A Tale of Two Turtles: Sympatry of Two Lotic Musk Turtle Species in the Pascagoula River Drainage

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Abstract.—Competition and hybridization between closely related species have remained topics of interest for decades. The ranges of the Razorback Musk Turtle (*Sternotherus carinatus*) and Stripe-necked Musk Turtle (*Sternotherus peltifer*) are mostly non-overlapping, but they are sympatric in south and central Mississippi, USA. In allopatry, each species fills the niche of a lotic, bottom-walking musk turtle and each can range in habitat from small, montane headwater streams to large, muddy bayous in the coastal plain. Using environmental, morphological, and genetic data, we assessed whether the two species exhibit different habitat associations, differ in morphology, and maintain reproductive isolation in sympatry. The two species differed significantly in habitat association in sympatry, with the Stripe-necked Musk Turtle occurring primarily in small streams or headwater stream habitats and the Razorback Musk Turtles frequenting larger riverine habitats. The two species occurred in syntopy in intermediate habitats, and while we detected three individuals with mixed ancestry, hybridization is likely precluded by both pre- and postzygotic barriers, notably the significant differences in body size between species and the reversed sexual size dimorphism exhibited by each species.

Key Words.—hybridization; Razorback Musk Turtle; species interactions; *Sternotherus carinatus*; *Sternotherus peltifer*; Stripe-Necked Musk Turtle; sympatry; syntopy

Introduction

Competition between closely related species has long been a focal point in ecology. Voltera (1926) and Gause (1934) were the first to posit that if the requirements of two species are sufficiently similar, then only one species should be able to persist. Later, Brown and Wilson (1956) coined the term character displacement to describe a mechanism that would allow two similar species to co-occur. Character displacement, as they defined it, is the divergent patterns of ecology, behavior, physiology, and/or morphology of two similar species where they occur together. Shortly thereafter, MacArthur (1958) demonstrated this in sympatric warbler species, five species of warbler shared common prey resources, but partitioned the tree canopy habitats, which reduced interspecific competition. This work led to the concepts of realized and fundamental niches of species. In the absence of a competitor, a species can generally occupy its fundamental niche and access the full range of available biotic and abiotic conditions under which can grow and reproduce. In contrast, when two species co-exist, the niche that each occupies should be narrower than their respective fundamental niches, and this concept is deemed their realized niche (Hutchinson 1957; Griesemer 1992). This coexistence between closely related forms can be defined in a few ways. Rivas (1964) helped clarify and define these terms by describing the overlap of species ranges as sympatry, but he reserved the term syntopy for a special form of sympatry in which the species co-occurred in the same locality. Similarly, Rivas (1964) defined allopatry as species with different geographic distributions, and allotopy as sympatric species that do not co-occur within the same locality.

Within chelonians, examples of resource partitioning in sympatry and syntopy are not uncommon. For example, niche overlap has been examined in marine turtles (Pike 2013), Australian turtles (Meathrel et al. 2002; Welsh et al. 2017), and South American turtles (Alcalde et al. 2010). Within the U.S., map and sawback turtles (genus *Graptemys*) are the most speciose group of turtles in the country (Vogt 1981; Fuselier and Edds 1994; Lindeman 2000) and provide many examples of character displacement. When two species of *Graptemys* co-occur within a river drainage, one species specializes on a molluscivorous diet with females (the larger sex) developing large, well-developed alveolar surfaces and mega- or mesocephaly (Lindeman 2000, 2013),
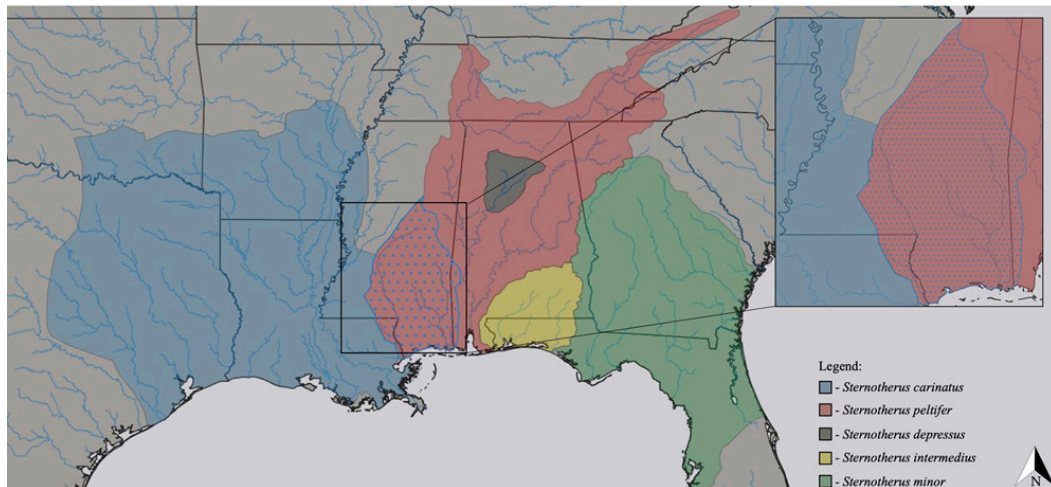
FIGURE 1. Range map of the lotic *Sternotherus* species in the southeastern U.S. The area of sympatry between Razorback Musk Turtles *(Sternotherus carinatus)* and Stripe-necked Musk Turtles (*Sternotherus peltifer*) is indicated on the map and inset.

whereas the congener has a small head used for a primarily spongivorous diet (Vogt 1981; Siegel and Brauman 1994; Lindeman 2013). This pattern is replicated across many Gulf Coast drainages from the Sabine to the Mobile Bay drainages (Lindeman 2013).

