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Spatial, Seasonal, and Sexual Variation in the Diet of *Graptemys flavimaculata*, a Threatened Turtle of the Pascagoula River System, Mississippi, USA

Will Selman¹ and Peter V. Lindeman²

The conservation of imperiled species often depends upon conserving their prey. *Graptemys flavimaculata* (Yellow-blotched Sawback) is an imperiled turtle endemic to the Pascagoula River system of Mississippi, USA. We investigated diet variability of *G. flavimaculata* relative to site geography, sex, seasons, and size. We captured individuals from May to October in 2007 and 2008 at two distant sites. One site is an inland freshwater tributary (Leaf River, LR) and the other site is coastal and tidally influenced (Pascagoula River, PR). Feces from males ($n=68$) and females ($n=74$) were collected and analyzed. Using the Index of Relative Importance (IRI; 0–100 scale, 100 = only item present in all samples), we found that *G. flavimaculata* are primarily sponge specialists for both males ($IRI_{LR}=85$, $IRI_{PR}=91$) and females ($IRI_{LR}=84$, $IRI_{PR}=65$). For both sexes, between-site differences were more varied than within-site differences; for the latter, prey items were typically similar for males and females at a single site, but importance varied. Seasonal comparisons suggest that both LR and PR females shifted diets towards mollusks during the spring and fall, possibly associated with increasing energy and calcium for reproduction. Based on the frequency of wood fragments in feces, submerged deadwood appears important for prey species, and therefore, managers should conserve deadwood along riverbanks (i.e., mature riparian corridors). If channel maintenance is needed, deadwood should be moved toward banks rather than removed to conserve structure for prey species colonization.

ANALYSIS of ecological data and life-history patterns across temporal and spatial scales is becoming increasingly important. Such broad studies are needed to document changes in species' populations, behaviors, and physiology because of anthropogenic landscape-level changes over time. Of particular importance for conservation efforts is an understanding of the diet of an animal species of concern, as it might be of equal importance to conserve its prey species or communities. Many studies of chelonians have reported dietary differences associated with variation in morphology and body size, physiological demands of reproduction, and differences in the reproductive roles between males and females (Tinkle, 1958; Berry, 1975; Dalrymple, 1977; Bulté et al., 2008a, 2008b). Comparison between the sexes is often made in dietary studies because sexual size dimorphism occurs in most chelonian species (Gibbons and Lovich, 1990) and can be extreme, as it is in all species of the genus *Graptemys* (Lindeman, 2008, 2013).

Species within the genus *Graptemys* (map turtles and sawbacks) are highly aquatic freshwater turtles, and many occur in single Gulf of Mexico river drainages. The genus is also considered the least-studied North American turtle genus (Lovich and Ennen, 2013), with many species lacking basic life-history and ecological information, even though many are listed as species of conservation concern (Buhlmann and Gibbons, 1997; Lindeman, 2013; van Dijk et al., 2014). *Graptemys* are typically divided into three main groups based on the relative head width of females (micro-, meso-, and megacephalic), with each group having diets tailored to the females' head morphology and feeding strategy. Megacephalic females specialize in feeding almost exclusively on mollusks, mesocephalic females feed on mollusks and other softer-bodied prey, and microcephalic females feed primarily on soft-bodied aquatic insects and algae, taking fewer mollusks (Lindeman, 2000, 2013).

One microcephalic species, *Graptemys flavimaculata* (Yellow-blotched Sawback), has been the focus of many ecological and physiological studies over the last 25 years (reviewed by Selman and Jones, 2011), primarily because it was listed as a federally threatened species in 1991 (U.S. Fish and Wildlife Service, 1991). This action led to a list of data deficiencies outlined in the species' recovery plan (Jones, 1993), including an emphasis on documenting the diet of *G. flavimaculata*. Seigel and Brauman (1994; see summary in Lindeman, 2013) studied the species' diet by dissecting museum specimens and by collecting feces. The museum specimens were from several upstream localities in the Pascagoula River, its two major tributaries (Leaf and Chickasawhay rivers), and another smaller tributary, Red Creek (localities reported in Cliburn, 1971), while the live specimens sampled for feces were from a different region, the lower Pascagoula River. They found that sponges, insects, and algae were the predominant prey and that turtles from the lower Pascagoula River also included mussels, with females eating substantially more mussels than males. However, because dissected museum specimens were collected at several upstream sites throughout the active season and across a wide temporal range, their ability to analyze variation either among sites or by season was limited. In addition, their upstream site specimens included seven juvenile females (<129 mm plastron length) but lacked adult females.

Although the range of *G. flavimaculata* is relatively small, there are many factors that might contribute to a varied diet throughout its range. First, it occurs across many different habitat types in the Pascagoula River system, ranging from swift, rocky headwater streams to sluggish coastal rivers and bayous (Selman and Qualls, 2009). Second, there are considerable differences in the species' body size and morphology throughout the system, with progressively larger individuals in downstream sections; downstream females also have larger relative head sizes compared to

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upstream females (Selman, 2012). Large relative head size in other species of the genus has been shown to be significantly related to diet, particularly the ability to consume hard-shelled mollusk species (Lindeman, 2000; Lindeman and Sharkey, 2001; Collins and Lindeman, 2006). Third, *G. flavimaculata* is sympatric with *Graptemys gibbonsi* (Pascagoula Map Turtle) throughout much of its range, particularly at upstream localities (Selman and Qualls, 2009; Selman and Lindeman, 2015). Thus, the dietary niche of *G. flavimaculata* might vary depending on the presence or absence of *G. gibbonsi*. Lastly, diet could change seasonally because of prey resource availability and certain prey might be fed upon selectively as it relates to differing seasonal physiological demands (e.g., females needing additional nutrients for egg production; Shelby et al., 2000; Horne et al., 2003). In summary, one might suspect that there could be considerable differences in the diet of *G. flavimaculata* throughout their range for multiple reasons.

