Ecomorphological variation in shell shape of the freshwater turtle *Pseudemys concinna* inhabiting different aquatic flow regimes

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**Synopsis** Populations of species that inhabit a range of environments frequently display divergent morphologies that correlate with differences in ecological parameters. The velocity of water flow (i.e., flow velocity) is a critical feature of aquatic environments that has been shown to influence morphology in a broad range of taxa. The focus of this study was to evaluate the relationship between flow velocity and shell morphology for males and females of the semi-aquatic freshwater turtle *Pseudemys concinna*. For both sexes, the carapace and plastron show significant morphological differences between habitats characterized by slow-flowing (i.e., lentic) and fast-flowing (i.e., lotic) water. In general, the most prominent pattern for both sexes is that the shells of individuals from lotic habitats are more streamlined (small height-to-length ratio) than the shells of individuals from lentic habitats. Of the two shell components (carapace and plastron), the carapace shows greater divergence between habitats, particularly for males. These results are consistent with adaptations to flow velocity, and suggest that variation in shape may be more constrained in females. I also provide empirical evidence for an adaptive benefit of the observed shape change (i.e., drag reduction) and a brief comment on the relative roles of genetic divergence and phenotypic plasticity in generating shape differences observed in this species.

**Introduction**

Populations of species that inhabit a wide range of environments frequently display divergent morphologies that correlate with differences in ecological parameters. Many studies examining intraspecific morphological divergence have focused on the effects of biotic features of the environment, such as resource competition (Adams and Rohlf 2000; Grant and Grant 2006; Pfennig et al. 2006; Adams and Collyer 2007) and the effects of predator–prey interactions (Bronmark and Miner 1992; Milano et al. 2002; Langerhans and DeWitt 2004; Eklov and Svanback 2006; Brookes and Rochette 2007). However, abiotic, or physical, features of the environment can also drive phenotypic divergence among intraspecific populations. The velocity of water flow, hereafter referred to as flow velocity, is a critical feature of aquatic environments that impacts numerous aspects of biology, including reproduction (Denny et al. 2002; Riffell and Zimmer 2007), feeding (Okamura 1984, 1985; Marchinko 2003; Pratt 2008), displacement of free-swimming taxa (Gibbins et al. 2007), and dislodgement of sessile taxa (Carrington 2002; Koehl et al. 2008; Stewart 2008). In addition, flow velocity has been shown to influence morphology in a broad range of taxa, including plants and algae (Puijalon and Bornette 2004; Boller and Carrington 2006; Stewart 2008), invertebrates (Marchinko 2003; Holomuzki and Biggs 2006), and vertebrates (Pakkasmaa and Piironen 2001; McGuigan et al. 2003; Peres-Neto and Magnan 2004). Such patterns of morphological variation have been identified in numerous species of fishes inhabiting different flow regimes (Brinsmead and Fox 2002; Keeley et al. 2005; Blob et al. 2008). While many of these studies are limited to the identification of a pattern of association between environment and morphology, several others have attempted to determine the adaptive benefits of divergent morphologies (Boily and Magnan 2002; Ojanguren and Brana 2003; Kerfoot Jr and Schaefer 2006). In general, these studies have observed that the shape of the body and caudal fin, as well as steady swimming performance differs in a predictable manner between lentic (i.e., slow flowing) and lotic (i.e., fast flowing) regimes (for review, see Langerhans 2008). More specifically, fishes inhabiting lentic flow regimes tend to have posteriorly deep bodies, low-aspect ratio caudal fins, and low steady-swimming performance. In contrast, fishes from lotic environments possess streamlined bodies, high-aspect ratio caudal fins, and increased steady-swimming performance (Langerhans 2008). In addition, several other...
studies have examined the relative contribution of environmental and genetic factors on the resultant morphology (Pakkasmaa and Piironen 2001; Imre et al. 2002; McGuigan et al. 2003; Peres-Neto and Magnan 2004; Keeley et al. 2007; Langerhans 2008). While morphological specializations to different flow regimes have been well established in fishes, the extent to which such patterns might extend to other vertebrates is uncertain because fishes live exclusively in water and, as a result, selection on body shape for lower hydrodynamic resistance is expected to be maximized. In contrast, many tetrapods use both aquatic and terrestrial environments. For example, semi-aquatic freshwater turtles perform several vital functions on land (e.g., nesting and basking) as well as in water (e.g., feeding and copulation). Despite the potential constraints of a rigid shell, semi-aquatic freshwater turtles have adapted to life in a diverse array of aquatic flow regimes, ranging from ponds and lakes to fast flowing rivers (Ernst et al. 1994). At the most basic level, compared with terrestrial turtles, aquatic turtles possess flatter and more symmetrical shells; both of these characteristics are believed to increase swimming performance (Claude et al. 2003; Rivera and Claude 2008). Furthermore, many species of freshwater turtles inhabit both lotic and lotic environments. Two studies examining intraspecific variation in morphology across different flow regimes have suggested that the shells of freshwater turtles are suited to the hydrodynamic environments in which they are found (Aresco and Dobie 2000; Lubcke and Wilson 2007). Aresco and Dobie (2000) presented the first quantitative data, by showing that the shells of river cooters (Pseudemys concinna) from lotic sites were flatter than those from lentic sites. More recently, Lubcke and Wilson (2007) found that western pond turtles (Actinemys marmorata) from lotic habitats were flatter and narrower than those from lentic habitats. Though both of these studies identified body shapes expected to reduce drag in high-flow environments, there are several limitations to these analyses. First, the morphological data used were based on only two (length and height of shell; Aresco and Dobie 2000) or three morphological variables (length, height, and width of shell; Lubcke and Wilson 2007); as a result, the manner in which changes in these variables occur are unknown. For example, while we may know that shell shape ranges from “flat” to “highly-domed,” we do not know what specific structural differences are responsible for these morphologies. Second, the geographic areas examined were limited to two physiographic regions within the state of Alabama (Aresco and Dobie 2000) and three sites within a single county in California (Lubcke and Wilson 2007). Third, it is possible that the flow environment could differentially influence shape in the two components of the shell (i.e., carapace and plastron), but these components have not yet been examined separately. Fourth, while both studies suggest that the association between flow velocity and shell morphology may be based on reducing hydrodynamic resistance, empirical effects of shell shape on hydrodynamics are yet to be tested. Lastly, as is common in studies examining correlations between environmental characteristics and morphology, an important question is whether the differences observed are the result of natural selection or of phenotypic plasticity (DeWitt et al. 1998; Rivera and Claude 2008; Langerhans 2008). Consequently, while these studies provide support for ecomorphological variation associated with flow velocity in turtles, many important questions remain unanswered.

