Turtle Communities in the Upper Midwest, USA
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ABSTRACT

We analyzed the composition of upper Midwestern turtle communities, trends with latitude, and the effects of habitat and geographic region. The relative abundance (RA) of many species correlated negatively with the RA of Trachemys scripta. Neither richness nor equitability correlated with latitude; however, species diversity correlated positively with latitude. Riverine communities were significantly richer than ecotonal and lacustrine habitats, most likely because of the complex habitat structure of rivers. The RA of species within turtle communities could be partitioned into two discriminant functions, one explaining lentic species and one explaining lotic species. Turtle communities clustered by habitat, indicating that habitat is a strong force in shaping the structure of the community. Mississippi River communities were richer compared to southern Illinois lacustrine habitats. Although not as dominant as the clustering by habitat, temporal isolation has also shaped the structure of upper Midwestern freshwater turtle communities.

INTRODUCTION

Biological communities are commonly defined using descriptive variables and indices such as relative abundance (RA), species richness, species diversity, and equitability (Krebs 1989). The relationships between these descriptive variables and the biotic and abiotic environment can reveal community structure. For example, species richness in reptiles is primarily associated with environmental factors such as annual rainfall (Schall and Pianka 1977 and 1978, Owen and Dixon 1989, Iverson 1992a). In temperate zone freshwater habitats hydroperiod, winter anoxia, predation, and competition determine the structuring (Welborn et al. 1996). These factors can be expressed as gradients and analyzed for their effects on the community structure of ectotherms, such as latitudinal trends in range size (Heenar 1999) and species richness (Iverson 1992a) in turtles.

Because turtles are long-lived, typically comprise a large amount of the biomass, and have low annual biomass productivity within freshwater ecosystems (Iverson 1982, Congdon et al. 1986), their roles in nutrient cycling and trophic structuring within ecosystems are important. Most studies analyzing higher-level associations in freshwater turtles have focused on interactions within guilds to elucidate niche dynamics (Vogt 1981, Williams and Christiansen 1981, Pluto and Bellis 1986, Vogt and Guzman Guzman 1988, Moll 1990, Fuselier and Edds 1994, Fachin-Teran et al. 1995). Such studies are important in terms of competition, social structure, and resource partitioning; however, higher-level interactions among all community members are not as well understood (Bury 1979). Within the United States, turtle communities in the upper Midwest are the best represented in the literature. There are five studies in the primary literature pertaining to community structure (Cagle 1942, Wade and Gifford 1964, Vandewalle and Christiansen 1996, DonnerWright et al. 1999, Bodie et al. 2000) with additional information on structure in theses and unpublished technical reports (Moll 1977, Pierce 1992, Gritters and Maudlin 1994, Dreslik 1996, Tucker et al. 1997a). Structural data of communities are required to assess interspecific interactions such as competition and to differentiate along latitudinal, habitat, and regional gradients.
The goals of our study were a) to summarize data for upper Midwestern freshwater turtle communities and examine how the relative abundance (RA) of species within the community relates to all other species, richness, equitability, and diversity; b) to examine if RA, richness, equitability, and diversity varied with latitude; and c) to assess whether communities differed between habitats and geographic regions.

METHODS AND MATERIALS

We reviewed turtle community studies in the upper Midwest north of the confluence of the Ohio River and the Mississippi River because multiple studies were available for this region. We omitted sites with ≤ 50 captures because we considered them not representative of the turtle community. Six studies were selected for the analysis, and all used multiple capture methods (Table 1).

Summary community attributes we used were RA, richness, diversity, and equitability. The RA of a turtle species was its proportion respective to the entire

<table>
<thead>
<tr>
<th>Reference</th>
<th>Study Site</th>
<th>No. Captured</th>
<th>Location</th>
<th>Habitat/Region</th>
</tr>
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<tr>
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<td>Gritters and</td>
<td>Pool 8 (PL8)</td>
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<td>Maudlin, 1994</td>
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<td>Bodic et al.</td>
<td>Baited hoop traps and aquatic drift fences</td>
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<td></td>
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<td>2000</td>
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<td>2201</td>
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*a Exact numbers for Pierce (1992) are unknown and proportions came from E.O. Moll (unpubl. data).