Lotic musk turtles (genus *Sternotherus*, excluding *S. odoratus*) follow a similar distribution across river drainages of the southeastern U.S., but unlike for *Graptemys*, rivers typically support only one species per drainage. There are currently five recognized forms of lotic *Sternotherus* (from west to east: Razorback Musk Turtle, *S. carinatus*, Stripe-necked Musk Turtle, *S. peltifer*, Flattened Musk Turtle, *S. depressus*, Intermediate Musk Turtle, *S. intermedius*, and Loggerhead Musk Turtle, *S. minor*; Scott et al. 2018) that share very similar ecologies and have mostly non-overlapping distributions (Fig. 1). The exceptions are *S. peltifer* and *S. depressus*, which come into contact at the Fall Line of the Black Warrior River, and *S. carinatus* and *S. peltifer* in the Pearl and Pascagoula River drainages (Ernst and Lovich 2009). Whereas contact between *S. depressus* and *S. peltifer* is limited to a geologic feature (the Fall Line), Stripe-necked and Razorback Musk turtles are sympatric throughout two river drainages (the Pearl and Pascagoula) at the eastern- and westernmost extent of the ranges of each species (Fig. 1).

Sternotherus carinatus and *S. peltifer* occupy very similar ecological roles in lotic habitats in allopatry, i.e., east of the Pascagoula (*S. peltifer*) and west of the Pearl (*S. carinatus*; McCoy et al. 1978, 2020). For example, *S. peltifer* can be found throughout most of the Mobile River drainage and large portions of the Tennessee River drainage, from small streams dominated by boulders and cobble in the Blue Ridge Mountains of the Southern Appalachians to the large, turbid, and slow-moving Alabama River (Peter Scott, pers. comm.). Similarly, *S. carinatus* is found in montane creeks of the Ouachita uplands down to the bayous of the Gulf Coast (Kavanagh and Kwiatkowski 2016; pers. obs.). For some time, *S. peltifer* was presumed to be absent in the Pascagoula (Iverson 1977) until Vogt et al. (1978) trapped the species in the Chickasawhay River at Waynesboro, Mississippi (see also McCoy et al. 2020).

No studies have attempted to fully document the distribution and abundance of *S. peltifer* within the Pearl and Pascagoula drainages. Since the species was confirmed in the Pascagoula River drainage in 1978, only seven other localities (seven individuals) for *S. peltifer* have been reported from the entirety of the Pascagoula River drainage with very few localities known within the Pearl River drainage (Iverson 1977). Although no hybrids between these two species have ever been reported from the wild, hybridization events are not uncommon in turtles (Parham et al. 2013; Godwin et al. 2014) and hybridization has previously been documented between *S. peltifer* and *S. depressus* at the Fall Line in Alabama (Scott and Rissler 2015; Scott et al. 2019).

While some studies have looked at species of *Sternotherus* in syntopy (Berry 1975; Brown 2008), these studies focused on interactions between the lotic *S. minor* (Berry 1975) and *S. carinatus* (Brown 2008) with a lentic species (*S. odoratus*). No work

has focused exclusively on the overlap of two lotic *Sternotherus* species, however, which would provide a unique opportunity to better understand the ecological (abiotic and/or biotic) drivers influencing their distributions. We investigated potential interactions between the *S. carinatus* and *S. peltifer* in the Pascagoula River system. Specifically, we asked: (1) do the two species differ significantly in their habitat association; (2) do the species differ in morphology; and (3) are the two species maintaining reproductive isolation, particularly at sites of syntopy?

MATERIALS AND METHODS

Site selection.—We used Stratified Random Sampling to select 60 potential trapping locations from points of public access (boat launches, bridge crossings, etc.) for the 2018 trapping season. We used the Elevation Derivatives for National Application (EDNA) watershed layer for the Pascagoula river drainage from the U.S. Geological Survey as well as GIS data for Mississippi roads from Mississippi Geospatial Clearinghouse (http://www.census.gov/geo/www/tiger). After intersecting these two layers, we created a pool of potential access points to streams and rivers, which we then combined with coordinates for public boat launches on rivers within the Pascagoula drainage.

We classified sites into one of three groups based on discharge data from the EDNA watershed layer: small stream (0.5–10 m^3/sec), intermediate-sized streams (10–100 m^3/sec), and larger rivers (100+ m^3/sec). We randomly selected 20 sites from each category. These sites were screened with GoogleMaps (www.maps.google.com) to verify that the stream crossing selected represented a natural, lotic environment and not irrigation ditches, which were common on the landscape.

Trapping.—During systematic trapping efforts in 2018, we accessed stream or riverine sites by wading (small streams), canoe (intermediate streams and rivers without boat launches), or johnboat (rivers where boat launches were available). At each site, we set 15 collapsible 36" × 12" minnow traps (Promar & Ahi USA, Gardena, California, USA) for two nights, for a total of 30 trap-nights per site. We set traps in shallow water (25–100 cm in depth) near suitable habitat (e.g., woody debris, log jams, or rock ledges) and baited them with one can of sardines in soybean oil. We tied all traps to a stationary point (i.e., secure instream deadwood or the bank). To account for any fluctuations in water level and to reduce the risk of drowning by a turtle, we placed an empty water bottle in each trap. We checked traps every 24 h for 48 h. We also hand caught turtles opportunistically while setting and checking traps.

Data collection.—For each *Sternotherus* species trapped and/or caught, we recorded standard morphometrics, mass (g), and the presence of any injuries or abnormalities. We also collected a small genetic sample (5–10 mm piece of interdigital tissue from the hind food), which was stored in 95% ethanol. We also collected additional genetic and morphometric data opportunistically outside of the 2018 field season for other studies and were included in this study, but environmental and trap data were not collected at those sites and were not included in subsequent analyses of habitat associations.