We sought to address many of the diet-related topics outlined in the recovery plan for *G. flavimaculata* (Jones, 1993). Our objectives were to compare the diets of *G. flavimaculata* 1) between males and females, 2) across a range of body sizes within each sex, 3) between two sample sites with differing riverine habitats, and 4) among seasons (spring, summer, and fall).

MATERIALS AND METHODS

Study sites and field sampling.—From May to October of 2007 and 2008, we sampled turtles at the Leaf River (LR, Forrest County) and the lower Pascagoula River (PR, Jackson County) once per month for 3–5 days each month. The LR is a small to moderate-sized, inland freshwater tributary system with abundant emerged and submerged deadwood. It also has large meanders, with abundant sandbars and cutbanks. Conversely, the PR site is a large, deep (up to 12 m; Jones, 1996), sluggish coastal river with low-salinity influence because of its proximity to the Gulf of Mexico (approx. 23 river km north). It also has abundant deadwood present in the river, but only a few small sandbars are present. Additional habitat characteristics for the sites are presented by Selman (2012).

At both sites, turtles were trapped by attaching open-topped basking traps (made of 3/4" [1.9 cm] mesh PVC coated crawfish wire; The Fish Net Company, Jonesville, LA) to deadwood structures that turtles used for basking platforms (Selman et al., 2012). Traps varied in size from 56 × 46 × 31 cm to 122 × 61 × 25 cm and were affixed to logs, branches, stumps, and tree crowns with nails and cotton twine, with up to 15 traps used during a trapping day. Traps were checked approximately every hour by rapidly approaching trap logs by motorized boat, which startled any basking turtles into the traps. Turtles were also captured opportunistically by hand or dip net at both sites. These methods did not use bait to capture turtles and therefore should not introduce bias into our dietary samples.

After capture, individuals were sexed when possible based on the presumption that males were smaller, had longer foreclaws, and longer tails than females, with the cloaca posterior to, rather than even with, the carapace rim (Selman and Jones, 2011). Midline plastron lengths (PL) of turtles were measured to the nearest 1 mm using tree calipers. Turtles were permanently marked with holes made by an electric drill on marginal scutes (Cagle, 1939), which allowed

for future identification of captured individuals. Recaptured individuals were not included in data analyses.

Following marking and measuring of turtles, they were placed individually in 18.9 L buckets with a small amount of water (~5 cm deep) to keep fecal contents moist, with water shallow enough to keep the turtle from swimming continuously. Individuals were brought back to the lab overnight and the following morning, fecal contents were collected by straining the contents in a 1 mm sieve and retained in jars with 70% ethanol. Sex of individual, date of collection, and identification number were recorded for each sample. Turtles were released the following day at their capture sites, even in cases in which no fecal contents were collected.

Diet analysis.—Preserved prey remains were sorted under a dissecting microscope, and the volume of each prey item category was determined via volumetric displacement of water to the nearest 0.1 ml. Categorical samples that displaced <0.1 ml were estimated to constitute 0.05 or 0.01 ml. Samples were then sorted into sex (M or F) and month (May through October) categories. Because we had small sample sizes in some months, the monthly category was later broadened as spring (May, June), summer (July, August), or fall (September, October) to be able to make seasonal dietary comparisons. For each prey category *i* within each class of turtle and month, data on mean percent total volume (%V_{*i*}) and percent frequency of occurrence (%F_{*i*}) were used to calculate an Index of Relative Importance (IRI; Hyslop, 1980; as modified by Bjørndal et al., 1997):

$$IRI_i = 100V_iF_i/\Sigma(V_iF_i).$$

IRI_{*i*} values sum to 100 for all prey categories.

Two separate Chi-square analyses were used to determine if the frequency of wood fragments in the feces was different by site for males and females (analyzed separately). Because molluscan prey have been shown to be of high importance to some species of *Graptemys* (Lindeman, 2013), we used a Wilcoxon Rank Sum Test to determine if percent molluscivory (i.e., total mollusk volume divided by total fecal sample volume) was similar for males and females, with each site analyzed separately. Nonparametric Wilcoxon tests were used because of the nonnormal distribution of percent molluscivory (i.e., many "0" values). We used separate Spearman's rank correlations for males and females to determine if percent molluscivory was related to body size. We used JMP (v9.0.0, SAS Institute Inc.) for all statistical analyses and accepted significance of tests at $\alpha = 0.05$.

RESULTS

Sample summary.—We collected fecal contents from 59 individuals at the LR (25 males, 34 females) and 83 individuals from the PR (43 males, 40 females; Table 1); for females, 5 from the LR and 3 from the PR overlapped with male size ranges but were analyzed as females. For males, 26 samples were collected in the spring (10 LR, 16 PR), 27 during the summer (10, 17), and 15 in the fall (5, 10). For females, 26 samples were collected in the spring (12 LR, 14 PR), 37 in the summer (17, 20), and 11 in the fall (5, 6).

Sexual comparisons.—The principal dietary item for males and females at both sites was freshwater sponges (Spongillidae), in percent frequency (males: 92–98%; females: 85–91%), mean percent volume (males: 67–71%; females: 56–62%), and IRI (males: 85–91; females: 65–84; Table 2). The only other prey

Table 1. Comparative morphometric data for *G. flavimaculata* collected for dietary samples from the Leaf and Pascagoula river sites. Abbreviations: PL—plastron length (cm), BM—body mass (g), SD—standard deviation.

