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INTRADRAINAGE VARIATION IN POPULATION STRUCTURE, SHAPE MORPHOLOGY, AND SEXUAL SIZE DIMORPHISM IN THE YELLOW-BLOTCHED SAWBACK, *GRAPTEMYS FLAVIMACULATA*

WILL SELMAN

*Department of Biological Sciences, The University of Southern Mississippi,
118 College Dr. #5018, Hattiesburg, Mississippi 39406, USA
Rockefeller Wildlife Refuge, Louisiana Department of Wildlife and Fisheries,
5476 Grand Chenier Hwy., Grand Chenier, Lousiana 70643, USA;
e-mail:*

***Abstract.*—*Graptemys flavimaculata* (Yellow-blotched Sawback) is a small, highly aquatic turtle that is endemic to rivers and large creeks of the Pascagoula River system of southeastern Mississippi, USA. Little is known about geographic variation in population structure, shape morphology, and sexual size dimorphism (SSD) throughout the drainage. I captured and measured *G. flavimaculata* from three sites in 2005 and 2006. I analyzed female head width at two of these sites in 2008. Results indicate that body size and population structure vary across a geographic gradient; turtles from the Pascagoula River site were generally larger (both body mass and plastron length) relative to two upstream sites on two tributaries, the Leaf and Chickasawhay rivers. Additionally, body shape in females varied among populations, with Pascagoula River females having a more domed shape than upstream sites where turtles have a more streamlined shape. There was little difference in male shapes among sites. Female-biased SSD typified all three populations with SSD being less pronounced in the two upstream sites. Female head width was significantly different across sites (Pascagoula > Leaf), while there was no difference among sites for male claw length. Presumably, synergistic factors influence population structure, shape morphology, and sexual size dimorphism in *Graptemys flavimaculata* including: 1) food availability; 2) presence of competitors; 3) thermal environment; 4) presence of alligators; and 5) fluvial conditions.**

Key Words.—demography; geographic variation; *Graptemys*; Pascagoula River; sexual size dimorphism; turtle

INTRODUCTION

Graptemys flavimaculata (Yellow-blotched Sawback; Cagle 1954) is a small, riverine turtle that is endemic to the Pascagoula River system of southeastern Mississippi (Selman and Qualls 2009; Selman and Jones 2011). The species is found primarily in large rivers to medium-sized creeks within the Pascagoula River basin (Cliburn 1971; Selman and Qualls 2009), which is considered one of the least hydrologically impacted river systems in the contiguous United States (Dynesius and Nilsson 1994) and which is located within a global turtle biodiversity hot spot (Buhlmann et al. 2009). There is also considerable habitat variability within the Pascagoula River basin from the smaller, rocky, moderate-high gradient headwater streams to the larger, sluggish, low-gradient coastal rivers and bayous (Selman and Qualls 2009).

Graptemys flavimaculata home ranges are generally small (< 6 river km), with individuals sometimes using associated riverine wetlands including oxbow lakes and bayous (Jones 1996). Because individuals of this species occupy well-defined home ranges and there is considerable variation in biotic and abiotic factors within streams occupied, there may be associated phenotypic attributes (e.g., body size, shape morphology) that would be advantageous in a specific habitat type (Rivera 2008; Germano and Bury 2009). Studies of *G. flavimaculata* have shown that individuals from the Pascagoula River are significantly larger than those from upstream sites, with food availability or competition with a similar species as possible reasons for size differences (Lindeman 2000; Shelby and Mendonça 2001). Conversely, Jones and Hartfield (1995) found considerable variation in body size of *Graptemys oculifera* (Ringed Sawback) among sites within the Pearl River system, but little correlation of body size with location of site along the river continuum.

Many turtles also exhibit either male or female-biased sexual size dimorphism (SSD). Geographic variation of SSD is likely the result of selection for larger female body size for larger clutch size (Ralls 1976; Schoener et al. 1982), competitors (Schoener 1977), or niche partitioning (Schoener 1967, 1968). Within the family Emydidae, many species exhibit female-biased SSD, particularly within the genus *Graptemys*, which exhibits extreme SSD. *Graptemys* females sometimes attain up to twice the body length and 10 times the body mass of males (Ernst and Lovich 2009; Lovich et al. 2009), while some have enlarged heads/jaws for crushing mollusks (Lindeman 2000). Adult female *G. flavimaculata* from the Pascagoula River attain up to seven times the mass of adult males (Jones 1996; Selman and Jones 2011), while females also have larger heads relative to males.

