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Habitat-Related Variation in Body Size and Reproductive Output and an Examination of Reproductive Allometry in the Sabine Map Turtle (*Graptemys sabinensis*) across Three River Drainages

Amy K. Fehrenbach¹, Irvin Louque², Stacy L. McFadden¹, Cybil Huntzinger², Eddie Lyons², Stephen H. Shively³, Will Selman⁴, and Peter V. Lindeman¹

The Sabine Map Turtle (*Graptemys sabinensis*) inhabits the Sabine-Neches, Calcasieu, and Mermentau river drainages of southwestern Louisiana and east Texas. Sparse data in the literature mark it as having among the smallest body sizes and smallest clutch sizes among the 14 species of the genus *Graptemys*. All available data on life history originate from the upper Sabine and upper Calcasieu drainages, which are relatively high-gradient rivers with fast currents and numerous sandbars. Downstream segments of these drainages and the entire Mermentau drainage have almost no gradient, with little perceptible current and no sandbars. We sampled *G. sabinensis* from the Mermentau River and upper and lower portions of both the Sabine and Calcasieu drainages. We collected data on body size and radiographed gravid females in the lower Calcasieu and Mermentau drainages to examine clutch size and egg width and compared our data to literature records and measurements of museum specimens. Both males (to 104 mm in midline plastron length) and females (to 202 mm) were considerably larger in the Mermentau and lower reaches of the Sabine and Calcasieu drainages than in the upper Sabine and upper Calcasieu drainages (to 92 mm and 176 mm, respectively). Clutch sizes were also significantly larger in the Mermentau and lower Calcasieu (mean 5.3 eggs, range 3–7) compared to previously reported clutch sizes for the upper Sabine and upper Calcasieu drainages (mean 2.3 eggs, range 1–4). Comparison with recent findings for other species of *Graptemys* indicates that it is typical for populations in faster-current habitats to be smaller in body size, although no previous report has shown the magnitude of differences exhibited by *G. sabinensis* in the present study. Examination of the allometry of reproductive output complemented previous studies of *Graptemys* in that both egg width and clutch size were hypoallometrically related to female body size, consistent with the hypothesis of anatomical constraints on egg width. The difference between egg width and pelvic aperture width grew larger as females increased in size, suggesting that anatomical constraints may have applied only to smaller females, leaving egg-size optimization possible in larger females. We could not determine the reason for a significant difference in egg width between the Mermentau and lower Calcasieu after correction for female body size, as pelvic aperture width did not vary between the drainages; however, other potential anatomical constraints on egg width were not measured.

GRAPTEMYS *sabinensis* is a narrow-headed species of *Graptemys* (“microcephalic,” *sensu* Lindeman, 2000, 2013) that feeds on aquatic vegetation and insects (Shively and Jackson, 1985). *Graptemys sabinensis* was described by Cagle (1953a) and inhabits the Sabine-Neches, Calcasieu, and Mermentau river systems in southwestern Louisiana and east Texas. Although it was known as a subspecies, first of the False Map Turtle (*G. pseudogeographica*; see Cagle, 1953a) and then of the Ouachita Map Turtle (*G. ouachitensis*; see Vogt, 1993), some recent authors have regarded it as a separate species due to its allopatric distribution and diagnosability relative to those two species (e.g., Buhlmann et al., 2008; reviewed in Lindeman, 2013).

Few studies have been conducted on the ecology of *G. sabinensis*. Since Cagle’s (1953a) report of specimens he and his students collected from the Sabine and Calcasieu rivers and specimens taken from the Mermentau River in the 1890s, the only field studies of the species prior to ours have concerned habitat use and diet in Whisky Chitto Creek, a tributary of the Calcasieu (Shively and Jackson, 1985); basking surveys of abundance in Louisiana (Shively, 2001); reproduction in the middle reaches of the Sabine and the upper reaches of the Calcasieu (Ewert et al., 2004); and

basking ecology on the upper Sabine in Texas (Coleman and Gutberlet, 2008).

Across the three river systems in which *G. sabinensis* is found, there are two very distinct habitats. All field studies of *G. sabinensis* prior to the present study and all reports of body size, except two Mermentau specimens that Cagle (1953a) noted, have concerned populations in the upper Sabine and upper Calcasieu rivers. Both are fast-flowing, sinuous rivers with abundant sandbars. These habitats are very different from the lower Sabine, lower Calcasieu, and Mermentau river drainages, which have almost no gradient and are wide, sluggish, and devoid of sandbars.

Cagle (1953a) gave ranges of maximum plastron length for adult males (64–95 mm; mean 74.5) and adult females (126–140 mm; no mean reported) from his large type series from the Sabine River, while also noting larger size for two female specimens from the Mermentau River (164 and 168 mm). Subsequent statements in the literature about body size in *G. sabinensis* have emphasized its small size relative to congeners. Vogt (1993) stated that carapace length (typically 5–10% longer than plastron length in *Graptemys*; P. Lindeman, unpubl. data) reaches 80 mm in males and 120 mm in females; he later revised those figures to 106 and 155 mm, respectively (Vogt, 1995), still small for the genus. A

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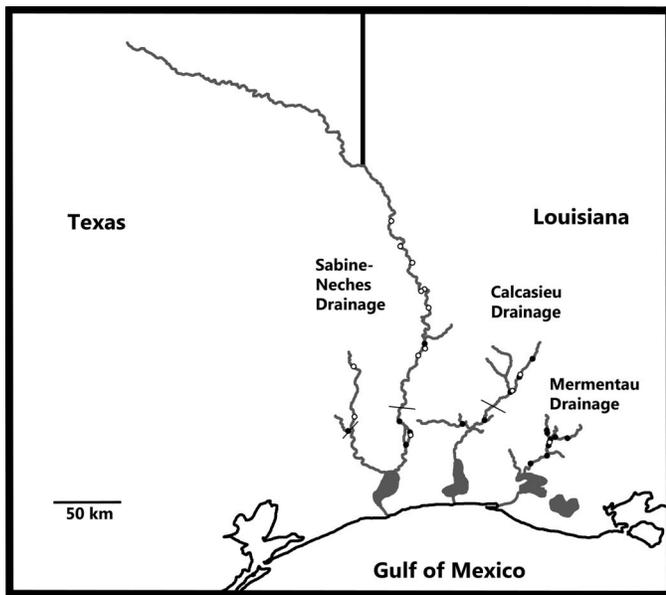


