	Reaches	Segments surveyed	Total river km (rkm)	*n*	*n*/rkm	Proportion	*n*	*n*/rkm	Proportion	*n*	*n*/rkm	Proportion	*n*	*n*/rkm	Proportion	*Graptemys* ratio
2015–2018 surveys																
Pearl	Main stem reaches[a]	21	118.2	411	3.5	0.11	2864	24.2	0.80	309	2.4	0.08	286	2.4	0.07	7.0
	Tributary reaches	17	69.6	114	1.6	0.21	191	2.7	0.35	252	3.6	0.45	115	1.7	0.17	1.7
	Larger tributaries[a]	9	39.7	85	2.1	0.24	79	2.0	0.23	195	4.9	0.53	81	2.0	0.18	0.9
	Smaller tributaries	10	29.9	29	1.0	0.16	112	3.8	0.55	58	1.9	0.30	34	1.1	0.15	3.9
	Total	40	187.8	525	2.8	0.13	3055	16.3	0.75	561	3.0	0.12	401	2.1	0.09	5.8
Pascagoula	Main stem reaches[b]	14	70.2	240	3.4	0.20	840	12.0	0.70	126	12.0	0.10	46	0.7	0.04	3.5
	Tributary reaches	17	65.1	137	2.1	0.30	66	1.0	0.14	255	1.0	0.56	77	1.2	0.14	0.5
	Larger tributaries[b]	8	37.0	83	2.2	0.43	53	1.4	0.27	57	1.4	0.30	31	0.9	0.14	0.6
	Smaller tributaries	9	28.1	54	1.9	0.21	13	0.5	0.05	198	0.5	0.74	46	1.6	0.15	0.2
	Total	31	135.3	377	2.8	0.22	906	6.7	0.56	382	6.7	0.22	123	0.9	0.07	2.4
Combined data, 2006–2018																
Pearl	Main stem reaches	22	121.0	455	3.8	0.11	3035	25.1	0.80	342	2.8	0.08	286	2.4	0.08	6.7
	Total	41	190.5	569	3.0	0.12	3226	16.9	0.75	594	3.1	0.12	401	2.1	0.10	5.7
Pascagoula[c]	Main stem reaches	24	144.7	547	4.3	0.22	1568	12.4	0.61	379	3.0	0.17	69	0.5	0.03	2.8
	Tributary reaches	27	194.7	275	2.0	0.33	122	0.9	0.12	559	4.0	0.55	127	0.9	0.12	0.4
	Larger tributaries	15	139.4	200	2.0	0.38	99	1.0	0.14	258	2.6	0.47	64	0.6	0.10	0.4
	Smaller tributaries	12	55.3	75	2.0	0.25	23	0.6	0.08	301	7.9	0.67	63	1.6	0.14	0.3
	Total	51	339.4	822	3.1	0.25	1690	6.4	0.47	938	3.5	0.27	196	0.7	0.05	1.9

[a] Pearl River drainage main stem reaches were the Pearl and West Pearl rivers, while tributaries categorized as large were the Yockanookany, Strong, Bogue Chitto, and East Pearl rivers.

[b] Pascagoula River drainage main stem reaches were the Pascagoula, Leaf, and Chickasawhay rivers, while tributaries categorized as large were Tallahala, Buckatunna, Big Black, Black, and Red creeks.

[c] Because not all turtles were consistently recorded in 2006–2007 surveys, totals for calculations of corrected basking densities in this row are based on 45 total reaches: 23 main stem reaches totaling 126.5 km, 12 reaches of large tributaries totaling 100.3 km, and 10 reaches of small tributaries totaling 38.2 km; only the *Graptemys* ratio is based on data from all 51 reaches.

Table 3. Summary of catch per unit effort (CPUE) and relative abundance for *Graptemys* species in the Pearl and Pascagoula river drainages based on numbers of turtles captured in basking traps and fyke nets (see Supplemental 1). The unit effort is a trap day, defined as a basking trap checked multiple times throughout a day, or a trap night, defined as a fyke net left in place overnight, with trap days and trap nights weighted equally for combined CPUE. Also given is the percent of each species in the total catch of turtles of all species and the ratio of each sawback species to its sympatric megacephalic map turtle species.

	G. pearlensis			*G. oculifera*			*G. pearlensis*	*G. oculifera*	
Pearl River drainage sections	Basking traps	Fyke nets	Combined	Basking traps	Fyke nets	Combined	Percent of all turtles captured		*Graptemys* ratio
Main stem reaches[a]	0.08	0.00	0.08	0.50	0.06	0.49	0.14	0.81	5.8:1
Tributary reaches	0.14	0.03	0.13	0.14	—	0.13	0.38	0.33	0.9:1
All reaches	0.09	0.02	0.09	0.45	0.02	0.43	0.17	0.79	4.6:1
	G. gibbonsi			*G. flavimaculata*			*G. gibbonsi*	*G. flavimaculata*	
Pascagoula River drainage sections	Basking traps	Fyke nets	Combined	Basking traps	Fyke nets	Combined	Percent of all turtles captured		*Graptemys* ratio
Main stem reaches[a]	0.11	0.02	0.11	0.32	0.20	0.32	0.22	0.73	3.3:1
Tributary reaches	0.12	0.38	0.15	0.09	0.03	0.08	0.32	0.30	0.9:1
All reaches	0.11	0.17	0.11	0.30	0.13	0.30	0.24	0.72	3.0:1

[a] Main stem reaches in each drainage were the Pearl and West Pearl rivers and the Pascagoula, Leaf, and Chickasawhay rivers, respectively.

$F_{2,38} = 3.71$, $p = 0.038$; *G. flavimaculata*: $F_{2,38} = 8.74$, $p = 0.0008$). *Graptemys pearlensis* had highest densities on main stem reaches and lowest densities on small tributaries, with only the 2 extreme categories different in a Tukey test. Tukey's test identified no pairs of categories different for *G. gibbonsi*, although the trend was similar to that for *G. pearlensis*, with larger reaches averaging highest basking densities. For both sawbacks, main stem reaches had significantly higher densities than both large and small tributaries, which did not differ significantly from one another. In the Pascagoula River drainage, earlier surveys (2006–2008) had significantly higher densities than later surveys (2015–2018) for both *Graptemys* species (*G. gibbonsi*: $F_{1,38} = 3.71$, $p = 0.038$; *G. flavimaculata*: $F_{1,38} = 8.74$, $p = 0.0008$).

Trapping Results. — Total trapping effort over all years was 1868 trap days for basking traps and 50 trap nights for fyke nets in the Pearl River drainage vs. 2920 trap days for basking traps and 79 trap nights for fyke nets in the Pascagoula River drainage (Supplemental Material 1; https://doi.org/10.2744/CCB-1414.1.s1). We captured 2808 total turtles of 14 native species: 183 *G. pearlensis*, 390 *G. gibbonsi*, 841 *G. oculifera*, and 1169 *G. flavimaculata*, plus 225 turtles of 10 other species (2 other emydids, 4 kinosternids, 2 trionychids, and 2 chelydrids). We also captured 1 specimen each of 2 nonnative species of *Graptemys* (*Graptemys pseudgeographica* and *Graptemys sabinensis*) in the Pearl River near Jackson. Totals include 224 recaptures recorded at sites where we marked all turtles, accounting for 10% of total captures at those sites.

More *Graptemys* were caught in basking traps than in fyke nets, both in absolute terms (2154 vs. 25) and in terms of CPUE (0.45 TTD vs. 0.19 TTN; numbers for all 4 native *Graptemys* species from all years in both cases; breakdown by species in Table 3). Fyke nets were particularly ineffective in sampling *Graptemys* in the Pearl River drainage (0.04 TTN vs. 0.30 in the Pascagoula River drainage). In contrast, basking traps caught *Graptemys* at a slightly higher CPUE in the Pearl River drainage (0.54 TTD vs. 0.41 in the Pascagoula River drainage).