Even though head width is larger in females, *G. flavimaculata* are still considered microcephalic in relation to other *Graptemys* species (Lindeman 2000). There are relatively few studies to date that compare turtle SSD or secondary sexual characteristics (i.e., male claw length, female head width) across a geographic gradient, with only a single study of this type in the genus *Graptemys* (Jones and Hartfield 1995). Due to the lack of comparative information on population parameters in *G. flavimaculata*, and *Graptemys* species in general, I wanted to determine if there was geographic variation in: (1) population structure (i.e., body size distribution and mean body size); (2) sexual size dimorphism in body size; male claw length or female head width; and (3) shape morphology.

Materials and Methods

Study sites.—I conducted field work in 2005 and 2006 at three sites within the Pascagoula River basin of southeastern Mississippi, USA (Fig. 1). Study sites included the Leaf River (Forrest County), Chickasawhay River (Greene County), and Pascagoula River (Jackson County). I sampled Leaf and Pascagoula River sites in 2008 for female head width comparisons. The three sample sites are found in distinct subregions within the Pascagoula River basin, with all sites being separated by > 140 river km (Pascagoula to Chickasawhay: 142.4 km; Pascagoula to Leaf: 220.4 km; Leaf to Chickasawhay: 164.6 km). Sample sites varied in size and habitat characteristics, but they were representative of most large to small riverine habitat types encountered within the range of *G. flavimaculata* (Table 1).

Sampling technique.—During April through October of 2005–2006, I sampled each of the three sites once per month for three to five days each month (only two sites sampled in 2008). I trapped turtles by attaching open topped basking traps (made of 1.9 cm [0.75 in] PVC coated crawfish wire; The Fish Net Company, Jonesville, Louisiana) below or beside known turtle basking structures. Traps varied in size from 56 × 46 × 31 cm to 122 × 61 × 25 cm and I affixed them to logs, branches, stumps, and tree crowns with nails/cotton twine. I used a maximum of 15 traps during a trap-day. During a typical trapping day, I checked traps every hour by rapidly approaching “trap logs” by motorized boat, which startled basking turtles into the traps. I also captured turtles opportunistically by hand/dip net at all sites.

Determining sex and measurements of captured turtles.—After capture, I determined sex when possible based on the assumptions that males were smaller, had longer foreclaws, taller carapacial spines, and longer tails compared to females (Selman and Jones 2011). I measured midline plastron length (PL), carapace height (CH; measurement on third vertebral scute not including the spine), carapace width (CW), and male claw length (MCL; longest foreclaw on either forelimb) to the nearest mm with tree calipers. I also measured body mass (g) for both males and females with a hanging scale. Additionally, I collected data from two sites in 2008 (Leaf and Pascagoula) for female head width (FHW), which was measured as the distance (mm) between the right and left lower jaw insertion point. I permanently marked turtles with holes made by an electric drill on marginal scutes (Cagle 1939), which allowed for future identification of captured individuals. I did not include recaptured individuals in the data analyses. Population specific growth patterns using

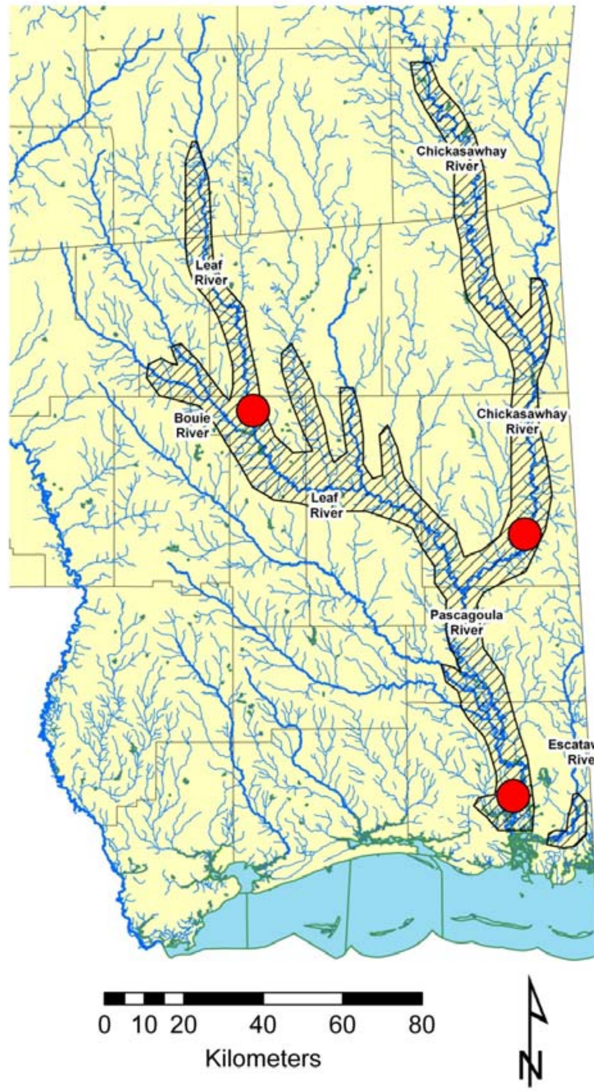

Figure 1. The Pascagoula River system of southeastern Mississippi with approximate range of *Graptemys flavimaculata* (crosshatched area; based on Selman and Qualls 2009). Localities of sample sites from 2005–2008 are indicted by red dots.