*b Because Missouri River sites were pooled by year and because the locality information between Hartsburg and Missouri City was not specific enough, those sites are only used in the regional analysis.
community. For diversity, we calculated the natural log Shannon index ($H' = \sum p_i \log p_i$, where $p_i$ is the proportion of the $i^{th}$ species in the total sample) and maximum diversity ($H'_{\text{max}} = -S((1/S)\log(1/S))$, where $S$ is the total number of species in the community. Equitability, a measure of the heterogeneity with respect to maximal diversity, was calculated as $J = H'/H'_{\text{max}}$. We divided communities into three gross habitat categories (riverine, lacustrine, and ecotonal) and into five regional categories (Illinois River, Mississippi River, Ohio-Wabash River, Missouri River, and southern Illinois lacustrine systems). All proportional data were arcsine-square root transformed to meet the assumptions of parametric statistics.

We summarized the statistics for each community and performed a partial correlation analysis between RAs and latitude, while controlling for gross habitat. We used one-way ANOVAs to determine if diversity and equitability differed among habitats and regions. Because richness is ordinal scale data, we used the Kruskall-Wallis $H$ test to determine if richness differed between gross habitat and regional categories. We then used discriminant function analysis (DFA) to determine if groupings occurred by gross habitat and region. However, a DFA conducted on RA grouped by habitat would exhibit regional variation and a DFA conducted on RA grouped by region would exhibit habitat variation. Therefore, before we conducted a DFA on gross habitat, we removed the effects of region on the RA of each species using linear regression, and the same process was repeated for region. We then used the residuals from the regressions as the variables for the DFA. Thus, the DFA for gross habitat used the residuals derived from the region to RA regressions, and the DFA for region used the residuals from the gross habitat to RA regressions. Univariate F tests were conducted on the RA of each species using Wilks' $\lambda$. Finally, we used ANOVA to determine if discriminant function (DF) scores differed between community groups. All significant tests were subject to means comparison with parametric Bonferroni and nonparametric Tukey-Kramer HSD post hoc means comparison tests (Day and Quinn 1989, Zar 1996). The nominal $\alpha$ level for all tests was set a priori at 0.05, and Bonferroni penalties were taken where appropriate. Finally, we constructed UPGMA (unweighted pair-group method using arithmetic mean) trees using Euclidean distance of RA for the composite data set and the DF scores from the habitat and regional analyses to examine community similarity. All statistics were calculated using SPSS 6.1™ or in Microsoft Excel™ spreadsheets.

RESULTS

Of the twenty communities reviewed, ten were dominated by *Trachemys scripta*, six by *Chrysemys picta*, three by *Graptemys pseudogeographica*, and one by *Apalone mutica*. Among the 19 sites used in the analyses, species richness ranged from three to ten species, the Shannon indices ranged from 0.72 to 1.52, and equitability ranged from 0.40 to 0.92 (Table 2). The initial UPGMA of RA presented no distinct pattern of community relatedness (Fig. 1). Partial correlation analysis controlling for gross habitat categories resulted in 14 significant correlations. The RA of *T. scripta* correlated negatively with the RA of *A. spinifera* ($r_p = -0.53$), *C. picta* ($r_p = -0.43$), and *G. geographica* ($r_p = -0.66$). The RA of *A. mutica* correlated negatively with the *Chelydra serpentina* ($r_p = -0.53$) and positively with the RA of *G. ouachitensis* ($r_p = 0.808$). Species richness correlated positively with the RA of *A. spinifera* ($r_p = 0.75$). Species diversity correlated positively with the RA of *A. spinifera* ($r_p = 0.75$), *G. geographica* ($r_p = 0.68$), and negatively with the RA of *T. scripta* ($r_p = -0.55$). Equitability correlated positively with the RA of *C. serpentina* ($r_p = 0.53$). The RA of *A. spinifera* ($r_p = 0.73$), *C. picta* ($r_p = 0.54$) and *G. geographica* ($r_p = 0.67$) were positively associated with latitude, whereas the RA of *T. scripta* ($r_p = -0.69$) was negatively associated with latitude. Finally, there
was no latitudinal trend present for richness or equitability; however, diversity increased with latitude ($r_p = 0.60$).