Relative Abundance in Basking Counts and Trapping. — In point counts and basking density surveys, the sawback:megacephalic ratio was consistently more favorable to *G. gibbonsi* (i.e., lower, with fewer sawbacks per megacephalic) than to *G. pearlensis*, except in small tributaries in the data for point counts from all years (Tables 1 and 2). There was a preponderance of the megacephalic species *G. gibbonsi* in point counts and basking density surveys on tributary reaches of the Pascagoula system, while there was a preponderance of the sawback species *G. oculifera* in tributary reaches of the Pearl system in basking density surveys but not in point counts. Relative abundance among all species of turtles observed in basking counts were largely similar by species and category of river reach between point counts and basking density surveys (Tables 1 and 2; Fig. 1), with the biggest discrepancy by type of survey being for *G. oculifera* on small tributaries, where they were much more relatively abundant in boat surveys than in point counts (55% vs. 4%). For both megacephalic *Graptemys* species, relative abundance among all turtle species (all years) varied little among main stem, large tributary reaches, and small tributary reaches (range, 11%–25% for *G. pearlensis*, range 21–38% for *G. gibbonsi*). In contrast, sawback relative abundance was generally much higher on main stem reaches (67% for point counts and 80% for boat surveys for *G. oculifera*, 46% and 61% for *G. flavimaculata*) than on tributary reaches (10% and 35% for *G. oculifera*, 5% and 12% for *G. flavimaculata*), as pooled other species were high in relative abundance in the tributaries of both river systems (range, 45%–67%) compared with main stem reaches (range, 8–33%). For

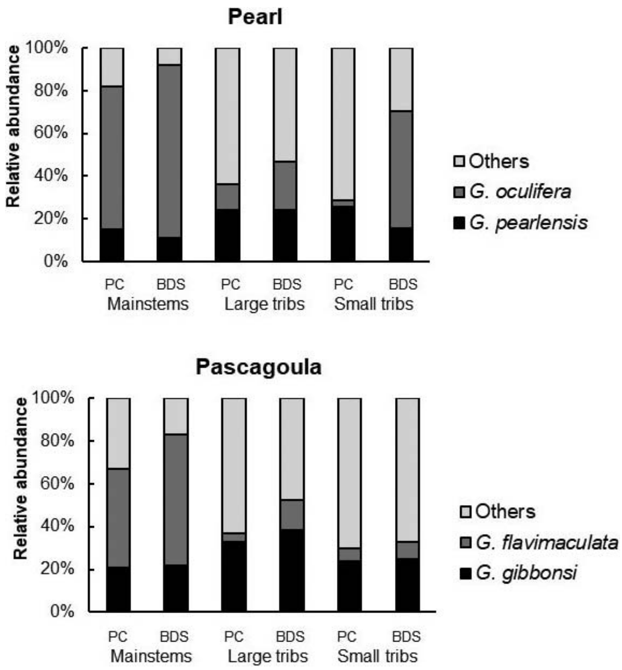

Figure 1. Relative abundance of *Graptemys* species and other turtle species, comparing point counts (PC) made from bridges or riverbanks with basking density surveys (BDS) made during boat cruises, for main stem reaches, large tributaries, and small tributaries.

2015–2018 data from both drainages, the differences in distribution of sightings between megacephalic map turtle species and sympatric sawbacks among the 3 categories of river reach were highly significant, in both point counts (Pearl: $\chi^2_2 = 98.2$, $p < 0.0001$; Pascagoula: $\chi^2_2 = 184.1$, $p < 0.0001$) and boat surveys (Pearl: $\chi^2_2 = 196.6$, $p < 0.0001$; Pascagoula: $\chi^2_2 = 177.0$, $p < 0.0001$).

Similar trends in relative abundance occurred in trapping data (Table 3). Sawback captures outnumbered megacephalic map turtle captures on main stem reaches of both river systems, almost twice as strongly so in the Pearl River as in the Pascagoula, Leaf, and Chickasawhay rivers; that is, the main stem *Graptemys* ratios were more favorable toward *G. gibbonsi* than toward *G. pearlensis*. In tributary reaches, megacephalic map turtles dominated in both river systems by lesser margins. Other turtle species became more prevalent in trapping results on tributaries, as pairs of sympatric *Graptemys* species made up 95% of the total turtle catch in main stem reaches of each river system, compared to just 71% in Pearl tributaries and 62% in Pascagoula tributaries.

We captured the 2 megacephalic *Graptemys* at lower CPUE rates than the 2 sawback species overall, and the megacephalics also contrasted with the sawbacks in having slightly higher CPUE on tributary reaches than on main stem reaches compared to much higher CPUE on main stem reaches for the sawbacks (Table 3). *Graptemys pearlensis* had slightly lower CPUE than *G. gibbonsi*.

Population structure based on 451 total captures (Table 4) were similar for the 2 species of megacephalic map turtles ($\chi^2_4 = 5.39$, $p = 0.25$). Sex ratios of captured turtles larger than minimum male size were 55♂:31♀ (or 1.8♂:1♀) for *G. pearlensis* and 141♂:124♀ (1.1♂:1♀) for *G. gibbonsi*, with the former but not the latter departing significantly from unity ($\chi^2_1 = 6.70$, $p = 0.0010$ and $\chi^2_1 = 1.09$, $p = 0.30$, respectively; Table 4). Operational sex ratios (i.e., discounting immature females) were significantly skewed toward males for *G. pearlensis* (55♂:12♀, or 4.6♂:1♀; $\chi^2_1 = 28$, $p < 0.0001$) and for *G. gibbonsi* (141♂:48♀, or 2.9♂:1♀; $\chi^2_1 = 46$, $p < 0.0001$). Unsexed juveniles, including hatchlings in their first full growing seasons and 1-yr-olds, were commonly captured at many sites (Table 4), accounting for 18% of all *G. pearlensis* and 24% of all *G. gibbonsi*, the latter of which had especially high frequencies of hatchlings, mostly via hand or dip net captures, at 2 sites on the upper Chickasawhay and Chunky rivers (58% and 63% of all turtles captured at those sites, respectively).

Total Range, with New Tributary Records and Upstream Range Extensions. — The total range we found to be occupied by *G. pearlensis* was 1279.6 rkm, with 632.6 rkm (49%) in the main stem Pearl and West Pearl rivers and the remaining 647.0 rkm (51%) in various tributaries. Of these totals, ~ 33.6 rkm of the middle Pearl River's original channel is submerged under the Ross Barnett Reservoir, which has 61.5 km of shoreline. The total range we found to be occupied by *G. gibbonsi* was 1733.7 rkm, with main stem reaches of the Pascagoula, Leaf, and Chickasawhay rivers totaling 623.1 rkm (36%) and various smaller tributaries totaling 1110.6 rkm (64%). Of these totals, ~ 10.1 rkm of upper Okatibbee Creek is submerged under Okatibbee Reservoir, which has 26.7 km of shoreline.

Between 2015 and 2018, *G. pearlensis* was detected for the first time in 5 tributaries, and other new records document upstream range extensions within 4 additional tributaries (Table 5). Assuming a continuous range within these stream reaches, the total newly discovered range for *G. pearlensis* sums to 188.3 rkm. *Graptemys gibbonsi* was detected for the first time in 3 tributaries, and other new records document range extensions within 4 additional tributaries (Table 5). Its newly discovered range sums to 133.3 rkm. New tributaries and upstream range extensions were also recorded for the sympatric sawback species (4 and 2, respectively, totaling 102.5 rkm for *G. oculifera*, and 1 and 3, respectively, totaling 55.5 rkm for *G. flavimaculata*). These records include a total of 8 new county records for *Graptemys* species (3 vouchering previous sight records and 5 establishing previously unknown county occurrences; Lindeman 2017a, 2017b, 2017c).