TABLE 1. Characteristics of sampling localities and turtle densities for *Graptemys flavimaculata* (2005–2006, 2008) within the Pascagoula River system. I collected discharge data from USGS Real-Time Water database from 1 April 2005 to 31 October 2008.

Site (Years Sampled)	River Width (m), Discharge Range (m^3/sec)	Dominant Riparian Tree Species	River Habitat Characteristics	Turtle Density† (per river km)
Chickasawhay* (2005, 2006)	30–90, 11–793	Black Willow (*Salix nigra*), Sycamore (*Platanus occidentalis*), Bald Cypress (*Taxodium distichum*), Loblolly Pine (*Pinus. taeda*), Water Oak (*Quercus nigra*)	Medium river with alternating sandbar & bendway sections; high snag density and small oxbow lakes	93
Leaf (2005, 2006, 2008)	20–50, 7– 623	Sycamore, Water Oak, Loblolly Pine, Red Maple (*Acer rubrum*), White Oak (*Quercus alba*)	Small-medium river with alternating gravel-sandbar & bendway sections; gravel runs between bendways and high snag density	80–120
Pascagoula (2005, 2006, 2008)	50–150, 34–2832	Bald Cypress, Water Oak, Spruce Pine (*Pinus glabra*), Chinese Tallow Tree (*Triadica sebifera*)	Large river with associated bayous, large oxbow lakes and cypress ponds; few sandbars present and high snag density	281–602

† Estimates of turtle density are derived from Selman and Qualls (2009).
*Chickasawhay site not sampled for FHW in 2008.

scute annuli were unreliable due to multiple growth rings for one year (i.e., the presence of "false annuli" [Shealy 1976]). Following marking and measuring of turtles, I released turtles at their point of capture.

Data analysis.—For population structure comparisons, I used one-factor ANOVAs to determine differences in plastron length and body mass by site, with sexes analyzed separately due to dramatic sexual dimorphism observed in this species (Selman and Jones 2011). For female body mass, I excluded gravid females, which I palpated (n = 7; six females from Pascagoula and one female from Chickasawhay), from the analysis to remove additional variation associated with clutch mass. If these analyses were significant, I used a Tukey-Kramer post hoc comparison to delineate differences among the sites. I also used a Chi-squared contingency table to determine if populations deviated from a 1:1 sex ratio at each sample site.

For morphological comparisons among the three sites, I used separate linear regressions for males and females for CH and CW by PL, which generated individual residual values. I used one-factor ANOVAs to compare CH and CW residual values among sites for males and females. By using residual values for both sexes, I could delineate body shape differences (streamlined shells [wide, shallow] vs. blocky shells [narrow, deep]), while correcting for differences in overall body size among sites. If significant differences were found, I used a Tukey-Kramer post hoc comparison to detect differences among the sites.

To determine differences in SSD among the three sites, I calculated the sexual dimorphism index (SDI; Lovich and Gibbons 1992) for each site by dividing the mean PL of females by the mean PL of males and then subtracting one. To determine differences in secondary sex characteristics, I used ANCOVAs for FHW (Leaf and Pascagoula sites only) and MCL (all three sites) with PL as the covariate, sample site as a factor, and a factor by covariate interaction term. For FHW and MCL analyses, I considered only individuals with discernable secondary sexual characteristics (females > 11.0 cm PL and males > 6.0 cm PL). I used JMP 8.0 (SAS Institute Inc., Cary, North Carolina, http://www.jmp.com) for all statistical analyses with significance levels of $P \leq 0.05$.

RESULTS

In 2005 and 2006, I captured 456 individuals at the three study sites: 221 individuals from the Pascagoula River site, 123 from the Leaf River site, and 112 from the Chickasawhay River site (Table 2). In 2008, I captured 42 females from the Pascagoula River site and 22 from the Leaf River site for FHW analysis.