Several factors make freshwater turtles an ideal group in which to evaluate morphological variation associated with different flow regimes, as well as the effects of such variation on locomotor performance. First, individual species inhabit a variety of aquatic habitats, encompassing a wide range of flow velocities within a relatively small geographic area (Ernst et al. 1994). Additionally, both components of the turtle shell are covered by keratinized scutes, the intersections of which form a large number of easily identifiable landmarks that can be used to assess morphological variation using landmark-based geometric morphometric analyses (Slice 1993, 1996; Claude et al. 2003; Valenzuela et al. 2004; Myers et al. 2006; Rivera and Claude 2008). The rigid shell also makes it possible to digitize these landmarks accurately and with high repeatability. Furthermore, because the shell limits axial mobility, propulsion in turtles is limited to the forces generated by movements of the forelimbs and hind limbs (Pace et al. 2001; Rivera et al. 2006), which results in a decoupling between the morphology of propulsory structures and overall shape (i.e., shell morphology). In contrast, studies examining the association between flow velocity and the morphology of fishes have to interpret the complex interactions between modifications of the body and fins that reduce drag and those that increase propulsion (though see Blob et al. 2008). Turtles are also an excellent system in which to use physical models to evaluate the effects of shape on hydrodynamic forces (Koehl 2003). Given that turtle shells are rigid, data collected from rigid models will closely approximate...
in vivo forces, as shown in studies of other rigid-bodied taxa (e.g., boxfish, Bartol et al. 2003, 2005). Finally, shell shape in turtles has been shown to possess a heritable genetic component (Myers et al. 2006), an essential requirement for divergent natural selection.

The broad goal of this study was to evaluate the relationship between flow velocity and shell morphology in a semi-aquatic freshwater turtle, the river cooter (P. concinna). The specific objectives of this article are three-fold. First, I test for three-dimensional (3D) differences in shell morphology between turtles from lentic and lotic flow regimes, while concomitantly testing whether the carapace and plastron demonstrate the same propensity for environmentally correlated differences. Second, I use physical models to test whether morphological differences of the shell confer reductions in drag. Finally, I provide preliminary data regarding the potential role of phenotypic plasticity in generating the morphological variation observed in turtles between the two flow regimes.

Materials and methods

Study system

The river cooter (P. concinna) is a large freshwater turtle that inhabits a broad array of aquatic environments throughout southeastern North America. Much of the species’ range is divided by the Fall Line, a physiographic feature that delineates the higher elevation Piedmont (i.e., foothills of the Appalachian Mountains) in the east and uplands in the west from the flat and low-lying Coastal Plain. Because the populations used in this study were from either the Piedmont (sensu stricto) or the Coastal Plain, hereafter, sites located above the Fall Line are referred to as “Piedmont” and those below the Fall Line are referred to as “Coastal Plain.” Rivers above the Fall Line tend to be fast flowing (i.e., lotic), whereas flow velocity below the Fall Line is considerably slower (i.e., lentic). The difference between the two flow regimes can be attributed to the elevation gradient between the Piedmont and Coastal Plain. While, lotic environments inhabited by this species are mostly limited to rivers above the Fall Line, lentic habitats include rivers below the Fall Line, lakes, oxbows, bayous, and floodplain deltas.

Study sites

I examined carapace and plastron morphology in P. concinna using fluid-preserved museum specimens collected from nine sites throughout the species’ range (Fig. 1; Table 1). The list of measured specimens is given in Appendix 1. Because the specific flow velocities encountered by the specimens in vivo are unknown, the flow regime of each site was categorized as lentic or lotic. Preliminary assessment of flow velocity was based on geography, with riverine habitats above the Fall Line classified as lotic and those below the Fall Line classified as lentic. In addition, within both of these regions (Piedmont and Coastal Plain) non-flowing bodies of water (e.g., lakes and bayous) were considered lentic flow regimes. The classification of sites was confirmed using historical flow data from the USGS National

Fig. 1 Map showing the range (shaded area) of P. concinna in North America. Bold line indicates the position of the Fall Line, which separates the Upland/Piedmont (above) and Coastal Plain (below). Locations of the nine populations used in this study are indicated by open triangles (lentic), filled squares (lotic), and open circle (Reelfoot Lake).

Table 1 Sample sizes for populations

<table>
<thead>
<tr>
<th>Site</th>
<th>State</th>
<th>Male Carapace</th>
<th>Female Carapace</th>
<th>Male Plastron</th>
<th>Female Plastron</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lentic</td>
<td></td>
<td>87</td>
<td>37</td>
<td>84</td>
<td>38</td>
</tr>
<tr>
<td>Coon Creek Lake</td>
<td>Texas</td>
<td>27</td>
<td>5</td>
<td>26</td>
<td>6</td>
</tr>
<tr>
<td>Southern LA</td>
<td>Louisiana</td>
<td>14</td>
<td>11</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td>Mobile River Delta</td>
<td>Alabama</td>
<td>35</td>
<td>10</td>
<td>32</td>
<td>9</td>
</tr>
<tr>
<td>White River</td>
<td>Arkansas</td>
<td>11</td>
<td>11</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>Lotic</td>
<td></td>
<td>41</td>
<td>16</td>
<td>40</td>
<td>16</td>
</tr>
<tr>
<td>Black Warrior River</td>
<td>Alabama</td>
<td>18</td>
<td>4</td>
<td>18</td>
<td>4</td>
</tr>
<tr>
<td>Cahaba River</td>
<td>Alabama</td>
<td>9</td>
<td>6</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>Coosa River</td>
<td>Alabama</td>
<td>8</td>
<td>2</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Tallapoosa River</td>
<td>Alabama</td>
<td>6</td>
<td>4</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Reelfoot Lake</td>
<td>Tennessee</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>137</td>
<td>63</td>
<td>133</td>
<td>63</td>
</tr>
</tbody>
</table>
Eight of the nine sites fit clearly into one of the two flow regimes (i.e., lentic or lotic; Table 1). However, turtles from the remaining site (Reelfoot Lake) represent a population that inhabits a lentic environment, but whose ancestors inhabited a lotic environment <200 years ago. Reelfoot Lake is a natural lake located within the New Madrid Seismic Zone, the center of a series of large earthquakes between 1811 and 1812. These events formed the lake’s basin (Mirecki 1996), which was subsequently filled with water and colonized by turtles from the lotic Mississippi River (Fig. 2). This unique history provides the opportunity to examine whether turtles inhabiting the lake display morphologies associated with lentic or lotic environments. The presence of lotic morphotypes would suggest that neither selection (natural or sexual) nor phenotypic plasticity has acted on the ancestral (i.e., lotic) morphotype. However, because the lake has existed for a short period of time and because P. concinna has a long generation time, the presence of lentic morphotypes is more likely to suggest a role of phenotypic plasticity than of natural or sexual selection.