For sites visited in 2018, we collected stream habitat variables at each site to investigate if there were differences in habitat use by each species. We collected these data 24 h after we set traps. Stream habitat metrics were taken at 25, 50, and 75% of the length of transect. At these three points along each transect, we collected the following stream metrics at 25, 50 and 75% of the wetted stream width: (1) stream substrate composition (using a modified Wentworth scale where 1 = silt/mud, 2 = sand, 3 = pea-sized gravel, 4 = large gravel, 5 = cobble, and 6 = bedrock and/or soapstone; Cummins 1962); (2) amount of deadwood (0 = absent, 1 = small amount woody debris, and 2 = abundant deadwood); (3) stream width (m); (4) stream depth (cm); (5) canopy cover (approximated categorically to 0%, 25%, 50%, 75% or 100%); and (6) turbidity (0 = very clear, 1 = clear with tannins, 2 = turbid, and 3 = very turbid). From GIS, we used the National Hydrology Plus database to extract the cumulative upstream drainage area (CDA) at each site as a descriptor of stream size (https://www.usgs.gov/national-hydrography/access-national-hydrography-products).

Statistical analysis.—We used only adult turtles in statistical analyses of morphology (> 80 mm carapace length [CL] in *S. carinatus* and > 70 mm CL in *S. peltifer*; modified from Iverson 1977). For adults, we used a Two-factor Analysis of Variance (ANOVA) with species and sex as factors to test three null hypotheses: (1) the two species were equal in mass; (2) the two sexes were equal in mass; and (3) there was no interactive effect on mass between species and

sex. We chose mass to test these hypotheses as many turtles exhibited damage to the carapace or plastron, which affected length measurements. After a log transformation of mass, data for each hypothesis met the necessary assumptions of normality and equal variances. We used a post hoc test (Tukey HSD) to determine where significant differences occurred. We performed all statistical analyses in the stats package in R v. 4.1.2, and we set all alpha values at 0.05.

For habitat data, we used a Canonical Correspondence Analysis (CCA) using the vegan package in R to determine any habitat associations between turtles and different lotic habitats. A CCA is used to evaluate the associations between two sets of variables and allows one to visualize these associations in ordination space (ter Braak 1986; Legendre and Legendre 2012). Because stream characteristics can be highly correlated, we checked for multicollinearity across habitat variables by examining the variance inflation factor scores (VIF scores; Legendre and De Cáceres 2012), and if two variables were too highly correlated (VIF scores > 4; Hair et al. 2011), we removed one from the analysis and we re-evaluated VIF scores before proceeding with the CCA. We used a PERMANOVA with either stream metric or CCA axes as fixed variables with 10^5 permutations to detect whether that axis or variable explained a significant amount of the variance in the dataset. We set alpha levels at 0.05. In the first CCA, we included environmental data where *Sternotherus* were detected to test for habitat associations between these two species and in a second CCA, we plotted the habitat associations of every turtle species with > 5 detections (i.e., observed > 10% of the time).

Genetic analyses.—We collected tissue from 210 *S. carinatus* and *S. peltifer* from trapping in the spring, summer, and fall of 2018. We collected an additional 185 tissue samples from *S. carinatus* and *S. peltifer* opportunistically for other studies of these species. In total, we analyzed tissues from 433 lotic *Sternotherus* in our study, and we genotyped 211 *S. carinatus* and 222 *S. peltifer* from the Pascagoula River drainage across six diagnostic microsatellite loci. We confirmed the identification (to species) of each individual *Sternotherus* through genetic analyses of microsatellite loci and a mitochondrial marker. Total genomic DNA was extracted from tissue samples with a DNeasy Tissue Kit (QIAGEN Inc., Valencia, CA). Brown and Kreiser (2020) identified six diagnostic microsatellite loci (Scar06, Scar08, Scar26, Scar27, Scar29, and Scar39) for *S. carinatus* and *S. peltifer*

with species-specific allele sizes that do not overlap with those present in the other species. Polymerase chain reaction conditions and thermocycler profiles followed Brown and Kreiser (2020). Microsatellite alleles were visualized on a polyacrylamide gel using a LICOR 4300 DNA Analyzer. Alleles were sized using GeneProfiler ver. 4.05 (LICOR Co.). We tested for linkage disequilibrium among loci within each species using Genepop on the Web (Raymond and Rousset 1995; Rousset 2008). We applied a Bonferroni correction to the alpha value to account for multiple comparisons (Rice 1989).

We used STRUCTURE v. 2.3.4 to determine the proportion of the ancestry of each individual for both *S. carinatus* and *S. peltifer*. We tested for a K of 2 for the two species, without using location as a prior and assuming correlated allele frequencies with admixture between groups. We performed 10 independent runs of a K of 2 with a burn in of 50,000 and 100,000 MCMC replications. We used CLUMPP (Jakobsson and Rosenberg 2007), as performed by StructureSelector (Li and Liu 2018), to average all 10 runs, which were then subsequently visualized using Distruct v. 1.1 (Rosenberg 2004).

