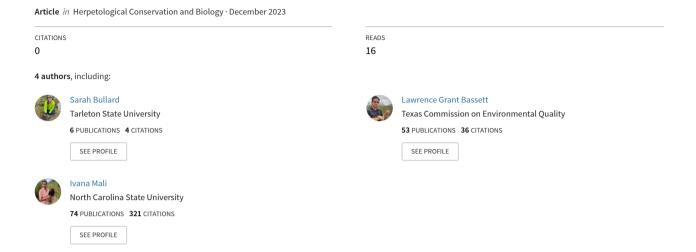
Diet of Apalone spinifera emoryi (Texas Spiny Softshell) and Trachemys scripta elegans (Red-eared Slider) in the Pecos River, Texas, USA



DIET OF APALONE SPINIFERA EMORYI (TEXAS SPINY SOFTSHELL) AND TRACHEMYS SCRIPTA ELEGANS (RED-EARED SLIDER) IN THE PECOS RIVER, TEXAS, USA

SARAH BULLARD^{1,4}, LAWRENCE G. BASSETT², IVANA MALI³, AND MICHAEL R.J. FORSTNER¹

¹Department of Biology, Texas State University, 601 University Drive, San Marcos, Texas 78666, USA

²Texas Commission on Environmental Quality, 12100 Park 35 Circle, Austin, Texas 78753, USA

³Fisheries, Wildlife, and Conservation Biology Program, North Carolina State University, Box 8008,

Raleigh, North Carolina, 27695, USA

⁴Corresponding author, e-mail: sbullard0222@gmail.com

Abstract.—The Pecos River of the southwestern USA is a degraded river system that is experiencing decreased flow, increased salinity, pollution, and invasion by exotic flora and fauna due to human endeavors. We sought to quantify the diet of Texas Spiny Softshells (Apalone spinifera emoryi) and Red-eared Sliders (Trachemys scripta elegans) and to examine the niche breadth and overlap of these two turtle species in the Pecos River of west Texas. During the summers of 2020 and 2021, we used fecal content analysis of trapped turtles to examine the diet of A. s. emoryi and T. s. elegans at four sites on the Pecos River. As expected, insects were the most important prey type for A. s. emoryi whereas vegetation was the most important food type/category for T. s. elegans. Both species frequently consumed insects from the orders Coleoptera, Hymenoptera, Odonata, and Orthoptera, indicating that some allochthonous subsidies are readily exploited. The average percentage volume of vegetation in T. s. elegans fecal samples was significantly higher than that of A. s. emoryi. To overcome the drawbacks associated with fecal content analysis, we encourage supplementary study of turtle diets and resource availability in this imperiled river system (e.g., stable isotope analysis and metabarcoding). Characterization of dietary habits and resource selection is useful for habitat management as it identifies those taxa upon which A. s. emoryi and T. s. elegans depend to persist in this degraded river system.

Key Words.—allochthonous subsidies; aquatic turtles; Chihuahuan Desert; fecal content analysis; niche

Introduction

Turtle populations often constitute a substantial biomass in freshwater systems (Iverson 1982; Congdon et al. 1986) and significantly influence the ecological communities they occupy (Lovich et al. 2018). For example, turtle occupancy has been shown to expedite nutrient cycling and increase arthropod abundance in lentic water bodies (Lindsay et al. 2013). Furthermore, carnivorous chelonians structure aquatic ecosystems by controlling irruptions of species occupying lower trophic levels (Silliman and Bertness 2002). Some freshwater turtles act as facultative scavengers (e.g., Donini 2018; Platt and Rainwater 2018; Sepúlveda-Seguro 2021) that regulate water quality (Santori et al. 2020) and may provide stability to ecological communities (Wilson and Wolkovich 2011; Beasley et al. 2019). Freshwater turtles can be carnivorous, omnivorous, or herbivorous (Ernst and Lovich 2009), and the many trophic interactions resulting from these diverse diets are likely to maintain species richness within freshwater systems through topdown control of community structure (Smith and Smith 2015). Given the ecological importance of freshwater turtles, it is useful to analyze their dietary habits. Such work identifies the prey taxa most important to turtle species and enables management agencies to ensure the perpetuity of those nutritional resources. This is especially critical in imperiled river systems that are subjected to anthropogenic degradation.