Morphological measurements

Previous studies have noted that secondary sexual characteristics in P. concinna are apparent in males with carapace lengths >16.0 cm (Fahey 1987; Aresco and Dobie 2000). Based on this information, all specimens used in this study had a carapace length of at least 16.0 cm to facilitate accurate classification of sex. Turtles were sexed based on the presence or absence of elongated foreclaws and precloacal tail length, which is considerably larger in males (Fahey 1987; Buhlmann and Vaughan 1991). As the position of the intersections of scutes was the basis of morphometric data, specimens displaying developmental scute deformations were excluded from the study. Individuals with localized damage to scutes (e.g., cracks along the marginal scutes) were included as long as all landmarks on either the left or right side of the shell were intact. In some cases, when shells were damaged, only one of the two shell components (carapace or plastron) was digitized for a given specimen, producing minor differences in sample sizes between these components (Table 1).

To quantify the shape of the shell, 3D coordinate data (x, y, z) were collected for 74 landmarks on the carapace (sensu Slice 1993) and 17 landmarks on the plastron (Fig. 3) using a 3D digitizing system (Microscribe G2LX, Immersion Corp., San Jose, CA, USA; accuracy of 0.30 mm). These landmarks were formed by the intersections of keratinized scutes covering the carapace and plastron and are type 1 (Bookstein 1991). Two replicates of each configuration (i.e., set of landmarks) were collected for both shell components. These replicates were averaged and became the basis of the geometric morphometric (GM) analysis.
In order to reduce redundancy in the data and linear dependence among shape variables, only the coordinates of the right side of the shell were used for GM analyses (Bookstein 1996; Claude et al. 2003; Valenzuela et al. 2004). For specimens in which the right side was damaged, but the left side was not, landmarks from the left side of the shell were mirrored to form a “right side.” In addition, for the carapace, there were five pairs of closely associated landmarks; one landmark from each pair was excluded because (1) they provided minimal information about shape relative to the other nearby landmark, and (2) in several cases, the two landmarks within a pair appeared to occupy the same position. Similarly, a single point on the plastron was removed from the configuration. This point was along the periphery of the plastron, and for specimens in which the plastron had been cut from the carapace, the position of this landmark was not considered accurate.

The removal of the aforementioned landmarks from each configuration produced 33 landmarks for the carapace and 11 landmarks for the plastron (Fig. 3). Many species of turtle, including P. concinna, display sexual dimorphism (Gibbons and Lovich 1990; Aresco and Dobie 2000). For this reason, each sex was analyzed separately. Each of the four sets of configurations (male carapace, female carapace, male plastron, and female plastron) was then separately superimposed (scaled, translated, and rotated) using generalized Procrustes analysis (GPA) (Rohlf and Slice 1990). GPA removes information not related to shape (scale, position, and orientation) from configurations and allows shape to be examined independent of size (i.e., centroid size). First, GPA scales all configurations to the same centroid size. Translation occurs by moving the centroid of each configuration to the same point in 3D space. Finally, configurations are rotated about all three axes to minimize the sum-of-square distances between homologous landmarks.

Following GPA, each configuration occupied a position in a curved, non-Euclidean shape space and was subsequently projected onto a tangent plane (Slice 2001). A principal component analysis (PCA) was conducted on the coordinates of the tangent-space projected configurations to examine the major components of morphological variation. The PC scores generated from this analysis represent the shape variables which were subsequently used in several multivariate tests (SYSTAT, v.10; nested MANOVA, discriminant function analysis, and correlation analysis) to examine the relationship between shape and flow regime. The software package morphologika (O’Higgins and Jones 1998; available online at http://hymn.fme.googlepages.com/resources) was used to conduct GPA, tangent projection, and PCA of the configurations. In addition, morphologika provided the ability to visualize shape variation by “warping” between the extremes of the PC axes, thus allowing for a qualitative description of shapes associated with lentic and lotic flow regimes.

Drag measurements
I also examined how the observed differences in shape influence drag, a force that resists forward motion. This examination was limited to males because variation in the shape of males is less likely to be confounded by other factors (e.g., reproductive pressures). I selected two populations that conformed to the lentic and lotic morphotypes [based on discriminant function analysis (DFA); see Table 2]. Morphologika was used to calculate the mean configuration for each population, which was the average of the GPA superimposed configurations prior to tangent-space projection. I then selected the individual from each population that displayed the shape most similar to the mean shape of the entire population (based on minimum Procrustes distance) and used these two “average” specimens to generate plastic models. Specimens were immersed in liquid silicone (Oomoo 30, Smooth-on, Inc., Easton, PA, USA) to generate a mold. After the mold was set, specimens were removed and the spaces into which the head and limbs had extended were filled with silicone putty. This allowed for the examination of hydrodynamic properties of the shell, without confounding effects associated with the orientation of the head and limbs (e.g., interactive effects from the head and arms can make the effective drag on the shell higher), which differed between the two specimens. Low-viscosity liquid plastic (Smooth-cast 300, Smooth-on, Inc.) was then poured into the silicone mold. Upon curing, remnants of the neck and limbs were sanded and smoothed-over using epoxy putty.

Each model was mounted caudally to a support rod, called a sting, in the center of a flow tank (working area, 120 cm × 333 cm × 336 cm). The horizontal sting extending posteriorly from the model was fastened to a vertical sting connected to a 1 kg bending load cell (EBB-1, Transducer Techniques Inc., Temecula, CA, USA) positioned above the flow tank (Fig. 4). Data output from the load cell was amplified by a Vishay conditioning bridge amplifier (model 2120B; MicroMeasurements Group, Raleigh, NC, USA) and collected at a rate of 1000 Hz for 40 s using a customized data-acquisition program in LabVIEW (v.6.1; National Instruments Corp., Austin, TX, USA). Data were collected for...
nine trials, including three replicates each of drag incurred by the lotic model, the lentic model, and the sting only. Each trial contained an initial 5 s segment with no flow to provide a baseline value and a 30 s segment with flow velocity at 0.67 ms$^{-1}$, the maximum velocity at which flow remained laminar. The average force measured from the sting apparatus was subtracted from the average overall force.