Riverine communities were the most species rich, followed by ecotonal and then lacustrine habitats (Table 2). Ecotonal habitats were the most species diverse, whereas lacustrine habitats had the highest equitability. Among gross habitat categories, there were no significant differences in diversity ($F = 1.37, p = 0.28, df = 18$) or equitability ($F = 1.27, p = 0.31, df = 18$). However, species richness did significantly differ between habitats ($\chi^2 = 6.38, p = 0.04, df = 2$), and riverine and ecotonal communities were equally species rich but were richer than lacustrine communities. There were two discriminant functions with the following eigenvalues: \(DF_1 = 16.08\) (Wilks’ $\lambda = 0.03$) and \(DF_2 = 0.81\) (Wilks’ $\lambda = 0.55$). When considering the variables individually, the residual variation in RA of all species significantly differed between gross habitats (Table 3). The residual variation in RA of $A.\ mutica$, $A.\ spinifera$, $G.\ geographica$, $G.\ ouachitensis$, $C.\ picta$, and $C.\ serpentina$ correlated positively with DF1, whereas the RA of $G.\ pseudogeographica$, $Sternotherus\ odorus$ and $T.\ scripta$ correlated positively with DF2 (Table 4). When classified by gross habitat, the RAs of community members formed distinct riverine, ecotonal, and lacustrine communities (Fig. 2). There was a significant difference between habitats for both DFs (\(DF_1 - F = 120.6, p < 0.001, df = 18\); \(DF_2 - F = 6.09, p = 0.012, df = 18\)). Riverine habitats had lower DF scores than ecotonal habitats and both had lower scores than lacustrine habitats for DF1. Lacustrine and riverine habitats had greater DF scores than ecotonal habitats for DF2. The UPGMA tree for habitat showed distinctive and clear breaks among gross habitat categories, with the largest difference occurring between lacustrine communities and riverine-ecotonal communities (Fig. 1).

When categorized by region, Mississippi River communities averaged seven species, and Illinois River communities averaged six species (Table 2). For diversity, Illinois River communities were qualitatively the most diverse and equitable, whereas southern Illinois lacustrine communities were the least species rich and diverse. However, neither diversity ($F = 1.17, p = 0.35, df = 17$) nor equitability ($F = 1.60, p = 0.23, df = 17$) differed significantly among geographic regions. Species richness differed significantly ($\chi^2 = 7.98, p = 0.05, df = 3$) with Mississippi River sites having more species than all other communities. In addition, Illinois River and Ohio-Wabash River communities were equally species rich, and both had more species than southern Illinois lacustrine communities. The residual variation in the RA of $G.\ geographica$ was removed.