The Pecos River of the southwestern U.S. (i.e., New Mexico and Texas) is an important water resource of the Chihuahuan Desert that has been seriously altered by human activities. Historic and ongoing threats include declining flow due to encroaching phreatophytes (deep-rooted plants that obtain water from near the water table) and agricultural diversion (Thomas 1959; Harley and Maxwell 2018), increased salinity due to reduced flows and greater evapotranspiration (Hoagstrom 2009), heavy metal pollution from fossil fuel extraction (Schmitt et al. 2004), pesticide pollution from agricultural practices (Schmitt et al. 2004), and invasion by non-native plant and animal species (Hillis et al. 1980; Bestgen et al. 1989; Nagler et al. 2011). These changes correspond with the apparent extirpation of various freshwater vertebrates, including 13 fish species (Hoagstrom 2009).

The Red-eared Slider (Trachemys scripta elegans) and Texas Spiny Softshell (Apalone spinifera emoryi) are two turtle species that occur in the Pecos River (Degenhardt and Christiansen 1974; Rhodin et al. 2017; Bassett and Forstner 2020a; Bassett et al. 2020). Previous research has shown that A. spinifera are primarily carnivorous (Degenhardt et al. 1996; Ernst and Lovich 2009), with crayfish, fish, and insects representing important prey items in multiple studies (Lagler 1943; Williams and Christiansen 1981; Cochran and McConville 1983). Occasional reports of large amounts of plant matter in the stomach contents of A. spinifera (Platt et al. 2008; Heyborne and Sigg 2017) suggest that this species may purposefully supplement its mostly carnivorous diet with vegetable matter. Trachemys scripta has a diet that is more omnivorous (Ernst and Lovich 2009), with juveniles being highly carnivorous and individuals growing increasingly herbivorous with age (Clark and Gibbons 1969; Hart 1983). Documented diet items of T. s. elegans include a diverse array of plant and animal taxa including, but not limited to, algae, vascular plants, mollusks, crustaceans, arachnids, insects, fish, reptiles, amphibians, and birds (Ernst and Lovich 2009).

Understanding the dietary habits of A. spinifera and T. scripta in the Chihuahuan Desert can broaden our knowledge of how turtle species survive in degraded systems. Webb (1962) found coleopterans, hymenopterans, ephemeropterans, odonates, and plant matter including roots, seeds, stems, and bark in the stomachs of two A. s. emoryi from the Rio Grande at Lajitas, Texas. Bassett and Forstner (2020b) reported a T. s. elegans scavenging on the carcass of a White Bass (Morone chrysops) on the Pecos River at Red Bluff Reservoir, and Bassett et al. (2021) observed a T. s. elegans consuming a Gulf Killifish (Fundulus grandis) in a baited hoop-net trap on the Pecos River in Ward County, Texas. Bassett and Forstner (2021) found several invertebrates, Balcones Elimia (Elimia comalensis), Red-rimmed Melania (Melanoides tuberculata), and Red Swamp Crayfish (Procambarus clarkii), in the fecal contents of a single T. s. elegans. These results were generally corroborated for the T. s. elegans population inhabiting San Felipe Creek by stable isotope mixing models (Bassett et al. 2022). These scattered reports are informative but do not allow for generalizations regarding what prev are most important for the A. s. emoryi and T. s. elegans populations inhabiting the Pecos River.

The species composition of the Chihuahuan Desert is considerably different from habitats within which *T. scripta* and *A. spinifera* diet have been previously investigated. We suspect that such differences do not dramatically affect the general composition of turtle diets (e.g., herbivory versus carnivory), and instead

result in dietary constituents of differing taxonomic identities. Given the lack of information regarding A. s. emoryi and T. s. elegans diets in the Pecos River, and the potential importance of that information for wildlife management agencies, scientific investigation of the topic is worthwhile. Furthermore, although A. s. emoryi and T. s. elegans are not globally threatened, they may be at risk within particular sections of the Pecos River. Moreover, understanding turtle diets in degraded systems such as the Pecos River is useful for predicting if and how the dietary habits of freshwater chelonians shift in response to habitat alteration. Herein we examine fecal samples collected from A. s. emoryi and T. s. elegans in the Pecos River of west Texas to identify the most important prey taxa that can inform wildlife management strategies in this imperiled river system.