We surveyed basking turtles in point counts on several additional tributaries that had no previous records of the 2 megacephalic map turtle species as well as upstream of the known ranges on many occupied streams (Supplemental Material 2; https://doi.org/10.2744/CCB-1414.1.s2). No *G. pearlensis* were detected in 16

Table 4. Population structure as indicated by trapping results for *Graptemys pearlensis* and *Graptemys gibbonsi*, 2005–2018. Unsexed juveniles were smaller than the minimum size of adult males and in at least their second season of growth, while juvenile females were larger than minimum male size but lacked the male secondary sexual characteristic of an enlarged tail and were < 180 mm in plastron length. Recaptures are not included.

Trapping site	Hatchlings	Unsexed juveniles	Adult males	Juvenile females	Adult females
G. pearlensis, Pearl River drainage					
Pearl River downstream of Highway 19 north of Philadelphia	2		7		
Pearl River at Carthage					
Pearl River at Jackson					
Pearl River at Highway 28 east of Georgetown		1	3		1
Strong River at Highway 28 west of Pinola			5	1	4
Pearl River at Monticello					
Pearl River at Columbia			28	10	1
Bogue Chitto River at Walkers Bridge Water Park west of Tylertown	4	3	5	2	2
East Pearl River at Napoleon		2	4	5	1
Additional sites, each with < 5 captures	3	3	3	1	3
Total	9	9	55	19	12
Percentage	9	9	53	18	12
G. gibbonsi, Pascagoula River drainage					
Leaf River at Beaumont	2		7	2	1
Leaf River upstream of Hattiesburg	3	3	30	33	22
Tallahala Creek at Morriston Road northeast of Morriston	4	3	3	2	4
Bowie River at Glendale Road in Hattiesburg	1		3	4	
Chunky River at Griffis Fountain Road in Chunky	10	1			5
Chickasawhay River at Stonewall		3	15	8	4
Chickasawhay River at County Road 690 east of Desoto	18	2	6	5	
Chickasawhay River at Shubuta		1	6	3	2
Chickasawhay River at Highway 184 in Waynesboro	2		2	1	2
Chickasawhay River downstream of Leakesville	3	11	54	6	4
Leaf River/Pascagoula River at Merrill	1	2	3	1	1
Pascagoula River at Wade		3	2	1	
Pascagoula River at Ward Bayou		3	5	10	
Additional sites, each with < 5 captures	4	2	5		3
Total	48	34	141	76	48
Percentage	14	10	41	22	14

tributaries (24 sites, 32 total counts), and we also conducted 42 surveys at 21 total sites upstream of their known range in 8 streams known to be occupied farther downstream. No *G. gibbonsi* were detected in 20 tributaries (38 sites, 52 total counts), and we also conducted 82 surveys at 49 total sites upstream of their known range in 18 streams known to be occupied farther downstream. Other turtle species were often recorded during these out-of-range point counts (n = 228 turtles, in 208 total counts).

Global Population Estimates. — Based primarily on basking density surveys made by boat and secondarily on results of point counts, we divided each river drainage into river reaches typified by high, moderate, low, and very low density of their resident megacephalic map turtle species (Fig. 2). In the Pearl River drainage, we assigned these categories typical basking densities of 10, 3, 1, and 0.7 *G. pearlensis*/rkm, respectively, and these categories comprised 3%, 68%, 16%, and 14%, respectively, of the total range of *G. pearlensis*. In the Pascagoula River drainage, we assigned these categories typical basking densities of 5, 4, 2.5, and 0.5 *G. gibbonsi*/rkm, respectively, comprising 33%, 6%, 38%, and 23%, respectively, of the total range of *G. gibbonsi*. On the assumption that we saw on average 15% of the population during basking surveys, we estimated global populations to be 21,841 *G. pearlensis* and 34,081 *G. gibbonsi*. Two main factors caused the 56% difference in global population estimates: 1) *G. gibbonsi* occurred at greater densities in main stem reaches, and 2) the Pascagoula River system has more occupied tributaries than the Pearl River system, particularly in terms of smaller tributaries.

Comparisons of various drainage segments by the proportion of the total range length they constitute and the percent of the estimated global population that inhabits each segment are presented in Table 6. For *G. pearlensis*, 61% of the estimated global population occurs in main stem reaches, and 34% occurs in 4 large tributaries, with half of the latter total (3749 turtles) in the Bogue Chitto River, leaving 6% spread among 11 smaller tributaries, of which only Lobutcha Creek exceeded n = 300. For *G. gibbonsi*, 57% of the estimated global population occurs in main stem reaches, and 25% occurs in 5 large tributaries, primarily in Tallahala, Buckatunna, and Black creeks (each $n > 2500$), with 18% spread among 19 smaller tributaries, in particular Okatibbee and Souinlovey creeks, the Bogue Homa, and the Chunky River (each $n > 750$).

Table 5. Range extensions measured in river km (rkm) recorded for *Graptemys* species in 2 river drainages during most recent fieldwork (2015–2019) in newly documented tributaries and upstream of records in tributaries already known to be occupied. Known ranges as of 2014 are based on records published prior to the start of the present study (Lindeman 2013, 2014a, 2014b). Voucher photos deposited in the University of Florida digital collection are listed by catalog number where available.

		New tributaries			Extended tributaries					
River drainage	Species	Tributary	Occupied range (rkm)	Voucher photos	Tributary	Known range as of 2014 (rkm)	Upstream extension, 2015–2018 (rkm)	Revised occupied range (rkm)	Voucher photos	Total added range (rkm)
Pearl	*G. pearlensis*	Tuscalometa Creek	24.9	179335–36	Lobutcha Creek	30.8	14.6	45.4	181008–09	188.3
		Pelahatchie Creek	5.6	No photo	Yockanookany River	24.1	50.7	74.8	179333, 179352–54	
		Purvis Creek	1.9	No photo	Strong River	74.3	13.1	87.4	179083	
		Hobolochitto and West Hobolochitto creeks	41.5	184624–26	Topisaw Creek	1.0	15.5	16.5	181013	
		Magees Creek	20.5	181011–12						
	G. oculifera	Lobutcha Creek	8.0	No photo	Strong River	23.4	50.9	74.3	181019, 184623	102.5
		Tuscalometa Creek	0.5	No photo	Yockanookany River	34.0	12.0	46.0	181016–17	
		Pelahatchie Creek	5.6	181018						
		Hobolochitto and West Hobolochitto creeks	25.5	No photo						
Pascagoula	*G. gibbonsi*	Shubuta Creek	34.0	181026	Chunky Creek	0.4	4.1	4.5	181028	133.3
		Atkinson Creek	5.8	185750	Okatibbee Creek	58.4	30.3	88.7	179392, 181027	
		West Tallahala Creek	4.3	189685	Souinlovey Creek	24.7	37.2	61.9	179355	
					Oakohay Creek	19.6	17.6	37.2	179397–98	
	G. flavimaculata	Okatibbee Creek	17.8	179314	Leaf River	215.4	20.4	235.4	179315	55.5
					Chickasawhay River	253.1	6.5	259.6	*[a]	
					Tallahala Creek	72.9	10.8	83.7	181059	

[a] * Range extension in uppermost 6.5 rkm of Chickasawhay River by virtue of specimen found upstream in the river's tributary, Okatibbee Creek.