Fig. 1. Map of the Sabine-Neches, Calcasieu, and Mermentau river drainages in eastern Texas and southwestern Louisiana showing sites of sample collections of *Graptemys sabinensis* made in the present study (filled symbols) and earlier sampling (open symbols; Shively, 1982; Lindeman, 2000, 2008; P. Lindeman, unpubl.). Thin lines separate upper drainages in the Sabine-Neches and Calcasieu drainages, where there are abundant sandbars and moderate flow due to gradients in elevation, from sluggish lower drainages that are near sea level and lack sandbars. Drainages are drawn to the upstream extent of known habitation by *G. sabinensis* (Lindeman, 2013; Ilgen et al., 2014; Louque, 2014).

specimen from the upper Sabine River that measured 116 mm maximum plastron length was noted to be the smallest gravid female *Graptemys* on record (Lindeman, 2005). Measurements of midline plastron lengths of museum specimens ranged to 92 mm for males and 176 mm for females and were among the smallest for the genus for both maxima and mean values (Lindeman, 2000, 2008). Clutch sizes ranged from 1–4 eggs per clutch with a mode of two eggs (Ewert et al., 2004), by far the smallest clutches of any of the 14 species of *Graptemys* (reviewed in Lindeman, 2013).

Small body size poses interesting questions about the life history of *G. sabinensis*. Organisms divide their available energy among various aspects of their life histories. Extra energy allocated toward reproduction will be used to either increase the number of offspring or increase offspring size. Optimal offspring-size theory predicts that as females grow larger, they produce more eggs of an optimum size rather than producing larger eggs (Smith and Fretwell, 1974; Brockelman, 1975).

Many reptile species display a positive correlation between female body size and clutch size but no correlation of egg size with female body size, which is expected under optimal egg-size models (Congdon and Gibbons, 1987). However, many turtle species also show a correlation between egg size and female body size (Congdon and Gibbons, 1983; Lindeman, 2005; Ryan and Lindeman, 2007). This phenomenon can be explained by the anatomical-constraints hypothesis, under which smaller females are physically unable to lay eggs of the optimum size because of the restricted size of the caudal gap of the shell and the pelvic aperture (Tucker et al., 1978; Congdon and Gibbons, 1987). In such cases, the relationship between egg size and maternal body size is typically

hypoallometric: because both clutch size and egg size increase simultaneously, neither is able to increase isometrically with body size. Positive hypoallometric relationships of both clutch size and egg width with female body size have been reported in two species of *Graptemys* and two other emydid turtles (Lindeman, 2005; Ryan and Lindeman, 2007), a batagurid turtle (Naimi et al., 2012), and a kinosternid turtle (MacÍp-Rios et al., 2012).

Because previous studies of the species have been restricted to faster-flowing upper reaches, while slow-flowing, lower reaches present such a difference in habitat, we investigated whether *G. sabinensis* is truly a small species with small egg clutches range-wide or whether body and clutch size depend on the habitat in which they are found. We also investigated the reproductive allometry of the species to determine whether *G. sabinensis* has positive correlations of both clutch size and egg size with maternal body size and to examine the allometry of these relationships. If *G. sabinensis* has an optimized egg size, no correlation between egg size and female body size should be evident, and an isometric relationship between clutch size and plastron length would be expected. If *G. sabinensis* is influenced by anatomical constraints, energy would be distributed between increasing both egg size and clutch size so that each increases only hypoallometrically with female body size.

MATERIALS AND METHODS

The Sabine-Neches (hereafter simply Sabine) and Calcasieu drainages have an elevational and flow-rate dichotomy not evident in the Mermentau drainage. Lower reaches of the Sabine and Calcasieu drainages, as well as the entire Mermentau drainage, are extremely low-gradient streams with little detectable current and a lack of large open sandbars on inner bends. Upper reaches of the Sabine and the Calcasieu have higher gradients that result in greater flow rates that act to maintain prominent sandbars on inner bends of the rivers. Sandbar-dominated upper reaches of the Neches River that are inhabited by *G. sabinensis* (see dot-distribution map in Lindeman, 2013) total ca. 93 mainstem river kilometers (rkm) plus 30 rkm in a tributary, Village Creek, with river elevations at the upstream range limit in the Neches reaching 22 m above sea level (asl). Sandbar-dominated upper reaches of the Sabine River inhabited by *G. sabinensis* total ca. 700 mainstem rkm plus 42 rkm of a tributary, Anacoco Bayou, with river elevations at the upstream range limit in the Sabine reaching 122 m asl. A total of ca. 200 rkm are inhabited by *G. sabinensis* in the sandbar-dominated reaches of the upper Calcasieu River and its major tributaries, Whisky Chitto Creek and Bundick Creek, where river elevations reach as high as 32 m asl.

The character of the rivers changes at ca. 4 m asl in the Neches, 9 m asl in the Sabine, and 3 m asl in the Calcasieu (as determined from GoogleEarth; Fig. 1). Below these points, the Neches River includes ca. 70 rkm, in which the distribution of *G. sabinensis* is poorly known based on museum specimens and was not further investigated in the present study; the Sabine River includes ca. 70 mainstem rkm and 18 rkm in the East Sabine River that we found to be inhabited by *G. sabinensis*; and the Calcasieu drainage includes ca. 47 rkm on the mainstem Calcasieu that we found to be inhabited by *G. sabinensis*, as well as portions of the West Fork/Houston River and smaller tributaries that we found to be inhabited, including the Little River and Indian, English, and Serpent bayous, with a combined total of ca. 55

rkm. All portions of the Mermentau River and its major tributaries that are inhabited by *G. sabinensis* (ca. 140 rkm; Ilgen et al., 2014) are situated at <1 m asl.

In 2011–2013 and 2015, we used fykenets, hoop nets baited with fish, and basking traps to capture *G. sabinensis* at various locations on the three drainages (Fig. 1). Turtles were permanently and individually marked by a series of notches or drilled holes in the marginal scutes of the carapace (Cagle, 1939), and data from recaptures are not included in the present study. We measured midline plastron length (PL) using a flexible ruler and body mass (BM) using Pesola spring scales. Additional data on midline PL were obtained via measurements of museum specimens (Lindeman, 2000, 2008; P. Lindeman, unpubl. data) and two field-captured specimens (P. Lindeman, unpubl. data from 2001) as well as measurements reported by Shively (1982). For turtles captured by AKF, SLM, and PVL, numbers of growth annuli on the pectoral scutes of the plastron (Zug, 1991) were recorded when discernible.