### Table 2

<table>
<thead>
<tr>
<th>Excluded population</th>
<th>Jackknifed (Known)</th>
<th>Unknown</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Lentic (N)</td>
<td>Lentic (% Correct)</td>
</tr>
<tr>
<td>Male carapace</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black Warrior River</td>
<td>87</td>
<td>98</td>
</tr>
<tr>
<td>Cahaba River</td>
<td>87</td>
<td>94</td>
</tr>
<tr>
<td>Coosa River</td>
<td>87</td>
<td>92</td>
</tr>
<tr>
<td>Tallapoosa River</td>
<td>87</td>
<td>91</td>
</tr>
<tr>
<td>Coon Creek Lake</td>
<td>60</td>
<td>90</td>
</tr>
<tr>
<td>Southern LA</td>
<td>73</td>
<td>92</td>
</tr>
<tr>
<td>Mobile River Delta</td>
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<tr>
<td>White River</td>
<td>76</td>
<td>88</td>
</tr>
<tr>
<td>Female carapace</td>
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<td></td>
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<tr>
<td>Black Warrior River</td>
<td>37</td>
<td>89</td>
</tr>
<tr>
<td>Cahaba River</td>
<td>37</td>
<td>84</td>
</tr>
<tr>
<td>Coosa River</td>
<td>37</td>
<td>81</td>
</tr>
<tr>
<td>Tallapoosa River</td>
<td>37</td>
<td>78</td>
</tr>
<tr>
<td>Coon Creek Lake</td>
<td>32</td>
<td>75</td>
</tr>
<tr>
<td>Southern LA</td>
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<tr>
<td>Mobile River Delta</td>
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<tr>
<td>White River</td>
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<td>69</td>
</tr>
<tr>
<td>Male plastron</td>
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<td></td>
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<tr>
<td>Black Warrior River</td>
<td>84</td>
<td>83</td>
</tr>
<tr>
<td>Cahaba River</td>
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<tr>
<td>Coosa River</td>
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<td>Tallapoosa River</td>
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<td>Coon Creek Lake</td>
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<tr>
<td>Southern LA</td>
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<tr>
<td>Mobile River Delta</td>
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<td>White River</td>
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<td>74</td>
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<td>Female plastron</td>
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<td>Black Warrior River</td>
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</tr>
<tr>
<td>White River</td>
<td>26</td>
<td>77</td>
</tr>
</tbody>
</table>

N = number of actual individuals in this category. Tests used to examine the influence of each population on the function’s overall ability to correctly classify individuals into the two flow regimes. For each test, individuals of the excluded population were coded as “unknown” and classified as “lentic” or “lotic” based on the remaining individuals. Lentic populations are Coon Creek Lake, Southern LA, Mobile River Delta, White River; Lotic populations are Black Warrior River, Cahaba River, Coosa River, Tallapoosa River.
Fig. 4 Apparatus for measuring drag. Model turtle is suspended in water column of flow tank by a horizontal sting extending posteriorly from the model and connecting to a vertical sting. The vertical sting is connected distally to a load cell located above the tank (not shown). Water flows from left to right (anterior to posterior relative to turtle). Grid = 1 cm.

measurement, leaving only the drag produced by the model. Comparisons of drag were performed using the drag coefficient (CD, an empirically derived coefficient that is fixed for a particular shape; see Vogel 2003) for each model, which was calculated using the equation [CD = (2 × D)/(ρw × A1 × u2)], where D is drag, ρw is the density of water (1 kg m⁻³), A1 is frontal area (m²), and u is the water velocity. Furthermore, a variant of the preceding equation (D = 0.5 × CD × ρw × A1 × u²) is used to calculate the drag incurred by the two morphotypes at a range of biologically relevant speeds.

Results
I examined morphological variation of the carapace and plastron among lentic and lotic populations of the river cooter, P. concinna. The data were treated as four distinct units: carapaces of males, carapaces of females, plastrons of males, and plastrons of females; each of these datasets was analyzed separately. Descriptions of differences in shell morphology between turtles inhabiting lentic and lotic flow regimes, as well as the results of nested MANOVA, DFA, and correlation analyses, are detailed in the sections below. While the population from Reelfoot Lake was used in generating the new dataset (i.e., PC axes); for all statistical tests, this population was analyzed independently (see Discussion section for rationale).

Morphological comparisons
Carapaces of males
PCA of the Procrustes superimposed data for all nine sites (N = 137) listed in Table 1 produced 92 PCs. Of these, the first 31 accounted for 95.1% of the total variation, while the first 54 accounted for 99.0% of the total variation. PC 1 (22.4%) and PC 2 (15.6%) accounted for a total of 38% of the total variation (Fig. 5A). Low scores for PC 1 identify individuals with strongly domed (i.e., high carapace height-to-length ratio) carapaces. The domed shell is a result of steeply oriented costal scutes. Due to the high steepness, the carapace is narrow. The width of the carapace does not vary considerably along the length of the body. Additionally, the marginal scutes are narrow and angled more steeply than are the costal scutes. In contrast to low scores, high scores for PC 1 depict individuals with dorsoventrally flattened and wider carapaces. This morphology is predominantly the result of less steeply oriented costal scutes. In addition, the angle between the costal and marginal scutes is decreased, causing the marginal scutes to “flare out.” The posterior end of the carapace is also visibly wider than the anterior end. Low PC 1 scores correspond to morphologies displayed by “lentic” individuals, while high PC 1 scores correspond to morphologies displayed by “lotic” individuals (Fig. 5C). Low PC 2 scores also describe domed carapaces. The domed shape is generated by increasing the mediolateral width of the costal scutes, rather than by changing the angle of their orientation. The possession of wide costal scutes also increases the overall width of the carapace. Additionally, the marginal scutes are oriented downward. In contrast, high PC 2 scores are characterized by a more dorsoventrally flattened and narrower carapace. The height and width of the carapace decreases because the width of the costal scutes decreases. Finally, the marginal and costal scutes are oriented at the same angle. Low PC 2 scores correspond to morphologies displayed by “lentic” individuals, while high PC 2 scores correspond to morphologies displayed by “lotic” individuals (Fig. 5C).

Results of a nested MANOVA on the eight focal populations (Table 1) using the first 31 shape variables (i.e., 95% of the variation in shape) indicated that there is a significant effect of flow regime on carapace shape (Wilks’ Lambda: F31,90 = 17.62, P < 0.001), as well as a significant effect of site (Wilks’ Lambda: F186,539 = 3.909, P < 0.001), which was nested within the effect of the flow. Univariate F-tests identified six PCs that differed significantly between flow regimes at the 0.05-level (PCs 1–3, 9, 14, 18). These six PCs accounted for 54.8% of the total variation. I used DFA (on the first 31 variables) to determine the level of difference in shape between the two groups. Based on jackknifed results, turtles were
correctly classified 91% of the time (lentic = 92%, lotic = 90%).

In order to examine the influence of each population on the DFA’s overall ability to correctly classify the two groups, multiple DFA were performed on the dataset, each excluding one population at a time (Table 2). Concomitantly, individuals of each excluded population were coded as “unknowns” and were classified as belonging to either lentic or lotic morphotypes based on the
remaining individuals (Table 2). Results show that the exclusion of individuals from the Black Warrior River (BWR) population produced the largest increase in the rate at which individuals were classified correctly, from 91% to 97%. Furthermore, when treated as “unknowns,” individuals from this population were classified correctly 33% of the time (Table 2).