MATERIALS AND METHODS

Study sites.—We sampled four sites located on the Pecos River in Texas, USA (Fig. 1). The sites were the following four road crossings or termini intersecting the river: State Line Road, Texas Highway 302, Texas Highway 18, and Texas Rock Road. The Pecos River at State Line Road is lentic, impounded immediately downstream by Red Bluff Dam. Water at this site is highly turbid, and dominant riparian vegetation includes Saltcedar (Tamarix ramosissima), an introduced, invasive plant, and cattail (Typha sp.). Texas Highway 302 is situated downstream of Red Bluff Dam and had the most consistent, strongest instream flow of all our sites. Texas Highway 18 had high water clarity and gentle flow, as did Texas Rock Road. The dominant aquatic and riparian plants at these last three sites were stonewort (Chara sp.) and T. ramosissima.

Trapping and sample collection.—During the summer of 2020, we trapped turtles at State Line Road, Texas Highway 302, and Texas Highway 18. During the summer of 2021, we trapped turtles about five river km upstream of Texas Rock Road. Trapping sessions were separated by a minimum of 27 d, beginning in May and ending in August. We trapped each site three times. During each trapping session, we deployed 45 hoop-net traps (Memphis Net and Twine Company, Memphis, Tennessee, USA) at each site for a total of 48 h. Each trap was 50 cm in diameter, fiberglass, single opening, and wide-mouthed with 2.5 cm mesh and four hoops per net. We baited each trap with half of a can of sardines (about 50 g) placed into a plastic container drilled with holes. Additionally, we baited every third trap with a single leaf of romaine lettuce. We deployed traps across a distance of 368 to 890 river-meters at each site. We measured flow and turbidity on each trapping occasion

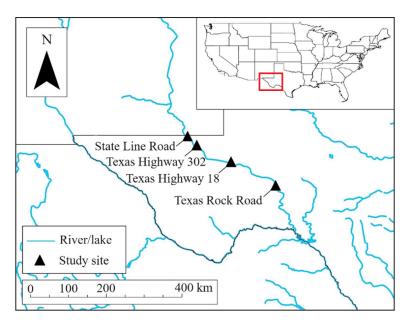


FIGURE 1. Inset map of the USA with the study region outlined in red. Base map shows rivers and lakes (blue) and study sites (black triangles) located on the Pecos River in Texas. River data were provided by the U.S. Geological Survey (2022. North American Rivers and Lakes. Available from https://www.sciencebase.gov/catalog/item/4fb55df0e4b04cb937751e02 [Accessed 24 January 2022]) and state boundary data provided by the U.S. Census Bureau https://www.census.gov/geographies/mapping-files/time-series/geo/carto-boundary-file.html [Accessed 24 January 2022]).

at each site using a MF Pro portable flow meter (OTT HydroMet, Loveland, Colorado, USA) and a Secchi disk. We took measurements at the beginning, middle, and end of each trap line.

We shell-notched captured turtles in cohort based on the year of capture (Cagle 1939). We weighed turtles with a digital scale and measured straight-midline carapace length (method D in Iverson and Lewis 2018) using tree calipers (Haglöf Sweden AB, Långsele, Sweden). While processing turtles at the field site, we kept a random subset of turtles in separate 23-L plastic tubs with water from the Pecos River poured through a 1.24 mm sieve to maintain thermal stability and hydration. We kept turtles in the water-filled tubs for no longer than 4 h while at the field site and released them before the end of the day. We kept turtles in a shaded area at the field sites and monitored water temperature once every 2 h to ensure that turtles did not experience heat stress. Fresh filtered water from the Pecos River was added to the tubs as necessary to maintain a suitable water temperature within 2° C of the recorded temperature of water at the center of the river. When turtles defecated, we poured the contents of the plastic tubs through a 1.24 mm mesh sieve to retain fecal material, which we then transferred into 50 ml Falcon tubes with 95% ethanol.

Fecal content analysis.—We examined fecal material with a Leica EZ4 dissection microscope (Leica Microsystems GmbH, Wetzlar, Germany) with a magnification range of 8–35×. We identified and sorted

fecal content to the lowest possible taxonomic level. We dried excess ethanol from sorted samples by gentle blotting with paper towels and measured the volume of each taxonomic group using volumetric displacement to the nearest 0.1 ml.

