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DIMORPHISM IN SHELL SHAPE AND STRENGTH IN TWO SPECIES OF EMYDID TURTLE

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ABSTRACT: This study investigates the mechanical implications of shell shape differences between males and females of two North American turtle species: *Chrysemys picta* and *Glyptemys insculpta*. These species show patterns of sexual dimorphism that are common to many species of turtle. Females have wider and more highly domed shells, whereas males tend to have flatter, more streamlined shells. In addition, the males of many terrestrial species have concave plastra, most likely to accommodate the domed shells of the females while mating. The purpose of this study was to determine whether the known morphological differences in male and female turtle shells are also associated with differences in shell strength. Landmark coordinate data were collected from the shells of males and females of both species. These data were used to create digital models of each shell for finite-element (FE) analysis. FE models were generated by transforming a single base model of a turtle shell to match the shapes of each specimen examined in this study. All models were assigned the same material properties and restraints. Twelve load cases, each representing a predator's bite at a different location on the carapace, were applied separately to the models. Subsequently, Von Mises stresses were extracted for each element of each model. Overall, the shells of females of both species exhibited significantly lower maximum and average stresses for a given load than those of their male counterparts. Male *G. insculpta* exhibited significant increases in stresses because of the concave shape of their plastra. We suggest that the mechanical implications of shell shape differences between males and females may have a large impact on many aspects of the biology of these turtle species.

Key words: *Chrysemys picta*; Finite-element analysis; Functional morphology; *Glyptemys insculpta*; Mechanical stress; Sexual dimorphism; Turtle shell

ONTOGENETIC growth differences between male and female turtles lead to sexual dimorphism in shell shape in adults (Brophy, 2006). These differences in male and female shell shape likely reflect sex-specific selective pressures. Females possess larger, taller shells that increase body volume, potentially enabling them to hold larger clutches of eggs (Kaddour et al., 2008). Males, in contrast, have flatter shells with larger openings for their limbs, enhancing their ability to move their limbs and tail and thus improving success in mating, dispersal, and courtship (Kaddour et al., 2008). In addition, the plastra of males of terrestrial species are often concave to accommodate the curved shell of the female and prevent the male from falling backward during mating (Pritchard, 2008). Males and females of aquatic species have flat or slightly convex plastra.

These differences in shape between males and females of the same species have implications for the ability of their shells to withstand loads, such as might be experienced during a predator's bite, without breaking. For example, the increased height of their shells may increase females' ability

to resist loads (Tucker et al., 1998). However, although the taller shell is beneficial for protection and reproduction, it may negatively affect the hydrodynamic properties of female turtle shells by increasing drag (Rivera, 2008). The narrower, flatter shell of male turtles probably produces a lower drag coefficient (Rivera, 2008) and increases swimming performance, but this flatter shell may make the shell weaker during loading. These potential functional differences can in turn affect other aspects of turtle natural history. For example, shell shape differences could explain differences in the predator avoidance strategies of males and females (Bellis and Pluto, 1986).

The goal of this study was to investigate the mechanical implications of sexual differences in shell shape in two species of emydid turtle: *Chrysemys picta* (Painted Turtle), an aquatic species, and *Glyptemys insculpta* (Wood Turtle), a terrestrial species. Female *C. picta* have a more dome-shaped carapace relative to males, whereas males have flatter shells with a wider posterior end (Adams et al., 2004). Female *C. picta* are larger than the males. Male *G. insculpta*, like many terrestrial species, have a concave plastron, whereas

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females have a taller, more domed shell and smaller apertures for the limbs than males (Barbour and Ernst, 1989). In this species, females are smaller (Ernst et al., 2008).