Population structure.—For all sites, male and female PL approached normal distributions, but female PL was slightly skewed toward larger individuals at the Pascagoula and Leaf sites (Fig. 2). All sites lacked captures in the juvenile size classes with only nine

TABLE 2. Comparisons of male, female, and juvenile plastron lengths (PL; cm), body mass (g), female head width (FHW; cm), and male claw length (MCL, cm) among three sample sites for *Graptemys flavimaculata*. Significant differences among sampling sites for males/females are indicated by different letters. Site names are abbreviated: Chickasawhay (C), Leaf (L), and Pascagoula (P).

	Males			Females			Juveniles		
	C	L	P	C	L	P	C	L	P
PL									
n	58	78	132	49	42	88	5	3	1
Mean	7.7[c]	8.5[b]	9.0[a]	13.2[b]	14.1[b]	15.9[a]	4.5	4.9	-
Min	6.1	5.8	7.6	6.5	6.6	9.8	3.8	4.0	-
Max	9.3	10.9	11.8	17.0	16.8	18.9	5.3	6.6	6.5
SE	0.09	0.08	0.05	0.29	0.31	0.22	0.38	0.85	-
Mass									
n	58	78	132	48	42	82	5	3	1
Mean	88.5[c]	118.9[b]	145.5[a]	505.6[b]	591.5[b]	900.3[a]	23.0	30	-
Min	45	25	80	60	60	175	10	15	-
Max	210	250	220	1050	950	1550	30	50	55
SE	3.4	3.2	2.4	31.8	32.3	35.2	4.4	10.4	-
FHW									
n				-	22	42			
Mean				-	1.78[b]	2.00[a]			
MCL									
n	54	78	132						
Mean	0.98[a]	1.14[a]	1.15[a]						

small turtles of undetermined sex at all sites (Table 2). The Leaf (χ^2 = 11.5, df = 1, P < 0.001) and Pascagoula (χ^2 = 8.9, df = 1, P = 0.003) sites deviated significantly from a 1:1 sex ratio, while the Chickasawhay site (χ^2 = 0.76, df = 1, P = 0.380) did not deviate from a 1:1 sex ratio.

There was significant variation in *G. flavimaculata* PL for both males ($F_{2,268}$ = 88.6, P < 0.001) and females ($F_{2,179}$ = 30.2, P < 0.001). Pascagoula males were larger than both Leaf and Chickasawhay males, and Leaf males were larger than Chickasawhay males (Table 2). Maximum PL for a Pascagoula male (11.8 cm) was 8% greater than the largest Leaf male (10.9 cm) and 27% greater than the largest Chickasawhay male (9.3 cm; Fig. 2). Pascagoula females were significantly larger than Leaf or Chickasawhay females, but Leaf females were not different from Chickasawhay females (Table 2). In a similar pattern to males, maximum PL for a Pascagoula female (18.9 cm) was 12% longer than the largest Leaf female (16.8 cm) and 11% longer than the largest Chickasawhay female (17.0 cm; Fig. 2).

There was also a significant difference in body mass among study sites for both males ($F_{2,268}$ = 87.9, P < 0.001) and females ($F_{2,179}$ = 41.9, P < 0.001). Pascagoula males were significantly heavier than both Leaf and Chickasawhay males, while Leaf males were heavier than Chickasawhay males (Table 2). Maximum

