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Habitat Partitioning Among Three Sympatric Species of Map Turtles, Genus *Graptemys*

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ABSTRACT.—Three species of map turtles, genus *Graptemys*, were trapped in rivers, streams, and lakes of southeastern and south-central Kansas, and 32 environmental variables were measured at each trap site to compare overlap in habitat use among species. *Graptemys ouachitensis* and *G. pseudogeographica* were collected in rivers with abundant basking sites. However, *G. geographica* was found exclusively in shady streams over rock and gravel substrata. The three species had high habitat overlap index values, but discriminant analysis based on environmental variables separated them into distinct groups. Variables most useful in distinguishing among groups were, in order of decreasing discriminating power, percentage rock substratum, percentage bare shoreline, dissolved carbon dioxide, percentage mud substratum, percentage shade, dissolved oxygen, pH, and stream width. *Graptemys pseudogeographica* was commonly found together with *G. ouachitensis*, but sites of co-occurrence were distinguishable from sites where only one of these species occurred.

Habitat use by map turtles, genus *Graptemys*, is poorly understood. Three of the 11 map turtle species, *G. ouachitensis*, *G. pseudogeographica*, and *G. geographica*, occur in eastern Kansas, but the extent of habitat overlap and partitioning among these species is unknown.

Shively and Jackson (1985) described habitat variables important in determining densities of Sabine map turtle (*G. ouachitensis sabinensis*). Movements of *G. geographica* in both lentic and lotic environments have been investigated, but information on habitat utilization has been limited to basking site selection, nesting areas, and hibernacula locations (Gordon and MacCulloch, 1980; Pluto and Bellis, 1986). Flaherty and Bider (1984) showed that social function influenced the distribution of *G. geographica* in Quebec, but most partitioning studies have concentrated on food habits. Vogt (1981a) showed overlap in food preference among *Graptemys p. pseudogeographica*, *G. o. ouachitensis*, and *G. geographica*, with no difference in food habits among males of these species. Other studies have suggested that food niche separation is common among turtles (Moll, 1976; Vogt and Guzman, 1988), but few have addressed habitat overlap, and none has investigated habitat partitioning among *Graptemys* species.

The purposes of this paper are to examine habitat partitioning among *G. ouachitensis*, *G. pseudogeographica*, and *G. geographica* in Kansas, using environmental variables to discriminate among groups, and to describe habitats of each species in areas of sympatry. Nomenclature follows Vogt (1993).

MATERIALS AND METHODS

We collected turtles at 186 sites in 41 counties of southeast and south-central Kansas, in the Marais des Cygnes, Neosho, Verdigris, Walnut, and lower Arkansas river drainages from April 1990 to September 1991. We used two sizes of commercially available 2.54 cm mesh nylon nets (1.83 m long × 0.76 m or 1.07 m diameter) and set two to 10 nets at each site, depending on size of water body. We trapped one to four days at each site, and number of net nights (one net set for one night) ranged from two to 40. Trapping locations are available from D. Edds. Analysis of variance (ANOVA) of net nights among sites of occurrence of each *Graptemys* species and sites with no *Graptemys* present showed no differences in net nights among sites ($F = 1.89$, $P > 0.1$), therefore equal trapping effort was assumed.

Fresh mussel and canned cream corn were the most successful baits for *Graptemys* species in preliminary trials (Voorhees et al., 1991). These baits were used at each site, along with fish, scallop, shrimp, crayfish, grasshopper, or mulberry. Bait was hung in the back of each net in punctured cans or plastic film canisters.

At each site we recorded the number of individuals of each species, and measured 32 environmental variables (structural or water characteristics). Structural variables included visual estimation of substratum type (percentage clay, mud, sand, gravel, rock, and bedrock); percentage shoreline bare, covered by grass, shrub, and trees; percentage of site covered by shade at noon; percentage of site covered by submerged and emergent vegetation; availability of basking sites (coded 0–4 for visual estimates of none, few, some, common, and plentiful, respectively); and percentage of site comprised of riffle, pool, and run or glide habitat. Water variables included surface water temperature; mean current speed (measured with a Teledyne Gurley pygmy current meter no. 625); water clarity (measured with current meter rod); mean depth; mean width; and estimated permanency of the water regime (coded 1 = intermittent and 2 = permanent). Water analyses conducted with a Hach kit (model AL-36B) included dissolved oxygen, dissolved carbon dioxide, pH, free and total acidity, phenolphthalein and total alkalinity, total hardness, and nitrate nitrogen (Hach DREL NitraVer method).