Carapaces of females

PCA of the Procrustes superimposed data for all nine sites (N = 63) produced 62 PCs. Of these, the first 25 accounted for 95.2% of the total variation, while the first 41 accounted for 99.0% of the total variation. PC 1 (21.9%) and PC 2 (17.1%) accounted for a total of 39% of the total variation (Fig. 5B). Low PC 1 scores characterize individuals with domed and narrow carapaces. In addition, marginal scutes are more steeply oriented than are costal scutes. In contrast, high PC 1 scores characterize individuals with dorsoventrally flattened and wider carapaces. Additionally, the angle between marginal and costal scutes is small (Fig. 5D). PC 2 depicts variation between short and thus more domed carapaces (low scores) and slightly elongated carapaces (high scores). Low scores for PC 1 and PC 2 correspond to morphologies displayed by “lotic” individuals, while high scores correspond to morphologies displayed by “lentic” individuals (Fig. 5D).

Results of a nested MANOVA using the first 25 shape variables (i.e., 95% of the variation in shape) for the eight focal populations indicated that there is a significant effect of flow (Wilks’ Lambda: F_{25,21} = 6.155, P < 0.001) and site (Wilks’ Lambda: F_{150,130} = 2.032, P < 0.001) on carapace shape. Univariate F-tests identified five PCs that differed significantly between flow regimes at the 0.05-level (PCs 1–4, 11). These five PCs accounted for 60.6% of the total variation. Using the jackknifed results of a DFA (on the first 25 variables), turtles were correctly classified 83% of the time (lentic = 78%, lotic = 94%).

In order to examine the influence of each population on the DFA’s overall ability to correctly classify the two groups, multiple DFA were performed on the dataset, each excluding one population at a time (Table 2). Concomitantly, individuals of each excluded population were coded as “unknowns” and were classified as belonging to either lentic or lotic morphotypes based on the remaining individuals (Table 2). Results show that the independent exclusion of two populations [BWR and Mobile River Delta (MRD)] increased the rate at which individuals were classified correctly from 83% to 88% (Table 2). Furthermore, when treated as “unknowns,” individuals from the BWR and MRD were classified correctly 50% or less of the time (Table 2).

Plastrons of males

PCA of the Procrustes superimposed data for all nine sites (N = 133) produced 26 PCs. Of these, the first 15 accounted for 95.4% of the total variation, while the first 21 accounted for 99.1% of the total variation. PC 1 (26.4%) and PC 2 (16.8%) accounted for a total of 43.2% of the total variation (Fig. 6A). In general, low scores for PC 1 describe a wide and dorsoventrally flat plastron. In contrast, high scores for PC 1 depict a narrower plastron in which the anterior and posterior ends are angled upward, producing a more 3D structure (Fig. 6C). Low PC 2 scores describe a wide plastron with the anterior and posterior edges slightly inclined. High scores for PC 2 indicate a narrower and dorsoventrally flattened plastron. Low scores for PC 1 and PC 2 correspond to morphologies displayed by “lentic” individuals, while high scores correspond to morphologies displayed by “lotic” individuals (Fig. 6C).

Results of a nested MANOVA using the first 15 shape variables (i.e., 95% of the variation in shape) indicated that there is a significant effect of flow (Wilks’ Lambda: F_{15,102} = 12.34, P < 0.001) and site (Wilks’ Lambda: F_{90,580} = 4.216, P < 0.001) on plastron shape. Univariate F-tests identified five PCs that differed significantly between flow regimes at the 0.05-level (PCs 1–3, 5, 9). These five PCs accounted for 63.5% of the total variation. Pearson correlation coefficients and significance values from a correlation analysis between the first three plastron PCs, which accounted for 54.4% of plastron variation, and the first five carapace PCs identified a number of significant correlations between shape variables of the carapace and plastron (Table 4). Using the jackknifed results of a DFA on the first 15 variables, turtles were correctly classified 78% of the time (lentic = 77%, lotic = 80%).

In order to examine the influence of each population on the DFA’s overall ability to correctly classify the two groups, multiple DFA were performed on the dataset, each excluding one population at a time (Table 2). Concomitantly, individuals of each excluded population were coded as “unknowns” and were classified as belonging to either lentic or lotic morphotypes based on the remaining individuals (Table 2). Results show that the exclusion of individuals from the MRD population produced the largest increase in the rate at which individuals were classified correctly,
from 78% to 90% (Table 2). Furthermore, when treated as “unknowns,” individuals from the MRD were correctly classified 31% of the time (Table 2).

Plastrons of females
PCA of the Procrustes superimposed data for all nine sites \( (N = 63) \) produced 26 PCs. Of these, the first 15 accounted for 95.5% of the total variation, while the first 20 accounted for 99.0% of the total variation. PC 1 (23.1%) and PC2 (14.6%) accounted for a total of 37.7% of the total variation (Fig. 6B). Low PC 1 scores for the plastrons of females describe a wide plastron with inclined anterior and posterior ends; the anterior end is inclined to a greater degree.

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**Fig. 6** PCA on the 3D coordinates for the plastron. (A) First two principal components (PC 1 and PC 2) for males. (B) PC 1 and PC 2 for females. (C) Shape variation along PC 1 and PC 2 for males. (D) Shape variation along PC 1 and PC 2 for females. For (C, D), turtle diagrams represent the extreme of each PC axis. Top image in each set represents the lateral (right-side) view of the plastron; bottom image represents the ventral view of the right side of the plastron. For all diagrams of shells, anterior is to the right. Symbols on the axis represent mean ± SE For (A–D), open triangles represent turtles from lentic habitats; filled squares represent turtles from lotic habitats. Sample sizes are given in Table 1.
In contrast, high PC 1 scores characterize individuals with narrower, longer, and more dorsoventrally flattened plastrons (Fig. 6D). PC 2 depicts variation between plastrons with a strongly inclined anterior end and a weakly inclined posterior end (low scores) and dorsoventrally flattened plastrons (high scores). Low scores for PC 1 and PC 2 correspond to morphologies displayed by "lentic" individuals, while high scores correspond to morphologies displayed by "lotic" individuals (Fig. 6D).

Results of a nested MANOVA using the first 15 shape variables indicated a significant effect of flow (Wilks' Lambda: \(F_{15,32} = 6.453, P < 0.001\)) and site (Wilks' Lambda: \(F_{90,186} = 2.321, P < 0.001\)) on plastron shape. Univariate F-tests identified two PCs that differed significantly between flow regimes at the 0.05-level (PCs 1–2). Pearson correlation coefficients and significance values from a correlation analysis between the first three plastron PCs, which accounted for 51.0% of plastron variation, and the first five carapace PCs identified a number of significant correlations between shape variables of the carapace and plastron (Table 4). Using jackknifed results of a DFA on the first 15 variables, turtles were correctly classified 83% of the time (lentic = 82%, lotic = 88%).