To evaluate maternal ancestry of each turtle, we used a diagnostic restriction fragment length polymorphism (RFLP) of the mitochondrial gene Cytochrome b (cytb). We modified the cytb-B and cytb-L primers of Shaffer et al. (1997) to better match the sequences available on GenBank for *S. depressus* (KT865054), *S. peltifer* (KF301364) and *S. carinatus* (HQ114563). The new sequences for these primers were cytb-B-f: CCCTCAAACATTTCAGCCTGATGAAA and cytb-L-r: TCTTCAACTGGTTGTCCTCCAATTCA. We then aligned sequences for other kinosternids (Shaffer et al. 1997; Scott and Rissler 2015) with Sequencher 4.10.1 (Gene Codes; Ann Arbor, Michigan) and determined that the restriction endonuclease DpnII produced species-specific fragment patterns. Using the polymerase chain reaction, we amplified this portion of the mitochondrial genome in 25-μL reactions consisting of 15.9 μL of dH2O, 2.5 μL 10× standard Taq (Mg-free) buffer (New England Biolabs), 2.0 μL 2 mM dNTPs, 2.0 μL 25 mM MgCl2, 0.3 uM of each primer, 0.5 units Taq polymerase (New England Biolabs), and 20–50 ng of DNA template. PCR cycling conditions were as follows: initial denaturation at 94° C for 2 min, 30 cycles of 1 min at 94°C, 1 min at a 50°C, and 1 min at 72° C, with a final elongation of 7 min at 72° C. Restriction digests using DpnII (New England Biolabs) took place in a 20-μL volumes of 7.9 μL of dH2O, 2 μL

10x DpnII reaction buffer (New England Biolabs), 0.1 μL of DpnII (New England Biolabs), and 10 μL of PCR product. We incubated samples at 37° C for 4 h. We visualized the restriction fragment digests and a 100-bp size standard (New England Biolabs) on a 1.5% agarose gel stained with ethidium bromide. We scored individuals as having a haplotype of either *S. carinatus* or *S. peltifer*.

Trapping.—We trapped 57 (20 small, 19 medium, and 18 large) riverine and stream sites. We chose 52 of these sites from the stratified random sampling of access points in GIS, and we selected five as known sites for each species (Table 1). The total effort we accumulated was 1,509 trap-nights across the Pascagoula River watershed (520, 523, and 466 trap-nights at small, medium, and large lotic sites, respectively). We lost 174 trap nights associated with Alligator Snapping Turtle (*Macrochelys temminckii*) interference, where the turtle would rip open nets and steal the tin of bait (Brown 2023), and we lost another 27 trap nights to water level fluctuations or meso-mammal interference.

TABLE 1. Summary of the 2018 field season in the Pascagoula River system, Mississippi, USA, including the number of sites where each turtle species was encountered, the number encountered, and catch per unit effort (CPUE) calculated from the number of turtles caught divided total trap nights (1509). Site-specific localities are available upon request, but they are withheld for the protection of these species.

Species	# Sites Detected	n	CPUE
Spiny softshell (*Apalone spinifera*)	8	10	0.007
Smooth Softshell (*Apalone mutica*)	1	1	0.001
Southeastern Mud Turtle (*Kinosternon subrubrum*)	1	1	0.001
Alligator Snapping Turtle (*Macrochelys temminckii*)	20	26	0.017
River Cooter (*Pseudemys concinna*)	3	3	0.002
Razorback Musk Turtle (*Sternotherus carinatus*)	22	88	0.058
Eastern Musk Turtle (*Sternotherus odoratus*)	6	7	0.005
Stripe-necked Musk Turtle (*Sternotherus peltifer*)	30	101	0.067
Pond Slider (*Trachemys scripta*)	21	64	0.042

RESULTS

In total, we captured 346 turtles of nine species across 53 of the 57 sites (Table 1); however, in addition to those species trapped, we observed three other species during this study that were not caught in traps. We encountered only two *Chelydra serpentina* near traps, as well as both map turtle species (Pascagoula Map Turtle, *G. gibbonsi,* and Yellow-Blotched Sawback, *G. flavimaculata*) which are more bait averse than other turtle species (Boyer 1965; Selman and Qualls 2009; Lindeman 2013).

We detected *Sternotherus* at 43 of the 57 sites (Table 1; Fig. 2). *Sternotherus carinatus* was found at 22 river and stream sites. We caught *Sternotherus peltifer* at 30 stream and river sites, and we detected both species in syntopy at nine sites (Fig. 2). In total, we trapped 189 *Sternotherus* during these systematic trapping efforts with *S. peltifer* the most frequently encountered turtle species (n = 101, plus nine hand captures; catch per unit effort [CPUE] = 0.07). The second most caught species was *S. carinatus* (n = 88, plus 12 hand captures; CPUE = 0.06), third most captured was the Pond Slider (*Trachemys scripta;* n = 64; CPUE = 0.04), and the Alligator Snapping Turtle (*M. temminckii*) was the fourth most encountered species (n = 26 juveniles; CPUE = 0.02). In addition, we caught seven *S. odoratus* at six sites, as well as three Southeastern Mud Turtles (*Kinosternon subrubrum*) at one stream site. Kinosternids made up 57.5% of all turtles caught. In addition to the trapping locations above, from 2015 to 2019, we opportunistically detected (through work on other projects) *S. carinatus* at an additional 15 sites, *S. peltifer* at an additional 11 sites, and five additional syntopic sites, for a total of 64 sites across the Pascagoula River drainage (Fig. 2).

