Diets of Syntopic Black-knobbed Sawbacks
(Graptemys nigrinoda) and Alabama Map Turtles
(Graptemys pulchra) in the Alabama River

PETER V. LINDEMAN

Abstract.—The emydid turtle genus Graptemys is characterized by intra- and interspecific dietary diversity. Sympatric species pairs typically differ in trophic morphology and dependence on bivalve mollusks in female diets, yet there is a lack of comprehensive comparisons of the diets of sympatric species. I collected feces from 92 black-knobbed sawbacks (G. nigrinoda) and 54 Alabama map turtles (G. pulchra) from the Alabama River at a site in Autauga and Lowndes counties, Alabama. Samples were analyzed separately for unsexed juveniles, adult males, juvenile females larger than the smallest mature males, and adult females of each species. Sponges, aquatic insects (particularly caddisfly larvae), and filamentous algae were the primary foods of G. nigrinoda. Native mussels, invasive Asian clams, and aquatic insects (but few caddisfly larvae) were the primary foods of G. pulchra. Each of the four sex and size classes exhibited substantially greater similarity with conspecific classes than with classes of the other species. Intraspecific interclass similarity in diet showed size-structured patterns in both species but with opposite patterns. In G. nigrinoda the classes that were most similar in diet were the smallest-bodied classes, unsexed juveniles and adult males, which fed most heavily on sponges; the largest-bodied class, adult females, fed most heavily on filamentous algae and was least similar in diet to other classes. In G. pulchra the classes that were most similar in diet were the two largest-bodied classes, adult and juvenile females, which fed most heavily on bivalve mollusks; the smallest-bodied class, unsexed juveniles, was least similar in diet to other classes. These results reinforce the importance of body size in determining Graptemys diets and suggest dietary differentiation of sympatric Graptemys species may extend beyond differentiation in adult females more often than is generally thought.

Introduction

Freshwater turtles exhibit extensive variation in the morphology of the skull, jaws, jaw musculature, and neck that results as species adapt to a variety of feeding niches (Herrel et al., 2002). Diverse freshwater turtle assemblages occur in some parts of the world, where species occupy a variety of feeding niches. The map turtles and sawbacks (Emydidae: Deirochelyinae: Graptemys) are important contributors to the high diversity of freshwater turtle assemblages along the coast of the Gulf of Mexico in the southeastern United States (Buhlmann et al., 2009; Lindeman, 2013). They are distinguished by: (1) their high species diversity that is associated with drainage-specific endemism (nine of the 14 recognized species occur in single Gulf Coastal drainages); (2) exceptional dietary diversity that is associated with morphological variation both within and across species; and (3) their exceptional degree of sexual size dimorphism, with adult males having less than half the shell length and around one-tenth the body mass of adult females (Gibbons and Lovich, 1990; Lamb et al., 1994; Lindeman, 2000a, 2008, 2013; Stephens and Wiens, 2009). Female Graptemys segregate into micro-, meso-, and megacephalic groups (essentially narrow-headed, moderately

1 Corresponding author: Telephone: (814) 732-2417; e-mail: plindeman@edinboro.edu
broad-headed, and extremely broad-headed) that differ according to the degree to which they depend on bivalve and gastropod mollusks in the diet (reviewed in Lindeman, 2000a, 2013). In contrast most reports of diets for the much smaller male conspecifics indicate low consumption of mollusks, regardless of female diet.

Co-occurrence of species of *Graptemys* shows a strong pattern of geographic segregation according to the trophic morphology of adult females (Lindeman, 2000a). In particular the five species that have microcephalic females are each sympatric with species having meso- or megacephalic females: (1) *G. sabinensis* with the mesocephalic species *G. pseudogeographica* in the Sabine-Neches, Calcasieu, and Mermentau drainages; (2) *G. ouachitensis* with *G. pseudogeographica* and in some regions with a second mesocephalic species, *G. geographica*, in the Mississippi drainage; (3) *G. oculifera* with the megacephalic species *G. pearlensis* in the Pearl drainage; (4) *G. flavimaculata* with the megacephalic species *G. gibbonsi* in the Pascagoula drainage; and (5) *G. nigrinoda* with the megacephalic species *G. pulchra* in the Mobile Bay drainage. There is also some overlap of the mesocephalic species *G. geographica* with the megacephalic species *G. pulchra*, and to a much lesser extent with the microcephalic species *G. nigrinoda*, in some upper reaches of the Mobile Bay drainages (Lindeman, 2013). In addition recent reports place two megacephalic species, *G. barbouri* and *G. ernsti*, in limited sympatry in part of the Choctawhatchee drainage (Godwin et al., 2014).