We investigated the mechanical behavior of the turtle shell by modeling a series of point loads distributed over the carapace and plastron. These loads are intended to simulate a predator's tooth being driven into the shell during biting. Modeling was performed using finite-element (FE) techniques. FE analysis is an engineering technique that is increasingly being used in biological research to analyze the behavior of complex skeletal structures (Dumont et al., 2005; McHenry et al., 2006; Pierce et al., 2008; Rayfield, 2005, 2007). Briefly, FE analysis builds up a computer model of a potentially complex structure (such as a female *G. insculpta* turtle shell) from simple geometric elements, and then sums the response of those elements to describe the behavior of the more complex structure under a given loading condition. Thus, by generating multiple FE models of turtle shells, and testing their response to multiple loads, an overall comparison can be made between the average shell strength of female and male turtles. These methods have been validated on turtle shells (Stayton, 2009), and mechanical testing on a subset of the individuals used in another study revealed a strong correlation between modeled maximum stress and actual load to failure ($r^2 = 0.81$; C. Stayton, personal observation).

In this study, we analyzed the shells of 68 specimens. All models were loaded under identical conditions. Von Mises stress values resulting from each of the loading experiments were used to assess differences in the structural strength of males' and females' shells. We hypothesized that the shells of females would exhibit lower modeled stress values for a given load than the shells of males of the same species, indicating that females have stronger shells. We also hypothesized that the concavity of male *G. insculpta* plastra would increase the modeled stress exhibited by those shells.

MATERIALS AND METHODS

Finite-Element Modeling

Ten *C. picta* were captured in Lewisburg, PA, USA, in accordance with PA Fish and

Boating Commission permit #210, and photographed at Bucknell University. Fifty-five *C. picta* (28 female; 27 male) and 23 *G. insculpta* (16 female; 7 male) were photographed at the Carnegie Museum of Natural History. All specimens were adults and ranged in size from 10.1 to 18.3 cm carapace length for *C. picta* and 16.4–27.0 cm for *G. insculpta*. Each specimen was photographed in dorsal, lateral, and ventral views. The camera was placed perpendicular to the specimens during photography and a scale was visible in all photographs. A piece of graph paper was used to check for distortion; this was found to be minimal in all views.

Fifty-nine landmarks located at three point junctions between scutes were digitized in the dorsal, lateral, and ventral view for each specimen (see Stayton, 2009 for the full set of landmark coordinates); separate files were created for each view. All landmark coordinates were compiled into a single three-dimensional file using a MATLAB routine (Stayton, 2009). FE models were constructed using the method of Stayton (2009). This method uses a thin-plate spline function fitted to geometric morphometric data to transform a pre-existing model into a model of the desired shape. In this study, a model of a bog turtle (*Glyptemys muhlenbergii*) was transformed to match the shapes of all *C. picta* and *G. insculpta* shells. *Glyptemys muhlenbergii* is in the same family (Emydidae) as, and shares a common shell construction with, both species. This original model consisted of 41,615 tetrahedral elements and was built from a series of scans obtained at the University of Texas at Austin high-resolution X-ray facility (see Stayton, 2009 for further details).

For male *G. insculpta*, the z -coordinates of the landmarks along the midline of the plastron were manipulated to achieve the concave shape seen in the specimens. To measure the degree of concavity, a string was placed longitudinally along the midline of the plastron of male *G. insculpta* specimens, and the distance from the string to the plastron was measured for all midline plastron landmarks. These distances were then used to adjust the coordinates of those landmarks to reflect the concavity of the plastron. This technique was used because the concavity of