Females were palpated for eggs. In 2012, gravid females from the Mermentau and lower Calcasieu drainages captured by AKF, SLM, and PVL were transported to a veterinary clinic to obtain digital radiographic images of their clutches and then released at their capture sites. Data were collected for clutch size (CS), mean and maximum egg width in each clutch (EW_{mean} and EW_{max}), and pelvic aperture width (PAW), with corrections made for shrinkage or enlargement using the coin technique of Graham and Petokas (1989). Additional data on clutch size from the upper Calcasieu and Sabine drainages were obtained from Ewert et al. (2004), whose data were from nests they discovered on sandbars and thus lack corresponding female measurements of PL.

Body-size distributions were compiled for males and females for each of five drainages or drainage segments: upper and lower Sabine, upper and lower Calcasieu, and Mermentau, with the dividing points for the first two being the transition from higher-gradient to low-gradient reaches described above and marked in Figure 1. We characterized sexual size dimorphism in both PL and BM within each drainage segment using the sexual dimorphism index (Gibbons and Lovich, 1990, as modified by Lovich and Gibbons, 1992), which gives the percent by which one sex is larger than the other on average. We used the same index to characterize differences in body size between turtles from upper and lower segments of the Sabine and Calcasieu drainages.

We logarithmically transformed our data in order to examine allometry vs. isometry in reproductive output. Using logarithmically transformed data creates linear relationships, permits comparison among populations and species, and allows analysis of slopes expected under the assumption of isometric increase of variables (King, 2000).

Log-transformed data were analyzed in S+, with all null hypotheses evaluated at $\alpha = 0.05$. The relationships of CS, EW_{mean} , and EW_{max} to female PL were analyzed by linear regression. In regression of a three-dimensional variable such as CS on a linear variable such as PL, a slope of 3 is expected, assuming isometric rates of increase in the two variables. An isometric slope of 1 is expected for the relationship of linear values (EW_{mean} , EW_{max} , or PAW with PL). A slope with a 95% confidence interval (CI) below the anticipated isometric slope value indicates a significantly hypoallometric relationship, a slope with a 95% CI including the anticipated value is considered isometric, and a slope with a 95% CI greater than the anticipated value indicates a significantly hyperallomet-

ric relationship. We also used analysis of covariance (ANCOVA) to compare EW_{mean} , EW_{max} , and PAW of lower Calcasieu and Mermentau females, with correction for the covariate, PL.

RESULTS

We captured 19 *G. sabinensis* of identifiable sex from the upper Sabine and 90 from the lower Sabine, 13 from the upper Calcasieu and 176 from the lower Calcasieu, and 253 from the Mermentau. Supplemental data sources increased the total sample sizes of sexed individuals to 72 for the upper Sabine and 92 for the lower Sabine, 49 for the upper Calcasieu, and 256 for the Mermentau; no additional data were available for the lower Calcasieu (Fig. 1; Table 1).

Wide, sluggish, low-elevation river reaches had larger *G. sabinensis* (Table 1, Fig. 2). Males from low, sluggish reaches ranged from 78–102 mm in PL in the Mermentau drainage, from 75–98 mm in the lower Calcasieu drainage, and from 69–104 mm in the lower Sabine drainage. By contrast, males ranged from 65–79 mm in the upper Calcasieu drainage and from 63–92 mm in the upper Sabine drainage.

Females from lower reaches ranged from 80–190 mm in PL in the Mermentau drainage, from 75–189 mm in the lower Calcasieu drainage, and from 70–202 mm in the lower Sabine drainage. By contrast, females ranged from 90–127 mm in the upper Calcasieu drainage and from 66–176 mm in the upper Sabine. The 176 mm female from the upper Sabine was collected from Forest Lake, a floodplain lake of the upper Neches River. The two next largest females from the upper Sabine were 131 and 155 mm PL. The larger of these two specimens was captured in 2001 at a site just 15 rkm upstream of the Neches River transition point from sandbar-dominated, faster-flowing reaches to sluggish, low-gradient reaches, which is considerably closer to the downstream reaches than any other specimen locality from the upper Sabine drainage. Thus, 131 mm may be more representative of the typical upper limit on female PL in the upper Sabine drainage (see Discussion).

Adult male PL differed significantly among drainage segments ($F_{4,294} = 107.5$, $P < 0.0001$). *Post hoc* Tukey's tests revealed that smaller males from the upper Sabine and upper Calcasieu were similar in size and significantly smaller than males from the lower Sabine and Mermentau, which also were similar in size; lower Calcasieu males were intermediate in size but much closer to the latter two groups in size (Table 1). Adult female PL also differed significantly among drainage segments ($F_{4,224} = 52.2$, $P < 0.0001$). *Post hoc* Tukey's tests revealed that smaller females from the upper Sabine and upper Calcasieu were similar in size and significantly smaller than females from the lower Sabine, lower Calcasieu, and Mermentau, which all were similar in size (Table 1). Combining samples, turtles from sluggish, low-elevation reaches of the drainages were on average 24% longer (males) and 30% longer (females) than turtles from higher-flow, sandbar-dominated upper reaches (Fig. 2).

There was similar variation in BM among drainage segments. Male BM differed significantly ($F_{4,247} = 21.2$, $P < 0.0001$), with *post hoc* Tukey's tests revealing that upper Sabine and upper Calcasieu males were similar in size but significantly smaller than males of other drainage segments and that lower Sabine and Mermentau males were also similar in size; lower Calcasieu males were intermediate but much closer to the latter two groups in size (Table 2). Adult female BM also differed significantly ($F_{4,208} = 22.3$, $P <$

Table 1. Plastron lengths (PL) of *Graptemys sabinensis* from sections of three river drainages, with samples derived from present and past field studies and museum specimens as indicated. For females, the two entries are for all females, including juvenile females as large as the smallest male, and for adult females, i.e., those as large as the smallest known gravid female for the drainage section. Entries in columns marked with the same letter do not differ. Also given are sexual dimorphism indices, based on body sizes of mature animals.

Drainage	Males										Females									
	Sample sizes					Mean					Sample sizes					Mean				
	Present study	Museum specimens ^a	Field specimens ^b	Shively (1982)	Total n	PL±SE (mm) (range)	Present study	Museum specimens ^a	Field specimens ^b	Shively (1982)	Total n	PL±SE (mm) (range)	Present study	Museum specimens ^a	Field specimens ^b	Shively (1982)	Total n	PL±SE (mm) (range)	Sexual dimorphism index	
Upper Sabine	4	30	—	—	34	73.9±1.20 (63–92) A	15	22	1	—	38	104.8±3.90 (66–176)	—	—	—	—	38	104.8±3.90 (66–176)	0.72	
Lower Sabine	40	—	—	—	40	92.0±1.40 (69–104) C	50	2	—	—	52	127.3±4.13 (111–176) A	—	—	—	—	52	127.3±4.13 (111–176) A	0.80	
Upper Calcasieu	6	6	1	10	23	72.0±0.93 (65–79) A	7	2	—	17	26	165.8±2.23 (155–202) B	—	—	—	—	26	165.8±2.23 (155–202) B	0.68	
Lower Calcasieu	63	—	—	—	63	87.7±0.59 (75–98) B	113	—	—	—	10	121.2±1.17 (116–127) A	—	—	—	—	113	150.5±2.53 (75–189) B	0.89	
Mermentau	139	—	—	—	139	91.3±0.43 (78–102) C	114	3	—	—	117	155.0±2.39 (80–190) B	—	—	—	—	117	155.0±2.39 (80–190) B	0.81	

^aLindeman (2000, 2008, unpubl.); based on sampling specimens in the Auburn University Museum, Carnegie Museum of Natural History, Texas Cooperative Wildlife Collection, Texas Natural Heritage Collection, and Tulane University.
^bP. Lindeman, unpubl. data from 2001.