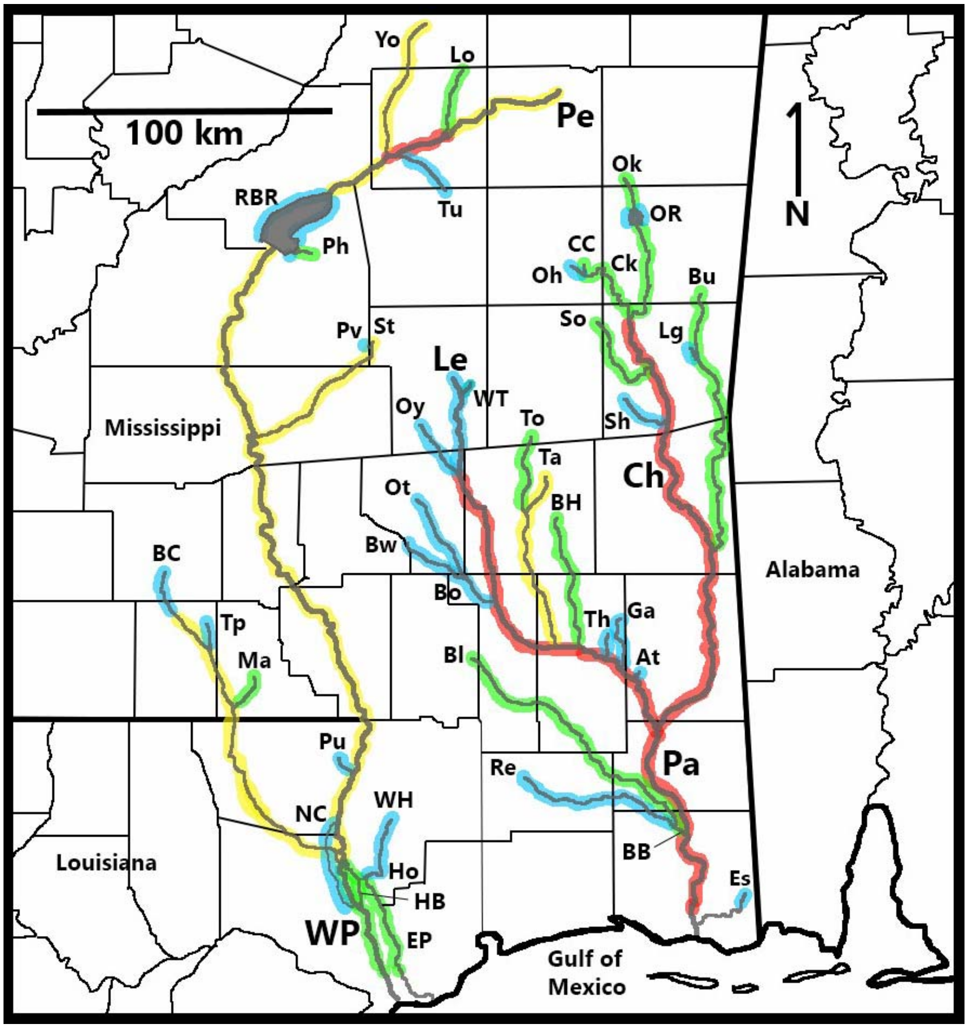

Figure 2. Map of the 2 river drainages studied, with river segments drawn to the upstream known range extents of the megacephalic map turtles *Graptemys pearlensis* and *Graptemys gibbonsi*. Shading represents river reaches with basking densities designated high (red), moderate (yellow), low (green), and very low (blue) for calculation of global population estimates (see text for representative densities used). The Pearl and West Pearl (Pe and WP) and Pascagoula, Leaf, and Chickasawhay (Pa, Le, and Ch) main stem reaches are indicated with larger labels along with their tributaries, which have smaller labels (see Table 6 for abbreviations).

DISCUSSION

The general picture of basking turtle abundance for the Pearl and Pascagoula drainages is a gradient from larger channels at downstream localities that are dominated by their respective federally listed sawback species, with declining *Graptemys* abundance farther upstream and into tributaries, to the point where first sawbacks and later the megacephalic species disappear, but other species rise in relative abundance and continue to be seen farther upstream. While all 4 *Graptemys* species in these river systems decline in abundance in smaller river channels, the gradient is far steeper for the 2 sawbacks. The 2 focal species of megacephalic *Graptemys* show considerably less variation in their relative abundance than the sawbacks and combined other species, making up a more or less constant proportion of the basking turtle fauna throughout their respective ranges. Both absolute and relative abundance of *G. gibbonsi* in the Pascagoula River drainage are more robust than are those of *G. pearlensis* in the Pearl River drainage, although both species show evidence of long-term historical declines in abundance.

Main Stem vs. Tributary Abundance. — Generally, the 4 resident species of *Graptemys* were most abundant in basking surveys and in CPUE in larger main stem river reaches and least abundant in small tributaries, but the gradient of basking density or CPUE was considerably steeper for the 2 sawbacks. In main stem river reaches of both drainages, sawbacks achieved high abundance (*G. oculifera* basking densities: mean 12.4/rkm, maximum 88.1/rkm; *G. flavimaculata* basking densities: mean 25.1 turtles/rkm, maximum 99.6 turtles/rkm). Average and maximum basking densities of sympatric megacephalic species were considerably lower than the sawback levels (*G. pearlensis*: mean 3.8/rkm, maximum 16.1/rkm; *G. gibbonsi*: mean 4.3 turtles/rkm, maximum 17.2/rkm).

The above interspecific differences mirror previous reports of basking density in *Graptemys*. Basking surveys

Table 6. Percent of occupied range and percent of total estimated population for *Graptemys pearlensis* in the Pearl River drainage and *Graptemys gibbonsi* in the Pascagoula River drainage. Tributaries are arranged from north to south according to where they join main stem rivers, with indented entries for tributaries of tributaries and impoundments (Fig. 2).

Stream	Code	Tributary class	Range (rkm)	Density class	Population estimate	Percentage of total range	Percentage of total population
Pearl River drainage main stem reaches							
Pearl	Pe	—	33.4/519.8	High/moderate	12,626	43	58
Ross Barnett Reservoir	RBR	—	61.5[a]	Very low	287	3	1.3
West Pearl	WP	—	45.8	Low	305	4	1.4
Pearl River drainage tributaries and connected channels							
Lobutcha Creek	Lo	Small	45.4	Low	303	4	1.4
Tuscolometa Creek	Tu	Small	24.9	Very low	116	1.9	0.5
Yockanookany	Yo	Large	74.8	Moderate	1498	6	7
Pelahatchie Creek	Ph	Small	13.8	Low	92	1.1	0.4
Strong	St	Large	87.4	Moderate	1749	7	8
Purvis Creek	Pv	Small	1.9	Very low	9	0.1	0.04
Pushepatapa Creek	Pu	Small	11.0	Very low	51	0.9	0.2
Bogue Chitto	BC	Large	182.8/19.5	Moderate/very low	3749	16	17
Topisaw Creek	To	Small	16.5	Very low	77	1.3	0.4
Magees Creek	Ma	Small	20.5	Low	136	1.6	0.6
Hobolochitto Creek	Ho	Small	10.3	Very low	64	0.8	0.3
West Hobolochitto Creek	WH	Small	31.2	Very low	129	2	0.6
Pearl Navigation Canal	NC	Small	32.4	Very low	151	3	0.7
East Pearl	EP	Large	56.71	Low	379	4	2
Holmes Bayou	HB	Small	17.91	Low	120	1.4	0.5
Pascagoula River drainage main stem reaches							
Pascagoula	Pa	—	119.9	High	4001	7	12
Leaf	Le	—	194.6/49.2	High/very low	6654	14	20
Chickasawhay	Ch	—	259.4	High	8651	15	25
Pascagoula River drainage tributaries and connected channels							
West Tallahala Creek	WT	Small	4.3	Very low	15	0.2	0.04
Oakohay Creek	Oy	Small	37.9	Very low	127	2	0.4
Bowie	Bo	Small	23.7	Very low	79	1.4	0.2
Bowie Creek	BC	Small	38.9	Very low	129	2	0.4
Okatoma Creek	Ot	Small	44.8	Very low	149	3	0.4
Tallahala Creek	Ta	Large	98.0	Moderate	2615	6	8
Tallahoma Creek	To	Small	46.4	Low	775	3	2
Bogue Homa	BH	Small	72.1	Low	1202	4	4
Thompson Creek	Th	Small	14.3	Very low	48	0.8	0.14
Gaines Creek	Ga	Small	29.6	Very low	99	1.7	0.3
Atkinsson Creek	At	Small	5.8	Very low	19	0.3	0.06
Chunky	Ck	Small	45.1	Low	752	3	2
Chunky Creek	CC	Small	4.5	Low	75	0.3	0.2
Okahatta Creek	Oh	Small	6.5	Very low	21	0.4	0.06
Okatibbee Creek	Ok	Small	82.4	Low	1374	5	4
Okatibbee Reservoir	OR	Small	26.7[b]	Very low	89	—	0.3
Souinlovey Creek	So	Small	63.2	Low	1054	4	3
Shubuta Creek	Sh	Small	34.0	Very low	113	2	0.3
Buckatunna Creek	Bu	Large	176.0	Low	2935	10	9
Long Creek	Lo	Small	7.8	Very low	25	0.4	0.07
Big Black Creek	BB	Large	9.2	Low	153	0.5	0.4
Black Creek	Bl	Large	155.5	Low	2592	9	8
Red Creek	Re	Large	93.8	Very low	312	5	0.9
Escatawpa	Es	Small	6.7	Very low	23	0.4	0.07