| Apalone mutica | 0.18 | 2.38 | 23.00 | 2.50 | 0.00 | 9.06 | 0.00 | 0.10 |
| A. spinifera | 9.80 | 8.64 | 2.37 | 0.50 | 0.00 | 7.94 | 0.00 | 7.52 |
| Chrysemys picta | 31.13 | 33.10 | 4.83 | 4.90 | 31.75 | 24.03 | 31.75 | 30.10 |
| Chelydra serpentina | 3.10 | 5.58 | 12.03 | 6.10 | 6.75 | 7.72 | 6.75 | 2.62 |
| Graptemys geographica | 3.70 | 5.70 | 0.00 | 0.00 | 0.00 | 3.52 | 0.00 | 3.80 |
| G. ouachitensis | 0.50 | 0.84 | 7.40 | 0.00 | 0.00 | 2.80 | 0.00 | 0.84 |
| G. pseudogeographica | 0.18 | 25.02 | 0.17 | 46.30 | 0.00 | 14.02 | 0.00 | 0.10 |
| Pseudemys concinna | 0.00 | 0.02 | 5.93 | 0.00 | 0.00 | 0.01 | 0.00 | 3.56 |
| Sternotherus odoratus | 6.72 | 0.50 | 1.07 | 0.00 | 13.50 | 0.87 | 13.50 | 7.64 |
| Trachemys scripta | 41.02 | 18.18 | 43.17 | 39.70 | 55.50 | 30.00 | 55.50 | 39.30 |

| Richness | 6.2 | 7.4 | 5.7 | 6 | 3.8 | 6.6 | 3.8 | 6.4 |
| Diversity | 1.24 | 1.11 | 1.01 | 1.16 | 0.98 | 1.09 | 0.98 | 1.23 |
| Equitability | 0.70 | 0.55 | 0.66 | 0.65 | 0.74 | 0.61 | 0.74 | 0.68 |

Table 2. Mean relative species abundance (%), richness, species diversity, and equitability of 19 chelonian communities categorized by geographic region and habitat type.
Figure 1. UPGMA trees using Euclidean distance for upper midwestern turtle communities A = relative abundance, B = habitat, C = region.
from the analysis because it did not meet the minimum tolerance for inclusion into the DFA (Norušis 1994). The three DFs with respective eigenvalues were DF1 = 5.24 (Wilks' $\lambda = 0.03$), DF 2 = 3.24 (Wilks' $\lambda = 0.16$), and DF3 = 0.49 (Wilks' $\lambda = 0.67$). When considering the variables individually, there were no significant differences in the residual variation in RA for any species between regions (Table 3). The residual variation in RA for all species was positively correlated with DF3 (Table 4). When classified by region, the residual variation in RA formed distinct clusters in some cases, but discriminant scores generally overlapped (Fig. 3). There were significant differences among regions for DF1 ($F = 24.5, p < 0.001, df = 18$) and DF2 ($F = 15.1, p = 0.001, df = 18$) but not DF3 ($F = 2.27, p = 0.125, df = 18$). Ohio-Wabash River sites had greater scores than all other sites, and Illinois River sites had greater scores than Mississippi River sites for DF1. Mississippi River and Ohio-Wabash River sites had greater DF scores than Illinois River and southern Illinois lacustrine sites for DF2. The UPGMA tree for region was less precise because communities were intermixed among groups (Fig. 1).

**DISCUSSION**

**Community Structure**

Some communities clustered, such as the Mississippi River communities and southern Illinois lacustrine systems, but extensive variation obscured most structuring. Communities with high RAs of *T. scripta* were less diverse and had lower RAs of *A. spinifera*, *C. picta*, and *G. geographica*. When *T. scripta* was the dominant member of the community, it accounted for > 60% of the turtle community. Because we have accounted for gross habitat in the analysis, some other factor such as competition, a physiological constraint, or environmental quality may explain the associations. Because *T. scripta* is an opportunistic species (Moll and Legler 1971, Ernst et al. 1994), its niche characteristics may overlap and limit other species. Although others have suggested that *C. picta* and *T. scripta* are competitors where they co-occur (Cagle 1942, Cagle and Chaney 1950, Ernst 1971, Moll and Legler 1971), there is no direct evidence that *T. scripta* competitively excludes *C. picta* or any other turtle species.