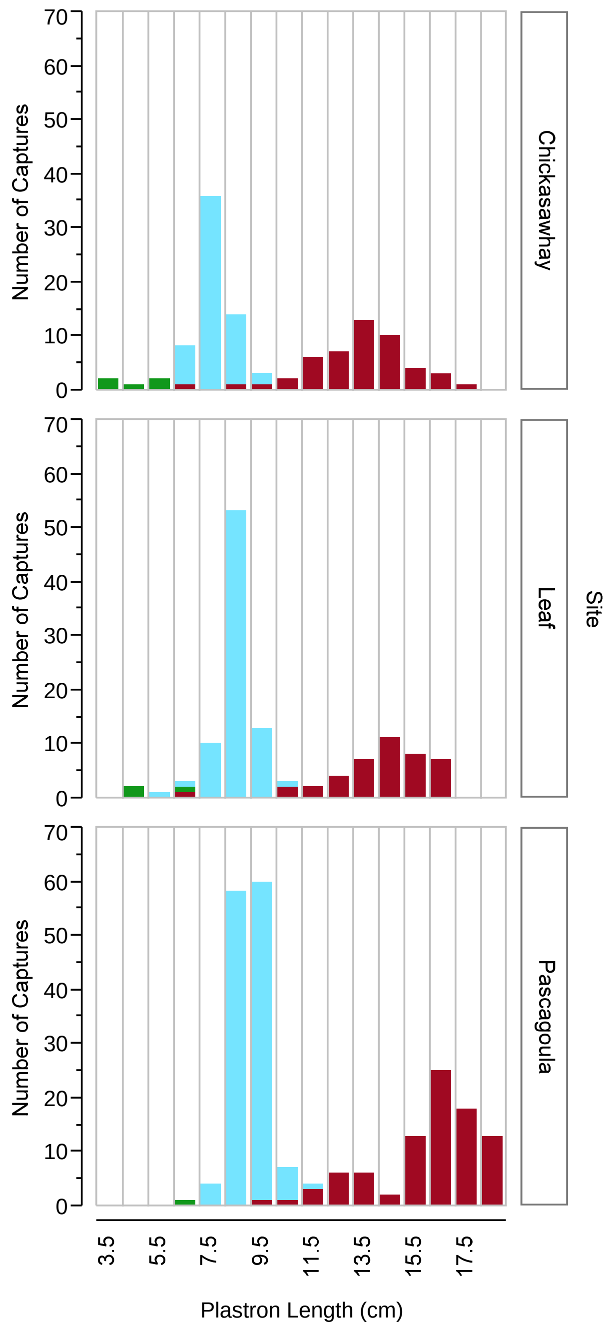

FIGURE 2. Number of captures for different size classes of *Graptemys flavimaculata* at the three sample sites. Unknown sex juveniles are in green, males in light blue, and females in dark red. For plastron length size classes, all individuals captured in a particular size class (e.g., 7.5 range) have plastron lengths beginning with that whole number (e.g., 7.0 and 7.9).

male mass was similar across sites (Pascagoula = 220 g; Leaf = 250 g; Chickasawhay = 210 g). Pascagoula females were significantly heavier than Leaf or Chickasawhay females, with no significant difference among Leaf and Chickasawhay females (Table 2). The largest Pascagoula female (1550 g) was 63% heavier than the largest Leaf female (950 g) and 48% heavier than the largest Chickasawhay female (1050 g).

Sexual size dimorphism and secondary sex characteristics.—Sexual size dimorphism was pronounced for *G. flavimaculata* at all sites, with females attaining mean plastron lengths greater than males. Sexual dimorphism index values varied among the three sites, with values of 0.66 for the Leaf site, 0.73 for the Chickasawhay site, and 0.76 for the Pascagoula site.

Female HW was significantly and positively correlated to PL ($F_{1,63}$ = 100.9, $P < 0.001$) and there was a significant difference in female HW by site ($F_{1,63}$ = 8.87, P = 0.004; Fig. 3). Pascagoula females had significantly wider heads relative to body length than Leaf females. The interaction term was not significant ($F_{1,63}$ = 3.08, P = 0.08). Male claw length was significantly and positively correlated to PL ($F_{1,258}$ = 67.72, $P < 0.001$), but there was no significant difference in MCL among sites ($F_{2,258}$ = 0.48, P = 0.62; Table 2) or a significant interaction term ($F_{2,258}$ = 2.50, P = 0.08).

Shape morphology.—For males, there was no significant difference for CH:PL across the three sites ($F_{2,264}$ = 1.22, P = 0.29), while CW:PL was significantly different across sites for males ($F_{2,265}$ = 6.40, P = 0.002). Pascagoula males were significantly wider than Leaf males but not Chickasawhay males. There was no difference between Chickasawhay or Leaf males. For females, there were similar results for CH and CW relative to PL. Carapace height and CW were significantly different by site (CH: $F_{2,179}$ = 4.01, P = 0.02; CW: $F_{2,179}$ = 4.00, P = 0.02). Pascagoula females had significantly deeper and wider shells than Leaf females but not Chickasawhay females. There was no difference between Chickasawhay or Leaf females.

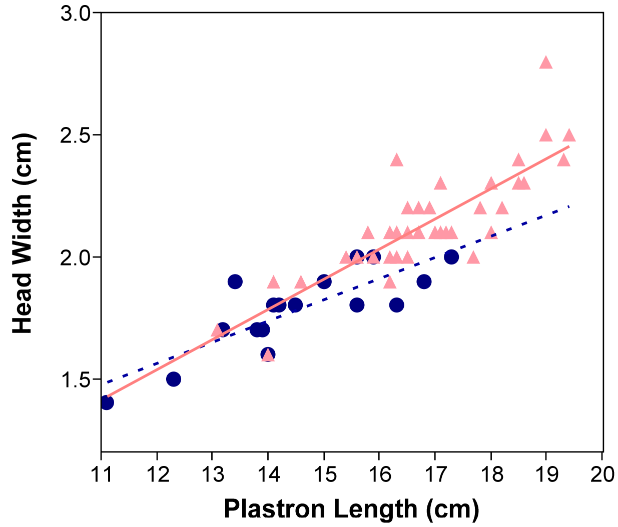

FIGURE 3. Regression of *Graptemys flavimaculata* female head width on plastron length for Leaf (dashed blue line and blue dots) and Pascagoula river females (solid pink line and pink triangles).