[a] Value represents shoreline km of Ross Barnett Reservoir; the 33.6 rkm of Pearl River submerged by the reservoir is subtracted from the value for the Pearl River above.
[b] Value represents shoreline km of Okatibbee Reservoir; the 10.1 rkm of Okatibbee Creek submerged by the reservoir is subtracted from the value for Okatibbee Creek above.

of narrow-headed *Graptemys* species commonly report basking densities averaging over 20 turtles/rkm and ranging to over 100/rkm (reviewed in Ilgen et al. 2014). Megacephalic species of *Graptemys*, in contrast, have been reported to occur at site-specific basking densities that average > 10/rkm in only 2 rivers and exceed 15/rkm for single sites only rarely (Table 7). Narrow-headed *Graptemys* feed on sponges and other invertebrates and algae that they graze from submerged deadwood (Shively and Jackson 1985; Lindeman 2016; Selman and Lindeman 2018; P.V.L., W.S., and R.L.J., unpubl.). These communities are sunlight dependent (Shively and Jackson 1985); thus, higher densities in larger river channels may reflect prey abundance. High densities of narrow-headed species are reported to occur in large, sluggish, low-gradient channels near the coast as well as at upstream confluences with reservoirs (Fehrenbach et al. 2016; Jones 2017). Megacephalic species rely primarily on benthic mussels

Table 7. Basking densities reported for megacephalic species of *Graptemys* from rivers to compare to a similar table for narrow-headed *Graptemys* species in Ilgen et al. (2014). Indented drainages are tributaries of the rivers listed above them. No corrections are made for unidentified turtles observed. NR = not reported.

Species	Drainage	Source	Basking density (no./river km)	Range
G. pearlensis	Pearl	Present study (2006–2018)	3.8	0.3–16.1
	Yockanookany		4.6	3.4–5.2
	Strong		1.5	1.3–2.5
	West Pearl		1.3	0.6–2.6
	Bogue Chitto		2.6	—
	East Pearl		0.7	0.2–1.4
	Various smaller tributaries		1.5	0–4.4
	Pearl	Lindeman (1998, 1999)	7.1	0–22.1
	Tributaries		3.2	1.3–4.5
	Bogue Chitto	Shively (1999)	6.6	1.5–15.4
	Pearl	Dickerson and Reine (1996)	1.8	0.1–4.7
	West Pearl		0.1	0–0.4
	Bogue Chitto		1.6	—
G. gibbonsi	Pascgoula	Present study (2006–2018)	3.9	1.6–7.8
	Leaf		5.4	1.9–17.2
	Chickasawhay		3.4	1.0–7.0
	Various smaller tributaries		1.8	0–8.1
	Pascgoula	Lindeman (1998, 1999)	8.9	4.0–17.4
	Leaf		3.1	0–7.0
	Chickasawhay		8.1	0–30.9
	Various smaller tributaries		5.4	0–13.3
G. pulchra	Tensaw	Godwin (2001, 2003)	0.2	0–0.5
	Tombigbee		0.5	0–0.7
	Black Warrior		0.1	0.1–0.1
	Alabama		2.7	0–7.5
	Cahaba		1.8	0.3–2.5
	Coosa		4.8	1.7–9.6
	Tallapoosa		1.8	1.2–5.2
G. ernsti	Yellow	Godwin (2000)	2.6	0.2–7.0
	Conecuh		24.9	0.5–63.3
	Tributaries		6.2	4.7–8.1
	Escambia	Aresco and Wallace (2006)	5.0	—
G. barbouri and *G. ernsti*[a]	Choctawhatchee	Godwin (2002)	0.5	0–3.1
	Pea		1.2	0–4.2
	Choctawhatchee	Enge and Wallace (2008)	2.4	0.1–7.0
	Choctawhatchee	Mays and Hill (2020)	10.6	1.9–25.6
G. barbouri	Ochlockonee	Enge and Wallace (2008)	0.1	0.1–0.1
	Apalachicola	USFWS (1992 unpubl.; summarized in Lindeman 2013)	7.8	7.6–7.9
	Chipola Cut-Off		8.0	—
	River Styx		5.0	—
	Apalachicola	Mays and Hill (2020)	21.8	5.0–51.5
	Chipola		7.1	1.0–20.3
	Ochlockonee		0.7	0–1.1
	Chipola	Moler (1986)	2.6	NR
	Chattahoochee	Hepler et al. (2015)	2.4	NR
	Tributary		0.9	NR
	Flint		9.7	NR
	Tributaries		1.1	NR
	Ocklockonee		0.5	NR

[a] *Graptemys barbouri* is numerically dominant over *G. ernsti* in the Choctawhatchee, but the 2 species are difficult to distinguish in basking surveys and also hybridize; densities listed are for combined numbers.

(Sanderson 1974; Shealy 1976; Lindeman 2016; J. Vučenović and P.V.L., unpubl. data, 2015–2018), and no reports suggest that well-insolated or large, sluggish channels near the coast or upstream ends of reservoirs show any particular pattern regarding the abundance of these turtles.

Tributary populations are not as dense as main stem populations, yet some tributaries contain large populations of *G. pearlensis* and *G. gibbonsi*, including many that have only recently been discovered. For example, presence of *G. pearlensis* in the Yockanookany was first established in 1994, and extensive upstream range extensions have now been reported in the Yockanookany, Strong, and Bogue Chitto rivers (Lindeman 1998, 2010, 2013, 2014a, 2017c); these 3 tributaries together are inhabited by nearly one-third of our estimated global population (Table 6), with nearly half occurring in stretches not known to be part of the species' range prior to the present century. Likewise, *G. gibbonsi* occurs in relatively large numbers in upper Tallahala and Tallahoma creeks, Souinlovey and Buckatunna creeks, and the Bogue Homa, which collectively house over one-fifth of our estimated global population; all but the lower sections of Tallahala Creek were unreported populations until the first decade of this century (Selman and Qualls 2009; Lindeman 2017b).

No major channel alterations or impoundments have occurred on the Pascagoula or the 2 major tributaries that form the Pascagoula. In contrast, 33.6 rkm of the middle Pearl River is inundated by the Ross Barnett Reservoir, and downstream channel alterations have diverted considerable flow from the East Pearl into the West Pearl and the Pearl River Navigation Canal (Piller et al. 2004; Tipton et al. 2004). We found the reservoir and all 3 downstream distributaries to be very-low-density or low-density reaches, suggesting that substantial loss of population in the lower reaches of the Pearl River drainage has occurred historically due to river engineering. Dickerson and Reine (1996) also reported much lower basking density of *G. pearlensis* in the West Pearl than in the upper Pearl (Table 7).

