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SEXUAL DIMORPHISM AND FEEDING ECOLOGY OF DIAMOND-BACKED TERRAPINS (*MALACLEMYS TERRAPIN*)

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Abstract: Natural and sexual selection are frequently invoked as causes of sexual size dimorphism in animals. Many species of turtles, including the Diamond-backed Terrapin (*Malaclemys terrapin*), exhibit sexual dimorphism in body size, possibly enabling the sexes to exploit different resources and reduce intraspecific competition. Female terrapins not only have larger body sizes but also disproportionately larger skulls and jaws relative to males. To better understand the relationship between skull morphology and terrapin feeding ecology, we measured the in-lever to out-lever ratios of 27 male and 33 female terrapin jaws to evaluate biomechanics of the trophic apparatus. In addition, we measured prey handling times by feeding Fiddler Crabs (*Uca pugnax*), a natural prey item, to 24 terrapins in the laboratory. Our results indicate that although females have disproportionately larger heads, they have similar in:out lever ratios to males, suggesting that differences in adductor muscle mass are more important in determining bite force than jaw in:out lever ratios. Females also had considerably reduced prey handling times. Understanding the factors affecting terrapin feeding ecology can illuminate the potential roles male and female terrapins play as top-down predators that regulate grazing of Periwinkle Snails (*Littorina irrorata*) on Cord Grass (*Spartina alterniflora*).

Key words: Bite force; Emydidae; Handling time; Head size; Jaw musculature

Sexual dimorphism is a widespread phenomenon driven by sexual selection, natural selection, or both (Slatkin, 1984; Gibbons and Lovich, 1990; Bulté et al., 2008). In species that have male–male competition, sexual selection often favors larger males because they typically have more success in obtaining mates (Gibbons and Lovich, 1990; Perry, 1996; Lovich et al., 1998). Sexual dimorphism driven by natural selection can favor larger females, however, by conferring increased success in acquiring energy from larger prey items, thereby allowing females to produce more offspring (Slatkin, 1984; Bulté et al., 2008). Competitive displacement also can result in the evolution of sexual size dimorphism, by favoring increased body size in either males or females to reduce overlap in diet (Slatkin, 1984; Camilleri and Shine, 1990; Gibbons and Lovich, 1990; Bulté et al., 2008).

Sexual dimorphism resulting from natural selection is often manifested in changes to relative head size and shape, both of which can affect bite force (Emerson, 1985; Camilleri and Shine, 1990; Herrel et al., 2002, 2007; Claude et al., 2004). A larger head, and the resulting increase in bite force, can play a significant role in determining dietary divergence between the sexes and can reduce competition within the species (Emerson, 1985; Herrel et al., 2002). Individuals having larger heads or stronger bite forces can generally consume larger prey; thus, they can expand their diet or select prey items that reduce competition with the opposite sex (Wainwright, 1991; Herrel et al., 2002). There is a trade-off, however; stronger bite force can often result in slower prey capture responses (Emerson, 1985; Herrel et al., 2002, 2007). Thus, organisms that require high bite forces to consume durable prey often sacrifice the ability to capture fast-moving, elusive prey.

Bite force is an important functional metric because of its correlation with feeding habits. In some species of lizards, a greater bite force

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strongly correlates to a reduced handling time, because it may allow for more efficient prey capture and consumption (Verwaijen et al., 2002; Anderson et al., 2008). However, such a correlation has not been documented in turtles (Herrel et al., 2001; Verwaijen et al., 2002; Anderson et al., 2008).

The two primary mechanisms for increasing bite force are to (1) increase the in-lever to out-lever ratio of the jaws (i.e., increase the mechanical advantage of the jaws) and (2) increase the adductor muscle mass (Emerson, 1985; Pfaller et al., 2011). Increasing mechanical advantage allows for a greater proportion of the muscle force to be transferred to bite force, and increasing head size allows for greater jaw adductor muscle size and resulting muscle force (Emerson, 1985; Herrel et al., 2007). Although female Diamond-backed Terrapins (*Malaclemys terrapin*) are considerably larger than males, it is not known whether one of these mechanisms is more responsible for increasing the bite force in female terrapins (Gibbons and Lovich, 1990).