Dietary studies of sympatric species of *Graptemys* are limited to studies of female diets of two mesocephalic species and one microcephalic species in the Mississippi River in Wisconsin by Vogt (1981), who simply noted a qualitative similarity in the diets of males of the three species; studies of two of the same species (one meso- and one microcephalic) in a reservoir on the Tennessee River in western Kentucky (Lindeman, 1997, 2000b, 2013); and separate reports of the diets of syntopic microcephalic and megacephalic species that was limited with regard to the sample size of the latter (Seigel and Brauman, 1994; Selman and Lindeman, 2015). Prior to the present study, diets of sympatric species pairs of micro- and megacephalic species of *Graptemys* have not been compared with detailed attention to variation among size classes and between the sexes.

The primary objective of the present study was to conduct a comprehensive comparison of the diets of *G. nigrinoda* and *G. pulchra* of different age and sex classes for a site in the middle Alabama River where they are syntopic to determine the roles of body size, sex, and the trophic morphology of each species in determining diet. In addition diets of the two species are compared to those of congeners—particularly those of close relatives within the three-species sawback clade that includes *G. nigrinoda* and the five-species clade of species with megacephalic females that includes *G. pulchra* (Wiens et al., 2010)—to develop a more comprehensive view of dietary variation within and among species groups in the genus *Graptemys*.

**Methods**

*Study area.*—Turtles were sampled in a 2 km stretch of the Alabama River below Steele’s Landing, a boat ramp off County Rd. 1, on the border of Autauga and Lowndes counties, Alabama (32.4305° N, 86.8330° W). The Alabama River is the mainstem river of the eastern half of the Mobile Bay drainage. It is a large and deep river that is highly regulated by three lock and dam structures. Water level in the study area rose by ca. 1 m in the early afternoon each day during typical flows, when regular releases were executed ca. 21 river km upstream at the Robert F. Henry Lock and Dam. The river substrate was mud, gravel, and sand. Large fixed woody debris was abundant in the river channel and provided ample basking opportunities for *Graptemys*. 
Field methods.—Field work was conducted 27–31 May 2008, 14–22 May and 16–22 August 2009, 24 June–1 July 2010, 1–8 July 2011, 11–18 June 2012, and 21–25 June 2013. Most turtles were captured using unbaited fykenets (Vogt, 1980) and hoopnets modified as open-top basking traps (Lindeman, 2014), with greater reliance on the former in the first 3 y and greater reliance on the latter (with higher capture rates) in the last 3 y. Additional turtles were also captured using crawfish-wire basking traps (August 2009 only; Selman et al., 2012), a dipnet, and occasional hand capture.

Turtles were measured for plastron length (PL) to the nearest mm using a flexible plastic ruler pressed along the midline of the plastron. Body mass (BM) was measured using a series of Pesola spring scales, to the nearest 1 g for turtles <1000 g and to the nearest 10 g for larger turtles. Sex determination was made on the basis of the location of the cloaca relative to the rear rim of the carapace, with the cloaca distal in males and even with the rim in females (Vogt, 1980). Any individual larger than the minimum observed size of adult males but not exhibiting the cloaca distal to the carapacial rim was categorized as female, with females divided between mature and immature size classes based on the minimum sizes of females determined via palpation of eggs to be gravid (135 mm PL in *G. nigrinoda*, 185 mm in *G. pulchra*). Individuals smaller than the smallest mature male were categorized as unsexed juveniles, including hatchlings in their first full season of growth and 1 y olds exhibiting one post-hatching scute annulus, which were analyzed together due to small sample size of 1 y olds. Before release each individual was marked with a unique (for each species) set of two or three notches filed into the marginal scutes (Cagle, 1939).