0.0001), with *post hoc* Tukey's tests revealing that upper Sabine and upper Calcasieu females were similar in size and significantly smaller than lower Sabine, lower Calcasieu, and Mermentau females, which all were similar in size (Table 2). Combining samples, turtles from low-elevation reaches of the drainages were on average 79% heavier (males) and 142% heavier (females) than turtles from upper reaches.

Sexual size dimorphism was slightly reduced for smaller-bodied turtles from upper reaches of rivers than for larger-bodied turtles from lower reaches. Adult females were 72% and 68% longer in PL than adult males in the upper Sabine and upper Calcasieu drainages, respectively, compared to figures of 80%, 89%, and 81% for the lower Sabine, lower Calcasieu, and Mermentau drainages, respectively (Table 1). Similarly, adult females were 394% and 436% heavier than adult males in the upper Sabine and upper Calcasieu drainages, respectively, compared to figures of 601%, 608%, and 559% for the lower Sabine, lower Calcasieu, and Mermentau drainages, respectively (Table 2).

Gravid females captured in the lower Calcasieu and Mermentau rivers had clutch sizes ranging from 3–7 eggs per clutch (means 5.2 and 5.4, respectively), whereas clutch sizes previously reported by Ewert et al. (2004) were smaller in females from the upper Sabine (mean 2.8; range 1–4) and upper Calcasieu rivers (mean 2.0; range 1–3; Fig. 3). There was significant variation in mean clutch size among the four samples ($F_{3,74} = 78.4, P < 0.0001$), with all samples being significantly different in *post hoc* Tukey's tests except the lower Calcasieu and Mermentau samples.

Minimum sizes of gravid females from low-gradient river reaches were 155 mm PL in the lower Sabine, 137 mm PL in the lower Calcasieu, and 134 mm PL in the Mermentau. In contrast, on the upper Calcasieu, females measuring 116 and 125 mm PL were gravid and on the upper Sabine, females measuring 111 mm PL and 118 mm PL were gravid. None of the 18 largest females from the two upper drainages (range 105–131 mm PL) exhibited growth annuli, whereas 10 of 14 females in the same size range from the lower drainages exhibited between 2 and 5 growth annuli (Fig. 4). In the lower drainages, 10 of 44 females in the size range 132–172 mm PL exhibited between 4 and 9 growth annuli, while none of the 36 larger females exhibited growth annuli (Fig. 4).

Regression of log(CS) on log(PL) showed a positive correlation, although it was not significant ($r = 0.30, P = 0.17$). The slope of 0.92 (95% CI –0.43–2.27) was significantly below the slope anticipated under isometry (3.00), consistent with a hypoallometric relationship of CS with PL (Fig. 5). Regression of log-transformed EW variables on log(PL) yielded significant positive correlations ($EW_{mean}, r = 0.57, P = 0.0043$; $EW_{max}, r = 0.44, P = 0.038$). The comparison of these one-dimensional measurements would have a slope of 1.0 under isometry, but slopes were 0.28 for EW_{mean} (95% CI 0.10–0.47) and 0.24 for EW_{max} (95% CI 0.02–0.46), indicating significant hypoallometry of egg width. Regression of log(PAW) on log(PL) yielded a significant positive correlation that was slightly hypoallometric but which did not differ significantly from isometry ($r = 0.51, P = 0.0001$; slope = 0.75, 95% CI 0.42–1.09).

In ANCOVAs with log(PL) as the covariate, log(EW_{mean}) was significantly greater in lower Calcasieu specimens than in Mermentau specimens and log(EW_{max}) approached significance, while there was no difference in log(PAW) between the two drainages (Table 3). Log-log slopes for the relationships of EW_{mean} , EW_{max} , and PAW with female PL were similar for the two drainages and similar to slopes for