We calculated habitat overlap between species with Pianka's (1973) index of overlap:

$$O_{jk} = \frac{\Sigma\, p_{ij} p_{ik}}{\sqrt{\Sigma\, p_{ij}^2\, \Sigma\, p_{ik}^2}}$$

where p_{ij} and p_{ik} are proportions of resource i utilized by species j and k, respectively. This index gives values for habitat overlap ranging from 0 (no overlap) to 1 (complete overlap). We also calculated niche breadth for each species with Levins' (1968) formula:

$$B = 1/\Sigma\, p_i^2$$

where p_i is the proportion of resource i utilized by the species.

We used SAS (SAS Institute Inc., 1985) for all statistical analyses. Percentage data were arcsine square root transformed where the transformation improved normality. Remaining variables were transformed using the appropriate power as calculated according to the ladder of transformations proposed by Mosteller and Tukey (1977).

Phenolphthalein alkalinity and free acidity were invariant and were not used in analyses. Sites where *G. pseudogeographica* and *G. ouachitensis* co-occurred were considered distinct from sites where individual species occurred, and will be referred to as "co-occurrence" sites.

We used General Linear Model (GLM) procedures for one-way ANOVA. We first compared individual species' sites with all other sites sampled (e.g., *G. geographica* sites with all other sites), and second compared *G. ouachitensis* and *G. pseudogeographica* sites with sites of co-occurrence of these species. We used canonical discriminant analysis (CANDISC) to determine the extent of species separation given 30 environmental variables. Discriminant analysis (DISCRIM) was used to classify each group based on a discriminant function derived from a linear combination of these variables.

Results

A total of 1503 turtles was collected, including 169 *G. ouachitensis*, 36 *G. pseudogeographica*, and 10 *G. geographica*. Other species collected were *Trachemys scripta* (688), *Apalone spinifera* (261), *Chelydra serpentina* (122), *Chrysemys picta* (105), *Apalone mutica* (85), *Sternotherus odoratus* (20), and *Pseudemys concinna* (7). Voucher specimens were deposited at the University of Kansas Museum of Natural History. Forty-seven of 186 sites had *Graptemys* species present; *Graptemys ouachitensis* was captured at 23 sites, *G. geographica* at seven, *G. pseudogeographica* at eight, and *G. ouachitensis* and *G. pseudogeographica* co-occurred at nine additional sites. Based on GLM, each of the three groups showed differences among values for environmental variables when compared to all sites sampled.

Graptemys geographica inhabited areas with rock ($\bar{x}$ = 36%) and gravel ($\bar{x}$ = 26%) substrata on creeks and streams, as opposed to river mainstems. Compared to other sampled sites, *G. geographica* sites had more shade at noon ($\bar{x}$ = 56%, $P < 0.002$), a higher percentage of bare shoreline ($\bar{x}$ = 14%, $P < 0.01$), and water with more CO_2 ($\bar{x}$ = 49 mg/L, $P < 0.01$), and greater total acidity ($\bar{x}$ = 63 mg/L $CaCO_3$, $P < 0.001$).

Graptemys pseudogeographica sites had a higher percentage mud substratum ($\bar{x}$ = 78%, $P < 0.001$) and abundance of basking sites ($\bar{x}$ = 2.8, $P < 0.01$). This species was never trapped on sand substrate or in areas with riffle habitat.

Graptemys ouachitensis ranged furthest west across Kansas and occurred in a wide range of habitats. *Graptemys ouachitensis* was found on mud, sand, and rock substrata, ranging from 0% to 100%. This species preferred deeper ($\bar{x}$ = 117 cm, $P < 0.001$), wider ($\bar{x}$ = 42 m, $P < 0.003$) runs ($\bar{x}$ = 65%, $P < 0.002$) on rivers, and was also found in areas with higher average water temperature ($\bar{x}$ = 26.9 C, $P < 0.004$) than other sites. *Graptemys ouachitensis* sites had higher values for water regime ($\bar{x}$ = 1.9, $P < 0.02$), more available basking sites ($\bar{x}$ = 2.2, $P < 0.01$), higher dissolved oxygen ($\bar{x}$ = 8.4 mg/L, $P < 0.03$), less emergent vegetation ($\bar{x}$ = 0.1%, $P < 0.03$), and less shade ($\bar{x}$ = 11%, $P < 0.04$) than other sites.

Sites of co-occurrence of *G. pseudogeographica* and *G. ouachitensis* differed from both *G. pseudogeographica* and *G. ouachitensis* sites in a higher percentage of rock substratum ($\bar{x}$ = 40%, $P < 0.006$) and more bare shoreline ($\bar{x}$ = 29%, $P < 0.003$). Co-occurrence sites had more variables in common with *G. pseudogeographica* sites than with *G. ouachitensis* sites; they had less mud substratum ($P < 0.003$) than *G. pseudogeographica* sites, but more pool, less run, lower water temperature, and lower pH than *G. ouachitensis* sites ($P < 0.02$).