In order to examine the influence of each population on the DFA's overall ability to correctly classify the two groups, multiple DFA were performed on the dataset, each excluding one population at a time (Table 2). Concomitantly, individuals of each excluded population were coded as "unknowns" and were classified as belonging to either lentic or lotic morphotypes based on the remaining individuals (Table 2). Results show that the exclusion of individuals from the MRD population produced the largest increase in the rate at which individuals were classified correctly, from 83% to 87% (Table 2). Furthermore, when treated as "unknowns," individuals from the MRD were correctly classified 67% of the time (Table 2).

Turtles from Reelfoot Lake

In order to classify Reelfoot Lake specimens into either lentic or lotic morphotypes, multiple DFA were performed on the four datasets (Table 3). Specimens from Reelfoot Lake were coded as "unknowns" and were classified as belonging to either lentic or lotic morphotypes based on the populations included in the analysis. The initial analyses, which used PCs accounting for 95% of the morphological variation and included all populations, did not produce clear results. Subsequent analyses using only the PCs identified as significant in the univariate tests identified a pattern suggesting that specimens from Reelfoot Lake are more similar to turtles from lotic habitats than lentic habitats (Table 3).

**Measurements of drag**

Specimens from Coon Creek Lake (lentic) and Tallapoosa River (lotic) were selected to represent the lentic and lotic morphotype, respectively. These two sites were selected based on their DFA classification for carapace (100% correct; see Table 2). The specimen from Coon Creek Lake (UTA 20875; CL = 22.3 cm) had a frontal area of 0.0064 m\(^2\) and a \(C_D = 0.56\). The specimen from Tallapoosa River (AUM 34147; CL = 18.1) had a frontal area of 0.0042 m\(^2\) and a \(C_D = 0.27\). When both specimens were scaled to the same size (CL = 22.3 cm), frontal area for both was 0.0064 m\(^2\). These results indicate that the shells of turtles inhabiting lotic environments incur considerably less drag than do those of turtles inhabiting lentic environments. The difference in carapace shape and the effects of flow velocity on drag for the two specimens are given in Fig. 7.

**Discussion**

**Morphological variation**

For both sexes of *P. concinna*, the carapace and plastron show significant morphological differences between lentic and lotic flow regimes. In general, the most prominent difference between the flow regimes in both male and female carapaces is that the shells of individuals from lotic habitats are more streamlined (i.e., lower height-to-length ratio) than are those of individuals from lentic habitats. Variation in carapace shape, particularly height of the shell, was achieved in two different ways. Among males, flattened (i.e., streamlined) carapaces are achieved by either (1) decreasing the width of vertically oriented costal scutes, or by (2) decreasing the inclination angle of wider costal scutes. In addition, the former method generates narrower carapaces, while the latter produces wider carapaces. For females, streamlined shells are generated through a series of small changes that either flatten or lengthen the carapace.

Differences in overall shape of the plastron are more subtle. For males, individuals from lentic habitats tend to have wider plastrons, although in some cases the posterior end of plastrons of individuals from lotic habitats appeared to widen relative to the anterior end (high PC 1 scores). In addition, there is variation in the orientation of the anterior end of the plastron, although no consistent morphology is apparent among males. Among females the plastron also tends to be wider in individuals
from lentic habitats. In addition, females also display variation in the orientation of the anterior end of the plastron; however, among females a consistent pattern is observed. The anterior edge of the plastron of females from lentic habitats is strongly angled upward, whereas the anterior edge of the plastron of females from lotic habitats is generally flatter.

Of the two shell components, the carapace appears to be more divergent (between the two flow regimes) than the plastron, based on the ability of DFA to correctly assign individuals to their respective flow regime (Tables 2 and 3). These results are consistent with adaptations to flow velocity, since variation in the shape of the carapace is more likely to affect hydrodynamics, particularly drag. The curved carapace encounters high pressures anteriorly and low pressures posteriorly, generating a large pressure drag; in contrast, the flat plastron has minimal influence on pressure drag. In addition, the carapace is the larger of the two structures, and thus, the larger surface area of the carapace relative to that of the plastron increases friction drag, which occurs at the interface between the shell and fluid (Vogel 2003). Furthermore, these results are also consistent with those of Claude et al. (2003), who found that for two major clades of turtles, the carapace exhibits similar differences in shape between aquatic and terrestrial environments but the plastron does not. These findings suggest that for aquatic turtles, forces producing differences in shape act more strongly on carapace shape than on plastron shape.

Moreover, the results of correlation analyses suggest that the significant effect of flow regime on plastron shape might be the result of correlated...
changes between the carapace and plastron (Lande and Arnold 1983). For instance, males with wider carapaces also tended to have wider plastrons (e.g., cPC 1 versus pPC 2, cPC 2 versus pPC 2, cPC 2 versus pPC 1; Table 4). For males, the correlation between the first three plastron PCs and the first five carapace PCs, indicated that 11 of the possible 15 correlations were significant. The same pattern may explain differences observed among females (e.g., wider carapace correlated with wider plastron: cPC 2 versus pPC 1), although fewer significant correlations exist. However, because the anterior edge of the plastron does not form contact points with the carapace, variation in the angle of the anterior edge of the plastron does not appear to be based on correlated changes.

The results also indicate that the level of morphological divergence differs between the sexes; habitat-associated differences are more distinct in carapaces of males than in those of females, while the plastrons of males and females show equivalent levels of divergence. This suggests that variation in carapace shape may be more constrained in females than in males. Factors associated with reproductive biology (e.g., space available for eggs; Rowe 1994; Tucker et al. 1998) and more complex modes of inheritance (Wayne et al. 2007) might limit morphological divergence in females.

Atypical populations

In addition to using DFA to examine the level of habitat-associated morphological divergence among the four structures (i.e., male carapace, female carapace, male plastron, and female plastron), a set of additional analyses examined the effects of excluding each population from the full dataset. Furthermore, I tested the ability of each model to correctly classify the excluded group to its respective flow regime. Of the 32 tests conducted (four structures and eight populations), there were nine cases in which the excluded groups were correctly classified at a rate of 50% or less (Table 2). Seven of these cases were from two populations, four from BWR and three from MRD. The ability of the model to correctly classify male carapaces increased from 91% to 97% when BWR was excluded, and increased to 94% when the MRD was excluded. However, it increased to 100% when both BWR and MRD were excluded. Based on the variation in shape described by PCs 1 and 2, the BWR population is contiguous with the other lentic populations but falls within a zone of overlap between individuals from lentic and lotic habitats (Figs. 5 and 8). In contrast, individuals from MRD
display both lentic and lotic morphotypes (Figs. 5 and 8). There are two possible reasons for the high morphological variance of MRD turtles. First, it is possible that selection pressure is weaker in lentic habitats, thus allowing for a broader range of morphologies. Selection for drag-reducing morphologies should be lower in lentic habitats because drag increases exponentially with water velocity. However, the other three lentic habitats do not display such a high level of morphological variation. A second possibility is that turtles from lotic habitats above the Fall Line have been displaced downstream and that gene flow from lotic to lentic habitats is responsible for the high variability in shape among turtles from MRD. The four lotic habitats examined in this study each eventually drain into the Mobile Bay through the MRD. Each lotic site is several hundred miles from the MRD, and while it is unlikely that turtles from the Mobile River could reach the lotic sites due to the distance and energy required to swim against flow, the flow of water could assist in the displacement of turtles downstream. This hypothesis can be tested using genetic markers for each population (i.e., microsatellites; Hankison and Ptacek 2008) to examine the direction (upstream versus downstream) and intensity of gene flow between each of the four lotic sites and the MRD.