Site	Male		Female	
	PR	LR	PR	LR
PL <i>n</i>	43	25	40	34
PL mean	9.1	8.5	16.0	13.8
PL SD	0.58	0.52	2.70	2.52
PL range	7.5–10.5	7.9–9.2	7.7–19.4	6.9–16.8
BM <i>n</i>	42	25	39	33
BM mean	147	116	947	571
BM SD	28.1	20.1	320	40.5
BM range	90–225	75–150	75–1500	70–920

taxon of even moderate importance was dark false mussels (*Mytilopsis leucophaeata*) for females at the PR (IRI = 33); all other IRI values for both sexes at both sites were <6. Male diets also included dark false mussels at the PR (IRI = 4.6) and other items of minor importance such as small mollusks (snails, introduced Asian clams at the LR site, and sphaeriid clams), insects, spiders, and plant and algal material; female diets included similar taxa of low importance (Table 2).

Female diets from the PR were dichotomous at body sizes >140 mm PL, with most large females being primarily either molluscivorous (>75% by volume) or spongivorous (>75%), with few female samples having intermediate values (Fig. 1). Only three females from the LR had intermediate molluscivory values (20–50%) and none had higher values for molluscivory. Only three of the 43 males at the PR were considered highly molluscivorous (>75% by volume), with intermediate values in four PR males (24–48%) and two LR males (25% and 33%).

Geographic comparisons.—Diversity of diet was more similar by site than by sex, with males and females sharing many of the same prey items within each site but in different levels of importance (e.g., IRI values for *M. leucophaeata* at the PR; males: 5, females: 33). Overall, diets from the LR were more diverse (5 prey categories >1.0 IRI for each sex) than diets from the PR (3 categories >1.0 for each sex). Many prey items were shared at the two sites, including sponges, caddisfly larvae, unidentified insect fragments, and vegetative material (mosses, filamentous algae, algal stalks, leaf fragments). Caddisfly larvae (Trichoptera) were more important in the diets of LR turtles, while different bivalve molluscan prey were found in fecal samples from the LR (*Corbicula* spp., fingernail clams) vs. the PR (*M. leucophaeata*).

Undigested wood fragments passed with feces in higher frequencies at the LR (males: 23 of 25, 92%; females: 32 of 34, 94%) than at the PR (males: 35 of 43, 81%; females: 27 of 40, 68%), although only the female difference was significant (males, $\chi^2_1 = 1.42$, $P = 0.23$; females, $\chi^2_1 = 8.06$, $P = 0.0045$). Polystyrene was commonly found in samples from the PR (males: 5 of 43, 12%; females: 13 of 40, 33%) but was absent from LR samples. Percent volume composed of mollusks was not different between males and females at the LR (male mean: 4.1%, female mean: 4.2%; $Z = 0.13$, $P = 0.90$) but differed at the PR (male mean: 4.2%, female mean: 32.4%; $Z = 3.76$, $P = 0.0002$). There was no correlation of percent molluscivory with PL in males (Spearman $\rho = 0.010$, $P = 0.94$) or females ($\rho = 0.21$, $P = 0.08$).

Seasonal comparisons.—Sponges were the primary food item for both males and females in all three seasons at both sites

(Fig. 2). The only notable seasonal difference occurred in female samples. Sponges had lower IRI values during the spring (LR 63, PR 44) and fall months (LR 38, PR 48) compared to summer (LR 96, PR 80), while mollusk species had higher IRI values in the spring and fall (*M. leucophaeata* IRI at the PR: spring 48, summer 19, fall 47; *Corbicula* spp. IRI at the LR: spring 3, summer 0.5, fall 22).

DISCUSSION

Sexual and body size comparisons.—We found that both males and females depended heavily upon freshwater sponges as their main dietary item throughout the year. The lack of a sexual difference in diets is contrary to other studies that have shown high divergence in diets of *Graptemys* between the sexes, primarily driven by divergence in trophic morphology (Lindeman, 2006, 2013; Richards-Dimitrie et al., 2013). Also, the high dependence upon sponges is unusual in a predator, with very few animal species specializing on sponges because of their toxicity, high silica levels, and their sharp spicules (Lahanas, 1982; Meylan, 1988).

Our results are similar to those of a previous unpublished study of the diet of *Graptemys flavimaculata* (Seigel and Brauman, 1994). The primary prey were sponges, aquatic insects, and algae, with different bivalve mollusks at the two sites that were particularly prevalent in samples from adult females. The report of Asian clams in the diet at the upstream (LR) site is a new finding, probably because no adult female specimens from upstream localities were available to be dissected by Seigel and Brauman (1994). We also report seasonal trends and body-size relationships to prey types that were not analyzed by Seigel and Brauman (1994).

The diet of a related species, *G. nigrinoda* (Black-knobbed Sawback) of the Mobile Bay basin of Alabama and north-eastern Mississippi, has been studied in two locations (Lahanas, 1982; Lindeman, 2013, 2016). At both locations, males and females preyed heavily upon sponges, which had the highest IRI values among prey (Mobile Delta: males 61, females 37; Alabama River: males 69, juvenile females 66, and adult females 45). Sponges were not reported for the diet of the third species of the sawback clade (*sensu* Wiens et al., 2010), *G. oculifera* (Ringed Sawback; Kofron, 1991). However, Kofron might not have recognized sponge remains, which are identified primarily by their spicules and gemmules that are visible only under higher magnification. We think it is likely that a future study of the diet of *G. oculifera* would confirm that this species also has a high prevalence of sponges in the diet.

