

Sexual dimorphism, bite force and diet in the diamondback terrapin

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Abstract

Sexual dimorphism in head size and shape has been documented in many animals and is often thought to be related to the consumption of different prey in males and females thus reducing competition between the two sexes. However, for this to be true, the difference in head size and shape should be associated with a difference in performance allowing one sex to exploit different prey resources. In many durophagous turtle species, females are bigger than males and have bigger heads for a given size. Here, we test whether the observed dimorphism in head size and shape in the durophagous *Malaclemys terrapin* is reflected in differences in bite force. Furthermore, we measure the forces needed to crush different prey items in order to evaluate whether the observed bite force dimorphism allows access to different dietary resources in females. Finally, we compare head size and shape and bite force between the durophagous *M. terrapin* and a generalist (*Trachemys scripta*). Our results show that females of *M. terrapin* have higher bite forces than males in line with their bigger heads relative to their body size. Moreover, the higher bite forces in females allow them to eat larger as well as different types of snails resulting in differences in diet. Finally, our results show that both sexes of *M. terrapin* have bigger heads and bite forces for their body size compared to the generalist *T. scripta*, even as juveniles. Moreover, *M. terrapin* bite harder even when taking into account differences in head size, suggesting intrinsic differences in the jaw musculature in durophagous species.

Introduction

Sexual dimorphism is common in the animal kingdom and usually reflects differences in reproductive roles between the sexes (Darwin, 1871; Shine, 1989). Body size dimorphism is typically attributed to either fecundity selection leading to female-biased dimorphism as observed, for example, in many snakes and some mammals (e.g. Ralls, 1977; Shine, 1989) or male–male combat leading to male-biased sexual size dimorphism as observed in many lizards, primates and pinnipeds (Ralls, 1977; Olsson *et al.*, 2002). Sexual dimorphisms in feeding structures are also common and may be the result of niche divergence in response to competition for trophic resources between males and females (Schoener, 1967; Slatkin, 1984). Alternatively, sexual head size dimorphism may be related to male–male combat and territory defense, in which case it may result in the evolution of enlarged jaws and heads in males (Anderson & Vitt, 1990; Lappin & Husak, 2005; Lappin *et al.*, 2006). Furthermore, selection on females to increase energy intake may also drive differences in trophic structures between males and females (Bulté, Irschick & Blouin-Demers, 2008a). In many cases, teasing apart the relative roles of sexual

selection versus trophic niche partitioning or selection on energy intake remains difficult (Vincent & Herrel, 2007) as the same system (the jaws) is involved in both aggressive interactions and resource utilization.

In turtles biting is used during courtship (Liu *et al.*, 2013) and as such may also be under sexual selection. Despite this, dimorphism in head size and shape in turtles has often been suggested to be related to resource use (Lindeman, 2000, 2006a,b; Bulté *et al.*, 2008a). Moreover, it has been suggested that head size and performance differences may be directly related to differences in reproductive allocation between the sexes with females investing more in reproduction compared to males and thus needing a higher energy intake (Bulté *et al.*, 2008a). In the northern map turtle *Graptemys geographica*, females ate prey of a hardness closer to the maximal bite force compared to males. Moreover, body condition and reproductive output increased with relative head width suggesting a direct link between head size and shape, performance and reproductive success (Bulté *et al.*, 2008a). The alternative hypothesis of intersexual competition was ruled out by conducting detailed diet and habitat use analyses (Bulté, Gravel & Blouin-Demers, 2008b).

Here, we provide data on body and head dimensions as well as bite forces for diamondback terrapins *Malaclemys terrapin* to explore whether the head size and shape dimorphism in this species is related to differences in diet and more specifically prey hardness. The diamondback terrapin is a wide-ranging species inhabiting brackish coastal marsh ecosystems throughout the Eastern US (Ernst & Lovich, 2009). This species is dimorphic in body size with females being larger than males and having wider heads (Tucker, Fitzsimmons & Whitfield Gibbons, 1995). Moreover, this species is considered to be durophagous with both sexes consuming a variety of gastropods, crabs and other hard-shelled prey (Tucker *et al.*, 1995; Butler, Heinrich & Mitchell, 2012; Denton *et al.*, 2016; Outerbridge *et al.*, 2017). Sexual differences in diet have been demonstrated for this species (Tucker *et al.*, 1995; Butler *et al.*, 2012) and it has been suggested that resource use may be limited by snail shell strength in diamondback terrapins (Tucker *et al.*, 1997). This makes this species an ideal candidate to investigate the relationships among head size and shape, bite force, diet and prey hardness (Table 1).