Where it occurs in the southeastern United States, the Diamond-backed Terrapin preys mainly on Periwinkle Snails (*Littorina irrorata*) but also eats various crabs, other mollusks, and barnacles (Tucker et al., 1995). Because the majority of these prey items have hard outer shells, some of which strengthen exponentially with size, a stronger bite force is needed to feed on larger prey, making bite force an important factor influencing feeding ecology (Tucker et al., 1997). The size disparity in Diamond-backed Terrapins applies not only to their overall size (mean plastron length [PL] males = 102.6 mm; females = 144.2 mm; Gibbons et al., 2001) but also to relative head size, with males having a smaller head width relative to body size than females. Tucker et al. (1995) showed that male terrapins eat smaller prey, whereas larger female terrapins can eat larger prey and a wider variety of prey items. The differences in overall size and head size in adult terrapins suggest that disparities of head-to-body scaling might result in intraspecific ecological divergence in feeding habits and diet between male and female Diamond-backed Terrapins (Tucker et al., 1995). Intersexual differences in diet and feeding strategies of terrapins can affect trophic dynamics in salt marsh ecosystems through top-down effects (Silliman et al., 2005; Bertness and Silliman, 2008).

Our objectives in this study were to examine (1) the sexual dimorphism between male and female terrapins, particularly in their skull morphology and biomechanics; and (2) the relationship between body size and prey handling time. These objectives were aimed at better understanding the mechanisms of bite force and the resulting intersexual trophic divergence in the species. We hypothesized that (1) females would have greater in-lever to out-lever ratios resulting in greater force transfer compared with males; (2) females would have a larger relative head depth (measured as dorsoventral height) than males; and (3) females would have reduced prey handling times compared with males.

Materials and Methods

Skeletal Measurements

We obtained 60 adult Diamond-backed Terrapin skeletal specimens (27 male, 33 female) from museum collections (Appendix). Using digital calipers, we took the following measurements (±0.1 mm): skull width, measured at the widest part of the skull; skull depth, measured at the highest point of the skull immediately posterior to the postorbital bone (Herrel et al., 2002); jaw out-lever and in-lever length; and plastron length (PL). We measured out-lever distance as the length from the jaw joint to the tip of the dentary bone, and we measured in-lever distance as the perpendicular distance from the three-dimensional coordinates of the jaw joint to the jaw muscle force vector (Fig. 1a; but see Pfaller et al., 2011). The jaw muscle force vector was determined from dissections of freshly dead specimens (three adult females, one adult male) obtained as road kills. An entire suite of muscles function to adduct the jaw (Pfaller et al., 2011) in terrapins and include the musculus (M.) adductor (add.) mandibulae (mand.) complex: M. add. mand. externus, M. add. mand. posterior, and M. add. mand. internus. We followed the nomenclature, identification, insertion, and attachment points for these muscles described by

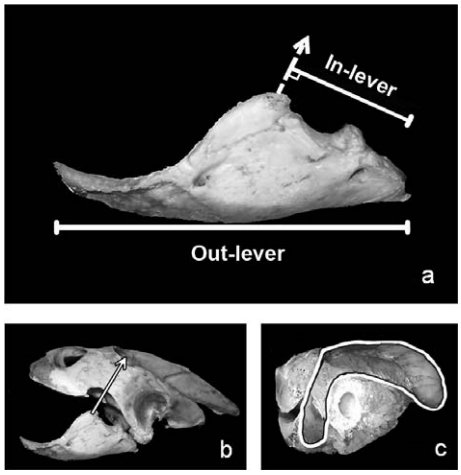

Fig. 1.—(a) In-lever and out-lever measurements of lower jaw of a Diamond-backed Terrapin. Solid lines represent measurements. Dotted line represents force vector direction. (b) Direction of force vector from insertion point of Pars superficialis-profunda complex. (c) Lateral view of P. superficialis, profunda muscle complex (outlined in white) in dissected adult female terrapin head.