To sample feces turtles were confined 1–2 nights in plastic tubs in a few cm of water. Feces were collected using a sieve and stored in ethanol for later analysis. Although recaptures were common (15% of all captures in the last 3 y of the study, both species combined), no individual was sampled twice for feces, with the exception of female *G. pulchra*, which were resampled to further assess the mollusks on which they feed; the data from those recaptures were withheld from calculation of dietary metrics described below. Based on a consideration of the adequacy of sample sizes, sampling of *G. nigrinoda* for feces was discontinued after 2011 with the exception of one juvenile female captured in 2012 and sampling of juvenile and male *G. pulchra* for feces was discontinued after 2012.

Data analyses.—A body-size index (Gibbons and Lovich, 1990) was used to characterize interspecific size differences of males and females of the two species and sexual size dimorphism within each species, with regard to both PL and BM. As modified by Lovich and Gibbons (1992), the index gives the proportion by which the larger species or sex exceeds the smaller species or sex in average size; proportional differences are herein reported as percentages. Attempts to transform PL and BM data to normality were unsuccessful, therefore Wilcoxon rank-sum tests were used in interspecific comparisons of male and female size.

Fecal samples were examined under a stereo dissecting microscope at up to 30× magnification. Prey remains were sorted into taxonomic categories to the degree possible for partially digested, fragmented remains and volume for each category in a sample was determined to the nearest 0.1 mL via volumetric displacement in a graduated cylinder. Caddisfly larval cases were relatively intact and thus could be analyzed separately from other insect remains, which were generally too fragmented to identify. Prey categories in a sample that failed to displace at least 0.1 mL were estimated to be either 0.01 or 0.05 mL in volume. Samples displacing <0.1 mL in total volume were withheld from further analyses, except in the case of samples from unsexed juveniles, which were retained for analyses regardless of total volume.
For each prey category $i$ within a class of turtles within a species, the percent frequency of occurrence ($\%F_i$) and mean percent of sample volume ($\%V_i$) were calculated and used to compute an Index of Relative Importance (IRI; Hyslop, 1980 as modified by Bjorndal et al., 1997) using the equation:

$$\text{IRI}_i = \frac{(\%F_i \cdot \%V_i)}{\sum (\%F_i \cdot \%V_i)}.$$ 

For a particular class of a species, values for IRI sum to 100 across all prey categories, therefore IRI values are a useful means of distilling data on percent frequency and percent volume and making comparisons among dietary data sets (Lindeman, 2013).

An index of dietary overlap ($O_{jk}$) was calculated for pairwise categories within and between species, using the equation of Lawlor (1980):

$$O_{jk} = \frac{\sum (p_{ij} \cdot p_{ik})}{\left[ \sum (p_{ij}^2) \cdot \sum (p_{ik}^2) \right]^{0.5}}$$

where $p_{ij}$ and $p_{ik}$ are the mean proportions by volume of the prey taxon $i$ for the turtle classes $j$ and $k$ being compared. Dietary overlap values were then converted to pairwise distance values ($D_{jk}$) using the equation

$$D_{jk} = -\ln(O_{jk})$$

and $D_{jk}$ values were used to construct a diagram using unweighted pairwise group mean averaging (UPGMA; Sneath and Sokal, 1973) to depict dietary similarity among the eight size and sex classes (four per species). For comparison a UPGMA diagram was also constructed to show dietary similarity among the four size and sex classes of each species of the only other case of a syntopic species pair of Graptemys for which diet has been quantified, *Graptemys ouachitensis* and *Graptemys pseudogeographica* in a western Kentucky reservoir (Lindeman, 1997, 2000, 2013).