More generally, it has been demonstrated that the consumption of hard-shelled prey in turtles impacts the shape of the skull leading to strong convergence in skull shape among durophagous species (Claude *et al.*, 2004). Additionally, the consumption of hard-shelled prey has been shown to result in the evolution of higher bite forces in turtles (Herrel, O'Reilly & Richmond, 2002; Pfaller *et al.*, 2010; Pfaller, Gignac & Erickson, 2011). Yet, little attention has been given to the relationships among head size and shape, bite force and resource utilization in turtles. Moreover, whether durophagous chelonian species differ from generalist chelonian species in absolute and relative bite performance remains poorly studied. Finally, whether specialization for durophagy facilitates the evolution of head shape dimorphism remains unknown. Indeed, in durophagous species an increase in head dimensions and bite force may allow access to novel food resources to one of the sexes thus reducing competition and/or allowing for increased energy intake. To explore these questions, we compare data for *M. terrapin* (Cagle, 1950; Clark & Gibbons, 1969) with data for its generalist closely related species *Trachemys scripta* (Spinks *et al.*, 2016).

Materials and methods

Animals

Animals examined were captured between 15 May and 28 September 2007 in Mill Neck Creek or Center Island Beach (Long Island, NY). They were captured by seine net or baited crab trap in Mill Neck Creek or by hand while nesting on Center Island Beach. An additional 16 laboratory-reared individuals were used in the bite force and head shape analyses. All wild captured terrapins were brought to the laboratory where the measurements were taken. All experiments were approved by the institutional animal care and use committee of Long Island University (C.W. Post Campus, protocol number 99-04), and animals were captured under a permit from the New York State Department of Environmental Conservation (Number 1661).

The weight of adult terrapins was measured to the nearest 25 g by placing an individual in a mesh bag and suspending it from a hanging fish scale (Chatillon). Juveniles (individuals that were too small to be sexed) were weighed using a digital scale (OHaus Scout Pro SPE123) to the nearest 0.01 g. Shell measurements of all turtles included midline carapace and plastron lengths, maximum carapace width and shell height at the deepest point between the highest ridge on the vertebral scutes and the plastron. Head measurements (head length, head width, head height, lower jaw length and snout length) were made to the nearest 0.1 mm using digital calipers (Mitutoyo, Roissy, France). Head length was measured from the anterior end of the premaxillary to the posterior edge of the parietal crest. Lower jaw length was measured from the anterior end of the dentary bone to the posterior edge of the retroarticular process. Head width was measured at the widest part of the head and includes potential bulging of the jaw muscles. Head height was measured at the deepest part of the head just posterior to the orbita. Snout length was measured from the back of the jugal bone to the tip of the snout. The jaw in-lever was then calculated by subtracting the snout length from the lower jaw length (see Herrel & O'Reilly, 2006). Shell measurements were taken to the nearest 1 mm using Haglof calipers (Haglof, Langsele, Sweden) and included midline carapace length,

Table 1 Means \pm standard deviations of the morphological traits and bite force in *Malaclemys terrapin*

	Females ($N = 48$)	Males ($N = 8$)	Juveniles ($N = 14$)
Carapace length (mm)	195.69 \pm 23.99	122.61 \pm 8.94	59.42 \pm 27.48
Plastron length (mm)	174.57 \pm 21.81	102.40 \pm 8.36	50.75 \pm 23.94
Carapace width (mm)	150.53 \pm 18.40	92.31 \pm 7.39	47.98 \pm 21.50
Carapace height (mm)	84.75 \pm 17.08	44.99 \pm 3.24	25.08 \pm 10.62
Mass (g)	1354.20 \pm 386.44	304.90 \pm 67.70	63.35 \pm 68.07
Head length (mm)	62.92 \pm 7.35	39.74 \pm 3.95	21.32 \pm 8.35
Head width (mm)	35.83 \pm 4.47	19.94 \pm 1.31	12.96 \pm 4.38
Head depth (mm)	24.06 \pm 2.78	13.98 \pm 0.66	10.04 \pm 3.36
Lower jaw length (mm)	38.06 \pm 4.48	24.00 \pm 1.11	14.61 \pm 5.15
Jaw in-lever (mm)	21.98 \pm 2.78	12.76 \pm 1.07	7.71 \pm 2.44
Head volume (mm ³)	29 375.89 \pm 7972.14	5900.42 \pm 1243.16	1981.85 \pm 1890.12
Bite force (N)	156.26 \pm 46.40	37.11 \pm 6.32	17.02 \pm 15.00

maximum carapace width, midline plastron length and shell height at the deepest point between the highest ridge on the vertebral scutes and the plastron. Head volume was calculated using the following equation: head volume = $(3.1415 \times \text{head length} \times \text{head width} \times \text{head depth})/6$ (Macías-Ordóñez & Draud, 2005).