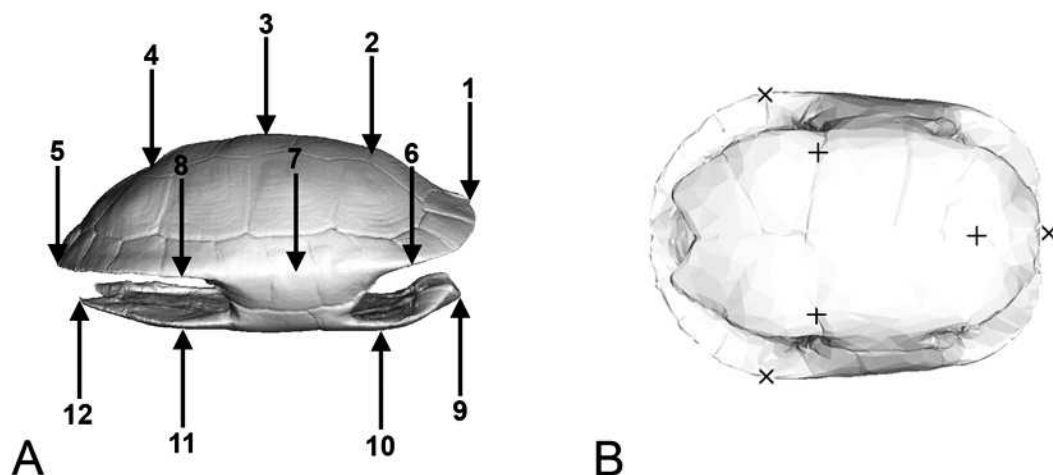


FIG. 1.—(A) Locations of load cases used for analysis: (1) anterior carapace, (2) anterior middle carapace, (3) middle carapace, (4) posterior middle carapace, (5) posterior carapace, (6) anterior mid-side carapace, (7) mid-side carapace, (8) posterior mid-side carapace, (9) anterior plastron, (10) anterior mid-side plastron, (11) posterior mid-side plastron, and (12) posterior plastron. (B) Locations of restraints on all models. The + represent restraints for loads on the carapace. The × indicate restraints for loads on the plastron.

the males' shells was not captured in the photographs.

FE analyses were performed on all shells in the sample. The FE files were imported into Strand7 finite-element analysis software (Strand7, 2007), and the models were cleaned to ensure that there were no extremely skewed elements that could produce artifactually high stresses during analysis. Two models were made for each male *G. insculpta*: one with the concave plastron and one with a flat plastron. After cleaning, all models were scaled to the same size. As stress is calculated as a force distributed over an area, models were scaled so that the ratio of applied force to surface area was identical for all. This scaling ensures that all differences in stress were exclusively the result of differences in shape rather than size (Dumont et al., 2009). This transformation, however, also produced unrealistically small models (on the order of 0.2 mm in length), so all models were subsequently scaled up by a factor of 1000 to produce models that were approximately 20 cm long. Note that this scaling to more reasonable sizes does not affect the relative stresses produced by the models, which is what is being investigated here.

By scaling all models to a comparable size, it is possible to investigate mechanical differences between males and females that are purely

due to differences in shell shape. However, size is a biological attribute that strongly influences mechanical strength (among other characteristics; LaBarbera, 1989); all else being equal, a larger structure will be capable of experiencing higher loads without breaking than will a smaller structure. Given that sexual size dimorphism is seen in both of these species (Barbour and Ernst, 1989), the influence of size, as well as shape, was also investigated. A second set of models was developed from the morphometric data, this time with all shells scaled to their actual size.

All 156 models (representing every specimen of this study, at both equivalent and actual sizes) were assigned the same set of material properties (Young's modulus = 10 MPa, Poisson's ratio = 0.3; typical values for Painted Turtle shell bone; C. Stayton, personal observation). In addition, the same 12 load cases (Fig. 1a) were applied to all models. Three restraints located on the plastron were used for loads on the carapace (loads 1–8); similarly, three restraints located on the carapace were used for plastral loads (9–12; Fig. 1b). Loads and restraints were placed on the same individual points in all models. We used 12 load cases (each 500 N) to simulate multiple loading situations and investigate the strength of the entire shell. All load cases and restraints were intended to

TABLE 1.—Average maximum Von Mises stress values (Pa) for 12 load cases for male and female *Chrysemys picta* and *Glyptemys insculpta*, and significance of those differences. All models scaled to the same size.