Relative Abundance. — The proportion of all *Graptemys* that were 1 or the other of the megacephalic species varied widely throughout both drainages, mainly due to strong variation in the basking density of their sympatric congeners, with low relative abundance of megacephalics on main stems that became higher on tributaries where sawback abundance declined precipitously, particularly on smaller tributaries, where the sawbacks were often absent. The most atypical part of this pattern was the relative abundance of *G. oculifera* on small tributaries in boat surveys (55% relative abundance compared to 23% on large tributaries), which may have been influenced by the fact that many of the small tributaries on the Pearl drainage were surveyed by boat at their downstream junctures with the Pearl and West Pearl main stems (Tuscolameta Creek, Pearl River Navigation Canal, Holmes Bayou, and Porter River) and may have supported populations that were continuous with those main stems. The proportion of all turtles that were megacephalic *Graptemys* also varied greatly due to congener trends and increased relative abundance of other species on small tributaries far upstream. Other species of turtles occurred well above the upstream range limits of the 2 megacephalic species but were far less important components of the basking turtle fauna on main stem reaches.

Population Structure of G. pearlensis *and* G. gibbonsi. — Both megacephalic *Graptemys* species showed evidence of considerable recruitment in trapping results, with unsexed juveniles accounting for 18% of *G. pearlensis* captures and 24% of *G. gibbonsi* captures and juvenile females being captured more frequently than adult females in both species. The overall sex ratio was somewhat male biased for *G. pearlensis* and almost exactly 1:1 for *G. gibbonsi*. Operational (i.e., adult) sex ratios were strongly male biased in both species, which is to be expected due to the exceptional sexual dimorphism in maturation age and thus size. Male *Graptemys* typically mature in 2–3 yrs (Lindeman 2013), while females mature much later; maturity may occur around 9 yrs of age in *G. pearlensis* and 11 yrs of age in *G. gibbonsi* (Vogt et al. 2019a, 2019b).

Without information on possible trapping biases, it is unclear what population structure indicates about population viability. For example, hand and dip net captures were almost exclusively juvenile turtles, particularly hatchlings, but hatchlings were captured in basking traps and fyke nets much less commonly. With the strong reliance on basking traps in the present study, any sexual differences or ontogenetic changes in basking proclivity would bias population structure. A comparison of trapping rates of different life stages with separate estimates of population size by life stage would be instructive. Estimating survival rates of adult males and adult females (e.g., Jones 2017) and a life table analysis would ultimately lead to a rigorous analysis of population viability.

Range Extensions and Their Significance to Conservation. — If range is measured in terms of the length of occupied stream reaches, our visual surveys increased the known ranges of the focal species by 15% for *G. pearlensis* (i.e., 188.3 of 1279.6 total rkm are range extensions) and by 8% *G. gibbonsi* (133.3 of 1733.7 total rkm). The positive nature of these findings is tempered, however, when the range extensions are viewed in light of our range-wide population estimates. Newly reported stream reaches account for just 9% of the global estimated population of *G. pearlensis* and 4% of the global estimated population of *G. gibbonsi* because most of the range extensions were in areas designated as low or very low density. In addition, without telemetry or wide-ranging mark-recapture sampling, it remains unknown how dependent turtles observed in the smallest tributaries may be on making seasonal forays into connecting larger tributaries and main stem river reaches for feeding, nesting, or refuge from drought and low water levels in small tributaries.

The USFWS recently decided not to list Barbour's map turtle (*G. barbouri*), another species with megacephalic females that had been part of the same listing petition as *G. pearlensis* and *G. gibbonsi* (Yarbrough 2017). Part of the rationale given for not listing *G. barbouri* was that the species had not disappeared from any portions of its known range, and in fact, during field surveys in the past decade and a half, the species was found in 2 new drainages and 3 tributary streams it had not been previously known to occupy in the Apalachicola River drainage (Hepler et al. 2015), with new findings extending the range of the species by 6% (Yarbrough 2017). As in our study, however, the newly reported tributaries and drainages had low populations of *G. barbouri* compared to main stem reaches of the Chattahoochee, Flint, and Apalachicola river system. We propose that the stated rationale likely overestimates the significance of the recent extensions of known range for *G.*

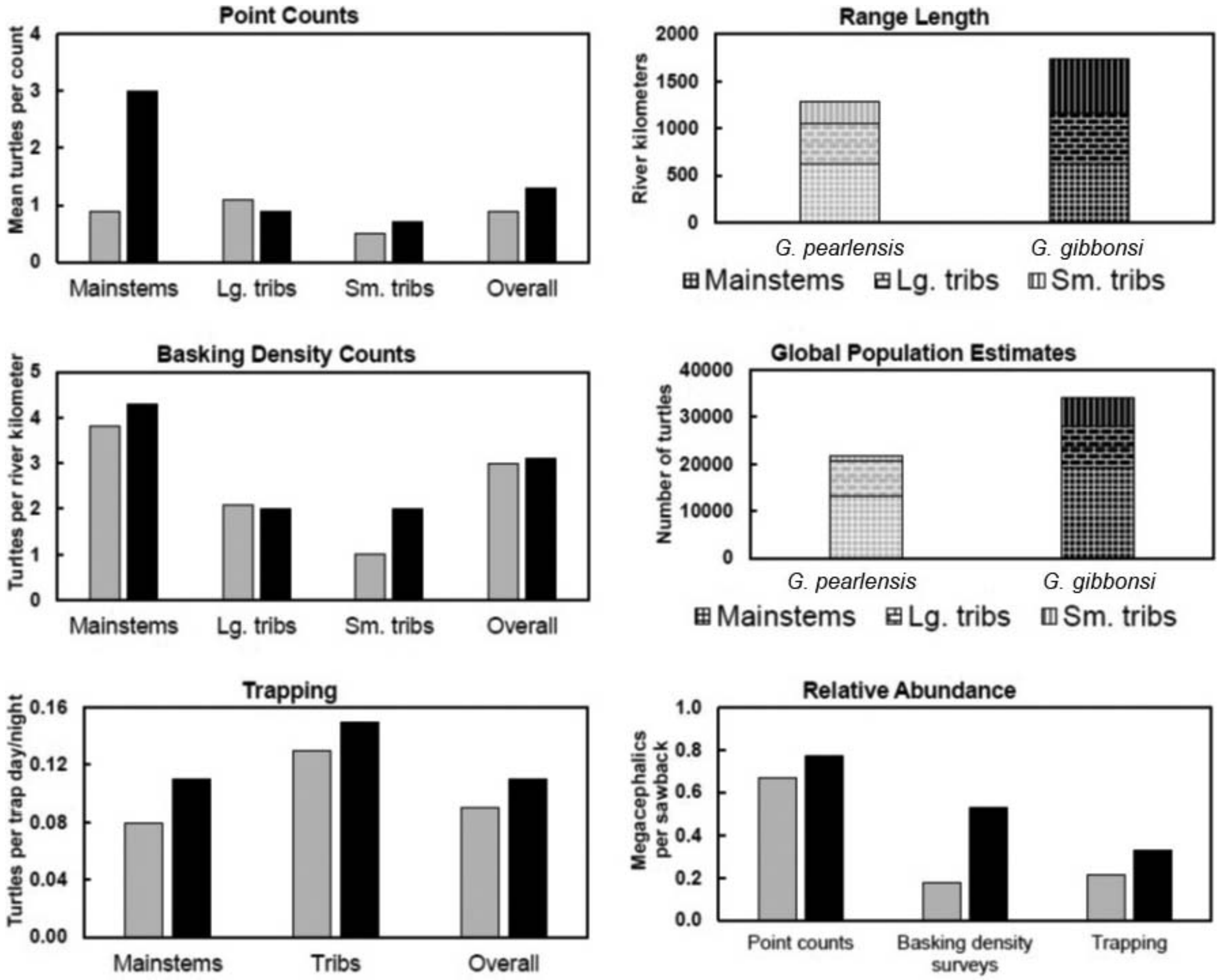

Figure 3. Summary comparison of *Graptemys pearlensis* (gray) and *Graptemys gibbonsi* (black) in main stem reaches, large tributaries, and small tributaries of their respective river drainages. Comparisons include mean number seen per point count, weighted mean basking density, catch per unit effort in basking traps (turtles per trap day) and fyke nets (turtles per trap night), river kilometers of known range, global population estimates, and relative abundance expressed in number of each species seen or captured per sympatric sawback species.

barbouri and caution against making a similar conclusion in the case of *G. pearlensis* and *G. gibbonsi*.