DISCUSSION

Population structure.—I did not capture many juveniles, which is not uncommon in *Graptemys* demographic studies (Gordon and MacCulloch 1980; Lahanas 1982; Jones and Hartfield 1995). Undersampling of juvenile turtles in this study was likely due to their cryptic nature, trapping methods used, and different basking behavior/basking locations of juveniles relative to adults (Selman and Qualls 2011). Body sizes of both sexes were different among sites, with both male and female Pascagoula turtles being larger, both in length and mass, than either Leaf or Chickasawhay turtles. There are multiple plausible and equally supported reasons that could contribute to Pascagoula turtles generally being larger than upstream turtles including: (1) dietary differences; (2) absence of competition from a sympatric *Graptemys* species; (3) a more stable thermal environment; and (4) presence of American Alligators (*Alligator mississippiensis*). First, due to the proximity of the Pascagoula River site to the Gulf of Mexico, some prey items were present in Pascagoula River turtle diets (e.g., *Mytilopsis leucophaeta*, a brackish mollusk) and absent from upstream individuals (Seigel and Brauman, unpubl. report; Lindeman and Selman unpubl. data). It is unknown if these prey differences relate to increased growth rates, but Avery et al. (1993) found that different diets, particularly as it relates to protein, greatly increased or decreased juvenile turtle growth rates. Second, *G. gibbonsi*, a mollusk specialist (Ennen et al. 2007; Lovich et al. 2009), is virtually absent from the Pascagoula River site, but occurs in much higher densities at the two upstream sites (Selman and Qualls 2009). Jones and Hartfield (unpubl. report) found a similar pattern in *G. oculifera*, with the smallest and largest mean PL in areas with the highest and lowest density of *G. gibbonsi* (now *Graptemys pearlensis*; Ennen et al. 2010b), respectively. Vogt (1981) found some level of dietary overlap in three Wisconsin *Graptemys* species and suggested that this overlap may influence female head widths. It is unknown whether there is any prey item/niche overlap between *G. flavimaculata* and *G. gibbonsi*, or whether competition can influence body size evolution in these turtles. Thirdly, the Pascagoula River system contains a larger volume of water relative to the two upstream sites, thus providing a more stable thermal environment for turtles (Fig. 4). Several studies have indicated that

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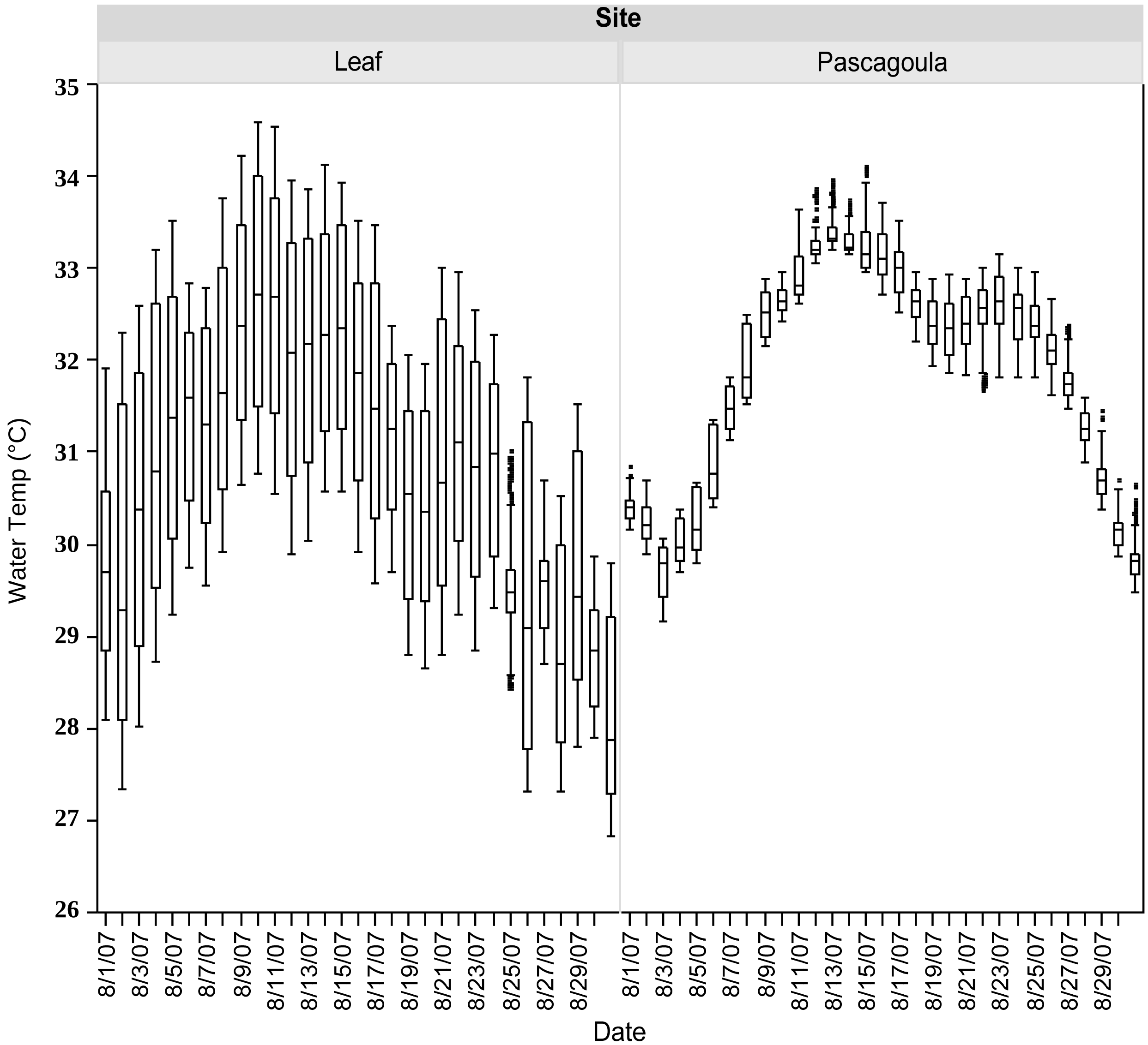