Location of load case	<i>Glyptemys insculpta</i>		<i>Chrysemys picta</i>	
	Males	Females	Males	Females
(1) Anterior carapace	7.80×10^7	$8.02 \times 10^{7**}$	2.73×10^8	$2.34 \times 10^{8**}$
(2) Anterior middle carapace	4.92×10^7	$4.45 \times 10^{7**}$	1.82×10^8	$1.50 \times 10^{8**}$
(3) Middle carapace	3.04×10^7	$2.77 \times 10^{7**}$	1.17×10^8	$9.63 \times 10^{7**}$
(4) Posterior middle carapace	5.66×10^7	$4.65 \times 10^{7**}$	1.92×10^8	$1.60 \times 10^{8**}$
(5) Posterior carapace	7.42×10^7	$6.20 \times 10^{7**}$	2.47×10^8	$2.00 \times 10^{8**}$
(6) Anterior mid side carapace	5.90×10^7	$4.13 \times 10^{7**}$	1.82×10^8	$1.40 \times 10^{8**}$
(7) Mid-side carapace	5.82×10^7	$3.14 \times 10^{7*}$	1.93×10^8	$1.55 \times 10^{8**}$
(8) Posterior mid-side carapace	1.32×10^8	$1.31 \times 10^{8**}$	4.72×10^8	$4.46 \times 10^{8**}$
(9) Anterior plastron	3.00×10^8	$1.93 \times 10^{8*}$	7.35×10^8	$4.73 \times 10^{8**}$
(10) Anterior mid side plastron	1.83×10^8	$1.53 \times 10^{8*}$	6.39×10^8	$4.62 \times 10^{8**}$
(11) Posterior mid side plastron	7.60×10^7	$6.23 \times 10^{7**}$	2.69×10^8	$2.19 \times 10^{8**}$
(12) Posterior plastron	1.09×10^7	$8.98 \times 10^{7**}$	3.02×10^8	$2.61 \times 10^{8**}$

* $P < 0.05$ after Bonferroni correction.
** $P < 0.001$ after Bonferroni correction.

approximate a bite from a predator, with the turtle being held in place on three teeth with a fourth tooth being forced onto the shell. This (500 N) is a strong bite from a medium-sized predator such as a coyote (Christiansen and Wroe, 2007) and thus represents a reasonable load that either of these species might encounter. Note that, although all boundary conditions are biologically reasonable, it is more important that they are identical for all models, as shell performance is being compared between models. A linear static analysis was conducted on the data, producing Von Mises stresses for all elements for 12 different load cases located on the specimens' shells.

The element with the highest Von Mises stress value for each load case was recorded along with its stress value. Von Mises stress is a type of combined stress that is useful in predicting failure of mechanical structures (Dumont et al., 2005). These maximum stresses represent areas in which the turtle shell would break first under a load, and thus represent biologically relevant parameters. As restraints can sometimes induce artifactually high stresses during loading, all models and loads were checked to ensure that these peak stresses did not occur close to the restraints. However, maximum stresses can still be the result of artifacts, even if they do not occur close to restraints. For this reason, average stresses were calculated for all load cases for each model as well. These maximum and average stresses were used for subsequent statistical analyses.

Statistical Analyses

Separate analyses were conducted on *C. picta* and *G. insculpta*. For each species, an ANOVA was conducted on both the maximum and average stress values observed for each load case to determine whether the sexes differed in their responses to individual loads. Males and females were compared with shells scaled to the same size (Table 1) and at actual size (Table 2).

To determine whether the concavity of the plastron resulted in greater stresses in male *G. insculpta*, a paired *t*-test was conducted on the maximum stresses exhibited by the models with and without concave plastra (Fig. 2; Table 3). Models were scaled to equivalent sizes for this analysis. α was set at 0.05 for all tests. Because multiple comparisons were conducted on each data set, a Bonferroni correction (Jackson, 1993) was applied to all *P*-values.

RESULTS

When considering only differences in shape, male turtle shells exhibited significantly greater stresses than female turtle shells for both species used in this study (Fig. 3; Table 1; Appendix 1). Average maximum stress values for all 12 load cases were higher for male *C. picta* than for females. Average maximum stress values for 11 of the 12 load cases were higher for male *G. insculpta*. The only load case for *G. insculpta* that produced significantly higher maximum stresses in

TABLE 2.—Average maximum Von Mises stress values (Pa) for 12 load cases for male and female *Chrysemys picta* and *Glyptemys insculpta*, and significance of those differences. All models scaled to their actual size.