Comparison of Abundance Between G. pearlensis *and* G. gibbonsi. — *Graptemys gibbonsi* was the more abundant of the 2 focal megacephalic *Graptemys* species in several metrics (Fig. 3): overall point counts (44% more *G. gibbonsi* than *G. pearlensis* for all counts, 333% more in counts on main stem reaches), overall basking density surveys (3% more *G. gibbonsi* for all counts, 13% more in main stem counts only), trapping results (22% more *G. gibbonsi* per trap day/night overall, 38% more on main stem reaches), total range length (35% more occupied rkm for *G. gibbonsi*), global population estimates (56% more *G. gibbonsi* than *G. pearlensis*), and more equitable ratios with its sympatric sawback species (1 *G. gibbonsi* per 1.3 *G. flavimaculata* vs. 1 *G. pearlensis* per 1.5 *G. oculifera* for point counts, 1 per 1.9 vs. 1 per 5.7 for surveys by boat, and 1 per 3.0 vs. 1 per 4.6 for trapping results). We believe it is clear that populations of *G. gibbonsi* are more robust overall than populations of *G. pearlensis*. A previous comparison of sawback:megacephalic species ratios in 1994–1995 (Lindeman 1998, 1999) did not consider the difference between the drainages because the 2 megacephalic species were at that time considered a single species under the name *G. gibbonsi* (Ennen et al. 2010). In replicated point counts conducted primarily on main stem sites (31 of 41 total sites, or 76%), the 2 sawbacks were 5.1 as abundant as the 2 megacephalics. However, in that study the sawback:megacephalic ratio was 9.6:1 for *G. oculifera* and *G. pearlensis* vs. 2.4:1 for *G. flavimaculata* and *G. gibbonsi*. Similarly, other reports, based on data included in the present study, also found more equitable ratios for the Pascagoula species pair (Selman and Qualls 2009) than for the Pearl species pair (Selman and Jones 2017).

The 2 river drainages are occupied by their respective megacephalic map turtle species to nearly identical extents along their main stem reaches (632.6 rkm for *G. pearlensis* vs. 623.1 rkm for *G. gibbonsi*), but *G. gibbonsi* occurs at greater densities along main stem reaches, as evidenced in point counts, basking density counts, and trapping results (Fig. 3). Habitat degradation is more extensive along the Pearl River than along the Leaf, Chickasawhay, and Pascagoula rivers. The Ross Barnett Reservoir has greatly reduced habitat suitability of 5% of the main stem Pearl River, and we also found low densities of *G. pearlensis* in the West and East Pearl rivers, whose flow was greatly altered by construction of the Pearl River Navigation Canal, which also has very low densities. Near Jackson, river channelization has also impacted *G. pearlensis* habitat negatively (Selman 2020), and channelization has also occurred along Tuscolameta Creek and the upper Yockanookany River. In the Pascagoula River drainage, only 1 small reservoir has been constructed within the range of *G. gibbonsi* on upper Okatibbee Creek, and no channelization has been undertaken.

Riparian land preservation is also more extensive in the Pascagoula River drainage. Upstream portions of the Pascagoula River drainage flow through Bienville and DeSoto national forests, and extensive habitat protection occurs downstream in 2 Nature Conservancy preserves near the confluence of the Leaf and Chickasawhay rivers (Lindeman 2013) and the Pascagoula and Ward Bayou wildlife management areas (WMA), which protect riparian habitat for almost the entire length of the Pascagoula River. The upper reaches of Okatibbee Creek in Okatibbee WMA and a short portion of lower Red Creek in Red Creek WMA are also protected. The most extensive habitat preservation on the Pearl River is the Bogue Chitto National Wildlife Refuge along the upper West and East Pearl and lower Bogue Chitto rivers, which is contiguous with the Pearl River WMA, which protects the area between the West and East Pearl rivers downstream to the Gulf of Mexico. Additional protection of *G. pearlensis* habitat occurs in the uppermost Pearl River in Nanih Waiya WMA, the Pearl River as it flows into Ross Barnett Reservoir in Pearl River WMA, and the upper Strong River in Bienville National Forest.

The human populations of the 2 river drainages provide a direct index of the degree of river degradation in each: according to 2010 US census data, the 16 Mississippi counties inhabited by *G. gibbonsi* have a combined human population of 608,072, while the 17 Mississippi counties and 2 Louisiana parishes inhabited by *G. pearlensis* have a combined population of 1,168,261 (92% higher). Much of the difference is due to the Jackson metropolitan area, as Hinds, Madison, and Rankin counties account for 41% of the total human population for counties and parishes in the Pearl River drainage. Human populations may also relate inversely to habitat preservation, as less populated areas provide better opportunities for habitat acquisition.

Given the greater concentration of estimated global population of *G. gibbonsi* in tributaries (43% vs. 39% for *G. pearlensis*), in a river system that is more tributary rich (Fig. 2), populations of *G. gibbonsi* should also prove to be more buffered against catastrophic declines due to anthropogenic degradation of habitat, as many such threats would not extend upstream into tributary channels. The point regarding insulation against threats in tributaries is important to the conservation status of these 2 species because the relatively tributary-poor Pearl River drainage is afflicted with considerably more plans for projects that would degrade habitat for these 2 species. Plans for new reservoirs on the Pearl River both upstream and downstream of Jackson have been or are being considered (Lindeman 2013; Selman 2020).

Although they are ecologically similar species, the reasons given for listing *G. oculifera* and *G. flavimaculata* differ (USFWS 1986, 1991) in ways that are relevant to comparing the status of *G. pearlensis* and *G. gibbonsi* and making listing determinations. The listing of *G. oculifera* was predicated primarily on possible future threats to the species via further river engineering (USFWS 1986), and such projects, including the most recent "One Lake" proposal (Selman 2020), would be at least as deleterious for *G. pearlensis*, perhaps more so. The listing of *G. flavimaculata*, in contrast, was a reaction to perceived declines in populations that were considered to have already occurred (USFWS 1991). In the Pearl River drainage, *G. oculifera* outnumbers *G. pearlensis* to a much greater degree than *G. flavimaculata* outnumbers *G. gibbonsi*, a situation that has held steady for more than a quarter century (Lindeman 1998, 1999; Selman and Qualls 2009; Selman and Jones 2017); thus, the declines *G. gibbonsi* has suffered appear to be less severe.

Long-Term Historical Changes in Abundance of G. pearlensis *and* G. gibbonsi. — Basking survey data for sympatric species pairs of *Graptemys* in the Pearl and Pascagoula river drainages have been collected beginning only in the 1980s, when the USFWS began conducting surveys (Lindeman 2013). Trapping and specimen data date back to the late 1800s for the Pearl River and to 1952 (except for a single specimen of *G. flavimaculata* collected in 1930) for the Pascagoula River (Lindeman 2013) and may be used to give some idea of relative abundance in past decades. Overall, the data suggest that more equitable ratios of the 2 species occurred in southerly main stem reaches of each river drainage several decades ago. For his 2 species descriptions, Baur (1890, 1893) acquired 15 *G. oculifera* and 6 *G. pearlensis* collected in the West Pearl River between 1888 and 1891, a sawback:megacephalic ratio of 2.5:1. Cagle (1953) reported a ratio of 0.5:1 for a collection of 153 *Graptemys* specimens in the West Pearl River, and Tinkle (1958) reported the same ratio for 87 *Graptemys* specimens collected at 3 main stem Pearl and West Pearl sites. Cliburn (1971) collected at 7 sites throughout the Pearl River drainage and reported a 0.6:1 ratio for 114 *Graptemys* specimens. In 1978–1979, the ratio was 0.97:1 for 421 *Graptemys* captured in the middle Pearl River in Copiah and Simpson counties, Mississippi (McCoy et al. 2020). At a site on the middle Pascagoula, initial collection by the Tulane Field Crew in 1952 was strongly skewed toward *G. flavimaculata*, with a ratio of

11.6:1 for 202 specimens (Lindeman 2013), although Tinkle (1958) gave a much more equitable ratio of 1.4:1 for 36 *Graptemys* collected at a site on the lower Chickasawhay. The ratio for all 261 known specimens that were collected prior to 1960 is 6.9:1. Cliburn (1971) collected at 16 sites throughout the Pascagoula River drainage and reported a 0.97:1 ratio for 213 *Graptemys* specimens. In 1978–1979, the ratio was 0.6:1 for 141 *Graptemys* captured in the lower Chickasawhay River in Greene County, Mississippi (McCoy et al. 2020).