Habitat associations.—In 2018, upstream drainage area ranged from 12.0 km² to 21,195 km² (the Pascagoula River). *Sternotherus* were detected at sites ranging from 17.8 km² to 17,162 km² (the Pascagoula River). The first CCA analysis of habitat associations between just *S. carinatus* and *S. peltifer* explained 65.2% of the variation in habitat use (i.e., constrained inertia). Because there were only two species in this model, there was only one CCA axis that explained a significant amount of variation in the dataset ($F_{1,41}$ = 78.80, P = 0.001), and this axis was driven by stream size. Four habitat variables were included in the model (all had VIF scores < 4; Hair et
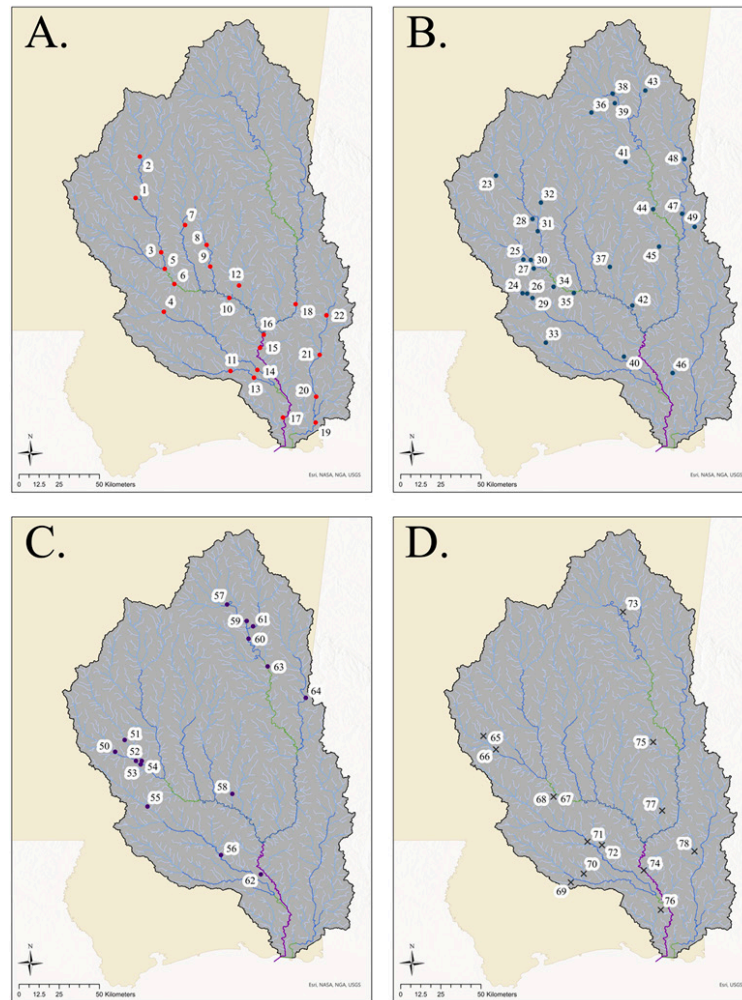
FIGURE 2. Capture locations within the Pascagoula River system, Mississippi and Alabama, USA, for (A) only Razorback Musk Turtles (*Sternotherus carinatus*), (B) only Stripe-necked Musk Turtles (*Sternotherus peltifer*), (C) syntopy, and (D) sites where no *Sternotherus* were detected. Stream size metrics for each site can be found in the appendix table.

al. 2011), and three of these were significant: stream depth ($F_{1,38}$ = 48.30, P = 0.001), water temperature ($F_{1,38}$ = 12.40, P = 0.005) and canopy cover ($F_{1,38}$ = 7.94, P = 0.005). *Sternotherus carinatus* and *S. pelti-fer* had an opposing and polar relationship along the first CCA axis (1.17 and -0.86 respectively), where *S. peltifer* was associated with smaller, cooler, heavily canopied streams, and *S. carinatus* was found in larger, warmer, open-canopied streams.

The analysis of the community dataset demonstrated similar patterns for the two musk turtle species, but the addition of other species to the model reduced the constrained variance explained to 23.1% (Fig. 3). The first axis (CCA1) remained significant ($F_{1,46}$ = 12.00, P = 0.001) as did the three habitat variables: stream depth ($F_{1,46}$ = 6.60, P = 0.001), canopy cover ($F_{1,46}$ = 3.93, P = 0.006), and water temperature ($F_{1,46}$

= 2.49, P = 0.027). CCA1 was again driven by stream size, and *S. carinatus* and *S. peltifer* are again polar in their position in ordination space (Fig. 3). *Trachemys scripta*, a well-known generalist (Gibbons 1990), occurred near the origin of the CCA, suggesting little habitat preference.

Genetics.—None of the six microsatellite loci demonstrated linkage disequilibrium after a Bonferroni correction. We did not explicitly test for Hardy-Weinberg Equilibrium as we were not interested in population subdivision in these species but rather the ancestry of each, which does not hold the genetic data to the same assumptions. Because loci were diagnostic for each species, we still included individuals with missing data into the STRUCTURE analysis, but the microsatellite dataset was 92%
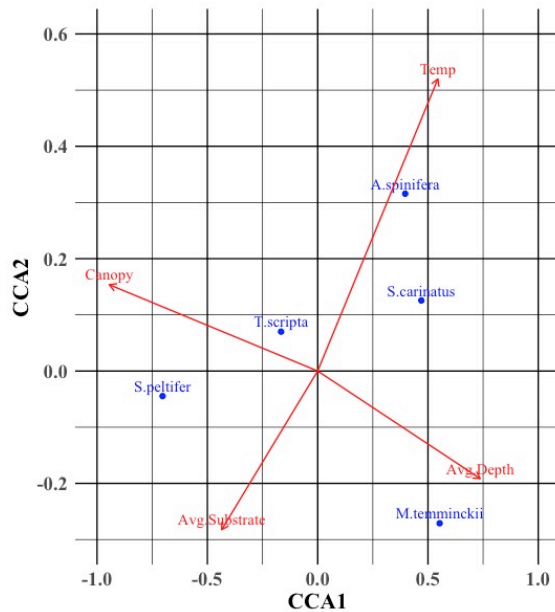
FIGURE 3. A Canonical Correspondence Analysis plot of all turtle species encountered at > 10% of all sites. Abbreviations are Temp = water temperature, Avg.Depth = average stream depth, Canopy = average percentage canopy cover, and Avg.Substrate = average substrate score. Species are in blue.

complete. Amplification of the mitochondrial cytb locus produced a 965-bp fragment. Digestion by DpnII produced different fragment sizes for *S. peltifer* (934 and 31 bp) and *S. carinatus* (794, 190 and 31 bp), with no other haplotypes observed in the 433 individuals screened.