**Turtles of Reelfoot Lake**

As previously noted, recent historical events have allowed turtles from the lotic Mississippi River to migrate into the lentic Reelfoot Lake. While a period of 200 years is likely too short a time for natural selection to effect changes on shell morphology for such a long-lived animal, this habitat transition provides the opportunity to test for effects of phenotypic plasticity. The premise for such tests is that if turtles from this population display the lotic morphotype, then plasticity is not a major factor determining morphology. However, if Reelfoot Lake specimens are more similar to lentic morphotypes, this would provide support for the importance of plasticity in the determination of shape. I used several DFA models to classify the Reelfoot Lake specimens as "lentic" or "lotic" (Table 3). Classifications based on all populations and the full complement of shape variables (i.e., 95% variation) were inconclusive. However, subsequent DFA models using only significant variables (as determined by MANOVA; see Results section) provided rather consistent results. Overall, these four tests (Table 3) found that the rate

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**Table 4** Pearson correlation values for carapace and plastron PCs (cPC1-5 versus pPC1-3)

<table>
<thead>
<tr>
<th></th>
<th>cPC1</th>
<th>cPC2</th>
<th>cPC3</th>
<th>cPC4</th>
<th>cPC5</th>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pPC1</td>
<td>0.51*</td>
<td>0.26*</td>
<td>-0.02</td>
<td>0.27*</td>
<td>0.29*</td>
</tr>
<tr>
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<td>0.60*</td>
<td>-0.01</td>
<td>-0.18*</td>
<td>-0.22*</td>
</tr>
<tr>
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<td>0.28*</td>
<td>0.10</td>
<td>-0.13</td>
<td>0.28**</td>
</tr>
<tr>
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<td></td>
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<td></td>
</tr>
<tr>
<td>pPC1</td>
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<td>0.61**</td>
<td>-0.38**</td>
<td>0.03</td>
<td>0.33**</td>
</tr>
<tr>
<td>pPC2</td>
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<td>-0.05</td>
<td>0.18</td>
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<tr>
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<td>-0.02</td>
<td>0.13</td>
<td>-0.11</td>
<td>0.44**</td>
</tr>
</tbody>
</table>

cPC, PC value for carapace; pPC, PC value for plastron.
*Denotes P-values < 0.05.
**Denotes P-values < 0.01.
Sample size (N) = 129 for males and 61 for females.

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**Fig. 8** PCA on the 3D coordinates for the carapace. First two principle components for males. (A) Positions of the lentic MRD (open triangles) and lotic BWR (filled squares). Plot of PC scores indicates considerable overlap between the two populations and peculiarly high PC 2 scores for MRD. (B) Position of Reelfoot Lake individuals relative to lentic and lotic populations. BWR and MRD have been excluded for clarity. Symbols are open triangles (lentic), filled squares (lotic), and shaded circles (Reelfoot Lake). Sample sizes are given in Table 1.
of classification as “lotic” for the four structures was as follows: male carapaces, 72%; female carapaces, 50%; male plastrons, 33%; and female plastrons, 78%. When the classification was based on only the significant PCs with the MRD and BWR populations excluded, the overall rate of classification as “lotic” was higher, but is consistent with the aforementioned average results: male carapace, 78%; female carapace, 60%; male plastron, 44%; and female plastrons, 78%. Because the ability to correctly classify unknown specimens was highest when the MRD and BWR populations were excluded, subsequent comments are based on these results (Fig. 8; Table 3). These results indicate that specimens from Reelfoot Lake display morphologies most similar to the examined “lotic” populations, suggesting that while phenotypic plasticity may play a role in the variation in shape between the two flow regimes, it is likely less than the contribution of genetic divergence. Still, laboratory studies that simultaneously examine the influence of genetic divergence and plasticity on differences in shell shape are required (Keeley et al. 2007; Langerhans 2008).

Effects of shape on drag

The measurement of drag from models indicates that habitat-associated morphological differences in the shells of turtles do have substantial effects on hydrodynamic characteristics. The drag coefficient \( (C_D = 0.27) \) of turtles from lotic habitats is approximately half that \( (C_D = 0.56) \) of turtles from lentic ones, meaning that for turtles of the same size and a particular swimming speed, the lotic morphotype only incurs half the resistance. Moreover, these values were calculated from the individuals that represented the two population means (Coon Creek Lake and Tallapoosa River; see Fig. 7). Based on the variation in shape described by PCs 1 and 2 (Fig. 7), there are other lentic–lotic pairs that display considerably more morphological divergence, suggesting that larger differences in drag \( (C_D) \) may be observed among individuals; this is important because selection acts on the performance of individuals. Finally, because the two models had the same frontal area when scaled to the same size \( (CL) \), the results provide an even more accurate estimate of differences in the drag associated with shape.

Alternative hypotheses

Geographic variation

While I identified significant morphological differences between populations from lentic and lotic habitats, it should be noted that these results also follow a geographic pattern—all four lotic populations were from eastern sites (i.e., east of the Mississippi River), while three of the four lentic populations were from western sites (i.e., west of the Mississippi River). While this could seem to suggest that an east-to-west trend in shell shape (i.e., shells of turtles are flat in the east and become more domed in the west) is responsible for the pattern observed in this study, data from Seidel and Palmer (1991) show that this is not the case. Seidel and Palmer (1991) determined that \( P. concinna \) from central Atlantic drainages were significantly less domed (lower shell height/carapace length; sensu Aresco and Dobie 2000) in the Piedmont than in the Coastal Plain. Within the Atlantic drainages, the Piedmont is located in the west and the Coastal Plain in the east. The findings of Seidel and Palmer (1991) for turtles within Atlantic drainages are consistent with results from Aresco and Dobie (2000) and those presented in this article for turtles within Gulf drainages, in that turtles inhabiting lotic sites in the Piedmont of the Appalachian Mountains (on the eastern or western slopes) possess flattened morphologies, whereas those inhabiting lentic sites in the adjacent Coastal Plains (in the Atlantic or Gulf drainages) are more domed. This demonstrates that the pattern is not simply a longitudinal trend, and provides additional support for the assertion that differences in flow velocity, which are associated with differences in elevational gradients, are the driving force that has produced the observed morphological variation.