Location of load case	<i>Glyptemys insculpta</i>		<i>Chrysemys picta</i>	
	Males	Females	Males	Females
(1) Anterior carapace	7.20×10^7	$8.72 \times 10^{7**}$	3.15×10^8	$2.05 \times 10^{8***}$
(2) Anterior middle carapace	4.55×10^7	$4.84 \times 10^{7**}$	2.09×10^8	$1.32 \times 10^{8***}$
(3) Middle carapace	2.81×10^7	$3.01 \times 10^{7**}$	1.34×10^8	$8.45 \times 10^{7**}$
(4) Posterior middle carapace	5.23×10^7	$5.06 \times 10^{7**}$	2.21×10^8	$1.40 \times 10^{8***}$
(5) Posterior carapace	6.85×10^7	$6.75 \times 10^{7**}$	2.84×10^8	$1.76 \times 10^{8***}$
(6) Anterior mid-side carapace	5.45×10^7	$4.49 \times 10^{7**}$	2.10×10^8	$1.23 \times 10^{8***}$
(7) Mid-side carapace	5.37×10^7	$3.41 \times 10^{7*}$	2.22×10^8	$1.36 \times 10^{8***}$
(8) Posterior mid-side carapace	1.22×10^8	$1.43 \times 10^{8***}$	5.43×10^8	$3.91 \times 10^{8***}$
(9) Anterior plastron	1.18×10^8	$8.89 \times 10^{7*}$	3.57×10^8	$1.75 \times 10^{8***}$
(10) Anterior mid-side plastron	1.21×10^8	$1.19 \times 10^{8*}$	5.25×10^8	$2.90 \times 10^{8***}$
(11) Posterior mid-side plastron	5.45×10^7	$5.27 \times 10^{7**}$	2.40×10^8	$1.49 \times 10^{8***}$
(12) Posterior plastron	6.95×10^7	$6.73 \times 10^{7**}$	2.39×10^8	$1.58 \times 10^{8***}$

* $P < 0.05$ after Bonferroni correction.
** $P < 0.001$ after Bonferroni correction.

females was the load placed at the anterior of the carapace. Males’ average maximum stress values ranged from 0.975 to 1.86 times the magnitude of females’ for *G. insculpta* and from 1.06 to 1.56 times higher than females’ for *C. picta* (Table 4). Analysis of average shell stress produced the same pattern of significance as did the maximum stresses.

When shells were scaled to their actual sizes, male *C. picta* still exhibited significantly greater stresses than female *C. picta* for all load cases. The situation for *G. insculpta* was more complicated. Females exhibited significantly higher stresses than males for 4 of the 12 load cases: 3 load cases along the anterior midline of the carapace and 1 along the posterior lateral edge of the carapace. Males exhibited significantly higher stresses than

females for all other load cases. Males’ average maximum stress values ranged from 1.39 to 2.04 times higher than females’ for *C. picta* and 0.826 to 1.57 times the magnitude of females’ for *G. insculpta*.

There were significant differences in the stresses exhibited by *G. insculpta* males due to the concavity of their plastron (Table 3). Stresses were higher for males with concave plastra in all except two load cases located on the carapace (posterior middle carapace and posterior mid-side carapace); more importantly, stresses were higher for all load cases located on the plastron.

DISCUSSION

When only shape (and not size) is taken into account, the shells of female *G. insculpta* and

TABLE 3.—Average maximum Von Mises stress values (Pa) for 12 load cases for male *Glyptemys insculpta* with flat and concave plastra. All models scaled to the same size.