For calculating summary statistics, we divided fecal content data into three broad groups (*j*): (1) Decapoda; (2) Insecta; and (3) vegetation. For each species, we calculated frequency of occurrence (%F) of each dietary component (*j*) found in the feces. We define %F as the number of fecal samples in which a particular dietary component occurred divided by the total number of fecal samples. We calculated average percentage volume (%V) of each dietary component (*j*). We define %V as the percentage of total volume a food item constituted in a sample, averaged across all samples. We calculated the Shannon-Wiener measure (*H*') of diversity to determine dietary diversity of each species:

$$H' = -\Sigma p_j \cdot \log p_j$$

where p_j is the proportion of turtles consuming dietary resource j. Because H' can range from 0 to ∞ , we standardized the index (H') on a scale of 0 to 1 by measuring evenness (J'):

$$J' = H'/log(n)$$

where n is the total number of prey groups. A high evenness indicates a more generalist diet, and a low evenness indicates a more specialized diet.

To rank the importance of dietary items relative to turtle species, we calculated the index of relative importance (IRI):

$$IRI = V_i F_i / \Sigma V_i F_i$$

where V_j is the average percentage volume of dietary component j measured across all fecal samples and F_j is the frequency of occurrence of dietary component j. Because our data were not normally distributed, we performed unpaired two-sample Wilcoxon tests in program R (R Development Core Team 2018) to determine whether there was a significant difference between the two species in regard to the average percentage volume of dietary components consumed. We inferred statistical significance at $\alpha = 0.05$.

RESULTS

Captures, samples collected, and sampling site characteristics.—Captures included 56 A. s. emoryi and 149 T. s. elegans, some of which we recaptured one or more times. We obtained 24 fecal samples from these turtles, 14 of which came from A. s. emoryi and 10 came from T. s. elegans (Table 1). All samples came from unique individuals. We collected fecal samples from both taxa at all sites except for Texas Rock Road, where we were only able to collect fecal contents from T. s. elegans. We collected samples from nine male and five female A. s. emoryi. Those individuals had a mean carapace length of 24.86 cm (range from 14.1–38.6 cm) and mass of 1.78 kg (range from 0.32-4.99 kg). We collected samples from three male and seven female T. s. elegans. Those individuals had a mean carapace length of 19.07 cm (range from 13.3–24.1 cm) and mass of 1.1 kg (range from 0.36–2.16 kg). Mean flow was 0 m/s at State Line Road, 0.22 m/s at Texas Highway 302, 0.01 m/s at Texas Highway 18, and 0.04 m/s at Texas Rock Road. Mean turbidity was 0.32 m at State Line Road, 0.43 m at Texas Highway 302, 0.52 m at Texas Highway 18, and 1.02 m at Texas Rock Road.

TABLE 1. Number of captures and number of fecal samples collected at each of our trapping sites for 14 Texas Spiny Softshells (*Apalone spinifera emoryi*) and 10 Red-eared Sliders (*Trachemys scripta elegans*) from the Pecos River, Texas, USA. All samples came from unique individuals. The abbreviation Rd = Road and Hwy = Highway.

	A. spinifer	a emoryi	T. scripta elegans		
Site	Captures	Samples	Captures	Samples	
State Line Rd	22	2	16	4	
Texas Hwy 302	11	10	2	1	
Texas Hwy 18	22	2	109	2	
Texas Rock Rd	1	0	22	3	

Apalone spinifera emoryi.—The most frequently encountered dietary items in A. s. emoryi feces were dicot vegetation, hymenopterans, and orthopterans (Table 2). Volumetrically, the most important food items were insects and vegetation (Table 3). The IRI values, which consider both frequency of occurrence and average percentage volume, indicate that insects were the most important prey item for A. s. emoryi (Table 3). Among the three defined dietary groups, decapods were the least important component for A. s. emoryi (Table 3). In total, we identified four orders of insects in fecal samples: Hymenoptera, Coleoptera, Orthoptera, and Odonata. Families we could identify from the hymenopterans included Formicidae and Pompilidae. The only family of coleopterans we could identify was Curculionidae from several mostly intact bodies and heads from different samples. The vegetation in A. s. emoryi samples consisted of both monocot and dicot taxa. Two of the samples contained many large seeds, possibly from a mesquite (Prosopis sp.), which are found along the Pecos River at all of our sites. Six of the samples contained plant stems with small, scale-like leaves, comparable to those found on T. ramosissima. Evidence of vertebrate prey items we encountered in A. s. emoryi samples included bird feathers in two samples and a fragment of bone from