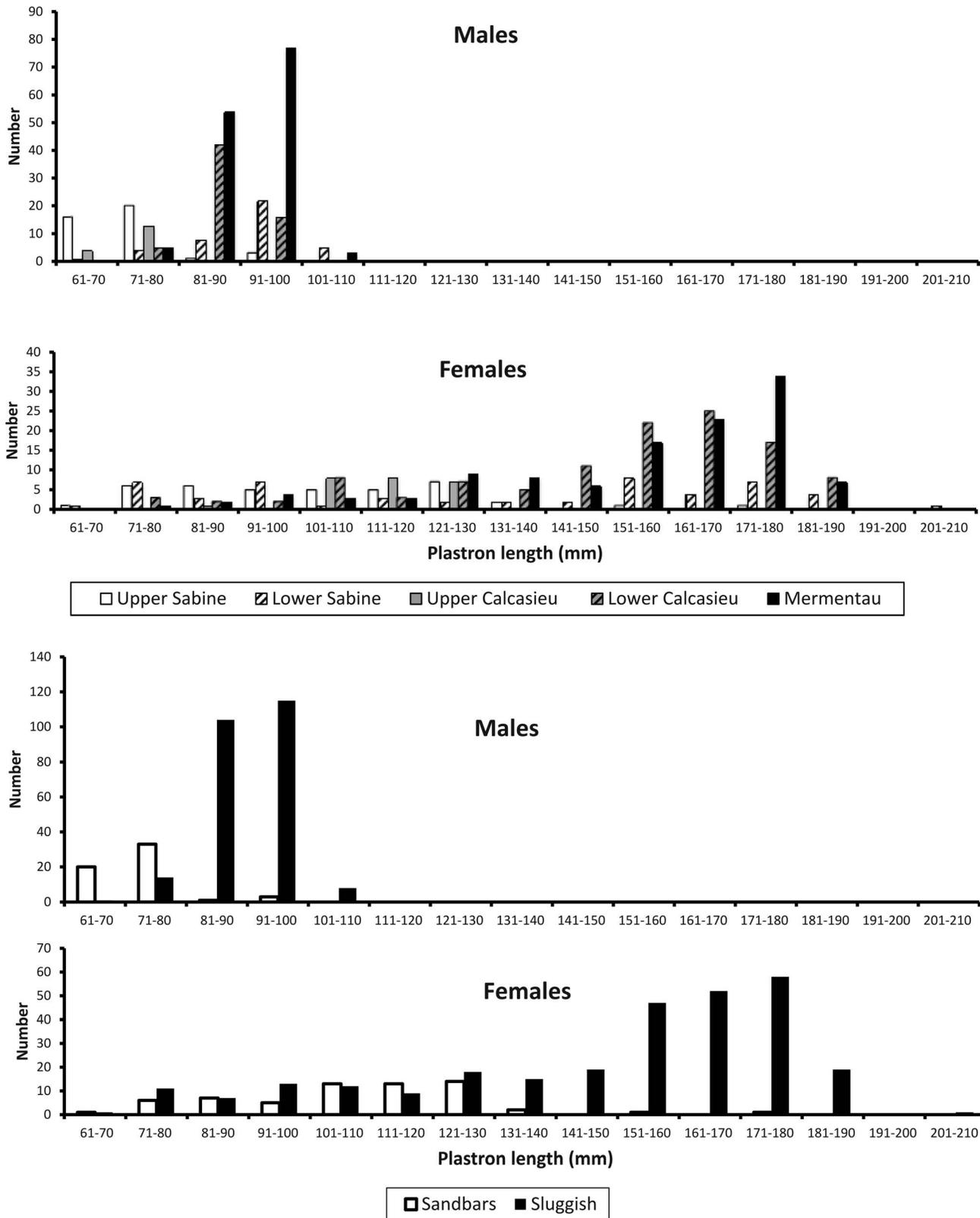


Fig. 2. Inter- and intradrainage variation in body size of *Graptemys sabinensis*. The lower pair of panels groups the data as such: the upper Sabine and upper Calcasieu drainages are high-gradient, sandbar-dominated river systems, while the lower Sabine, lower Calcasieu, and Mermentau drainages are low-gradient, sluggish river systems.

combined data reported above, but slopes for PAW were considerably steeper than for the EW variables (Table 3), with the effect that the difference between PAW and EW variables grew wider in larger females (Fig. 6).

DISCUSSION

The existing literature places *G. sabinensis* as the least fecund and among the smallest-bodied species of the diverse genus *Graptemys* (reviewed in Lindeman, 2013). However, our data

Table 2. Body mass (BM) of *Graptemys sabinensis* from sections of three river drainages. For females, the two entries are for all females, including juvenile females as large as the smallest male, and for adult females, i.e., those as large as the smallest known gravid female for the drainage section. Entries in columns marked with the same letter do not differ. Also given are sexual dimorphism indices, based on body masses of mature animals.

Drainage	Males			Females			Sexual dimorphism index
	<i>n</i>	Mean BM±SE (g) (range)		<i>n</i>	Mean BM±SE (g) (range)		
Upper Sabine	4	87.5±0.87 (85–89)	A	15	330.7±37.09 (87–495)		3.94
				9	432.2±11.08 (360–495)	A	
Lower Sabine	40	160.2±6.40 (73–220)	C	52	630.2±67.16 (77–1550)		6.01
				23	1123.8±47.16 (715–1550)	B	
Upper Calcasieu	6	81.7±5.94 (68–100)	A	7	397.9±28.39 (263–468)		4.36
				5	437.8±13.20 (392–468)	A	
Lower Calcasieu	63	140.7±2.67 (98–189)	B	110	843.3±34.53 (655–1620)		6.08
				76	995.5±26.09 (496–1620)	B	
Mermentau	139	152.6±1.90 (101–210)	C	114	863.3±34.14 (111–1450)		5.59
				91	1006.0±25.94 (450–1450)	B	

show this to be an accurate characterization only for high-gradient, flowing stream reaches of the upper Sabine and Calcasieu drainages that are dominated by sandbars. Such reaches would have been regarded as the typical habitat of the species before our studies recognized the existence of dense and wide-ranging populations in extremely low-gradient stream reaches located further downstream of previous sampling sites in the Sabine and Calcasieu drainages (Louque, 2014; P. Lindeman, unpubl. data) as well as throughout the Mermentau drainage (Ilgen et al., 2014). *Graptemys sabinensis* were found to have substantially larger body sizes and larger clutch sizes in the sluggish reaches of the lower Sabine, lower Calcasieu, and Mermentau drainages when compared to the faster-flowing, sandbar-dominated reaches of the upper Sabine and upper Calcasieu drainages.

The two largest female specimens from the upper Sabine drainage, at 176 and 155 mm in PL, may exemplify how habitat affects body size. The 176 mm female was collected from a floodplain lake near the upper Neches River, potentially a habitat more similar to the lower Sabine, lower Calcasieu, and Mermentau rivers than to the upper Neches River. The 155 mm female was captured from the lower sandbar-dominated reach of the Neches, very near the downstream transition to sluggish, low-gradient reaches. Given its proximity to these reaches, it is possible the specimen had made substantial use of the lower reaches of the river during its juvenile growth phase. Alternatively, the effect of habitat on body size may operate along a gradient near drainage transition points, rather than strictly dichotomously.

Examination of growth annuli further supports the intra- and interdrainage variation in body size we report. In *Graptemys*, distinct plastral growth annuli occur in younger/smaller specimens but are lost as their plastrons wear smooth shortly after maturation, once growth rate slows dramatically (Cagle, 1952, 1953a, 1953b, 1954; Shealy, 1976; Vogt, 1980; Jones and Hartfield, 1995; Lindeman, 1999, 2005). Cagle (1953a) reported that 16 female *Graptemys sabinensis* in the type series from the upper Sabine River labeled as “mature” (presumably via dissections, although this is not stated) were 126–140 mm in maximum PL (corresponding to ca. 121–135 mm midline PL) and all lacked growth annuli. Similarly, none of 18 females ranging from 105–131 mm PL that we caught at sites on the upper Sabine and upper Calcasieu exhibited growth annuli, suggesting they were older individuals that may have experienced prolonged periods of little to no growth. Most of the females in the same size range from the lower drainages exhibited low numbers of growth rings, suggesting they were immature turtles that were still growing rapidly. A consistent absence of growth annuli was not evident in females from the lower drainages until they were >172 mm PL.