The high frequency of wood fragments in the diets of both males and females at both sites suggest that both sexes forage

Table 2. Diet of male and female Yellow-blotched Sawbacks from the Pascagoula River (PR) and Leaf River (LR) sites, with taxon index of relative importance (IRI) calculated based on percent frequency (%F) and mean percent of total volume (%V) across samples within each group.

Taxon	Male						Female					
	PR (n = 43)			LR (n = 25)			PR (n = 40)			LR (n = 34)		
	%F	%V	IRI	%F	%V	IRI	%F	%V	IRI	%F	%V	IRI
Sponges	98	71	90.6	92	67	84.8	85	55	64.8	91	62	83.6
Asian clams				32	4	1.6				41	4	2.7
False mussels	35	10	4.6				75	32	33.0			
Fingernail clams				8	0.3	0.03						
Bryozoan colonies							10	2	0.2			
Caddisfly larvae	9	0.5	0.06	40	6	3.5	15	1	0.15	56	2	1.9
Insect fragments	14	3	0.5	48	5	3.6	5	0.04	0.003	26	3	1.3
Insect eggs				20	3	0.9				3	0.3	0.01
Arachnida				4	0.2	0.009						
Fish scales	2	1	0.02	8	1.4	0.16						
Leaf fragments	14	1	0.1	40	8	4.7	10	0.6	0.09	3	0.03	0.001
Vascular plant stems				4	1	0.06				3	0.08	0.004
Flowers	5	0.2	0.01									
Fruits							10	1	0.15			
Seeds	5	0.3	0.02									
Mosses	12	2	0.4	12	1	0.1	10	0.4	0.06	9	2	0.3
Filamentous algae	28	9	3.4				5	2	0.17	26	14	5.7
Algal stalks	16	1	0.3	20	2	0.5	25	3	1.1	26	11	4.5
Fungal hyphae							5	2	0.16			

primarily on submerged portions of deadwood for aquatic prey items. Indeed, Kofron (1991) reported that 66% of diet samples of *G. oculifera* had wood fragments present, indicative of deadwood “grazing,” with observations of nonselective grazing on submerged deadwood reported for *G. flavimaculata* and several congeners (Waters, 1974; Shively and Jackson, 1985; Selman and Qualls, 2008a; Lindeman, 2013). Because sponges and vegetative prey items (e.g., filamentous algae) likely co-occur on deadwood substrate and nonselective deadwood grazing has been observed, vegetation might not necessarily be associated with secondary ingestion of animal prey. Rather, *G. flavimaculata* might be foraging nonselectively on sections of deadwood with high prey densities of both vegetation and animal prey items. Selective grazing would need to be confirmed in future studies.

Compared to other broad-headed species of *Graptemys*, *G. flavimaculata* is considered a microcephalic species not specializing in molluscivory (i.e., it lacks the large jaws and jaw musculature necessary to crush mollusks; Lindeman, 2000). Even though mollusks were not a primary item in their diet, microcephaly did not inhibit both males and females from consuming the small mollusk species *M. leucophaeata* and *Corbicula* spp. Most females at both sites had a low percentage of their diet composed of mollusks, but a subset of large females at the PR (8 of 48 individuals) appeared to specialize on *M. leucophaeata*, with 80–100% of their diet composed of this species. Selman (2012) found the PR females have larger heads relative to their body size compared to LR females, which likely facilitates the higher level of molluscivory in PR females that we observed in this study. For males, only 9 of 68 individuals at both sites had mollusk species present in low to high percentages (24–83%), indicating a lesser importance of small mollusks in male diets. For the other sawback species, Lahanas (1982) found a similar relationship in the lower Mobile River system with

female *G. nigrinoda* having a greater propensity than males to consume mollusks, while upstream in the Alabama River, almost no molluscivory was noted in *G. nigrinoda* (IRI values for mollusks ≤ 1 for all groups; Lindeman, 2016). Kofron (1991) also found no mollusks in diets of *G. oculifera* from upstream sites.

Geographic comparisons.—Our study found that there were subtle differences in diets of *G. flavimaculata* at two distant riverine sites. Sponges predominated in the diet of both males and females at each site (all sex and site groups >56% sponges in mean percent volume and >66 IRI), but other items were found only at one site or the other. For example, the lower Pascagoula River is tidally influenced, therefore promoting a slightly brackish community as evident by the large number of *M. leucophaeata* in the diets of PR turtles. Similarly, *G. sabinensis* (Sabine Map Turtle) consumes *M. leucophaeata* in downstream portions of the Calcasieu River system in southwestern Louisiana (Fehrenbach et al., 2016), while *G. nigrinoda* likely also consumes *M. leucophaeata* in tidal portions of the lower Mobile River (possibly misidentified as *Modiolus* sp. [horseshell]; Lahanas, 1982). Conversely, the upper Leaf River is entirely freshwater and flow is seasonal, mainly dependent upon runoff from rain events. Therefore, it is not surprising that two primarily freshwater groups, freshwater mollusks (*Corbicula* spp. and fingernail clams [Family Sphaeriidae, Order Veneroida]) and caddisfly larvae (Order Trichoptera), were present. Caddisflies were also present at the PR, but were more important in LR turtle diets (Table 2). Caddisflies are particularly abundant in freshwater habitats and are considered important components of freshwater systems (Wiggins, 1996); they have frequently been found to be of high importance in the diets of males of species of *Graptemys* (Lindeman, 2013).