**RESULTS**

I captured 156 *G. nigrinoda* and 58 *G. pulchra* between 2008 and 2013. A total of 92 *G. nigrinoda* were sampled for feces: 19 adult females, 43 adult males, seven juvenile females, and 23 unsexed juveniles (all of the last group being hatchlings in their first full year of growth). A total of 54 *G. pulchra* were sampled for feces: 19 adult females, 20 adult males, 11 juvenile females, and four unsexed juveniles (three of the last group were hatchlings in their first full year of growth and one was a 1 y old). Samples from eight *G. nigrinoda* (seven males, one juvenile female) were withheld from analyses because they displaced <0.1 mL in total volume, while all samples from *G. pulchra* displaced at least 0.1 mL in total volume and were included in analyses.

Morphometric data for size and age classes (including individuals not sampled for feces) are given in Table 1. On average adult female *G. pulchra* were 23% longer in PL than adult female *G. nigrinoda* and 125% heavier in BM, with both differences being significant (PL: $Z = 5.78$, $P < 0.0001$; BM: $Z = 5.98$, $P < 0.0001$). Adult males exhibited less of an interspecific size difference, with *G. pulchra* males being 10% longer and 36% heavier, although both differences were again significant (PL: $Z = 4.92$, $P < 0.0001$; BM: $Z = 5.21$, $P < 0.0001$). Sexual size dimorphism was markedly greater in *G. pulchra* than in *G. nigrinoda*,
as adult females were 121% longer and 1071% heavier than adult males in *G. pulchra* vs.
only 97% longer and 607% heavier in *G. nigrinoda*.

The most important prey taxon of male *G. nigrinoda* was freshwater sponges (IRI = 69),
with caddisfly larvae (IRI = 19), other insects (IRI = 4), and filamentous algae (IRI = 7)
also achieving relatively high importance (Table 2). Freshwater sponges were less important
in the diets of females, although sponges were also their most important prey (IRI = 58 for
juvenile females, 48 for adult females); other important taxa were filamentous algae (IRI =
39 for adult females but absent from samples from juvenile females), insects (IRI = 13 for
juvenile females and 7 for adult females), and caddisfly larvae (IRI = 22 and 4, respectively).
Unsexed juveniles had the strongest reliance on sponges (IRI = 89). Sponges were most
prevalent in both percent frequency of occurrence and mean percent volume in the diet of
unsexed juveniles, followed by males and juvenile females, and then adult females. Small
wood fragments were present in 16 of 23 (70%) fecal samples from juveniles, 17 of 43 (40%)
samples from males, 3 of 7 (43%) samples from juvenile females, and 8 of 19 (42%) samples
from females. Samples that contained sponge remains were significantly more likely to
contain wood fragments (39 of 71, 55%; 5 of 21, 24%; \( \chi^2 = 6.29, P = 0.012 \)).

The major prey of male *G. pulchra* were invasive Asian clams (*Corbicula* spp.; IRI = 64),
followed by insects (IRI = 23) and native unionid mussels (IRI = 11; Table 3). The major
prey of female *G. pulchra* were Asian clams (IRI = 60 for juvenile females and 77 for adult
females) and native unionids (IRI = 37 and 22, respectively). For the four sampled unsexed
juveniles, three hatchlings (PL 35–45 mm) passed only insect fragments (IRI = 90 for all
four samples), while a 1-yr-old (PL 60 mm) passed primarily Asian clams (IRI = 9 for all four
samples).

Pairwise overlap indices were high for all intraspecific comparisons of sex and age classes
and low for all interspecific comparisons, which was reflected in a deep separation of the age
and sex classes between the two species in UPGMA clustering (Fig. 1). Clustering of sex and
age classes within each species proceeded in stepwise fashion according to relative body size,
albeit in reversed patterns for the two species: in *G. nigrinoda*, the two smallest-bodied
classes, unsexed juveniles and adult males, clustered first and were then joined in sequence
by juvenile females and adult females, while in *G. pulchra*, the two largest-bodied classes,
juvenile and adult females, clustered first and were then joined in sequence by adult males
and unsexed juveniles.