Other species of *Graptemys* exhibit trends in body size that are similar to what we report in the present study, albeit with less pronounced differences. *Graptemys versa* from a fast-flowing, upstream site in the South Llano River ranged from 57–79 mm PL in adult males and from 115–163 mm in adult females (Lindeman, 2005). Specimens collected from other portions of the Colorado drainage substantially exceeded the maximum PL in both males and females (Lindeman, 2005; P.

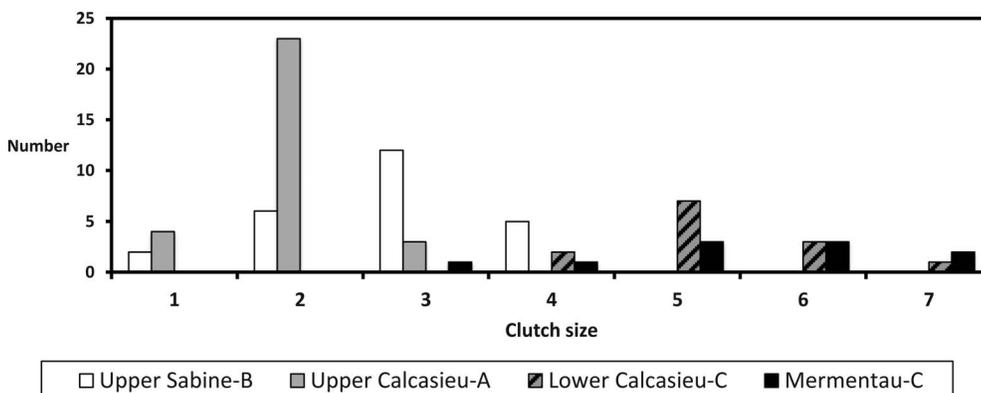


Fig. 3. Clutch size distributions for *Graptemys sabinensis*. The upper Sabine and upper Calcasieu drainages (data from Ewert et al., 2004) are high-gradient, sandbar-dominated river systems, while the lower Calcasieu and Mermentau drainages (data from present study) are low-gradient, sluggish river systems. Legends marked with the same letter denote drainage section samples that did not differ significantly.

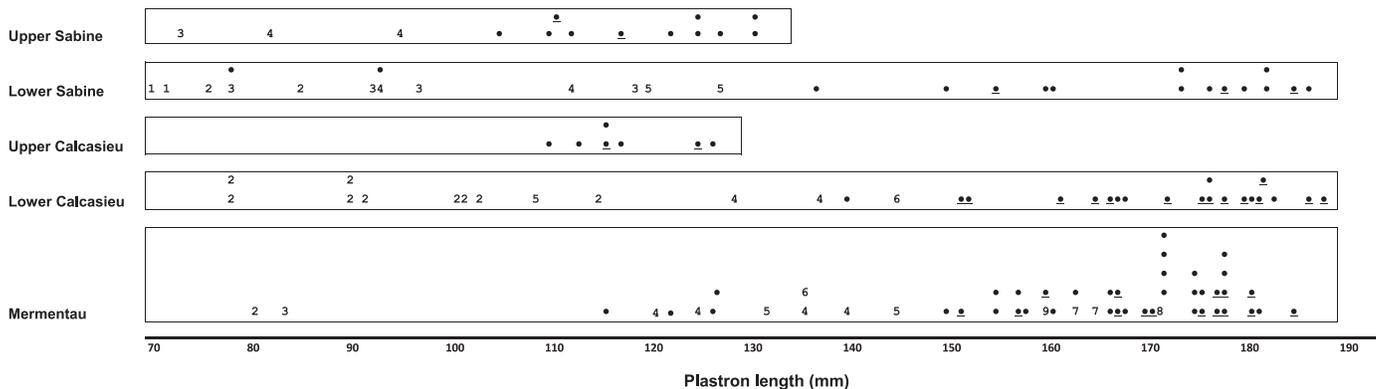


Fig. 4. Plastron length of females caught during May and June of 2011–2013 showing number of plastral growth annuli for each individual (• = a turtle lacking discernible annuli). Underlined symbols represent females that were determined to be gravid via inguinal palpation.

Lindeman, unpubl. data). Adults from other portions of the drainage were on average 12% (males) and 13% (females) larger than South Llano turtles. The South Llano is distinguished by generally faster current than most of the rest of the Colorado drainage. Additionally, syntopic Texas river cooters (*Pseudemys texana*) were similarly found to be small in body size in the South Llano compared to conspecifics in adjacent drainages (Lindeman, 2007).

Similar regional body size variation was reported for *Graptemys flavimaculata* in the Pascagoula drainage in Mississippi (Selman, 2012). Males from the lower Chickasawhay River and middle Leaf River—both faster-flowing tributary reaches with sandbars—ranged from 58–109 mm in PL, while females ranged from 65–170 mm. In the lower Pascagoula, a wide, sluggish river much further downstream in the drainage, males ranged from 76–118 mm and females from 98–189 mm. Compared to the two upper reaches, the lower Pascagoula males were on average 10% longer and 37% heavier and the lower Pascagoula females were on average 17% longer and 65% heavier.

A third species that exhibits intradrainage variation in body size is *Graptemys nigrinoda* of the Mobile Bay drainage in Alabama and eastcentral Mississippi (data in Lindeman, 2000, 2008 from museum specimens from various localities; also, P. Lindeman, unpubl. data). Males from the upper regions of the drainage ranged from 63–100 mm, while males

from the river’s delta region in Mobile and Baldwin counties, Alabama, ranged from 86–102 mm in PL. Females ranged from 68–180 mm in upper regions of the drainage and from 79–202 mm in the delta region. On average, adults from Mobile Bay sites were 20% (males) and 6% (females) larger than adults from upstream localities. Larger-bodied females from Mobile Bay also produced larger clutches than females from a middle reach of the Alabama River (Lahanas, 1982; Lindeman, 2013).

Intraspecific variation in the sexual size dimorphism of *G. sabinensis* was consistent with the interspecific trend among species of *Graptemys*, which tend toward greater size dimorphism in larger-bodied species (Gibbons and Lovich, 1990; Lindeman, 2008), as dimorphism was more pronounced for the larger-bodied samples from low-lying, sluggish river reaches. These results suggest that whatever ecological factors or selective forces act to make the turtles from the lower-drainage populations larger may have more influence in females than in males. If the difference in body size is due to ecological factors, differences in prey types or prey availability would be the most likely factors. If the difference is due to selection, it may be that selection favors larger female size in the lower reaches, with male size being enlarged to a lesser degree simply due to covariation between the sexes.