FIGURE 4. Daily water temperatures (°C) at the Leaf and Pascagoula River sites for August 2007 including the median daily temperature (horizontal line in box plot), upper and lower quartiles (upper and lower lines of box), and daily temperature range (vertical bars/outlier dots above and below box). Temperature data were collected at these two sites for a related study on turtle basking ecology and methods for temperature collection can be found in Selman and Qualls (2011).

a more stable thermal environment may provide longer periods of warm water temperatures, especially for rapidly growing juvenile turtles and ultimately, larger individuals at maturity (Gibbons 1970; Gibbons et al. 1979; Gibbons and Harrison 1981; King et al. 1998). Lastly, several authors have suggested that larger body sizes may be selected for in areas with high densities of predatory crocodilians (Gibbons 1990; Gibbons and Lovich 1990; Aresco and Dobie 2000). Turtles are a common and important food source for American Alligators (Delany and Abercrombie 1986; Taylor 1986; Barr 1997; Rice 2004). Even though there are no documented reports of alligators preying upon *G. flavimaculata*, there are records for other *Graptemys* species including *G. barbouri* (Neill 1971) and likely *G. oculifera* (Wolfe et al. 1987; reported as *Graptemys* sp.). Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP; unpubl. report) found that alligator population estimates were eight-fold greater in Jackson County relative to Greene County (Chickasawhay River site) or Forrest County (Leaf River site).

Sexual size dimorphism and secondary sex characteristics.—The SDI results for *G. flavimaculata* indicate that there are small differences in female-biased SSD (0.66 to 0.76) among the three sample sites. Jones and Hartfield (1995) found comparative SDIs (0.71 to 0.78) in *G. oculifera*, which has a similar life history, similar riverine habitat, and is a close phylogenetic relative of *G. flavimaculata* (Wiens et al. 2010; Ennen et al. 2010a). Other studies comparing SSD with turtles have found differences over similar small geographic scales (Gibbons and Lovich 1990), as well as larger geographic scales (Iverson 1985; Lovich et al. 1998; Lovich et al. 2010).

Differences among sites in FHW relative to PL indicate that females achieve greater head widths for their size at the Pascagoula River site compared to the upstream site. This is not unexpected as female *G. flavimaculata* from the lower Pascagoula River have been found to have the highest incidence of molluscivory in the genus (Seigel and Brauman, unpubl. report as cited by Lindeman 2000). However, *G. flavimaculata* is considered a microcephalic *Graptemys* species, with both sexes having considerably narrower heads relative to megacephalic mollusk specialists like *G. gibbonsi* (Lindeman 2000). Along with delineating species-level differences, Lindeman (2000) also found populations of the same species to have significantly different head widths across sampling localities in different states/drainages, specifically within the large ranging species of *G. geographica* (Common Map Turtle), *G. ouachitensis* (Ouachita Map Turtle), *G. p. kohnii* (Mississippi Map Turtle), and *G. p. pseudogeographica* (False Map Turtle). This is the first study to document such geographic differences in FHW from a drainage endemic *Graptemys* species over such small geographic scales. Further research is needed to understand the mechanisms that underlie the head width trait and the regional differences observed in this study. Using comparative dietary analysis relative to turtle community composition (e.g., density of *G. flavimaculata* vs. density of *G. gibbonsi*) may elucidate the driving forces underlying this trait.