Schumacher (1973). There are eight muscle subdivisions in total that collectively function to adduct the jaws: Pars (P.) superficialis, three subdivisions of the P. profunda, P. media, M. add. mand. posterior, M. pseudotemporalis, and M. pterygoideus (Pfaller et al., 2011). We measured the angle of insertion for each muscle and used this value to determine the direction of the muscle force vector (Fig. 1b). We then excised each jaw muscle, from both sides of each terrapin head, and weighed them. Together, the P. superficialis and P. profunda are the largest jaw adductor muscle complex in turtles. For our four specimens, these two muscles were 89.1 and 79.5% heavier for females and males, respectively, than the combined mass of the P. media, M. add. mand. posterior, M. pseudotemporalis, and M. pterygoideus muscles (Fig. 1c). Thus, we considered only the P. superficialis-profunda complex in generating the force vector, and consequently, for determining in-lever length. For each specimen, we calculated the ratio of in-lever to out-lever length to estimate biomechanical advantage.

Handling Time Analysis

During August 1989, 24 *M. terrapin* in total (six males, mean PL = 103 mm, range 95–112 mm; 18 females, mean PL = 142 mm, range 118–170 mm) were collected from tidal creeks along the Stono River on James Island, SC, USA, using trammel nets. Subjects were kept at the Savannah River Ecology Laboratory in Aiken, South Carolina, in 208-L Plexiglas® aquaria. The aquaria were filled with 15 cm of water treated with an artificial salt mixture to produce brackish water comparable to that of the terrapin natural habitat. Aquaria were placed at a slight tilt to provide shallow to dry areas for the turtles. Natural lighting was available, and ambient temperatures made heating the water unnecessary.

PL and head width were measured for each terrapin. To measure prey handling time, each terrapin was individually placed in a 75-L aquarium under similar conditions as described above with five, similarly sized adult Fiddler Crabs captured from Kiawah Island, South Carolina, and five Periwinkle Snails captured from the same location. Trials were video recorded from behind a black plastic blind so that equipment and observers would not affect terrapin behavior. From the recordings, an observer watched the feeding interaction and measured the handling time of the attacked prey. Handling time was defined as the time span from the instant the terrapin attacked the prey item to the moment it was completely ingested, and it focused on the attack and consumption of Fiddler Crabs. Five trials were conducted for each terrapin, from which the mean handling time in seconds was calculated.

Data Analysis

To examine potential differences in jaw morphology between sexes, we performed an analysis of covariance (ANCOVA) using *STATISTICA* 7.1 (StatSoft®, Inc., 2005, 2013). We used jaw in:out lever ratio as the dependent variable, sex as a categorical independent variable, and PL (to remove effect of increased female body size) as a continuous covariate. We assessed the possible effect of sex on terrapin prey handling time using ANCOVA, with handling time as the dependent variable, sex as a categorical independent variable, and PL as a continuous covariate. To assess differences in relative head width and depth between males and females, we used

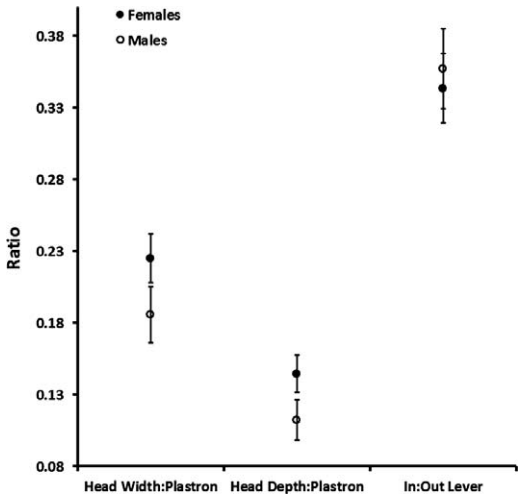

FIG. 2.—Mean head width to plastron length, head depth to plastron length, and in-lever to out-lever ratios between female ($n = 33$) and male ($n = 27$) Diamond-backed Terrapins. Vertical bars denote 0.95% confidence intervals. Females had larger relative head widths and head depths than males. Mean values for male and female in:out levers were similar.