Body size may be increased in lower reaches of the Sabine and Calcasieu drainages and throughout the Mermentau drainage due to increased ecological productivity of these reaches. In reservoir ecology, the most productive portion of a river is a transitional zone at some distance upstream of an impoundment, where declining current speed and increasing light penetration bring an optimal mix of nutrients carried by the current and light for algae that are the main base of the food web (Kimmel et al., 1990). Jones and Hartfield (1995) found that female *G. oculifera* immediately upstream of the Ross Barnett Reservoir (Ratliff Ferry site) were larger than turtles in freer-flowing upstream or downstream reaches. The slowing current of low-gradient reaches of coastal rivers may similarly be characterized by this optimal mix.

Alternatively (or in addition), larger female body size would be selected for if turtles in downstream reaches were taking advantage of a molluscan prey source unavailable in more upstream reaches. Females of low-gradient downstream populations of *G. nigrinoda* in Mobile Bay and *G. flavimaculata* in the lower Pascagoula River include the dark false mussel (*Mytilopsis leucophaeata*) in their diets in areas where

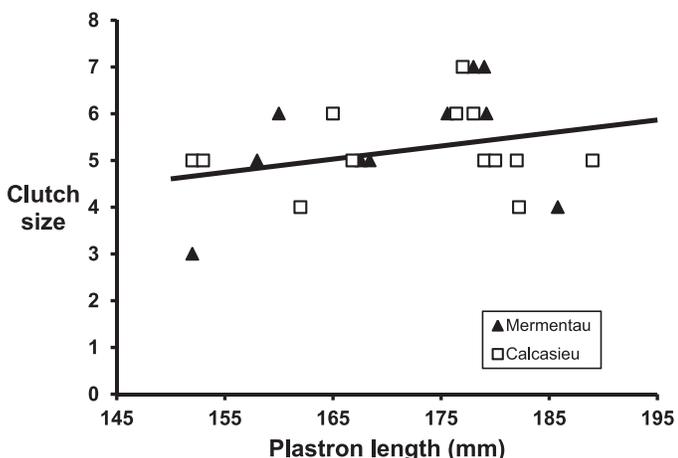


Fig. 5. Relationship of clutch size to female plastron length in *Graptemys sabinensis* from the lower Calcasieu and Mermentau river drainages, with a regression line based on log-transformation of both variables.

Table 3. Results of ANCOVAs comparing mean and maximum egg width (EW) and pelvic aperture width (PAW) for radiographs of gravid *Graptemys sabinensis* from the lower Calcasieu and Mermentau drainages, with results of simple linear regression for each drainage. Significant *P*-values are indicated in boldface.

Dependent variable	ANCOVA results						Regression results							
	Covariate (Plastron length)		Drainage		Interaction		Lower Calcasieu (n = 13)				Mermentau (n = 10)			
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	Slope	y-intercept	<i>r</i> ²	<i>P</i>	Slope	y-intercept	<i>r</i> ²	<i>P</i>
EW _{mean}	12.58	0.002	6.86	0.017	0.012	0.91	0.25	0.80	0.39	0.023	0.27	0.77	0.33	0.084
EW _{max}	5.40	0.031	4.00	0.060	0.0028	0.96	0.22	0.87	0.21	0.12	0.21	0.91	0.18	0.23
PAW	19.97	0.0003	0.41	0.53	0.048	0.83	0.70	-0.14	0.46	0.011	0.77	-0.31	0.61	0.007

sympatric, broader-headed congeners that might compete with them are effectively absent (Lahanas, 1982; Selman, 2012; Selman and Lindeman, unpubl. data). We observed dense colonies of *M. leucophaeata* in the lower Calcasieu drainage, shells of which were shed abundantly in the feces of female *G. sabinensis* held for radiographic study of clutches and visible in four of the 13 radiographs (e.g., Fig. 7). Selection might favor larger body size in females if it enables greater capacity to crush and consume mussels, as appears to be the case for the large-bodied megacephalic species of *Graptemys* (Lindeman, 2008, 2013). However, *M. leucophaeata* was not observed in the lower Sabine or the Mermentau and

was absent from dietary samples of adult female *G. sabinensis* from the Mermentau drainage (O. Zaleski and P. Lindeman, unpubl. data). Additionally, a broader-headed species, *G. pseudogeographica*, is present in the lower Sabine and lower Calcasieu at greater relative abundance than broader-headed congeners are present in Mobile Bay and the lower Pascagoula—it appears to have suffered a catastrophic but relatively recent decline in the Mermentau drainage, however (Ilgen et al., 2014)—thus competitive release of *G. sabinensis* in the lower-gradient rivers does not seem to comprise a sufficient explanation of their larger body sizes there.

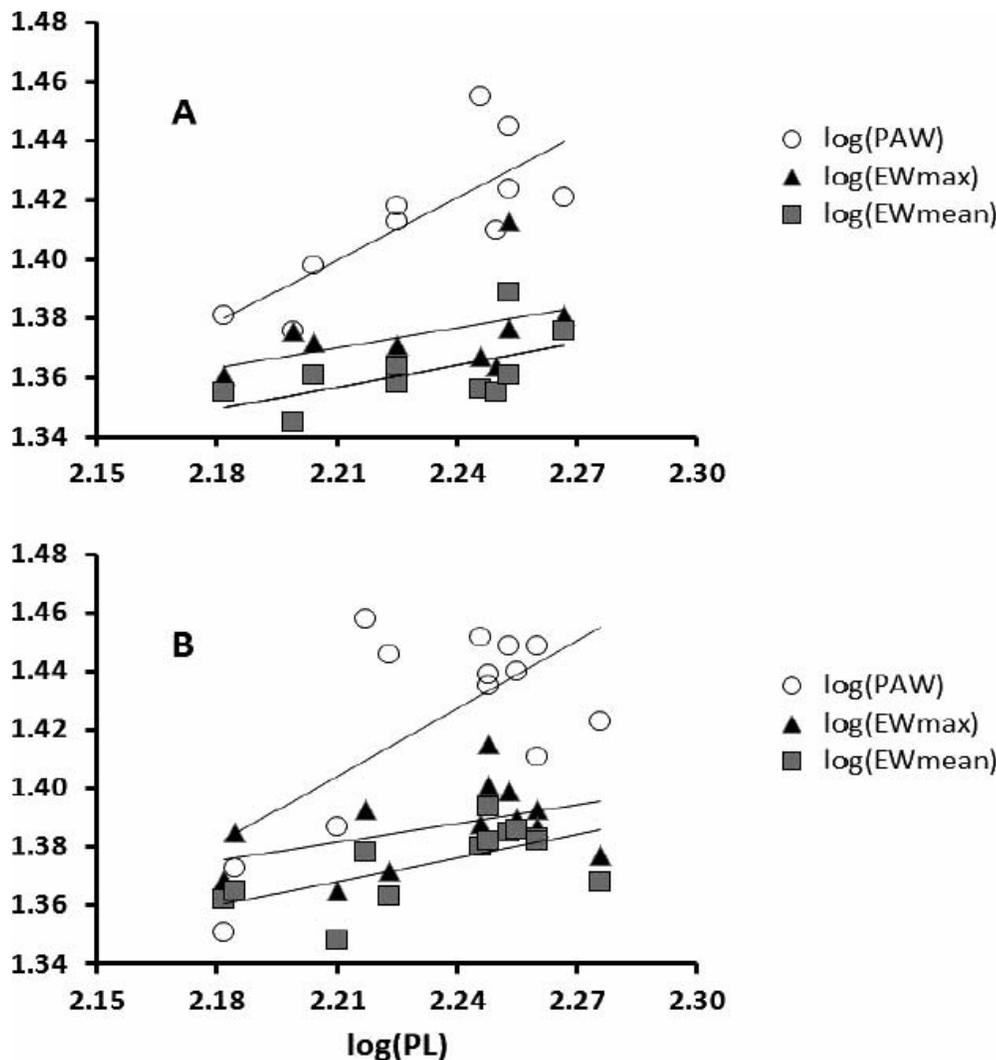
**Fig. 6.** Relationships of pelvic aperture width (PAW) and mean and maximum egg width (EW) in a clutch to female plastron length in *Graptemys sabinensis* for radiographs from the (A) Mermentau and (B) lower Calcasieu river drainages.