![Figure 2. Territoriality graph for discriminant scores derived from a DFA of turtle communities partitioned by habitat.](image-url)
Numerous proximate and ultimate factors other than competition, ranging from habitat productivity to clinal variation in reproductive traits, can explain the dominance of *T. scripta* over *C. picta*. *T. scripta* may have greater reproductive output compared to *C. picta*. On average, *C. picta* within the study region lay 8.7 eggs/clutch whereas *T. scripta* lay 15 (Moll 1973, Tucker and Moll 1997). Both species are capable of laying up to three clutches per year, but in *C. picta* clutch size and frequency decrease with latitude (Moll 1973, Tucker 1999). Although *T. scripta* may have greater reproductive output, this does not account for differential nest or hatchling survivorship. Persistent flooding can cause submergence of nests and hence embryonic mortality. Because riverine and other wetland habitats have hypervariable flood regimes, species that nest farther from and at higher elevations above flood zones would have increased nest survivorship. Studies of nesting in neotropical *T. scripta* found females would nest up to 400 m from the shore and approximately 10 m above the river level (Moll and Legler 1971), whereas in North America, *C. picta* typically excavated nests less than 200 m from the shore (Lindeman 1992, Ernst et al. 1994). If the environment is predictable, turtles could increase nest survivorship by timing nesting to coincide with lower water levels and emergence to coincide with high water levels. Neotropical *T. scripta* hatchlings emerged when water levels were highest (Moll and Legler 1971), and in Illinois *T. scripta* nesting coincided with the subsidence of spring flooding (Tucker et al. 1997b). Unfortunately, nothing is known about *C. picta* hatching emergence in populations that occupy rivers. Finally, one species may have greater embryonic and hatchling survival during prolonged inundation of the nest. Five of six eggs from a *T. scripta* nest submersed up to 60 min remained viable (Moll and Legler 1971). However, this phenomenon may be restricted to embryos in the early stages of development (Tucker et al. 1997). No comparative data exist on the tolerance of *C. picta* embryos and hatchlings to prolonged inundation.

Over a larger geographic scale, there was no correlation between the RA of *C. picta* and *C. serpentina* as previously reported by Bodie et al. (2000). However, the fact that RA of *A. mutica* correlated negatively with the RA of *C. serpentina* may result from finer scale habitat trends such as habitat quality and productivity for which we are unable to account. Only two species showed positive correlations with community attributes. The RA’s of *A. spinifera* and *G. geographica* were positively correlated with richer and more diverse communities, and the RA of *G. ouachitensis* correlated positively with

Table 3. Wilks’ λ univariate F-tests for DFAs on the residuals of species relative abundance regressions for habitat (df = 2,15) and regional associations (df = 3,14).

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Region</th>
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<tbody>
<tr>
<td></td>
<td>Wilks’ λ</td>
<td><em>F</em></td>
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<tr>
<td><em>Apalone mutica</em></td>
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<td>14.23</td>
</tr>
<tr>
<td><em>A. spinifera</em></td>
<td>0.58</td>
<td>5.49</td>
</tr>
<tr>
<td><em>Chrysemys picta</em></td>
<td>0.27</td>
<td>20.55</td>
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<td><em>Chelydra serpentina</em></td>
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<td>17.40</td>
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<tr>
<td><em>Graptemys geographica</em></td>
<td>0.42</td>
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<tr>
<td><em>G. ouachitensis</em></td>
<td>0.36</td>
<td>13.57</td>
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<td><em>G. pseudogeographica</em></td>
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<td><em>Stemotherus odoratus</em></td>
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<tr>
<td><em>Trachemys scripta</em></td>
<td>0.45</td>
<td>9.10</td>
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communities that were more equitable. If diversity or equitability of particular taxa are indicators of ecosystem health and functionality, then *A. spinifera*, *G. ouachitensis*, and *G. geographica* may be less tolerant of perturbations.