The presence of polystyrene in the diet of PR individuals appears to be from animals foraging for prey items on or

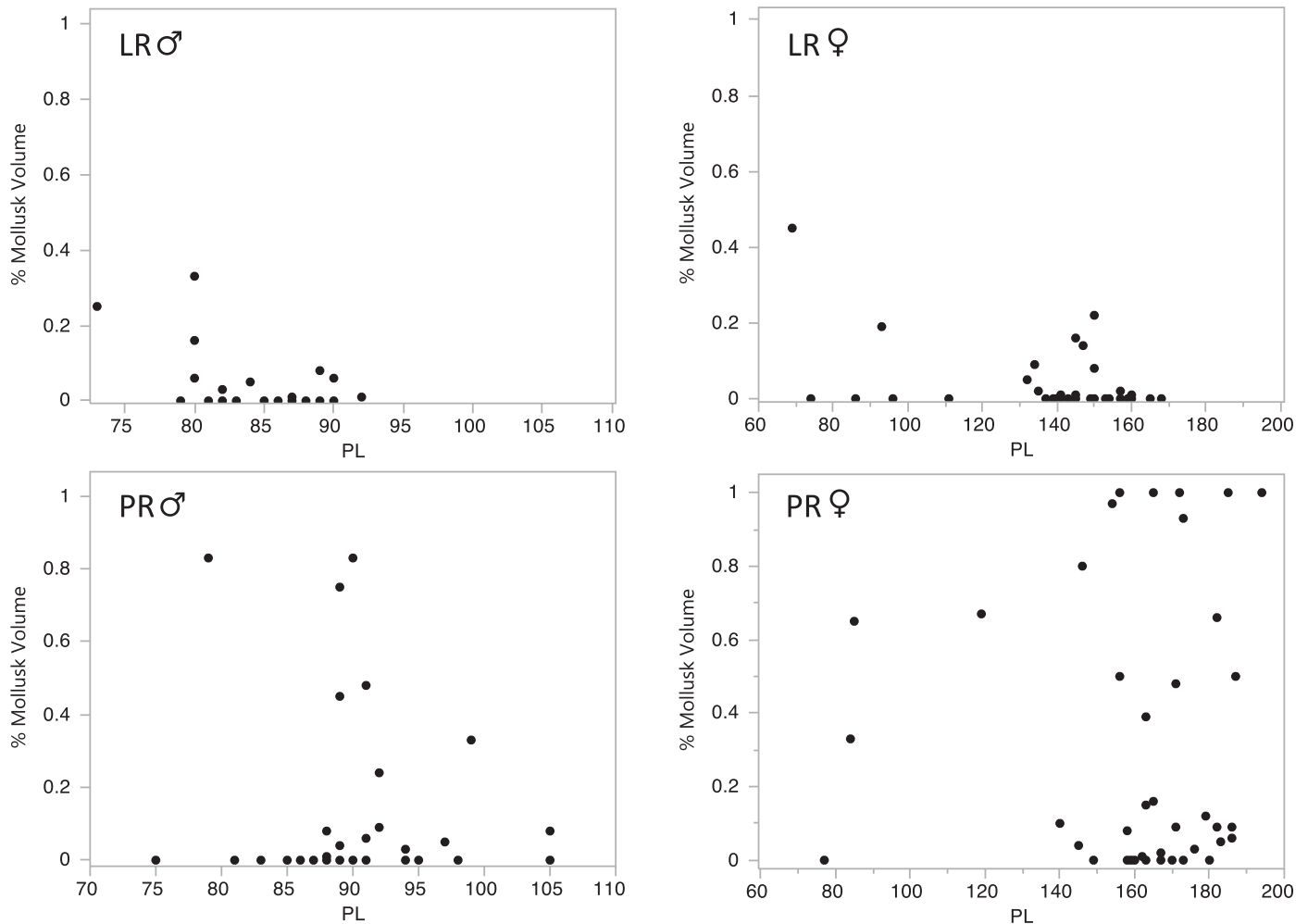


Fig. 1. Percent molluscivory of male and female *Graptemys flavimaculata* from the Leaf River (LR) and the lower Pascagoula River (PR).

embedded within this substrate rather than accidental ingestion. Polystyrene at the site is primarily available because of the presence of houseboats that use large polystyrene blocks for floatation (~48 floating houseboat units in 2008). Thus, it appears that *G. flavimaculata* forage on prey embedded within polystyrene on houseboat floats, as well as pieces that could have floated away because of damage to houseboats following major hurricanes (Selman and Qualls, 2008b). Although this by-product also entered the digestive tract, it is unknown how polystyrene impacted digestive efficiency, but anthropogenic debris has been shown to cause gut inflammations, obstructions, and difficulty passing fecal contents in sea turtles (McCauley and Bjørndal, 1999). Numerous studies have shown polystyrene in the diets of sea turtles (e.g., Guebert-Bartholo et al., 2011), with marine debris collectively having both lethal and sublethal impacts on sea turtles (for review see Schuyler et al., 2014). To our knowledge this is the first report of polystyrene in the diet of a freshwater turtle species.

Seasonal comparisons.—The only seasonal difference we observed was females consume more mollusks during the spring and fall than in the summer months. Females at the PR consumed 2–2.5X more *M. leucophaeata* during the spring and fall relative to summer, while females at the LR consumed 6.5–71.5X more *Corbicula* spp. during the spring

and fall relative to summer. Because mollusk species appeared to be available throughout the annual cycle (i.e., they are present in all months; W. Selman, pers. obs.), it does not appear that this seasonal dietary shift was related to seasonal availability, but was rather a result of prey selection by females. Mollusks might provide high caloric and calcium content for reproduction which supports follicular development during the fall (Mendonça and Licht, 1986; Selman et al., 2009) and final yolking of ovarian follicles the following spring (Shelby et al., 2000; Horne et al., 2003). Also, it does not appear that sponge availability was limited during the spring and fall months for females, because importance values for males were similarly high across all three seasons.