Within some *Graptemys* species, male claw length is an important secondary sex characteristic, with the males using claw displays during courtship (Ernst and Lovich 2009). In this study, larger males had longer foreclaws, potentially acting as a male ornament; such differences in ornaments may reflect differences in mate quality (Berglund et al. 1996). If so, claw length may confer a sexual selective advantage because female choice is believed to be the reproductive selective force in this species (Berry and Shine 1980).

Shape morphology.—For three of the four shape comparisons for both sexes (except male CH), Pascagoula turtles were deeper and wider than Leaf turtles, and Chickasawhay turtles were intermediate. Two factors likely determine *G. flavimaculata* shape morphology, specifically, the abundance of alligators at the Pascagoula River site and differing river flow conditions. First, gape limitations of alligators could be a significant selection pressure on turtle shell architecture (Aresco and Dobie 2000; Lovich et al. 2010). Shell architecture of females in this study (i.e., domed vs. streamlined) correlates well to the relative density of alligators found by MDWFP (unpubl. report). The Pascagoula River site had the highest alligator density, while turtles there had the most “domed” architecture. In comparison, the two upstream sites had lower alligator densities and turtles were more streamlined. However, this hypothesis does not completely explain this trait or explain why small turtle sizes and streamlined turtles would be advantageous in the absence of alligators. It is likely that river flow also plays an important role in shape morphology. In areas with well-defined channels and few backwater areas (Leaf and Chickasawhay sites), river flows fluctuate quite rapidly, whereas downstream areas (Pascagoula site) have larger channels and backwater areas, which moderate flow conditions. Because *G. flavimaculata* inhabit well-defined home ranges (Jones 1996), individuals must maintain connections to home ranges even during high flow events (Selman and Qualls 2008). A smaller and more streamlined shape is better suited in upstream sites to decrease drag, minimize energy expenditures related to swimming, and keep their position in the stream channel. At the Pascagoula River site, a more streamlined shell may not be advantageous as individuals are not subject to high, in-channel river flows and can move about in the flooded riparian forests (Jones 1996). Similar to this study, Rivera (2008) found that *Pseudemys concinna* (River Cooter) from lotic environments had a more streamlined shape compared to lentic sites, with lentic shapes being absent in lotic environments. Lotic shapes also led to a twofold decrease in drag at a flow velocity of 1.0 m/s. Lubcke and Wilson (2007) also found differences in shape of *Actinemys marmorata* (Western Pond Turtle) in the absence of a significant predator and attributed differences to flow conditions.

Conclusions.—As previously documented by many authors, including but not limited to Gibbons and Lovich (1990), Germano and Bury (2009), and Bury et al. (2010), multiple sites are needed to understand geographic variation and patterns in growth, population structure, and sexual size dimorphism within a turtle species. This study indicates that there are many geographic differences, sometimes dramatic, in the population structure, body size, shape, and sexual size dimorphism in the small range of *G. flavimaculata.* Many of these parameters are likely influenced by interacting biotic and abiotic factors (e.g., diet, competition, predation, river flow rates, and thermal environment) across their range.

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Will Selman is currently a Research Wildlife Biologist and Research Coordinator at Rockefeller Wildlife Refuge with the Louisiana Department of Wildlife and Fisheries. He received his Bachelor's degree in Biology from Millsaps College (2003) and thereafter completed his doctoral degree from the University of Southern Mississippi (2010). His dissertation focused on the conservation and ecology of the Yellow-blotched Sawback. Recent and current work at Rockefeller has centered on a broad range of conservation biology and applied wildlife conservation projects including translocation of rehabilitated Brown Pelicans (*Pelicanus occidentalis*) from the Gulf Horizon Oil Spill; life history, distribution, and abundance of Louisiana Diamondback Terrapins (*Malaclemys terrapin*); riverine turtle status in southwestern Louisiana; Whooping Crane (*Grus americana*) reintroduction to southwestern Louisiana; and impacts of oilfield exploration and disturbance on grassland bird diversity/abundance. (Photographed by Christine Selman)