**Latitudinal Associations**

Latitude was positively correlated with the RA of *A. spinifera*, *C. picta*, and *G. geographica* and negatively associated with the RA of *T. scripta*. Over-wintering survivability in the form of hibernation physiology and behavior may partially explain these trends. As latitude increases, the hibernation period increases, and turtles are forced to remain in anoxic environments for longer periods. Research suggests that *C. picta* had the highest anoxia tolerance of any taxa examined (Ultsch 1985). Although *C. picta* tolerates extreme anoxia, it may not often face such an extreme in the wild. In British Columbia *C. picta* hibernated close to the shoreline near the frozen surface where oxygen was richest (St. Clair and Gregory 1990). Conversely, both *G. geographica* and *A. spinifera* had lower tolerance to anoxic water (Ultsch 1985, Ultsch and Jackson 1995), and both species typically over-wintered in rivers avoiding anoxic conditions (Ultsch and Jackson 1995, Graham and Graham 1997, Plummer and Burnley 1997). Thus,

Table 4. Standardized discriminant function coefficients and correlations of the residual species RA for habitat and region classifications.

<table>
<thead>
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<th>Standardized Discriminant Function Coefficients</th>
<th>Habitat</th>
<th>Region</th>
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<tr>
<td></td>
<td>DF1</td>
<td>DF2</td>
</tr>
<tr>
<td><em>Apalone mutica</em></td>
<td>-10.27</td>
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<td><em>Graptemys geographica</em></td>
<td>0.31</td>
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<td><em>Sternotherus odoratus</em></td>
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<tr>
<td><em>Trachemys scripta</em></td>
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Correlations

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<th>Correlations</th>
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<th>Region</th>
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<td><em>Apalone mutica</em></td>
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<tr>
<td><em>Graptemys geographica</em></td>
<td>0.29</td>
<td>0.08</td>
</tr>
<tr>
<td><em>G. ouachitensis</em></td>
<td>0.33</td>
<td>0.30</td>
</tr>
<tr>
<td><em>G. pseudogeographica</em></td>
<td>0.29</td>
<td>0.70</td>
</tr>
<tr>
<td><em>Sternotherus odoratus</em></td>
<td>0.15</td>
<td>0.50</td>
</tr>
<tr>
<td><em>Trachemys scripta</em></td>
<td>0.26</td>
<td>0.36</td>
</tr>
</tbody>
</table>
hibernation strategies may contribute to the explanation of the trends in *G. geographica* and *A. spinifera*.

Because *T. scripta* survived prolonged anoxia as well as *C. picta* (Ultsch 1985), juvenile freeze tolerance may also contribute to the explanation of its latitudinal trend. Numerous studies on freeze tolerance in *C. picta* (Breitenbach et al. 1984, Storey et al. 1988, Paukstis and Shuman 1989, Packard and Packard 1990) indicate that hatchlings could survive up to 16 h at -8.9 °C, whereas juvenile *T. scripta* could survive -4 °C for only 4 h (Churchill and Storey 1992). The decrease in RA of *T. scripta* with latitude might result from limited hatchling freeze tolerance, whereas increased tolerance to freezing and anoxia might explain the latitudinal trend in *C. picta*. Additionally, hatching success at lower incubation temperatures may be reduced in *T. scripta* compared with *A. spinifera*, *C. picta*, and *G. geographica*; however, comparative data are not available to confirm this idea.

Figure 3. Territoriality graphs for discriminant scores derived from a DFA of turtle communities partitioned by region. Missouri River sites (Bodie *et al.*, 2000) are not included because data were pooled for all sites between years. Symbols represent Mississippi River communities (●), Illinois River communities (◆), Ohio-Wabash River communities (▲), and southern Illinois lacustrine communities (■).
Increased embryonic mortality could be the limiting factor for the northern distribution of *C. serpentina* (Bobyn and Brooks 1994). In addition, ecological, environmental, and physiological effects may act in concert to influence latitudinal associations. For example, the ultimate determinant in the upstream distribution of *G. ouachitensis sabinensis* in Louisiana was stream width (Shively and Jackson 1985). When patches of favorable habitat became smaller and more isolated upstream, they were less used than downstream patches. Thus, upstream dispersal was progressively reduced, explaining the lower population sizes upstream.