Conclusions and management implications.—The diet of *G. flavimaculata* appears to be highly specialized toward sponges, with a smaller proportion of the female diet allocated towards consumption of mollusk species during parts of the year (spring/fall). We acknowledge the biases of using fecal contents for dietary analysis, and this includes the inability to detect easily digestible, soft prey items (i.e., worms, small insects). However, in a similar species, *G. versa* (Texas Map Turtle), stomach samples via flushing were found to poorly represent mollusks whereas feces had high frequencies of mollusk shell fragments; this indicated the difficulty of flushing shell fragments out of the stomach. Stomach

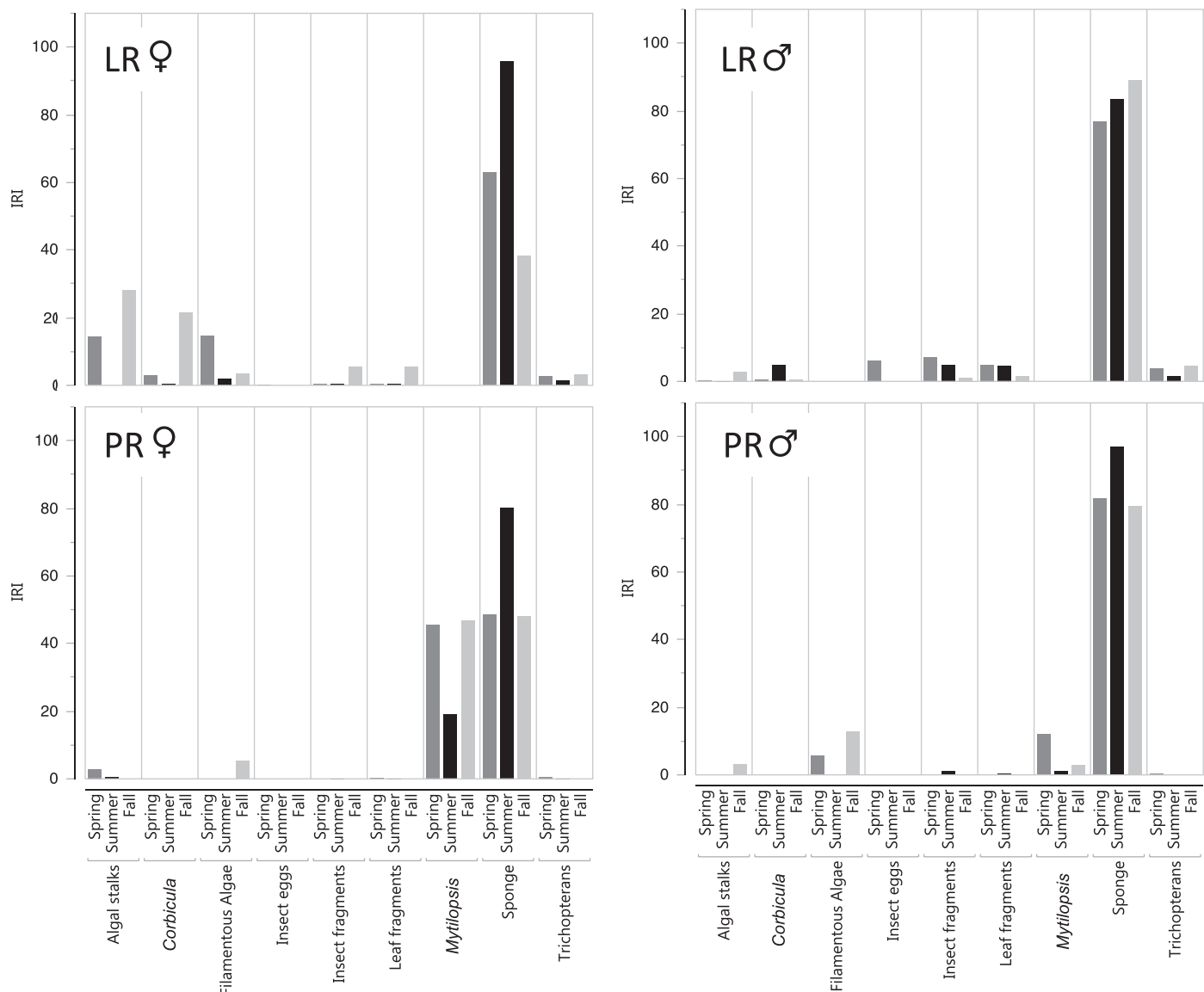


Fig. 2. Diets of male and female *Graptemys flavimaculata* from the Leaf (LR) and lower Pascagoula Rivers (PR) by season (Spring—dark gray, Summer—black, Fall—light gray). Prey items are sorted alphabetically with minor items not included.

flushing also can lead to unintended mortalities (Lindeman, 2006), and we considered this an unacceptable risk with a federally threatened species.

Most prey species of *G. flavimaculata* appear to be associated with deadwood substrates where turtles forage, further highlighting the importance of deadwood to this species beyond its importance as a basking substrate (Lindeman, 1999). Thus, river management via deadwood removal might negatively impact prey densities of *G. flavimaculata* (Lindeman, 1999). If channel maintenance is needed, instead of removing deadwood from rivers, managers could move deadwood from the center of the channel towards the river banks; this would conserve potential substrate for prey items to colonize. Managers should also maintain a riparian corridor of mature trees along the riverbanks (aka, streamside management zone), with this corridor providing a source of new deadwood when river cutbanks erode naturally (Sterrett et al., 2010; Lindeman, 2013). The removal of mature trees close to riverbanks should also be discouraged because it increases sedimentation that negatively impacts mollusk species (Neves et al., 1997). This practice would be particu-

larly important for female *G. flavimaculata* as well as megacephalic species of *Graptemys* that are mollusk specialists, such as sympatric *G. gibbonsi*, a congener which is also endemic to the Pascagoula River drainage (Shealy, 1976; Selman and Lindeman, 2015).