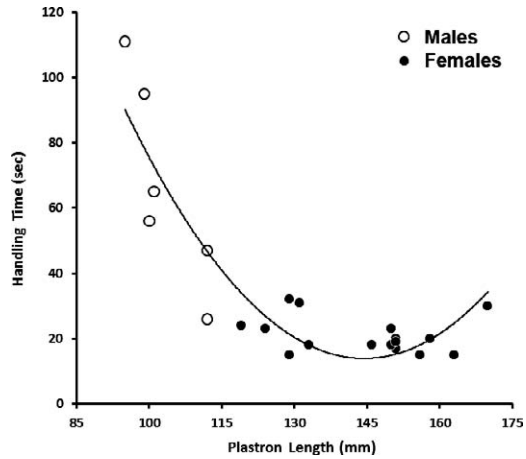

FIG. 3.—Handling time of adult female ($n = 18$) and male ($n = 6$) Diamond-backed Terrapins. Females had lower handling times than males. A quadratic smoothing function was fitted to the data for illlustrative purposes.

ANCOVA with head width or depth to plastron ratio as the dependent variable, sex as a categorical independent variable, and PL as a continuous covariate. All data were $\log_{10}$ transformed to improve linearity. Because ratio data tend to be skewed and thus potentially violate assumptions of a normal distribution, we performed arcsine square-root transformations to normalize the data (Zar, 1999).

RESULTS

We found that females were larger than males in both relative head width (head width to plastron ratio; Fig. 2, $F_{1,56} = 5.34$, $P = 0.025$) and relative head depth (head depth to plastron ratio; $F_{1,54} = 7.95$, $P = 0.007$). We found no effect of sex on in:out lever ratios in males and females (Fig. 2; $F_{1,57} = 0.27$, $P = 0.602$). The mean masses of the four jaw adductor muscles from the adult female subjects were as follows: P. profunda-superficialis complex = 4.09 g, P. media = 0.14 g, M. add. mand. posterior = 0.11 g, and M. pseudotemporalis, pterygoideus complex = 0.25 g. The masses of the same jaw adductor muscles from the adult male subject (means of the right and left side of the head) were as follows: P. profunda-superficialis complex = 1.05 g, P. media = 0.14 g, M. add. mand. posterior = 0.05 g, and M. pseudotemporalis, pterygoideus complex = 0.08 g. The average prey handling time for female terrapins was 21.125 s and was faster than that recorded for males, 66.667 s, when feeding on Fiddler Crabs (Fig. 3; $F_{1,19} = 5.22$, $P = 0.034$). We found no effect of plastron length on handling time ($F_{1,19} = 1.77$, $P = 0.20$).

DISCUSSION

The differences we found in the relative head widths and relative head depths between female and male terrapins are similar to the findings of Tucker et al. (1995) and indicate that adult females have disproportionately larger heads than adult males. We found no difference between female and male in-lever to out-lever ratios, however, indicating a similar mechanical advantage between the sexes in that regard. Mechanical advantage relates to the trade-off between force and speed in the jaw levers, with a greater mechanical advantage translating to a greater bite force (Emerson, 1985; Huber et al., 2006; Pfaller et al., 2011). Given that females have disproportionately larger heads and similar mechanical advantage compared with males, females likely achieve increased bite force

from increased adductor muscle mass and not from differences in jaw mechanics.

The rarity of freshly killed specimens limits our conclusions concerning the greater adductor muscle mass in female terrapins, compared with males. Because Diamondback Terrapin populations are declining (Cecala et al., 2008), it is difficult to obtain an adequate number of specimens to measure bite force and then rigorously measure adductor muscle mass between the sexes directly. Nevertheless, several studies have shown head depth and head width to be good predictors of bite force, including one study conducted on the sexually dimorphic Northern Map Turtle (*Graptemys geographica*; Bulté et al., 2008). Individuals with a greater head width and head depth have the space to accommodate more jaw adductor muscle mass (Huyghe et al., 2009), often leading to an increase in bite force (Emerson, 1985). Other factors, such as muscle architecture (including the degree and angle of pinnation, and muscle fiber length), also can affect bite force (Herrel et al., 2002). Furthermore, components of bite force, such as in:out lever ratios, muscle mass, and muscle architecture, can assume more significant roles in the biomechanics of some species than in others (Kaliontzopoulou et al., 2011).