Overlap index values for the three species were as follows: *G. pseudogeographica* and *G. ouachitensis*, 0.93; *G. pseudogeographica* and *G. geographica*, 0.87; *G. ouachitensis* and *G. geographica*, 0.83. Measures for testing the significance of overlap values are not available, but values 0.90 and greater have been considered "nearly com-

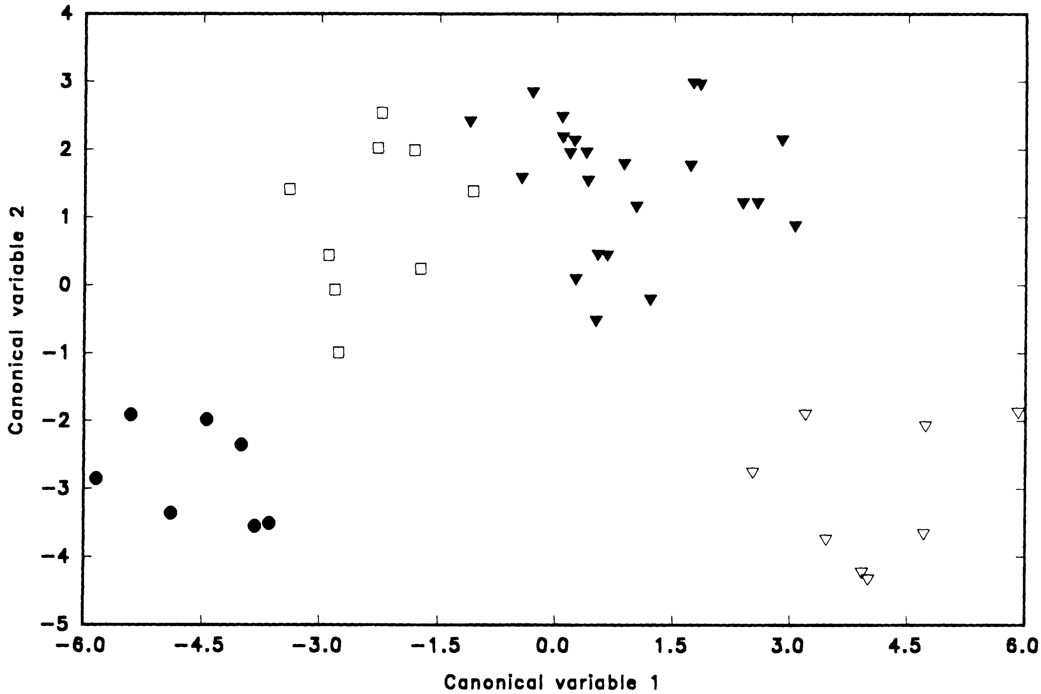

FIG. 1. Two-function plot of canonical axis 1 vs. axis 2; (▽ = *G. pseudogeographica* sites; ▼ = *G. ouachitensis* sites; ● = *G. geographica* sites; □ = *G. pseudogeographica* and *G. ouachitensis* sites of co-occurrence).

plete," and overlaps 0.75 or greater "very high" (Pianka and Pianka, 1976; Huey and Pianka, 1977). *Graptemys geographica* was most generalized in habitat choice, with a niche breadth of 15.5, higher than that of *G. pseudogeographica*, 13.6, and *G. ouachitensis*, 13.5.

Canonical discriminant analysis resulted in four distinct groups. Wilks' lambda value, a measure of group (species) differences, where values nearest zero denote high discrimination among groups (Klecka, 1980), was 0.0062 ($P < 0.004$). Mahalanobis pairwise squared distances between groups showed that *G. geographica* and *G. pseudogeographica* sites were most separated (79.6). *Graptemys ouachitensis* and "co-occurrence" sites had the closest group centroids (22.6). The first two canonical axes explained 84.8% of the variation among groups, and the two function plot resulted in four distinctly separated groups with no overlap (Fig. 1).

Variables most important in distinguishing among groups are those with highest total structure canonical coefficients (Table 1). Total structure coefficients are the best guide to interpreting the meaning of canonical discriminant functions, especially where there is high correlation among some variables (Klecka, 1980). Highest loading structure canonical coefficients on axis 1 ($> \pm 0.42$) were low percentage rock substratum, low percentage bare shoreline, low CO_2, and high percentage mud substratum. Axis 2 was most influenced ($> \pm 0.47$) by low percentage shade, high dissolved oxygen, high pH, and wide stream channels.

The discriminant function using all 30 environmental variables was 100% accurate for classifying species into four groups. To further test the accuracy of the discriminant function, 10 variables with the lowest standardized canonical coefficients on the first canonical axis were deleted. The resulting 20 variable function was also 100% accurate in classifying species.