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LITERATURE CITED

- Berry, J. F. 1975. The population effects of ecological sympatry on Musk Turtles in northern Florida. *Copeia* 1975:692–701.
- Bjorndal, K. A., A. B. Bolten, C. J. Lagueux, and D. R. Jackson. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. *Chelonian Conservation and Biology* 2:430–433.
- Buhlmann, K. A., and J. W. Gibbons. 1997. Imperiled aquatic reptiles of the southeastern United States: historical review and current conservation status, p. 201–232. *In: Aquatic Fauna in Peril: The Southeastern Perspective*. G. Benz and D. E. Collins (eds.). Lenz Design and Communications, Decatur, Georgia.
- Bulté, G., M.-A. Gravel, and G. Blouin-Demers. 2008a. Intersexual niche divergence in Northern Map Turtles (*Graptemys geographica*): the roles of diet and habitat. *Canadian Journal of Zoology* 86:1235–1243.
- Bulté, G., D. J. Irschick, and G. Blouin-Demers. 2008b. The reproductive role hypothesis explains trophic morphology dimorphism in the Northern Map Turtle. *Functional Ecology* 22:824–830.
- Cagle, F. R. 1939. A system for marking turtles for future identification. *Copeia* 1939:170–173.
- Cliburn, J. W. 1971. The ranges of four species of *Graptemys* in Mississippi. *Journal of the Mississippi Academy of Sciences* 16:16–19.
- Collins, D., and P. V. Lindeman. 2006. The influence of body size and trophic morphology on the size of molluscan prey of female Texas Map Turtles (*Graptemys versa*). *Herpetological Review* 37:416–418.
- Dalrymple, G. H. 1977. Intraspecific variation in the cranial feeding mechanism of turtles of the genus *Trionyx* (Reptilia, Testudines, Trionychidae). *Journal of Herpetology* 11:255–285.
- Fehrenbach, A. K., I. Louque, S. L. McFadden, C. Huntzinger, E. Lyons, S. H. Shively, W. Selman, and P. V. Lindeman. 2016. 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. *Copeia* 104:458–468.
- Gibbons, J. W., and J. E. Lovich. 1990. Sexual dimorphism in turtles with emphasis on the Slider Turtle (*Trachemys scripta*). *Herpetological Monographs* 4:1–29.
- Guebert-Bartholo, F. M., M. Barletta, M. F. Costa, and E. L. A. Monteiro-Filho. 2011. Using gut contents to assess foraging patterns of juvenile Green Turtles *Chelonia mydas* in the Paranaguá Estuary, Brazil. *Endangered Species Research* 13:131–143.
- Horne, B., R. Brauman, M. Moore, and R. Seigel. 2003. Reproductive and nesting ecology of the Yellow-blotched Map Turtle, *Graptemys flavimaculata*: implications for conservation and management. *Copeia* 2003:729–738.
- Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology* 17: 411–429.
- Jones, R. L. 1993. Yellow-blotched Map Turtle (*Graptemys flavimaculata*) recovery plan. U.S. Fish and Wildlife Service, Jackson, Mississippi.
- Jones, R. L. 1996. Home range and seasonal movements of the turtle *Graptemys flavimaculata*. *Journal of Herpetology* 30:376–385.
- Kofron, C. P. 1991. Aspects of ecology of the threatened Ringed Sawback turtle, *Graptemys oculifera*. *Amphibia-Reptilia* 12:161–168.
- Lahanas, P. N. 1982. Aspects of the life history of the southern Black-knobbed Sawback, *Graptemys nigrinoda delticola* Folkerts and Mount. Unpubl. M.S. thesis, Auburn University, Auburn, Alabama.
- Lindeman, P. V. 1999. Surveys of basking Map Turtles *Graptemys* spp. in three river drainages and the importance of deadwood abundance. *Biological Conservation* 88:33–42.
- Lindeman, P. V. 2000. Evolution of the relative width of the head and alveolar surfaces in Map Turtles (Testudines: Emydidae: *Graptemys*). *Biological Journal of the Linnean Society* 69:549–576.
- Lindeman, P. V. 2006. Diet of the Texas Map Turtle (*Graptemys versa*): relationship to sexually dimorphic trophic morphology and changes over five decades as influenced by an invasive mussel. *Chelonian Conservation and Biology* 5:25–31.
- Lindeman, P. V. 2008. Evolution of body size in the map turtles and sawbacks (Emydidae: Deirochelyinae: *Graptemys*). *Herpetologica* 64:32–46.
- Lindeman, P. V. 2013. The Map Turtle and Sawback Atlas: Ecology, Evolution, Distribution, and Conservation. University of Oklahoma Press, Norman, Oklahoma.
- Lindeman, P. V. 2016. Diets of syntopic Black-knobbed Sawbacks (*Graptemys nigrinoda*) and Alabama Map Turtles (*Graptemys pulchra*) in the Alabama River. *American Midland Naturalist* 175:194–205.
- Lindeman, P. V., and M. J. Sharkey. 2001. Comparative analyses of functional relationships in the evolution of trophic morphology in the Map Turtles (Emydidae: *Graptemys*). *Herpetologica* 57:313–318.
- Lovich, J. E., and J. R. Ennen. 2013. A quantitative analysis of the state of knowledge of turtles of the United States and Canada. *Amphibia-Reptilia* 34:11–23.
- McCauley, S. J., and K. A. Bjorndal. 1999. Conservation implications of dietary dilution from debris ingestion: sublethal effects in post-hatchling Loggerhead Sea Turtles. *Conservation Biology* 13:925–929.
- Mendonça, M. T., and P. Licht. 1986. Seasonal cycles in gonadal activity and plasma gonadotrophin in the Musk Turtle, *Sternotherus odoratus*. *General and Comparative Endocrinology* 62:459–469.
- Meylan, A. 1988. Spongivory in Hawksbill Turtles: a diet of glass. *Science* 239:393–395.
- Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity, p. 43–85. *In: Aquatic Fauna in Peril: the Southeastern Perspective*. G. Benz and D. E. Collins (eds.). Lenz Design and Communications, Decatur, Georgia.
- Richards-Dimitrie, T., S. E. Gresens, S. A. Smith, and R. A. Seigel. 2013. Diet of Northern Map Turtles (*Graptemys geographica*): sexual differences and potential impacts of an altered river system. *Copeia* 2013:477–484.
- Schuyler, Q., B. D. Hardesty, C. Wilcox, and K. Townsend. 2014. Global analysis of anthropogenic debris ingestion by sea turtles. *Conservation Biology* 28:129–139.
- Seigel, R. A., and R. J. Brauman. 1994. Food habits of the Yellow-blotched Map Turtle (*Graptemys flavimaculata*). Mississippi Museum of Natural History Museum Technical Report 28:1–18.