TABLE 2. Comprehensive lists of prey items and their frequency of occurrence (%F) found in the feces of Texas Spiny Softshells (*Apalone spinifera emoryi*) and Red-eared Sliders (*Trachemys scripta elegans*) in the Pecos River of west Texas, USA, during the summers of 2020 and 2021.

Apalone spinifera emoryi		Trachemys scripta elegans		
Food item	%F	Food item	%F	
Vegetation	85.7	Vegetation	80.0	
Dicot vegetation	71.4	Dicot Vegetation	50.0	
Monocot vegetation	35.7	Monocot vegetation	20.0	
Seeds	14.3	Seeds	10.0	
Vertebrata	21.4	Arthropoda	80.0	
Aves	14.3	Insecta	80.0	
Arthropoda	100	Coleoptera	20.0	
Decapoda	21.4	Curculionidae	10.0	
Insecta	92.9	Hymenoptera	30.0	
Coleoptera	28.6	Formicidae	20.0	
Curculionidae	7.1	Odonata	20.0	
Hymenoptera	42.9	Orthoptera	40.0	
Formicidae	14.3			
Pompillidae	7.1			
Odonata	28.6			
Orthoptera	42.9			
Unidentified matter	78.6	Unidentified matter	90.0	

TABLE 3. Frequency of occurrence (%F), average percentage volume (%V), and index of relative importance (IRI) for the diet of 14 Texas Spiny Softshell Turtles (*Apalone spinifera emoryi*) and 10 Red-eared Sliders (*Trachemys scripta elegans*) from the Pecos River, Texas, USA. Measures of dietary niche breadth, including diversity (H') and evenness (J') are provided for each turtle species in the bottom two rows.

	Apalone spinifera emoryi		Trachemys scripta elegans			
Dietary Category	%F	%V	IRI	%F	%V	IRI
Decapoda	21.4	12.2	0.04	0	0	0
Vegetation	85.7	21.5	0.31	80.0	59.1	0.80
Insecta	92.9	42.7	0.65	80.0	15.0	0.20
Diversity (H')	0.23			0.16		
Evenness (J')	0.48			0.51		

an unidentified vertebrate. Dietary diversity (H') for A. s. emoryi was 0.23, and the corresponding evenness measure (J') was 0.48 (Table 3).

Trachemys scripta elegans.—The most frequently encountered dietary items in T. s. elegans feces were dicot vegetation, orthopterans, and hymenopterans (Table 2). Volumetrically, the most important food items were vegetation and insects (Table 3). The IRI values indicate that vegetation is the most important diet item for T. s. elegans (Table 3). One sample contained plant stems with small, scale-like leaves, comparable to those found on T. ramosissima. Decapods were not present in any T. s. elegans samples. We identified the same four orders of insects in samples from T. s. elegans as we did in samples from A. s. emoryi (Hymenoptera, Coleoptera, Orthoptera, and Odonata). Among the hymenopterans, we found several formicid heads. Order Coleoptera was represented by several elytra in different samples and a single curculionid head. Dietary diversity (H') for T. s. elegans was 0.16, and the corresponding evenness measure (J') was 0.51 (Table 3).

Dietary differences.—The average percent volume of vegetation in fecal samples differed significantly between the two species (W = 35.5, P = 0.031; Fig. 2). The average percentage volume of insects in fecal samples, however, did not significantly differ between A. s. emoryi and T. s. elegans (W = 92, P = 0.146; Fig. 3). We did not test for a difference in average percentage volume of decapods in fecal samples because no T. s. elegans samples contained decapod material.