In the microsatellite dataset, STRUCTURE determined that of 433 turtles, only three demonstrated some level of mixed ancestry (q-score < 0.90; Fig. 4, Table 3). None of these turtles were missing microsatellite data, which can sometimes produce artificially high q-scores. We identified two

TABLE 2. Average ancestry coefficients (q-scores) of 211 Razorback Musk Turtles (*Sternotherus carinatus*) and 219 Stripe-necked Musk Turtles (*Sternotherus peltifer*) from the Pascagoula River drainage of Mississippi and Alabama, USA. The three S. peltifer of mixed ancestry were not included in the averages for the species, instead they are reported separately. The abbreviation SD = standard deviation.

Species	Average *carinatus* ancestry	Average *peltifer* ancestry	SD
S. carinatus	0.992	0.008	0.01
S. peltifer	0.007	0.993	0.007
S. peltifer of Mixed Ancestry			
Sp85	0.196	0.804	
Sp93	0.328	0.672	
Sp136	0.445	0.555	

in the field as *S. peltifer* while the third (ID# Sp136) appeared to have characteristics of both species, and it was noted as a putative F1 hybrid (see Brown 2021). Excluding the turtles of mixed ancestry, the average ancestry coefficient (q-score) for *S. carinatus* was 0.991 (standard deviation [SD] = 0.010), and the average q-score for *S. peltifer* was 0.993 (SD = 0.007; Table 2). Of the turtles with mixed ancestry, one was from an area of known syntopy; another from a small stream immediately upstream from a syntopic stretch of river, and the third from a small tributary near habitat that looked suitable for co-occurrence of the two, but trapping failed to detect either species. The individual identified in the field as a hybrid had q-scores reflecting approximately 50% ancestry from each species, whereas the other two had *S. peltifer*-dominated q-scores (0.80 and 0.67; Table 3). The two *S. peltifer* of mixed ancestry had S. peltifer mtDNA haplotypes as did the putative hybrid, and all remaining RFLP haplotypes matched species designation upon capture.

Morphology.—There was a significant effect of species ($F_{1,298}$ = 234.6, $P < 0.001$) and a significant interaction of species and sex ($F_{1,298}$ = 22.7, $P < 0.001$), but no significant effect of sex ($F_{1,298}$ = 0.024, $P = 0.878$). The significant interaction between sex and species indicated that *S. carinatus* was significantly heavier (mean = 240.6 ± 75.1 g) than *S. peltifer* (mean = 140.1 ± 44.2 g) in the Pascagoula River drainage and that both species exhibited sexual dimorphism within the Pascagoula River drainage, but in opposite directions. In *S. carinatus*, males were significantly heavier (mean = 261.2 ± 82.8 g) than females (mean = 219.7 ± 59.9 g), while in *S. peltifer*, females were significantly heavier (mean = 152.8 ± 44.9 g) than males (mean = 127.8 ± 40.1 g; Fig. 5).

DISCUSSION

Sternotherus carinatus and *S. peltifer* are both wide-ranging lotic *Sternotherus* species in the southeastern U.S. that occupy very similar niches across their geographic distributions. In allopatry, they can be found across the river continuum in headwater streams and feeder creeks to large rivers and bayous. Prior to this study, very little was known about *S. peltifer* from the Pascagoula River system, with only a handful of scattered records from throughout the drainage. We found *S. peltifer*

Sternotherus carinatus   *Sternotherus peltifer*
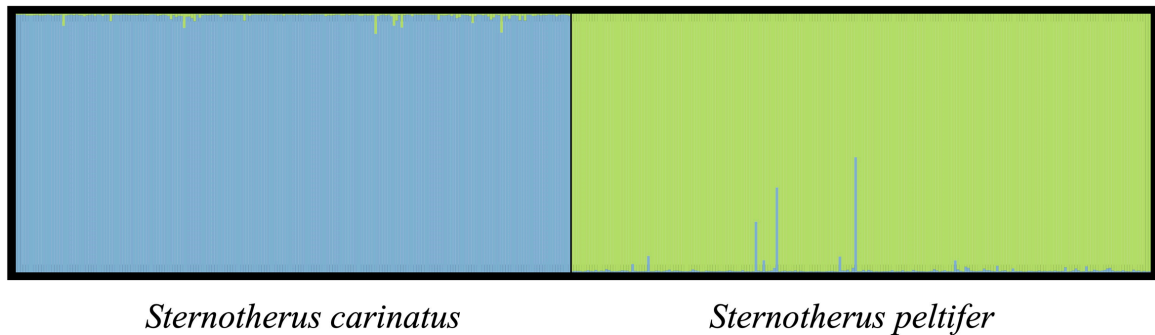
FIGURE 4. STRUCTURE plot for 211 Razorback Musk Turtles (*Sternotherus carinatus*) and 222 Stripe-necked Musk Turtles (*Sternotherus peltifer*) from the Pascagoula River drainage, Mississippi and Alabama, USA. The bars in this bar plot represent the percentage ancestry from each species for each turtle (1 bar = 1 turtle). Only three *S. peltifer* demonstrated evidence of mixed ancestry.

to be abundant (detecting 222 individuals) and distributed throughout most of the major tributaries of the drainage (except for the Escatawpa River). *Sternotherus carinatus* is well-known from the drainage; however, most data on the species were incidental to work with other species, notably the endangered *Graptemys flavimaculata* (Lindeman 1996; Lindeman 1999; Selman and Qualls 2009; Vogt 2020). Kinosternids made up 57.5% of all turtles caught, illustrating the effectiveness of using small, baited traps for these species (see Brown 2023).