Location of load case	Flat plastron	Concave plastron	Ratio of concave to flat
(1) Anterior carapace	7.80×10^7	$1.17 \times 10^{8**}$	1.51
(2) Anterior middle carapace	4.92×10^7	$7.59 \times 10^{7**}$	1.54
(3) Middle carapace	3.04×10^7	$4.82 \times 10^{7**}$	1.59
(4) Posterior middle carapace	5.66×10^7	$5.42 \times 10^{7**}$	0.958
(5) Posterior carapace	7.42×10^7	$8.47 \times 10^{7**}$	1.14
(6) Anterior mid-side carapace	5.90×10^7	$8.26 \times 10^{7**}$	1.40
(7) Mid-side carapace	5.82×10^7	$6.59 \times 10^{7**}$	1.13
(8) Posterior mid-side carapace	1.32×10^8	$1.28 \times 10^{8**}$	0.968
(9) Anterior plastron	3.00×10^8	$3.31 \times 10^{8**}$	1.10
(10) Anterior mid-side plastron	1.83×10^8	$2.20 \times 10^{8**}$	1.20
(11) Posterior mid-side plastron	7.60×10^7	$9.09 \times 10^{7**}$	1.19
(12) Posterior plastron	1.09×10^7	$1.54 \times 10^{8**}$	1.41

* $P < 0.05$ after Bonferroni correction.
** $P < 0.001$ after Bonferroni correction.

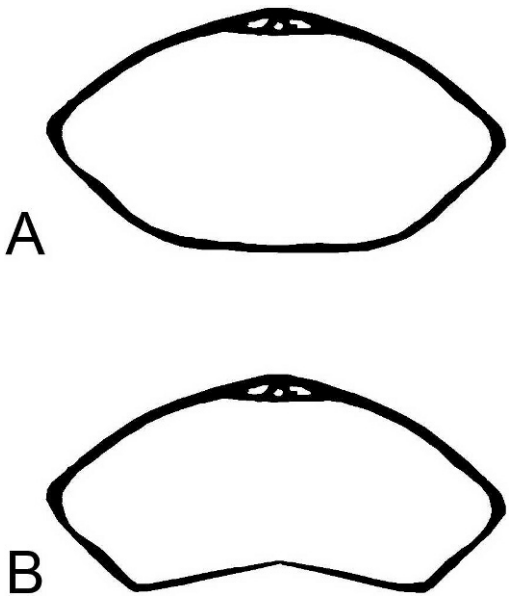


FIG. 2.—Frontal sections of a single male *Glyptemys insculpta* with (A) a flat plastron and (B) a concave plastron.

C. picta exhibit lower average stresses for a given load, and therefore may be said to be stronger than those of their male counterparts. Such a pattern is not unexpected—female turtles are known to develop taller, more rounded shells than males for many species (e.g., Tucker et al., 1998), and such shapes are conventionally considered to be

better at resisting failure during loading from predators (e.g., Rivera, 2008; Stayton, 2009). The greater stresses exhibited by *G. insculpta* models with concave plastras are also expected—a concave structure tends to exhibit larger amounts of tension, compared with a flat structure, when stressed (Currey, 2006; Wainwright et al., 1982). Nevertheless, this is the first study to quantify the magnitude and significance of these differences between males and females.

When size is taken into account, the shells of *C. picta* females still exhibit lower stresses than the shells of males. As females tend to be larger in this species (and were larger in the data set of this study), this is unsurprising. In this species, therefore, sexual size dimorphism enhances the mechanical differences between sexes. In the case of *G. insculpta*, the pattern is more complicated when size is considered—males exhibited lower stresses than females in four regions, most located along the anterior midline of the shell. In this species, sexual size dimorphism somewhat mitigates the mechanical differences between sexes. Although females still show lower average stresses overall, the differences are far less pronounced than they were when only shell shape was considered.