Predation

Aresco and Dobie (2000) proposed two hypotheses to explain morphological divergence between lentic and lotic flow regimes: (1) enhanced hydrodynamics in lotic populations, and (2) stronger shells that reduce alligator predation in lentic environments. Previous studies have examined relationships between flow and predator regimes in other vertebrates and invertebrates and found that predation can influence differences in shape (Langerhans and DeWitt 2004; Holomuzki and Biggs 2006). It is difficult to specifically test these hypotheses for \( P. concinna \) for two reasons. First, alligators do not inhabit lotic flow regimes, and second, alligators and \( P. concinna \) are sympatric in most lentic habitats. Nevertheless, here I propose that available evidence suggests that flow, rather than predation, is responsible for the observed morphological variation. First, lotic morphotypes are found in lentic habitats (e.g., MRD); however, lentic morphotypes are completely excluded from lotic populations. If flow
had no effect, domed turtles should be observed inhabiting both flow regimes. Second, the results of the drag tests indicated a significant reduction in drag for turtles inhabiting lotic flow regimes compared with those inhabiting lentic flow regimes. These results are also likely to be conservative, with respect to maximum drag reduction, as they were calculated using “mean specimens,” rather than being collected separately for each individual. As such, morphological differences between the two models were smaller than morphological differences between individuals at the extremes, suggesting that some “lotic” turtles may have even lower drag coefficients. In addition, Lubcke and Wilson (2007) found a similar pattern of flow-correlated shape variation for a different species of turtle (A. marmorata) in a system without a major predator dichotomy. Moreover, it is unknown whether the observed differences in shell shape would increase the strength of the shell, or if any increase would be large enough to resist an alligator attack. Furthermore, any advantage conferred by a change in shell shape would likely only be advantageous to larger individuals that are too big to be swallowed whole. Future studies should combine data on the forces exerted on the shells of turtles during attacks by alligators, collected from models of adult turtles subjected to alligator bites, and computational methods (e.g., finite element analysis) to examine the ability of shells of different shapes to withstand attacks.

Conclusions
This study demonstrates that P. concinna shows significant divergence in 3D shell shape between lentic and lotic flow regimes across a wide geographic range. In addition, significant differences were detected for the carapace and plastron of both sexes, with the level of morphological divergence being greater for the carapace. Using geometric morphometrics, I was able to describe the manner in which changes in shell shape have occurred. This study provides the first empirical evidence for an adaptive benefit (i.e., drag reduction) of the observed difference in shape. Finally, preliminary information collected from the Reelfoot Lake population suggests that phenotypic plasticity plays a limited role in shape variation between the flow regimes. While this study provides answers for many questions not addressed in earlier studies, it also generated several new ones. To better understand the ecomorphological divergence identified in this study, future studies should address several issues, including: (1) reproductive output between females from lentic and lotic habitats, (2) the cause of the increased shape variation observed in the MRD population, and (3) the relative effect of genetic and environmental factors on shape.

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Appendix 1: List of museum specimens

Abbreviations
AUM: Auburn University Natural History Museum
CM: Carnegie Museum of Natural History
KU: University of Kansas Natural History Museum
LSU: Louisiana State University Museum of Natural Science
UTA: Amphibian and Reptile Diversity Research Center, University of Texas, Arlington
†Specimen for which only the carapace was examined
‡Specimen for which only the plastron was examined
### Males

#### Coon Creek Lake
- UTA20847, UTA20848, UTA20860, UTA20861
- UTA20863, UTA20864, UTA20866, UTA20867
- UTA20868, UTA20870, UTA20871, UTA20872
- UTA20873, UTA20874, UTA20875, UTA20876
- UTA20878, UTA20879, UTA20880, UTA20881
- UTA20882, UTA20883, UTA20884, UTA20885
- UTA20886, UTA20887, UTA20888

#### Southern LA
- LSU38922, LSU43389, LSU43392, LSU74814
- LSU74816, LSU74817, LSU74818, LSU74825
- LSU74827

#### Mobile River Delta
- AUM10145, AUM11600, AUM11604, AUM11607
- AUM11610, AUM11815, AUM19359, AUM19360
- AUM19361, AUM6300, AUM9958, CM95897
- CM95906, CM95913, CM95914, CM95932
- CM95933, CM95934, CM95941, CM95943
- CM95944, CM95945, CM95946, CM95947
- CM95948, CM95949, CM95950, CM95951
- CM95952, CM95953, CM95954, CM95955
- CM95956, CM95957, CM95971

#### White River
- AUM27099, CM64089, CM94880, CM95179
- CM95180, CM95181, CM95182, CM95186
- CM95188, CM95189, KU3113, KU3353, KU3365, KU3368

#### Black Warrior River
- AUM12647, AUM12648, AUM12653, AUM12654
- AUM17810, CM95275, CM95289, CM95292
- CM95293, CM95294, CM95295, CM95296
- CM95297, CM95299, CM95715, CM95717, CM95718

#### Cahaba River
- CM67403, CM67418, CM95020, CM95383
- CM95587, CM95596, CM95597, CM95598, CM95999

#### Coosa River
- CM95705, CM95735, CM95736, CM95744
- CM95745, CM95774, CM95775, LSU75224

#### Tallapoosa River
- AUM34119, AUM34120, AUM34126, AUM34145
- AUM34147, AUM8849

### Females

#### Coon Creek Lake
- UTA20853, UTA20854, UTA20855, UTA20857
- UTA20858, UTA20865

#### Southern LA
- LSU18941, LSU38921, LSU41080, LSU41103
- LSU57179, LSU57180, LSU74824, LSU74826
- LSU74830, LSU75057, LSU75209

#### Mobile River Delta
- AUM10146, AUM10305, AUM6301, AUM9589
- CM67350, CM67382, CM95896, CM95958
- CM95959, CM95960

#### White River
- CM61677, CM95187, KU3352, KU3354, KU3355
- KU3357, KU3381, KU3383, KU3385, KU3445
- KU3446, KU3382

#### Black Warrior River
- AUM12651, AUM12656, CM94995, CM95298

#### Cahaba River
- CM67404, CM67419, CM95012, CM95612, CM95614, CM95698

#### Coosa River
- CM95737, CM95738

#### Tallapoosa River
- AUM14281, AUM34141, AUM34144, AUM6203

#### Reelfoot Lake
- CM95365, CM95445, CM95446, CM95449
- CM95450, CM96115, CM96149, CM96150, CM96151

### References


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Flow-associated shell shape in turtles