Our work is the first to evaluate the ecology and the co-occurrence of *S. carinatus* and *S. peltifer* in sympatry. Because they share such similar ecologies, this study touches on some of the earliest and central motifs of ecology: competition between closely allied forms (Darwin 1859). Competition is often more intense in closely related species, and the theory of competitive exclusion postulates that if two species are competing for the same limiting resources in an environment without differentiation (e.g., environmental, ecological, or morphological), one species will outcompete the other (Gause 1934, Gilbert et al. 1952; Harper et al. 1961). There are conditions, however, under which closely related species can coexist. Chunco et al. (2012) suggested that species can co-occur at intermediate environmental conditions, under the most extreme conditions, or independent of environmental conditions, but dependent on other biotic characteristics like dispersal ability. In the case of sympatric *S. carinatus* and *S. peltifer*, we found the two species differed significantly in their habitat associations, with *S. peltifer* inhabiting smaller streams (higher canopy cover with higher substrate score and cooler water temperatures) and *S. carinatus* occupying larger water bodies (which were deeper and warmer). For most sites (about 80%),

only one species or the other was detected; however, there were nine syntopic sites detected during 2018 trapping efforts and an additional five syntopic sites that were discovered through opportunistic and collaborative sampling for other studies. Most of these syntopic sites had environmental factors that made them suitable for both species as suggested by the framework of Chunco et al. 2012 (i.e., the intermediate environmental conditions). These sites were typically in headwater reaches of rivers (11 of 14) that had intermediate levels of canopy cover, high substrate scores, and provided an interface between small feeder streams and river stretches. This sort of syntopy between closely related species in intermediate habitats has also been documented in salamanders (Walls 2009), birds (Swenson 2006), mammals (Kamler et al. 1998), and fishes (Schaefer et al. 2011). Intermediate habitats could offer non-limiting resources allowing coexistence.

A potential consequence of syntopy in congeneric species is hybridization. The study of hybridization between closely related species or genetically distinct populations has been of interest and has important implications across a number of fields in biology, particularly in conservation biology (Todesco et al. 2016), systematics (Berger 1973), and evolutionary biology (Hilbish et al 2012). We used both nuclear and mitochondrial markers to determine not just whether there is gene flow between species, but also the directionality of the gene flow, as sometimes hybridization only happens unidirectionally (McGowan and Davidson 1992; Wirtz 1999; Beatty et al. 2010; Den Hartog et al. 2010; Scott et al. 2019). Because the two species in our study overlapped at intermediate habitats, we expected that there could by hybrid zones along these stream reaches. This was not the case, however, as we found no indication of a hybrid zone between these two species despite over
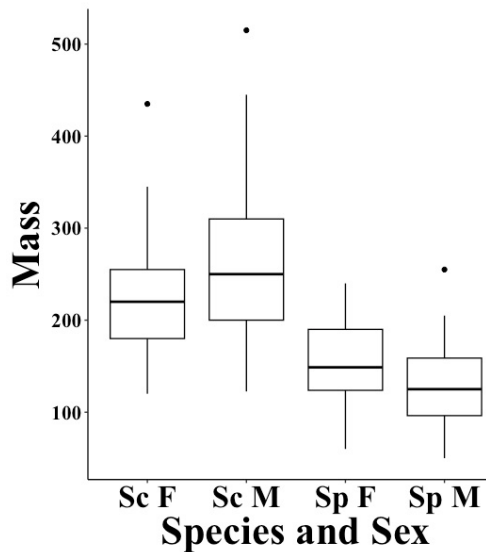
FIGURE 5. Masses of adult Razorback Musk Turtles (*Sternotherus carinatus*) and Stripe-necked Musk Turtles (*Sternotherus peltifer*). Dark horizontal bars represent median values; boxes represent the upper and lower quartiles, vertical lines represent the upper and lower extremes, and dots represent outliers in the dataset.

a dozen documented sites of syntopy. While there was one documented hybrid, and two potentially back-crossed individuals, these were very rare in the dataset (three of 433; a frequency of about 0.7%). In the Bouie River, we captured both *S. carinatus* and *S. peltifer* at the three sites sampled: a contact zone stretching a minimum of 24.1 km, and of the 27 *S. carinatus* and 20 *S. peltifer* captured, no turtles from this stretch of river exhibited evidence of mixed ancestry. Similarly, in Black Creek, both species spanned about 80 rkm of habitat, yet there was still no discernable hybrid zone nor hybrids detected.

While our study was not able to explicitly test whether pre- or postzygotic barriers prevented the formation of hybrid zones between these two species, some inferences can be drawn from phylogenetic, morphometric, and other data on these species. The phylogenetic position of *S. carinatus* and *S. peltifer* has fluctuated over time, but the most recent studies (Iverson et al. 2013; Scott et al. 2018) describe a clade that includes *S. minor, S. peltifer, S. depressus,* and *S. intermedius,* with the other two *Sternotherus* (*S. odoratus* and *S. carinatus)* as sister taxa. Morphologically, *S. carinatus* in the Pascagoula River drainage, is a significantly larger species than *S. peltifer.* Interestingly, the two species have opposing sexual dimorphism with males being the larger sex in *S. carinatus* and females being the larger sex in *S. peltifer.* Sexual dimorphism in razorback musk