A greater bite force can reduce handling time by limiting the number of gape cycles needed to consume a prey item (Huber et al., 2006). Although this is the first study to document variation in handling time as a function of bite force in turtles, this relationship has been documented in the lizards (*Lacerta oxycephala*, *L. vivipara*, *Podarcis melisellensis*, and *P. muralis*; Herrel et al., 2001; Verwaijen et al., 2002). These studies indicated a negative relationship between handling time and bite force (Herrel et al., 2001; Verwaijen et al., 2002). Female terrapins in our study had a significantly reduced handling time; this reduced handling time may be attributed to a greater bite force. We also note that although we offered both Periwinkle Snails and Fiddler Crabs to the terrapins in the handling time trials, only one terrapin chose to eat a Periwinkle Snail. The remaining 26 terrapins only attacked and ate Fiddler Crabs during the prey handling time trials. Thus, our results reflect the handling times from only those terrapins that consumed the Fiddler Crabs. Terrapins normally feed on snails above water (Tucker et al., 1997), a behavior that may account for not eating snails in our study.

Prey handling time is especially sensitive to variation in bite force when the prey species is hard-shelled, like Fiddler Crabs (Tucker et al., 1997). We were unable to perform in vivo bite force trials and instead measured two of the main drivers of bite force: mechanical advantage and adductor muscle mass (Emerson, 1985; Huber et al., 2006; Pfaller et al., 2011). Average mass of the main jaw adductor, the P. superficialis-profunda complex, was much larger for female specimens than the male (4.09 vs. 1.95 g), indicating that females might have an advantage in bite force.

Our results indicate that only sex, and not overall body size, affected the handling time. Because females are the larger sex, one would expect both sex and body size to affect handling time; however, this was not the case. This result might be explained by our small sample size of male terrapins. Our subjects were fed a hard-shelled prey item, and the ability of terrapins to crush through a crab's exoskeleton or a snail's shell is the largest factor affecting handling time. Because we found no difference in the mechanical advantage between male and female terrapins, and females had reduced handling times, it is likely that an increased amount of adductor muscle mass, the other main driver of bite force, is responsible for the reduced handling time.

One important consideration in our measurements of in:out lever ratios (i.e., mechanical advantage) between male and female terrapins, is dimensionality. Because of limited access to digital equipment, our measurements were made in the head depth and length plane (i.e., two-dimensionally) using digital calipers, compared with measurements using instruments and software that provide for geomorphic morphometric approaches; specifically, three-dimensional measurements incorporating head width as the third plane (Kaliontzopoulou et al., 2011). Studies have highlighted the importance of measuring biomechanical advantages using geometric

morphometrics that allow for more accurate measurements of the complex internal components of mechanical advantage and bite force beyond simple external linear measurements (McHenry et al., 2006; Wroe et al., 2008; Kaliontzopoulou et al., 2011). Our relatively simple linear measurements do not take into account all of the factors involved in bite force; thus, one must choose the most relevant morphological parameters (Kaliontzopoulou et al., 2011). Geometric morphometrics, however, can integrate the many factors involved in bite force into one model, allowing the geometric properties of the organism to be maintained while providing more accurate measurements (Kaliontzopoulou et al., 2011).

Sexual dimorphism in head size and shape in Diamond-backed Terrapins is a significant factor in their feeding ecology, because these differences in head morphology may affect their energy uptake. Optimal foraging theory predicts that an animal should behaviorally adjust its rate of energetic intake, specifically in relation to expenditure (Osenburg and Mittelbach, 1989; Preest, 1994). Typically, larger prey contain more energy; however, they are often more difficult to capture and ingest (Preest, 1994). Furthermore, prey selection, and thus energy acquisition, can be determined by whether or not the predator is capable of ingesting the prey item (Osenburg and Mittelbach, 1989). In the Spiny Lobster (*Panulirus interruptus*), the preferred size of molluscan prey increases with lobster body size; however, ingesting larger prey increased handling time by the lobster (Robles et al., 1990). Because terrapins feed mainly on hard-shelled prey, their ability to ingest prey is largely dependent on bite force, with a greater bite force being necessary to feed on larger or harder shelled prey (Tucker et al., 1997). Female Diamond-backed Terrapins likely have a greater bite force than males, and this difference may be partly because of their greater relative head size, allowing for more muscle mass. Thus, energy acquisition in terrapins is likely driven in part by sexual dimorphism in head size.