- Selman, W. 2012. Geographic variation in population structure, shape morphology, and sexual size dimorphism in *Graptemys flavimaculata*. *Herpetological Conservation and Biology* 7:427–436.
- Selman, W., J. Jawor, and C. Qualls. 2012. Seasonal variation of corticosterone levels in the Yellow-blotched Sawback (*Graptemys flavimaculata*), an imperiled freshwater turtle. *Copeia* 2012:698–705.
- Selman, W., and R. L. Jones. 2011. *Graptemys flavimaculata* Cagle 1954—Yellow-blotched Sawback, Yellow-blotched Map Turtle, p. 052.1–052.11. In: *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier (eds.). Chelonian Research Monographs No. 5. <http://www.iucn-tftsg.org/cbftt/>
- Selman, W., and P. V. Lindeman. 2015. Life history and ecology of the Pascagoula Map Turtle (*Graptemys gibbonsi*). *Herpetological Conservation and Biology* 10:781–800.
- Selman, W., and C. Qualls. 2008a. *Graptemys flavimaculata* (Yellow-blotched Map Turtle). Foraging behavior. *Herpetological Review* 39:215.
- Selman, W., and C. Qualls. 2008b. Impacts of Hurricane Katrina on a population of Yellow-blotched Sawbacks (*Graptemys flavimaculata*) in the Lower Pascagoula River. *Herpetological Conservation and Biology* 3:224–230.
- Selman, W., and C. Qualls. 2009. Distribution and abundance of two imperiled *Graptemys* species of the Pascagoula River system. *Herpetological Conservation and Biology* 4: 171–184.
- Selman, W., C. Qualls, and M. T. Mendonça. 2009. Impact assessment of Hurricane Katrina on the Yellow-blotched Sawback (*Graptemys flavimaculata*): Year 2. Report to the U.S. Fish and Wildlife Service and Mississippi Department of Wildlife, Fisheries, and Parks, Jackson, Mississippi.
- Shealy, R. M. 1976. The natural history of the Alabama Map Turtle, *Graptemys pulchra* Baur, in Alabama. *Bulletin of the Florida State Museum of Biological Sciences* 21:47–111.
- Shelby, J. A., M. T. Mendonça, B. H. Horne, and R. A. Seigel. 2000. Seasonal variation in reproductive steroids of male and female Yellow-blotched Map Turtles, *Graptemys flavimaculata*. *General and Comparative Endocrinology* 119:43–51.
- Shively, S. H., and J. R. Jackson. 1985. Factors limiting the upstream distribution of the Sabine Map Turtle. *American Midland Naturalist* 114:292–303.
- Sterrett, S. C., L. L. Smith, S. W. Golladay, S. J. Schweitzer, and J. C. Maerz. 2010. The conservation implications of riparian land use on river turtles. *Biological Conservation* 14:38–46.
- Tinkle, D. W. 1958. The systematics and ecology of the *Sternotherus carinatus* complex (Testudinata, Chelydridae). *Tulane Studies in Zoology* 6:3–56.
- U.S. Fish and Wildlife Service. 1991. Endangered and Threatened Wildlife and Plants: Threatened Status for the Yellow-blotched Map Turtle, *Graptemys flavimaculata*. *Federal Register* 56:1459–1463.
- van Dijk, P. P., J. B. Iverson, A. G. J. Rhodin, H. B. Shaffer, and R. Bour. 2014. Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status, p. 329–479. In: *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier (eds.). Chelonian Research Monographs No. 5. <http://www.iucn-tftsg.org/cbftt/>
- Waters, J. C. 1974. The biological significance of the basking habit in the Black-knobbed Sawback, *Graptemys nigrinoda* Cagle. Unpubl. M.S. thesis, Auburn University, Auburn, Alabama.
- Wiens, J. J., C. A. Kuczynski, and P. R. Stephens. 2010. Discordant mitochondrial and nuclear gene phylogenies in emydid turtles: implications for speciation and conservation. *Biological Journal of the Linnean Society* 99:445–461.
- Wiggins, G. B. 1996. Larvae of the North American Caddisfly Genera (Trichoptera). Second edition. University of Toronto Press Incorporated, Toronto.