Fig. 7. Radiograph of a female *Graptemys sabinensis* from the West Fork of the Calcasieu River (153 mm PL), showing a clutch of five eggs and an alimentary tract containing abundant shells of the dark false mussel, *Mytilopsis leucophaeata*. The large circle posterior to the turtle's withdrawn head is a U.S. quarter placed on the plastron as a size reference.

Clutch size was positively but not significantly correlated with body size. We attribute the lack of significance to the low amount of variation in clutch size. Had we been able to include some upper Sabine or upper Calcasieu females in the size range of 110–140 mm, with the one- to four-egg clutches that Ewert et al. (2004) reported, the positive regression likely would have been significant, as it typically is in species of *Graptemys* that exhibit greater variation in clutch size (Shealy, 1976; Vogt, 1980; Horne et al., 2003; Rosenzweig, 2003; Lindeman, 2005; Jones, 2006; Ryan and Lindeman, 2007). Artner (2001) reported three clutches averaging 3.0 eggs in captive *G. sabinensis*. Given that lower-drainage populations have been little noted and unsampled in the literature and museum collections since the 1890s (Ilgen et al., 2014), animals taken for the pet trade, such as Artner's, most likely originate from upper-drainage habitats, hence his reports for captives are consistent with the clutch sizes that Ewert et al. (2004) reported from these reaches.

Our findings with regard to reproductive allometry are consistent with those for two other species of *Graptemys* and other freshwater turtles (Lindeman, 2005; Ryan and Lindeman, 2007; Macip-Rios et al., 2012; Naimi et al., 2012). These previous studies also found that clutch size and egg width were both positively correlated with plastron length, but both increased at a proportionally slower rate than female body size. As females grow larger, they partition energy to not only increasing the size of the clutch, but also increasing egg size, such that neither can increase isometrically with female

body size (Lindeman, 2005; Ryan and Lindeman, 2007). These results thus further support the hypothesis that in *Graptemys* and many other freshwater turtles, anatomical constraints related to passing eggs from the body prevent smaller females from producing eggs of optimal size (Tucker et al., 1978; Congdon and Gibbons, 1987; Ryan and Lindeman, 2007).

Although egg width increased with female body size, it did so considerably more slowly than width of the pelvic aperture, for which the rate of increase was slightly hypoallometric but not different from isometry. This result may relate to the competing demands of increasing both clutch size and egg size as described above. Nevertheless, the effect is that the difference between egg width and width of the pelvic aperture grows greater in larger females, thereby relaxing any constraint on egg size. This pattern also fits a pattern described for *Chrysemys picta* by Rollinson and Brooks (2008), who suggested that the pattern might indicate that egg size is constrained in smaller females, which would therefore exhibit a correlation of egg width with female size, but optimized in larger females, which would show little correlation of egg width with female size. The analyses of Rollinson and Brooks (2008) did not use log-log transformation and so cannot be used to determine whether isometry or hypoallometry typifies smaller females (i.e., those that may have been constrained from producing eggs of optimal size). Sample sizes in the present study precluded use of the quadratic model Rollinson and Brooks (2008) used to fit egg width to female body size and compare to linear models.

Rothermel and Castellón (2014) analyzed reproductive allometry in the terrestrial turtle *Gopherus polyphemus* and found a pattern similar to the present results. Both clutch size and egg width were related to plastron length with log-log slopes that were each about half the slope values expected under isometry (1.67 and 0.49, respectively; no confidence limits on slopes were reported), while the slope of the relationship of pelvic aperture width to plastron length was nearly perfectly isometric (0.95). As in *G. sabinensis* in the present study, the difference between egg and pelvic aperture width grew greater in larger female *G. polyphemus*, suggestive of a relaxation of anatomical constraint on egg width. The results of Rothermel and Castellón (2014) are thus another case in which it appears that anatomical constraints on egg width apply to small adult females but are relaxed in larger females, who split the gain in reproductive output associated with growth to larger body sizes between increasing clutch size and egg size.

We suggest that future investigations of egg-width allometry in freshwater turtles may benefit from using “broken-stick” or piecewise regression (Toms and Lesperance, 2003), given large sample sizes of log-transformed data. A broken-stick model fits two regression lines to either side of a breakpoint in the independent variable, i.e., a measure of female size in the case of egg-width allometry. The expectation would be that females above a particular body-size breakpoint would have a slope of approximately 0, indicative of optimization of egg size, while females below the breakpoint would have a slope >0 , yet one that would likely be significantly hypoallometric, due to the competing demands of simultaneously increasing clutch size and egg size as females grow larger.

Females from the lower Calcasieu drainage had significantly wider eggs relative to their body size than females from the Mermentau drainage. Because no significant difference was found in width of the pelvic aperture between

the two drainages in spite of the difference in mean egg width, other possible anatomical constraints may have been responsible for the interdrainage difference in egg width. Only width of the pelvic aperture was measurable from radiographs. Height rather than width of the pelvic aperture or the size of the caudal gap (the space between the posterior edges of the carapace and plastron; Clark et al., 2001) might be responsible for interdrainage differences in this or other similar cases.

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