It is not clear whether the latitudinal span we examined (~7°) was broad enough to detect a trend in richness because of small sample sizes, although differentiation in diversity has been identified over a 7° span in other taxa (Zacharias and Rolf 2001). Further, a latitudinal trend in species richness may not hold in North America when considering the relatively species depauperate communities west of the Mississippi River basin (Iverson 1992b). Turtle species richness in Iowa decreased longitudinally with the main influence being the distance west of the Mississippi River drainage (Vandewalle and Christiansen 1996). Latitudinal trends in species richness have been reported for Iberia (Schall and Pianka 1977), but the trend is thought to be a relict of Iberia’s peninsular nature (Iverson 1992a). Of the suite of physiogeographic and environmental gradients analyzed, only annual rainfall correlated with turtle species richness on global, regional, and local scales (Schall and Pianka 1977 and 1978, Owen and Dixon 1989, Iverson 1992a). Only when accounting for the combined effects of species RA and richness through a diversity index does a latitudinal trend within the upper midwest become apparent.

**Habitat Associations**

Species richness was greatest in riverine habitats, a difference attributable to the complex habitat structure of rivers. Within river floodplains, habitats grade from riverine to ecotonal to lacustrine and the juxtaposition and proximity of these habitats may relate to increased diversity of freshwater species. Increased habitat heterogeneity at the landscape level explained diversity in Australian lizard (James and Shine 2000) and Mediterranean herpetofaunal communities (Atauri and de Lucio 2001). Thus as habitat heterogeneity increases, so may turtle species richness and diversity.

All species showed significant differences in RA when grouped by habitat. From greatest to least RA, *A. mutica, A. spinifera, G. ouachitensis*, and *G. pseudogeographica* showed a general trend of riverine-ecotonal-lacustrine. The primarily lentic species *C. picta, S. odoratus*, and *T. scripta* showed the reverse order of lacustrine-ecotonal-riverine, but *C. picta* was relatively uniform in RA across habitat type compared to all other species. Only *C. serpentina* was approximately equally abundant in riverine and lacustrine habitats but occurred with a lower RA in ecotonal habitats. Finally, *G. geographica* occurred in roughly equal abundance in riverine and ecotonal habitats but was generally in low abundance in lacustrine habitats. The general trend was for high abundances of lotic species in riverine habitats and lentic species in lacustrine habitats. This was similarly observed for wetlands along the Missouri River where RA of lotic species decreased with distance from lotic habitats, and the converse was observed for the RA of lentic species (Bodie et al. 2000).

When using the RA of species, all of the habitats formed distinct communities. In general, DF1 generally describes the abundance of lentic species, with the exception of *C. picta* and *C. serpentina*, whereas DF2 generally describes the abundance of lotic species, with the exception of *G. pseudogeographica*. UPGMA analysis, removing the effects of region, revealed three distinct clusters corresponding to the gross habitat categories. The
deepest differentiation occurred between lacustrine and the riverine-ecotonal clusters reflecting the marked differences between these habitat types. Considering the general habitat associations of the species examined, habitat provides the clearest explanation of variation in community structure. All species appeared in ecotonal habitats, albeit in lower abundances, and ecotonal communities were truly intermediate as shown by DFA and UPGMA. Varying hydrological regimes within floodplains allow connectivity between habitats and thus direct corridors of dispersal. Spring floods near the confluence of the Ohio River and the Wabash River create such dispersal corridors (Dreslik 1996). Upon the recession of flood waters, lotic species may become isolated in flood plain lakes and sloughs.