DISCUSSION

Turtles represent an important component of freshwater and terrestrial ecosystems. The diverse dietary strategies that have evolved among freshwater

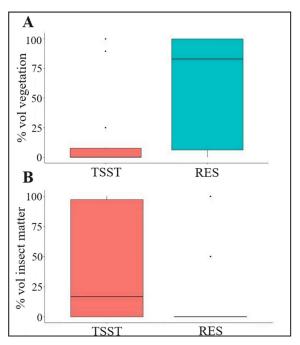


FIGURE 2. Percentage volume of broad dietary categories in feces for 14 Texas Spiny Softshell Turtles (*Apalone spinifera emoryi*) and 10 Red-eared Sliders (*Trachemys scripta elegans*) in the lower Pecos River, Texas, USA. (A) Percentage volume of vegetation in the feces. (B) Percentage volume of insect matter in the feces. The abbreviations TSST = Texas Spiny Softshell and RES = Red-eared Slider.

chelonians can structure and stabilize the communities they occupy, facilitate energy flow between terrestrial and aquatic systems, disperse seeds with some evidence of germination enhancement, and can even be used to restore degraded ecosystems (Silliman and Bertness 2002; Smith and Smith 2015; Lovich et al. 2018; Beasley et al. 2019). Therefore, it is important to understand resource selection of freshwater chelonians and their ecological role in the Pecos River system. Our study offers the only dietary information for *A. s. emoryi* and *T. s. elegans* from this imperiled river.

The results of fecal content analysis suggest A. s. emoryi in the Pecos River are primarily carnivorous, with diets consisting mostly of insects, supplemented by the frequent consumption of vegetation and the occasional consumption of crayfish (decapods). The indices of relative importance (measures of importance that incorporate both percentage occurrence and percentage volume) support this conclusion, as insects had the largest IRI, followed by vegetation and finally decapods. These findings are generally congruent with those of other studies on A. spinifera diet (Degenhardt et al. 1996; Platt et al. 2008; Ernst and Lovich 2009; Heyborne and Sigg 2017). The T. s. elegans samples we examined indicate a primarily herbivorous diet that is supplemented with insects. This is supported by a

high IRI for vegetation and lower IRI for insects. These findings also generally agree with previous research on *T. scripta* diet (Clark and Gibbons 1969; Hart 1983; Ernst and Lovich 2009). There appears to be little dietary niche overlap between the two species at our study sites given the significant difference in volumetric importance of vegetation for the two species. It appears that the overlap that does exist involves insect prey, and it is possible some competition may occur between the two species for allochthonous subsidies of insects. Both turtle species had intermediate evenness measures, indicating that neither were particularly specialized or generalist consumers at our sites.

Although affordable, one of the drawbacks of fecal content analysis is that it is oftentimes difficult to arrive at a refined taxonomic identity for particular prey items. Because fecal contents have undergone the process of digestion, the morphological characters needed to precisely identify prey are generally lost. This was especially true for much of the vegetation we examined in our samples. Further, varying degrees of digestibility between prey items can bias volumetric measurements so that less digestible items are overrepresented or more digestible items are underrepresented in a fecal sample. In future studies, other techniques such as stable isotope analysis (e.g., Bassett et al. 2022; Suriyamongkol et al. 2022) and metabarcoding (e.g., Ducotterd et al. 2021) would help refine our findings.

Nonetheless, our data show that A. s. emoryi and T. s. elegans populations in the Pecos River in Texas rely primarily on insects and vegetation, respectively. The continued effects of anthropogenic change on the Pecos River, such as increased salinization (Hoagstrom 2009) and water depletion (Thomas 1959), have the potential to impact the abundance of important dietary resources available to populations of A. s. emoryi and T. s. elegans. Berezina (2003) reported that the salinity tolerances of dipteran, odonate, and trichopteran insect larvae decreased at saline concentrations above 2000 mg/l, which is within the range of salinity reported in the lower Pecos River (Houston et al. 2019). The findings from Berezina (2003) imply the possibility of a decreased abundance of insect species that have an aquatic larval stage over long-term high levels of salinity, which could impact the availability of an important food category to both species. The continued increase in salinity in the Pecos River could also affect the composition of both aquatic and riparian plant communities (Hart et al. 1990). Such changes could impact the availability of plant foods and phytophagous insect prey for both species. Furthermore, increased salinity may have a negative impact on the total biomass of crayfish in the Pecos River. Sharfstein and Chafin (1979) reported an inverse relationship between the average growth rate of Procambarus clarkii and increasing salinity