A few caveats apply to the results of this study. First, we assumed that all shells showed identical material properties. However, bone

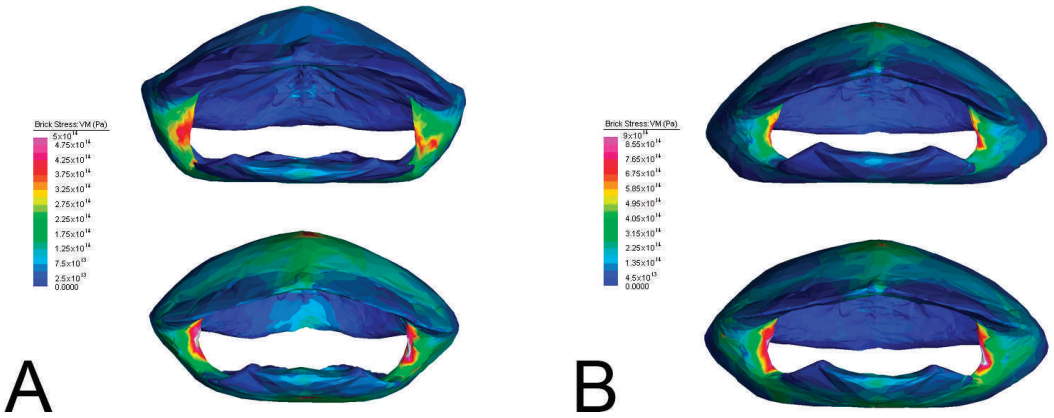


FIG. 3.—Representative results from finite-element modeling of turtle shell loadings. All figures show results from load case 2. Light colors (whites and light grays) indicate regions of high stresses; dark colors (blacks and dark grays) indicate areas of low stress. In the color version of this figure online and in the PDF, “Hot” colors (whites and reds) indicate regions of high stresses; “cool” colors (blues and greens) indicate areas of low stress. The scale is the same for females and males of the same species. Note that males generally show higher stresses in a given area than females. (A) Female (top) and male (bottom) *Glyptemys insculpta*. (B) Female (top) and male (bottom) *Chrysemys picta*.

TABLE 4.—Male/female ratio of average maximum stresses for 12 load cases for each study species, in models scaled to the same size and to their actual sizes.

Location of load case	<i>Glyptemys insculpta</i>		<i>Chrysemys picta</i>	
	Same size	Actual sizes	Same size	Actual sizes
(1) Anterior carapace	0.973	0.826	1.17	1.53
(2) Anterior middle carapace	1.11	0.939	1.21	1.58
(3) Middle carapace	1.10	0.934	1.21	1.59
(4) Posterior middle carapace	1.22	1.03	1.20	1.57
(5) Posterior carapace	1.20	1.02	1.23	1.61
(6) Anterior mid-side carapace	1.43	1.21	1.30	1.71
(7) Mid-side carapace	1.85	1.57	1.25	1.64
(8) Posterior mid-side carapace	1.01	0.854	1.06	1.39
(9) Anterior plastron	1.55	1.32	1.56	2.04
(10) Anterior mid-side plastron	1.20	1.01	1.38	1.81
(11) Posterior mid-side plastron	1.22	1.03	1.23	1.61
(12) Posterior plastron	1.22	1.03	1.16	1.52

can vary in strength or elasticity (Currey, 2006), and it is possible that presumptive “weaker” shells of males are composed of stronger bone than those of females, and thus are not actually weaker overall. Second, we compared the responses of shells that had all been loaded in the same way. If predators use different strategies when handling males and females (perhaps as the result of different defensive strategies on the part of the turtles), then males may never encounter loads that place relatively high stresses on their shells.

That said, both of our hypotheses received strong support from an analysis of these species. The mechanical effects of these differences in shell shape are thus elucidated. The results of this study are likely applicable to all turtle species that show the same patterns of shape dimorphism as are shown by *C. picta* and *G. insculpta*, with females having taller, more domed shells (especially in the posterior of the carapace) and males having flatter shells with larger apertures for the head, limbs, and tail and, in the case of terrestrial species, concave plastra.