Temporal differences may be a factor in our results because these studies spanned 50 years. A study of turtle communities in two farm ponds revealed a temporal shift in three species – C. serpentina, S. odoratus, and Kinosternon subrubrum (Stone et al. 1993). However, these wetlands were new at the onset of the study, and the shifts were attributed to colonization efficiency and habitat changes (Meylan et al. 1992, Stone et al. 1993). Additionally, because most turtle species tend to have long generation times and delayed sexual maturity, turtle populations and communities respond slowly to environmental changes (Frazer et al. 1990, Congdon et al. 1993 and 1994) and the studies chosen may span at most only three generations. Two decades of study at the E. S. George Reserve found temporal stability in community structure (Congdon and Gibbons 1996).

Regional Associations

Within the regions examined in this study, turtle communities averaged six species, whereas the lower Ganges-Brahmaputra and lower Mobile basins are the planet’s most species rich with 17 and 16 species respectively (Iversen 1992a and 1992b, Vogt and Benitez 1997). Mississippi River sites were the most species rich within the study region, whereas southern Illinois lacustrine systems were the least species rich. A combination of habitat quality and human impact may account for the regional differences. Habitat quality is highest in the upper reaches of the Mississippi River and declines through the lower impounded and unimpounded reaches where human impact and agricultural development are greatest (Theiling 1999). The Illinois River has been severely degraded by anthropogenic effects that have negatively impacted fish, mussel, bird, reptile, and amphibian fauna (Forbes and Richardson 1913, Mills et al. 1966, Starrett 1971, Bellrose 1979). Heavily modified river systems in Iowa have decreased turtle species richness, affecting mainly the less common species in the community (Vandewalle and Christiansen 1996). Such anthropogenic effects cause physical and chemical changes that result in a cascading decline in biodiversity upward through the higher trophic levels (May et al. 1997, Wang et al. 2000, Wang et al. 2001).

The RA of no species univariately differed between regions, and only when considered compositely was regional differentiation expressed. Even when the variation pertaining to habitat was removed, the resolution of the DFA by region was less clear than the DFA for gross habitat. Discriminant scores broadly overlapped for DF1 and DF2 between Illinois River and southern Illinois lacustrine sites and for DF2 and DF3 among Mississippi River and Ohio-Wabash River sites. UPGMA clustering of regions revealed overlap between southern Illinois lacustrine and Illinois River communities and overlap between Illinois River and Mississippi River communities, but Ohio-Wabash River communities were distinct.

Temporality in terms of glaciation events and wetland construction may explain the relationships observed among communities. In sequence, the distance observed for the Ohio-Wabash River communities is explained by glacial retreat. Glaciers would have
retreated from these drainages first, thus leaving suitable habitat earlier. The relationship between the Mississippi River and the Missouri River clusters follow the same logic of glacial retreat. Pool 26 and West Alton are near the confluence of the Mississippi River and the Illinois River. These two communities along with Havana may represent either unique Illinois River turtle communities or degraded communities due to anthropogenic changes within the Illinois River. Finally, the youngest turtle communities are those from lacustrine systems in southern Illinois. Many of these systems are impoundments and constructed ponds and their results appeared obscured because environmental changes and biotic interactions may have since changed the structure of communities. This is supported by the reduced explanatory power of the regional DFA compared to the habitat DFA.

ACKNOWLEDGMENTS

Funding for this research was provided by the Illinois Endangered Species Protection Board, Illinois Department of Natural Resources, and the Linnaeus Fund of the Chelonian Research Foundation. We thank E. Moll for providing unpublished data and for many insightful discussion on earlier versions of this manuscript, D. Moll, D. Shepard, J. Mui, A. Kuhns, and L. Page for their comprehensive reviews and suggestions on the manuscript, and D. Shepard and J. Tucker for help in explaining some of the associations and providing some very authoritative ideas and conversation on feasible alternatives to competition in the community relationship between T. scripta and C. picta.

LITERATURE CITED


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