| Body sizes (midline plastron length, PL, in mm and body mass, BM, in g) for two species of *Graptemys* in the Alabama River |
|---|---|---|---|---|---|---|---|---|
| *Graptemys nigrinoda* | *Graptemys pulchra* |
| Unsexed juveniles | Adult males | Juvenile females | Adult females | Unsexed juveniles | Adult males | Juvenile females | Adult females |
| N | 27 | 65 | 11 | 53 | 4 | 23 | 11 | 19 |
| Mean PL | 45.3 | 81.0 | 97.2 | 159.3 | 47.2 | 89.0 | 155.3 | 196.6 |
| SE | 1.43 | 0.66 | 5.60 | 1.39 | 4.68 | 1.43 | 8.36 | 1.32 |
| Mean BM | 25.1 | 99.3 | 176.3 | 701.7 | 25.4 | 134.6 | 794.7 | 1575.8 |
| SE | 2.61 | 2.49 | 30.82 | 15.62 | 7.09 | 6.35 | 111.85 | 42.95 |
Table 2.—Diet of the black-knobbed sawback (*Graptemys nigrinoda*), with index of relative importance (IRI) calculated from mean percent volume (%V) and percent frequency of occurrence (%F). Juvenile females were <135 mm midline plastron length, the size of the smallest gravid female.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Unsexed juveniles (N = 23)</th>
<th>Adult males (N = 43)</th>
<th>Juvenile females (N = 7)</th>
<th>Adult females (N = 19)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%V</td>
<td>%F</td>
<td>IRI</td>
<td>%V</td>
</tr>
<tr>
<td>Sponges</td>
<td>74</td>
<td>91</td>
<td>89</td>
<td>54</td>
</tr>
<tr>
<td>Insect fragments</td>
<td>11</td>
<td>43</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Caddisfly larvae</td>
<td>7</td>
<td>35</td>
<td>3</td>
<td>19</td>
</tr>
<tr>
<td>Spiders</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water mites</td>
<td>3</td>
<td>9</td>
<td>0.3</td>
<td>2</td>
</tr>
<tr>
<td>Bryozoan colonies</td>
<td>0.9</td>
<td>9</td>
<td>0.1</td>
<td>1</td>
</tr>
<tr>
<td>Asian clams</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Native bivalves</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moss</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf fragments</td>
<td>0.09</td>
<td>2</td>
<td>0.003</td>
<td>0.4</td>
</tr>
<tr>
<td>Fruits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stalked algae</td>
<td>0.05</td>
<td>2</td>
<td>0.002</td>
<td>12</td>
</tr>
<tr>
<td>Filamentous algae</td>
<td>4</td>
<td>22</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>Fungal fruiting bodies</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.—Diet of the Alabama map turtle (*Graptemys pulchra*) with index of relative importance (IRI) calculated from mean percent volume (%V) and percent frequency of occurrence. Juvenile females were <185 mm midline plastron length, the size of the smallest gravid female.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Unsexed juveniles (N = 4)</th>
<th>Adult males (N = 20)</th>
<th>Juvenile females (N = 11)</th>
<th>Adult females (N = 19)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%V</td>
<td>%F</td>
<td>IRI</td>
<td>%V</td>
</tr>
<tr>
<td>Asian clams</td>
<td>21</td>
<td>25</td>
<td>9</td>
<td>52</td>
</tr>
<tr>
<td>Native bivalves</td>
<td>14</td>
<td>55</td>
<td>11</td>
<td>39</td>
</tr>
<tr>
<td>Sphaeriid clams</td>
<td>2</td>
<td>10</td>
<td>0.2</td>
<td>2</td>
</tr>
<tr>
<td>Snails</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insect fragments</td>
<td>75</td>
<td>75</td>
<td>90</td>
<td>24</td>
</tr>
<tr>
<td>Caddisfly larvae</td>
<td>4</td>
<td>25</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Water mites</td>
<td>0.2</td>
<td>5</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Sponges</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf fragments</td>
<td>3</td>
<td>10</td>
<td>0.4</td>
<td>0.5</td>
</tr>
<tr>
<td>Filamentous algae</td>
<td>4</td>
<td>20</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>
Two syntopic species of *Graptemys* differed strongly in diet across all age and sex categories, with each species showing a body-size gradient in reliance upon its predominant prey. Sponges had high importance scores in the microcephalic species *G. nigrinoda*, particularly in the smaller-bodied classes, while bivalve mollusks had high importance scores in the megacephalic species *G. pulchra*, particularly in the larger-bodied classes.