DISCUSSION

Graptemys geographica was found in habitats different from those described for the species throughout its range. *Graptemys geographica* is considered "strictly riverine" in Wisconsin (Vogt, 1980, 1981b) and is otherwise known to inhabit lakes, backwaters, and oxbows with abundant aquatic vegetation, optimal basking sites, and soft clay or mud bottoms (Cahn, 1937; Pope, 1939; Ernst and Barbour, 1972; Gordon and MacCulloch, 1980; Caldwell and Collins, 1981; Vogt, 1981b; Collins, 1982; Flaherty and Bider, 1984; Pluto and Bellis, 1986; Johnson, 1987; Conant and Collins, 1991). *Graptemys geographica* is documented to prefer areas with rocky, wooded, or sandy shorelines and sandy substratum for nesting (Arndt, 1973; Bull and Vogt, 1979; Flaherty and Bider, 1984; Vogt and Bull, 1984; Cochran, 1986).

We found *G. geographica* at sites on small creeks and streams rather than rivers and oxbows. *Graptemys geographica* occurred on predominantly gravel substratum and was never trapped on sand or clay substrata. The species inhabited sites with bare shoreline and was not found in areas with high amounts of emergent or submerged vegetation. *Graptemys geographica* sites had the lowest mean availability of basking sites of the three species. Since *G. geographica* prefers different habitats within its range, food availability, rather than habitat, is likely a limiting factor for distribution of this species (Vogt, 1981a).

Graptemys pseudogeographica sites were similar to *G. ouachitensis* sites except that *G. pseudogeographica* was never collected on sand substratum. *Graptemys ouachitensis* sites with sand and higher water temperatures are indicative of its habitat farther west in Kansas where rivers are typically wider, sandier, and warmer than in eastern Kansas. *Graptemys pseudogeographica* preferred sites with more mud substratum and more basking sites, two habitat characteristics typically attributed to *G. geographica* (Collins, 1982; Johnson, 1987). Neither of these species lived in areas with abundant aquatic vegetation, a habitat characteristic typical in other parts of their range (Johnson, 1987). *Graptemys pseudogeographica* occurred as often alone (no other map turtles at the same site) as it occurred in nets with *G. ouachitensis*, and sites of co-occurrence were distinctly different from single species sites.

Habitat overlap values were "biologically significant" for each pairwise comparison of map turtle species (Zaret and Rand, 1971). However, based on the two-function plot of canonical scores, the four species groups are distinctly partitioned in terms of habitat use. Canonical scores for some individuals in the *G. ouachitensis* group are close to some in the "co-occurrence" group, but the four groups do not show the great amount of overlap suggested by the index values.

Variables most useful for discriminating among groups in discriminant analyses, with the exception of pH, were those variables that showed differences among groups in GLM analyses. *Graptemys geographica* sites scored low on axis 1 and are distinguished by more rock and less mud substrata, more bare shoreline, and higher dissolved CO_2. *Graptemys pseudogeographica* scored high on axis 1, therefore its distinguishing habitat characteristics are opposite those of *G. geographica*. Both co-occurrence sites and *G. ouachitensis* sites scored relatively high on axis 2, but lower scores for co-occurrence sites on axis 1 distinguish the two groups. Although the three map turtle species appear to use the same habitats, and pairwise comparisons indicate significant amounts of habitat overlap, certain habitat variables separate the species in this area of sympatry.

TABLE 1. Total canonical discriminant structure coefficients for 30 environmental variables on the first two canonical axes.

Variable	Canonical axis 1	Canonical axis 2
Rock	−0.5261	−0.0430
Bare shoreline	−0.5212	0.0667
Carbon dioxide	−0.4408	−0.2315
Mud	0.4267	−0.3056
Total acidity	−0.3984	−0.4230
pH	0.3224	0.4713
Basking sites	0.3059	0.1377
Width	0.2874	0.4587
Water temperature	0.2859	0.2847
Gravel	−0.2415	−0.1448
Shade	−0.2387	−0.6307
Run	0.2278	0.1937
Trees	0.2079	−0.0270
Pool	−0.2059	−0.2453
Submerged vegetation	0.2041	−0.0891
Water regime permanence	−0.2041	0.0891
Depth	0.1820	0.3964
Dissolved oxygen	0.1608	0.4965
Total alkalinity	−0.1580	0.0364
Bedrock	−0.1338	−0.1005
Sand	0.1083	0.3928
Nitrate nitrogen	0.1037	0.2812
Hardness	−0.1018	−0.2555
Emergent vegetation	−0.0845	−0.3733
Current speed	−0.0660	0.3333
Riffle	−0.0589	0.2112
Grass	0.0580	−0.1336
Clarity	0.0573	0.1614
Shrub	0.0285	−0.0069
Clay	0.0247	0.2074

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