We found that both *Graptemys* species in the Pascagoula River drainage were less abundant in our most recent (2015–2018) point counts and basking density counts than in earlier data (2006–2014), while no difference by time period was found for either species in the Pearl River drainage. Due to differences in survey technique, however, it is difficult to know how much if any of these significant differences should be attributed to actual declines. Earlier surveys in the Pascagoula drainage depended more heavily on the use of spotting scopes with higher magnification, while the more recent surveys have been done primarily using binoculars. Differences in turtle detection among observers or differences in flight initiation by basking turtles viewed using different survey techniques may also contribute to differences. Using the same trapping protocol 5 times over 25 yrs, Selman and Jones (2017) found that *G. pearlensis* declined in abundance at 3 of 5 sampling sites on the Pearl River.

Federal Action Under the ESA. — Given their relatively low density throughout almost all of their range, historical decline in relative abundance, and existing and proposed threats to their habitat, we believe that *G. pearlensis* should be federally listed as T. Populations of *G. gibbonsi* are more robust than those of *G. pearlensis*, less threatened by existing habitat degradation, and more insulated from potential future threats by more extensive tributary populations. Listing *G. gibbonsi* as T would recognize historical declines in its abundance, and recovery efforts could aim to stop further declines and rebuild populations. An alternative would be to list *G. gibbonsi* as T-SA due to the similarity of *G. pearlensis* and *G. gibbonsi*. A T-SA listing would protect the species from exploitation through the pet trade while focusing federal and state recovery efforts on the more dire status of *G. pearlensis*. On the other hand, a T-SA listing would exempt *G. gibbonsi* from the requirement of interagency consultation for potentially harmful activities funded or authorized by federal or state agencies as would be required with a T listing.

Given their low relative abundance compared to the 2 sympatric sawback species that have already long been listed as T, the possibility of a listing as E might also be considered. Given that both species have ranges extending farther upstream into tributary streams than the sawbacks and the fact that neither species has been extirpated from any segment of its range, however, we believe a listing as E is probably not warranted at this time. Reports of the possible imminent extinction of *G. pearlensis* (Alexander 2018) are almost certainly overstated, but the need for protection from further habitat degradation and from exploitation for the pet trade is clear.

Recommended Recovery Efforts. — The primary need for recovery planning is a better understanding of anthropogenic factors that limit populations of megacephalic *Graptemys* species and that may contribute to their decline. The highest priority of this effort should concern the prey base of *G. pearlensis* and *G. gibbonsi*—primarily invasive Asian clams (*Corbicula* spp.) and native mussels but with aquatic insect larvae also important prey for males and juveniles (J. Vučenović and P.V.L., unpubl. data, 2015–2018)—and how these taxa responds to impoundment, channel dredging, and sedimentation. Nesting by *G. pearlensis* and *G. gibbonsi* has not been studied in detail, and habitat requirements for sandbars or other nesting habitats may also be important factors in population viability. Finally, deadwood abundance and the preservation of its source in riparian forests are important determinants of riverine turtle abundance (Lindeman 1999; Sterrett et al. 2010, 2015). More detailed studies are needed comparing map turtle abundance and ecology in deadwood-poor river reaches with little riparian forest source vs. deadwood-rich areas located in areas with well-managed riparian forests.

In a comparison of numbers of published articles, *G. pearlensis* and *G. gibbonsi* were among the most sparingly studied of North American turtle species (Lovich and Ennen 2013). Much of what we do know about these 2 species is from data collected during recovery efforts focused on federally listed sympatric congeners (Selman and Qualls 2009; Selman and Lindeman 2015; Selman and Jones 2017); additional focused study of the basic ecology and life history of each megacephalic species is much needed.

Basking density and trapping surveys are valuable methods for monitoring *Graptemys* populations, particularly if the same methodology is used at the same sites (e.g., Jones 2017; Selman and Jones 2017). Given the diversity of techniques used to quantify basking density of *Graptemys* in the Pearl and Pascagoula river systems as well as in other river systems, there is a need to standardize basking survey methodology for future monitoring efforts along with designation of sites that will be monitored iteratively in the future. For the Pascagoula River drainage, we were unable to definitively determine whether data trends during the first 2 decades of the 21st century are indicative of real declines in abundance or simply artifacts of variation in survey methodology, with earlier basking density surveys having been more dependent on higher-magnification equipment (spotting scopes) employed from greater cover (bridges, riverbanks, and sandbars). Strong drainage-wide gradients in the number of basking turtles and their relative abundance also complicate efforts to compare sites over time if they are not from the same river reaches. We suggest that the USFWS and its cooperators establish standard survey methodologies for basking density surveys and/or trapping surveys on at least 6 stretches of the Pearl and West Pearl as well as 2 each of the Yockanookany, Strong, and Bogue Chitto rivers. Similarly, we suggest designation of at least 2 stretches each on the Pascagoula, Leaf, and Chickasawhay rivers and 1 each on Tallahala, Okatibbee, and Buckatunna creeks, the Chunky River, and the Bogue Homa.

Endangered species listing prohibits take for the pet trade, which would benefit populations of *G. pearlensis* and *G. gibbonsi*. Enforcement of the take prohibition, via detection of illegal collecting in the wild and illegal sale combined with prosecution of offenders, would be of paramount importance. Take is likely to be greatest near public boat ramps that facilitate access (Selman and Jones 2017); thus, spot checks by state or federal wildlife biologists for evidence of illegal trapping and educational outreach via boat ramp signage and pamphlets that encourage the public to report suspicious collecting activities they observe should be incorporated into recovery planning. Training of officers to recognize turtle species of the 2 river systems would be an important component of these efforts. A comparison of abundance and population structure in reaches near public access and areas insulated from public access would also be of interest. In addition, online trade in the 2 species should be monitored in order to be able to interdict poaching operations.

Finally, active habitat management will be necessary for rebuilding populations of *G. pearlensis* and *G. gibbonsi*. If mussel prey abundance is determined to be a limiting factor as suspected, mussel habitat restoration efforts (Haag and Williams 2014) and reduction of sedimentation will be an important part of recovery efforts. Sandbar nesting habitats may require control of nonnative vegetation and contouring to improve access to female turtles and control of nest predators, such as raccoons (*Procyon lotor*) and fish crows (*Corvus ossifragus*; Jones 2006). Experimentation with placement of deadwood in river reaches with less riparian cover may also be fruitful (Lindeman 2013).

Acknowledgments

We thank K. Travers, S. Shaffer, C. Pastorius, C. Gale, H. Smith, and numerous students from the University of Southern Mississippi and Millsaps College for their assistance in the field. Funding for the study was received from the USFWS, and fieldwork was carried out under permits issued by the USFWS and the states of Mississippi and Louisiana. Trapping and sample procurement were authorized by the Institutional Animal Care and Use Committees of Edinboro University of Pennsylvania (#2016-0101) and the University of Southern Mississippi (#07032201 and #11092206).

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Received: 1 October 2019

Revised and Accepted: 27 January 2020

Published Online: 31 December 2020

Handling Editor: Jeffrey E. Lovich