In a large-bodied population of *G. nigrinoda* from the delta of the Mobile Bay drainages, as in the present study, sponges were the most important prey and were more important in male diets than in female diets (Lahanas, 1982; see further quantification in Lindeman, 2013). Sponges are presumably taken via grazing on submerged deadwood, a behavior that has been described in *G. nigrinoda* (Lahanas, 1982; Waters, 1974) as well as for *G. flavimaculata, G. sabinensis*, and male *G. ernsti* (Shively and Jackson, 1985; Seigel and Brauman, 1994; Selman and Qualls, 2008; J. Godwin, pers. comm.). Ingestion of small wood fragments by *G. nigrinoda* probably occurred incidental to feeding on sponges. Wood fragments were more than twice as prevalent in samples that contained sponges as in samples that did not, supporting the link between sponge feeding and incidental ingestion of wood fragments.

The dependence upon freshwater sponges by all classes of *Graptemys nigrinoda* is remarkable, because relatively few vertebrates feed heavily on sponges, presumably due to the protective nature of sponge spicules and defensive chemicals (Hill et al., 2005). In marine environments the hawksbill turtle (*Eretmochelys imbricata*) is a selective sponge specialist and several coral reef fish species from diverse taxa also specialize on sponges (Meylan, 1988; León and Bjorndal, 2002; Andréa et al., 2007). In freshwater environments apparently minor sponge feeding typifies the Australian chelid *Rheodytes leurops* and traces of sponges occur in the diet of the Texas river cooter, *Pseudemys texana* (Legler and Cann, 1980; Tucker et al., 2001; Lindeman, 2007). However, the only reports of sponges predominating in freshwater turtle diets concern *Graptemys*. Besides *G. nigrinoda*, strong reliance on sponges also typifies the microcephalic species *G. flavimaculata* (Seigel and Brauman, 1994; W. Selman and P. Lindeman, unpubl. data). In addition Kofron (1991) reported high incidence of wood fragments in the stomachs of the microcephalic species *G. oculifera*; although he did not report sponges in the diet of the species, it is possible he simply did not recognize partially digested sponge remains in the museum specimens he dissected. If sponges are confirmed to also be an important prey of *G. oculifera*, it would mean that all three species of the “sawback” clade (sensu Wiens et al., 2010) are similar in this regard. Much lower importance of sponges in the diet has also been found for the microcephalic species *G. ouachitensis* and *G. sabinensis*, the mesocephalic species *G. pseudogeographica* and *G. versa*, and males of the megacephalic...
species *G. gibbonsi* (Lindeman, 1997, 2000b, 2006a; Selman and Lindeman, 2015; P. Lindeman, pers. observ.).

Native unionid bivalves have previously been reported in the diet of adult female *G. pulchra* from creeks in the Tallapoosa subdrainage of the Mobile Bay basin (Shealy, 1976). Megacephalic females of two closely related species (*G. ernsti* and *G. gibbonsi*) feed almost exclusively on invasive Asian clams, however, as do the mesocephalic females of *G. caglei* and *G. versa*, therefore the mix of native and nonnative bivalves reported herein for *G. pulchra* is a unique finding for the genus *Graptemys* (Shealy, 1976; Porter, 1990; Lindeman, 2006a; Ennen et al., 2007; Selman and Lindeman, 2015). In the kinosternid turtle *Sternotherus carinatus* in Oklahoma, local abundance of *Corbicula* was inversely related to prevalence of native mollusks (snails and unionid mussels) in the diet (Atkinson, 2013). Similarly, the diet of the kinosternid *Sternotherus odoratus* was more dominated by *Corbicula* in an urban creek in Arkansas that had abundant populations of the invader (Wilhelm and Plummer, 2012) than it was in a Missouri reservoir, where *Corbicula* and native unionid and sphaeriid mussels were all taken at similar moderate frequencies (Ford and Moll, 2004). It is possible *Corbicula* is a less dominant exotic invader in the mussel fauna of the middle Alabama River than in the other areas where the diets of mega- and mesocephalic *Graptemys* species have been studied, which would explain the contrast in the results of the present study.