levels in the water they inhabited. Additionally, Dörr et al. (2020) observed lowered survivorship of *P. clarkii* in relation to increased salinity. Although crayfish represented a prey item of low importance for *A. s. emoryi* in our study, other investigations have shown crayfish constitute a substantial portion of *A. spinifera* diet (Lagler 1943; Williams and Christiansen 1981; Cochran and McConville 1983). Our results may correspond to a generally low availability of crayfish at our study sites; quantifying available dietary items would be required to test this possibility. Regardless, higher salt concentrations throughout the Pecos River may decrease the availability of crayfish for *A. s. emoryi* consumption.

Our data show that both *A. s. emoryi* and *T. s. elegans* take advantage of allochthonous subsidies and thereby sequester energy from the terrestrial habitat into the aquatic community. For example, all insects identified in fecal samples were either terrestrial or flying insects. This indicates that particular insect species either rest or fall onto the surface of the water, at which point turtles ate them. Seeds, which were consumed by both turtle species, represent an additional allochthonous subsidy linking the terrestrial and aquatic portions of the Pecos River community.

We recognize that our study is limited in several ways. First, we had small sample sizes from A. s. emoryi (n = 14) and T. s. elegans (n = 10). Secondly, there are abiotic and biotic differences among our study sites that may influence turtle diets. Overrepresentation of State Line Road and Texas Highway 302 may have biased our findings. Lastly, we only gathered fecal samples during the summers of 2020 and 2021, which could have introduced a seasonal bias in the taxa that were present in fecal samples. For example, insects are especially abundant in the spring and summer months but less abundant in fall and winter. As a result, sampling other periods may indicate insects as a less important dietary item for both turtle species. Future studies that explore the specific effects of long-term increased salinity on the vegetation and arthropod taxa that inhabit the Pecos River would be beneficial to understanding how anthropogenic change along this river influences the availability of food resources for A. s. emoryi and T. s. elegans and would also better inform management decisions for the Pecos River.

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SARAH BULLARD earned her B.Sc. from Texas State University, San Marcos, Texas, USA, in 2022, where she conducted undergraduate research on the diet of freshwater turtles in west Texas. She has since worked for the Environmental Institute of Houston at the University of Houston - Clear Lake and for Texas Parks & Wildlife Department, USA. She will begin working toward her M.Sc. at Tarleton State University, Stephenville, Texas, in 2023, where she will conduct research on population demographics and occupancy modeling of Cagle's Map Turtle (*Graptemys caglei*). (Photographed by Brandi Giles).



LAWRENCE G. BASSETT is a Wildlife Biologist located in San Marcos, Texas, USA. He earned his B.Sc. in Wildlife Biology from Texas State University, San Marcos, Texas, in 2019. Two years later, he earned his M.Sc. from the same institution, studying the dietary habits and isotopic niche of the imperiled Rio Grande Cooter (*Pseudemys gorzugi*). Lawrence has worked previously as a Biological Technician for the U.S. National Park Service and currently maintains a broad interest in the biology of herpetofauna and arthropods. (Photographed by Laramie Mahan).



IVANA MALI received her B.Sc. from Henderson State University, Arkadelphia, Arkansas, USA, and her M.Sc. and Ph.D. from Texas State University, San Marcos, USA. She is an Associate Professor and Ecology Wildlife Foundation Distinguished Scholar for Conservation Biology at North Carolina State University, Raleigh, USA. She has worked extensively on freshwater turtle conservation issues in the states of Texas and New Mexico. Her research topics include freshwater turtle sustainability under anthropogenic stressors, distribution, reproductive ecology, testing field sampling assumptions and biases, and movement ecology. (Photographed by Michael Vandewege).



MICHAEL R. J. FORSTNER is a Regent's Professor in Biology at Texas State University, San Marcos, USA, and the Alexander-Stone Chair in Genetics. He has a B.Sc. from Southwest Texas State University, San Marcos, M.Sc. from Sul Ross State University, Alpine, Texas, and a Ph.D. from Texas A&M University, College Station. He has broad interests in the effective conservation of rare taxa, particularly reptiles and amphibians. The students and colleagues working with him seek to provide genetic and ecological data relevant to those conservation efforts. (Photographed by James Stout).