Tucker et al. (1995) reported that although both male and female terrapins fed largely on *L. irrorata*, female diets included snails averaging > 10 mm in size, whereas male and immature female diets consisted of snails < 10 mm. One reason for this disparity might be feeding energetics. Females of the sexually dimorphic lizard *Anolis carolinensis* showed decreased efficiency when ingesting comparatively sized prey items as males (Preest, 1994). As such, it was energetically more favorable for female *A. carolinensis* to eat larger amounts of smaller prey than smaller amounts of larger prey (Preest, 1994). Assuming that male and female terrapins have different bite forces, they may have evolved different ways to acquire prey in an energetically efficient way. For example, male terrapins might adopt a strategy similar to female *A. carolinensis*, wherein it is more energetically favorable to ingest large amounts of small prey items.

Before the late 1990s, it was assumed that salt marsh ecosystem productivity was controlled primarily by bottom-up forces, such as sulfide concentrations, nutrient availability in the substrate, and salt concentrations (Silliman and Zieman, 2001). However, some research has now indicated that Cord Grass (*Spartina alterniflora*) growth may be controlled primarily by top-down forces. These top-down forces include snails that feed directly on *S. alterniflora* and their predators, such as Diamond-backed Terrapins, that regulate snail densities and prevent overgrazing (Silliman and Zieman, 2001; Silliman and Bertness, 2002; Silliman et al., 2005; Bertness and Silliman, 2008). In one study, exclusion of snail predators from a marsh ecosystem allowed increased *L. irrorata* densities to such a degree that *S. alterniflora* marsh areas became denuded after two growing seasons (Silliman and Bertness, 2002). These findings suggest that predators, such as Diamond-backed Terrapins, help maintain productive salt marsh ecosystems.

During the early 20th century, Diamond-backed Terrapin populations were decimated by commercial harvest for their meat (Baldwin et al., 2005). Today, this species faces new anthropogenic threats, including crab trapping, watercraft strikes, road mortality, and destruction of nesting habitat (Gibbons et al., 2001; Tucker et al., 2001; Dorcas et al., 2007; Cecala et al., 2008). Because of their impor-

tant role in regulating snail densities, continued population declines in Diamond-backed Terrapins could lead to the degradation of salt marsh ecosystems (Silliman and Bertness, 2002).

We have demonstrated that female Diamond-backed Terrapins have reduced prey handling times and relatively larger heads, but similar jaw in:out lever ratios, compared with males. We suggest that because mechanical advantage is similar between the sexes, reduced handling time of females is a result of greater adductor muscle mass. The presumed difference in bite force between male and female Diamond-backed Terrapins plays an important role in their feeding ecology by facilitating resource partitioning between the sexes.

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Appendix

Malaclemys terrapin Specimens Examined.

Museum abbreviations follow Pérez (2010)

Cumberland, NJ, USA (AMNH 88231, 141067), Fairfield, CT, USA (AMNH 141059-60), New Haven, CT (AMNH 141065-6), New London, CT (AMNH 142303-5); Hofstra University (3745, 3749, 3751-4, 3756-8), no locality data; Baltimore City, MD, USA (CM 39729), New Kent, VA, USA (CM 64111), Ocean County, NJ (CM 96287, 108770), North Hampton County, VA (CM 125175, 130041, 146551); Pinellas, FL, USA (FLMNH 140783); Port Chico, LA, USA (FMNH 211590), Charlotte Harbor, FL (FMNH 211591); no locality data (FMNH 182816, 276324); no locality data (FSM 11063); Glynn, GA, USA (MCZ 37696); Cape May, NJ (MCZ 182820, 182823, 182842); no locality data (NMNH 9930, 51499, 59985-6, 220886); USA (NMNH 33899, 33912, 37016, 76605, 207131, 223998); New Haven, CT (YPM 10841-3, 12130), Charleston, SC (YPM 10910), Cape May, NJ (YPM 12245, 12627), no locality data (YPM 12627, 14347, 17209, 18485-6).