Also unique in the present results is the high incidence of bivalve mollusks in diets of male *G. pulchra*. In most reports strongly insectivorous males typify the other species of *Graptemys* that have meso- or megacephalic females (Lindeman, 2000b, 2006a, b; Sanderson, 1974; Shealy, 1976; Selman and Lindeman, 2015). Previous exceptions involving high rates of molluscivory in male *Graptemys* have concerned small gastropod prey rather than bivalve prey (White and Moll, 1992; Bulte et al., 2008; Richards-Dimitrie et al., 2013).

Bivalve mollusks were nearly absent from the diet of *G. nigrinoda* in the present study (IRI values ≤1). In the Mobile Bay delta, *G. nigrinoda* of both sexes reached larger sizes than specimens from the Alabama River (to 102 mm PL in males and 202 mm PL in females) and had moderate IRI values (7 for males, 16 for females) for a small native bivalve, *Mytilopsis leucopharata* (Lahanas, 1982; Lindeman, 2013). In the delta region, *G. pulchra* is rare enough to be effectively absent ecologically, raising the possibility that the large body size and moderate molluscivory of *G. nigrinoda* in the delta results from ecological release (Lindeman, 2013), as has also been postulated for *G. flavimaculata* in the near absence of *G. gibbonsi* in the lower Pascagoula River (Selman, 2012). However, *Mytilopsis leucopharata* is a small, thin-shelled, brackish-water species that does not occur in upstream reaches such as the middle Alabama River (Marelli and Gray, 1983). Therefore, the degree of molluscivory in these two populations is not directly comparable to the extent that it may be influenced by differences in factors such as size and shell hardness of the resident bivalve species.

The present study is the first published comprehensive report of dietary overlap among all age and sex classes of two syntopic species of *Graptemys*, as previous dietary studies of the genus have been carried out primarily on single species (reviewed in Lindeman, 2013). Descriptions of dietary differentiation in the genus *Graptemys* have tended to emphasize differences among the large adult females, for which trophic morphological differences are most well developed (Vogt, 1981; Lindeman, 2000a, 2013), yet all age and sex classes were strongly differentiated between species in the present study (Fig. 1).

The diets of syntopic *G. ouachitensis* (microcephalic females) and *G. pseudogeographica* (mesocephalic females) in western Kentucky were reported for combined age and sex classes in Lindeman (2000b), but further breakdown by class is given in other sources (Lindeman, 1997, 2013), allowing a UPGMA diagram to be constructed for comparison to
Figure 1. The result (Fig. 2) shows a pattern very different from the pattern in Figure 1, with close clustering of unsexed juveniles of the two species and close clustering of adult males of the two species but separation of female classes of the two species, with *G. pseudogeographica* females being more molluscivorous and *G. ouachitensis* females being more insectivorous.

The pattern in Figure 2 is similar to what Vogt (1981) reported for syntopic *G. ouachitensis*, *G. pseudogeographica*, and *G. geographica* in Wisconsin, although his lack of quantification for male diets, which he simply stated were very similar, does not allow construction of a UPGMA diagram. Also apparently similar to the Kentucky and Wisconsin results is the case of sympatric *G. flavimaculata* (microcephalic, primarily spongivorous females) and *G. gibbonsi* (megacephalic, primarily molluscivorous females) in the Leaf River of Mississippi (Seigel and Brauman, 1994; Selman and Lindeman, 2015), which have less differentiation of diets in males. Further dietary studies of species in syntopy, with quantification of diets from all classes, will be necessary to determine the prevalence of the two patterns reported to date, i.e., interspecific dietary differentiation that is strongly evident only for female classes (Vogt, 1981; Seigel and Brauman, 1994; Lindeman, 1997, 2000; Selman and Lindeman, 2015) vs. dietary differentiation that typifies all size and sex classes (present study).

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**Literature Cited**


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