turtles has been well-documented (Ernst and Lovich 2009; Kavanagh and Kwiatkowshi 2016), while most of the data on sexual dimorphism within the *minor* complex has focused on *S. minor* sensu lato, with little or no data published on sexual dimorphism in *S. peltifer.* Larger males in *S. carinatus* could be due to competition for resources, territories, or females. Many males in this study (Grover Brown, unpubl. data) showed damage to posterior marginals, similar to male-male aggression documented in *S. minor* (Pignatelli et al. 2023). As the smaller species, it may be that females in *S. peltifer* are the larger sex due to egg size constraints and/or optimal clutch sizes (i.e., fecundity selection). Heston et al. (2022) found such a trade-off between optimal egg size and morphological constraints in *S. minor* (a species more similar in size to *S. peltifer*). In their study, female turtles would produce suboptimal (i.e., small) eggs when young, converging on similar (but not allometric) egg sizes as adults along with an increase in clutch size, but little is known about egg and clutch sizes in *S. peltifer.*

The discrepancies between the opposing sexual dimorphism between species may explain the unidirectional gene flow seen in the mtDNA data of the three turtles of mixed ancestry that all had peltifer haplotypes. Gene flow was only observed from interspecific matings between male *S. carinatus* and female *S. peltifer.* Logistically, it seems more likely that a male *S. carinatus* would attempt to copulate with a similarly sized or smaller female *S. peltifer*, than for a diminutive *S. peltifer* male to attempt to mate with a significantly larger *S carinatus* female, but this is just speculation.

The results of our study closely parallel long-standing theories in ecology and evolutionary biology about the interactions and co-occurrence of closely related species (Gause 1934; Diamond 1975). Lotic *Sternotherus* provide a unique example within turtles to study the effects of closely related species that potentially compete for resources. Other species, like those in the genus *Graptemys*, have evolved to fill divergent niche space where congenerics co-occur (Lindeman 2008). When in sympatry, one *Graptemys* species typically exhibits megacephaly for a molluscivorous diet, while the other species is microcephalic for a diet of freshwater sponges or invertebrates (Lindeman 2008, 2013, 2016; Selman and Lindeman 2018; Vogt 2020). We found that *S. carinatus* and *S. peltifer* differed from *Graptemys* by separating primarily in habitat use, which is not unusual in lotic taxa. There are analogous examples

within fishes, most similarly in the Blackstripe Topminnow (*Fundulus notatus*) species complex found also in the Pascagoula drainage. Duvernell et al. (2013) and Duvernell and Schaefer (2014) found that when in sympatry, the Blackspotted Topminnow (*Fundulus olivaceus*) is typically more abundant in headwater stream habitats, whereas *F. notatus* is more abundant in larger rivers and backwater areas (Braasch and Smith 1965; Thomerson 1966; Thomerson and Wooldridge 1970; Duvernell et al. 2013). Hybrid zones of *Fundulus* are more common in intermediate habitats (Schaefer et al. 2009; Duvernell et al. 2013) compared to what we found in *Sternotherus*. Although *S. carinatus* and *S. peltifer* are similar in ecology in allopatry, in sympatry the two species differ in habitat, size, and sexual dimorphism. It is likely that some combination of these factors as well as their phylogenetic divergence preclude rampant hybridization between these species as has been seen in other syntopic *Sternotherus* species (e.g., *S. peltifer* and *S. depressus*; Scott et al. 2019).

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APPENDIX TABLE. List of sites found in Figure 2, and corresponding stream size data. The symbols + and - stand for present or absent, and UDA is an abbreviation of upstream drainage area in km^2.

Site #	carinatus +/-	peltifer +/-	UDA	Site #	carinatus +/-	peltifer +/-	UDA
1	+	-	633.1	40	-	+	25.4
2	+	-	373.0	41	-	+	88.4
3	+	-	2,719.5	42	-	+	146.0
4	+	-	543.9	43	-	+	194.8
5	+	-	2,795.6	44	-	+	4,278.0
6	+	-	4,698.2	45	-	+	35.4
7	+	-	1,232.0	46	-	+	68.6
8	+	-	695.3	47	-	+	1,319.0
9	+	-	922.4	48	-	+	45.8
10	+	-	7,815.6	49	-	+	80.6
11	+	-	953.1	50	+	+	565.6
12	+	-	312.2	51	+	+	527.9
13	+	-	1,152.2	52	+	+	770.9
14	+	-	1,952.2	53	+	+	788.1
15	+	-	17,162.3	54	+	+	697.3
16	+	-	17,093.9	55	+	+	445.4
17	+	-	21,367.4	56	+	+	1,740.8
18	+	-	6,986.4	57	+	+	942.8
19	+	-	2,323.2	58	+	+	546.5
20	+	-	1,694.9	59	+	+	1,320.9
21	+	-	1,315.7	60	+	+	2,392.7
22	+	-	815.9	61	+	+	977.6
23	-	+	34.3	62	+	+	17,508.3
24	-	+	35.8	63	+	+	3,341.1
25	-	+	57.0	64	+	+	1,026.2
26	-	+	50.8	65	-	-	65.9
27	-	+	1,563.5	66	-	-	12.6
28	-	+	144.4	67	-	-	84.5
29	-	+	30.1	68	-	-	256.4
30	-	+	30.7	69	-	-	48.0
31	-	+	27.7	70	-	-	82.9
32	-	+	245.0	71	-	-	1,257.4
33	-	+	49.0	72	-	-	60.6
34	-	+	33.4	73	-	-	20.2
35	-	+	17.9	74	-	-	17,363.7
36	-	+	40.8	75	-	-	168.9
37	-	+	550.0	76	-	-	21195.1
38	-	+	959.1	77	-	-	342.7
39	-	+	32.8	78	-	-	133.1