However, two questions remain for further study. First, what are the ultimate causes of the observed shape and size dimorphism in many turtle species? Second, what are the broader effects of these mechanical differences between males and females? Many causal explanations have been suggested for the differences in shell shape between males and females. For example, it has been suggested that females need to develop more volumi-

nous (and hence more spherical) shells using a given amount of shell material to increase clutch size (Brophy, 2006; Tucker et al., 1998; Willemsen and Hailey, 2003). Similarly, the flatter shells and larger limb apertures of males have been explained as adaptations to facilitate locomotion for dispersal or mate searching, and the concave plastra of terrestrial males have been suggested to increase stability during mating (Pritchard, 2008). Data from previous studies support some of these assertions: female turtles with taller shells can hold more or larger eggs (Tucker et al., 1998), and in many species males disperse farther and more frequently (Berry and Shine, 1980; Hall and Steidl, 2007; Parker, 1984; Remsberg et al., 2006; Tuberville et al., 1996) than females, although this pattern is not observed in all turtle species (Ernst, 1976; Thomas and Parker, 2000). The mechanical differences between the sexes are potentially unavoidable consequences of these adaptive differences in shell shape.

Similar arguments have been made for size dimorphism: in terrestrial species where male–male competition is common, selection favors larger males, whereas in aquatic species where such competition is rare, selection for increased fecundity favors larger females (Berry and Shine, 1980). Again, the observed mechanical patterns, with female *C. picta* exhibiting thoroughly stronger shells than males and male and female *G. insculpta* exhibiting more similar shell strengths, may be consequences of selection on other factors.

As of now, there are no data to suggest that selection on shell strength is the primary cause of the differences between males and females of these species. For example, there are no data to suggest that female *C. picta* or *G. insculpta* are more likely to encounter predators in the course of their life history, and one study even suggests the opposite (Wilbur, 1975), although this is not the case for other turtle species (Emmons, 1989; Gibbons and Lovich, 1990; Shealy, 1976; Siegel, 1980).

Even if they are not the direct target of selection, however, differences in shell strength can still affect certain aspects of turtle life history. Most obviously, female turtles may be better able to withstand predator attacks. Studies on *C. picta* have found more males than females killed by predators (Wilbur, 1975). However, studies on other aquatic species, which may be expected to show the same patterns of size and shape dimorphism as *C. picta*, have found that females are more likely to be killed by predators than males (Emmons, 1989; Gibbons and Lovich, 1990; Shealy, 1976), although these are also species in which females probably encounter more predators than males. In addition, previous studies have also found that female turtles show proportionally more injuries than males in some species, including *G. insculpta* (Ernst, 1976; Walde et al., 2003). These studies may suggest that females encounter more predators than males, or they may actually provide support for the idea that female turtles are better able to withstand predator attacks—the lower incidence of injuries among males may indicate that their encounters with predators more often end in death rather than injury.

If females are better defended against predators, this will likely have an effect on other aspects of their life history. Female turtles may survive more predator attacks than males and consequently live longer. Some aquatic emydid species, such as the spotted turtle (*Clemmys guttata*), do have females who are significantly longer lived than males (Litzgus, 2006). Males and females might use different tactics during predator encounters: female turtles may show a stronger tendency to use their shells as a primary defense, whereas males may more frequently use

escape tactics (Bellis and Pluto, 1986). Differences in shell strength could also have effects on turtle population structure. The female-biased ratios seen in some turtle populations (e.g., Lovich and Gibbons, 1990) could be due to many factors, but predation resistance is at least one. Clearly, studies on predator encounter rates and survival rates for many turtle species are crucial for understanding the impact of differences in shell mechanics on other aspects of turtle biology.

Such an understanding is important, as the results of this study could have important implications for turtle conservation. Turtle populations are already decreasing because of loss of habitat, road construction, pet trade, use as a food source, and increased predation and competition with invasive species (Gibbons et al., 2000). If males and females show different degrees of vulnerability to predation, then information on these differences will allow conservation biologists to focus their efforts to specifically help each sex. Additional information on the ontogenetic trajectory of shell shape and mechanical behavior would be useful in determining when males and females begin to diverge in terms of shell mechanics.

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