Bite force

Bite force was measured using an isometric Kistler force transducer (type 9203) mounted in a custom-built setup and connected to a Kistler charge amplifier (type 5995A; see Herrel *et al.*, 1999, 2001). The bite plates of the apparatus were placed in the open mouths of the terrapins until they forcefully bit down. The peak bite force was recorded and the procedure was repeated five times per individual. The maximum bite force recorded was considered to be the maximum force for that individual. Data for terrapins were compared to previously published data for red-eared sliders, a generalist semi-aquatic turtle (Herrel *et al.*, 2002; Herrel & O'Reilly, 2006).

Diet

To quantify the diet of *M. terrapin*, fecal analyses were conducted for 97 individuals (35 males, 62 females). Fecal analysis is the least invasive and harmful technique for determining diet in terrapins. Once captured, terrapins were transported to the laboratory where they were measured and kept individually. Every terrapin was isolated for 72–96 hours at 28–32°C and any fecal matter produced was removed daily. To collect the fecal samples, the individual was removed and water from its container was passed through a 1-mm sieve. The retained material was then stored in individual jars in 90% ethanol until it was sorted. Fecal samples were examined and compared visually to known local species present at the study site. All fecal samples for an individual collected over the 3- to 4-day period were combined. Per cent occurrence and per cent mass of each ingested species were calculated and terrapins were placed in one of the following four size classes: males (all males), large females (carapace length >190 mm), medium females (carapace length 170–190 mm) and small females (carapace lengths <170 mm).

Prey hardness

The same Kistler force transducer (type 9203) was also used to determine the compression resistance of potential prey items including crabs, snails, mussels and oysters. A screw was attached to the transducer and pushed upon the prey until failure occurred (Herrel *et al.*, 1999, 2001; Aguirre *et al.*, 2003). Each potential prey item was weighed to the nearest 0.001 g using a digital scale and measured to the nearest 0.1 mm using digital calipers (Mitutoyo). Carapace length, width and height, along with claw length and width were measured for crabs. Shell height of snails (base to apex), shell length of bivalves (hinge to ventral margin) and width at the widest point of both

snails and bivalves were measured. Snail operculum height and width were also taken when present.

Statistical analyses

All data were \log_{10} -transformed before analyses. To test for differences between male and female *M. terrapin*, we performed a MANCOVA on the head dimensions with carapace length as covariate. We next ran an ANCOVA on bite force, again with carapace length as covariate. As carapace lengths were not overlapping between males and females we also calculated the residuals of the different head dimensions and bite force of a regression of each trait on carapace length and tested for differences in head shape and bite force using a MANOVA and ANOVA respectively. We next determined what head dimensions best explained the overall variation in bite force using a stepwise multiple regression. Next, we ran another ANCOVA on bite force, but this time with head width as covariable. Since sizes are non-overlapping, we also calculated the residuals of a regression of bite force on head width and tested for differences between sexes using an ANOVA.

We subsequently tested for differences in head dimensions and bite force between *M. terrapin* and *T. scripta*, a generalist species for which data were collected using an identical protocol and by the same experimenter previously (Herrel *et al.*, 2002; Herrel & O'Reilly, 2006). Given the known sexual dimorphism, we tested for differences in head shape and bite force for each sex separately using a MANCOVA with carapace length as our covariate coupled to univariate ANCOVAs. We also tested for differences in head shape and bite force between species in juveniles to explore whether differences already exist at the juvenile stage. Finally, we ran a series of regression analyses testing for relationships between prey dimensions and the force needed to crush them and superimposed the mean bite forces of juvenile, male and female *M. terrapin* to explore whether ontogenetic and sexual differences in bite force allow animals to exploit different prey resources.

Results

Sexual dimorphism in bite force and head dimensions

A MANCOVA with carapace length as covariate detected significant differences in head shape between males and females (Wilks' lambda = 0.53; $F_{7,34} = 4.36$; $P = 0.002$). Subsequent univariate ANCOVAs showed that differences were significant for head width ($F_{1,40} = 21.41$; $P < 0.001$), head height ($F_{1,40} = 21.09$; $P < 0.001$) and head volume ($F_{1,40} = 19.99$; $P < 0.001$) with males having smaller heads for a given carapace length than females. A univariate ANCOVA with carapace length as covariate also indicated significant differences in bite force between the sexes ($F_{1,40} = 11.27$; $P = 0.002$) with females having larger bite forces than males for a given carapace length. These results were confirmed by analyses using the residuals of a regression of head dimensions on carapace

length showing differences in overall head shape (Wilks' lambda = 0.30; $F_{6,36} = 14.13$; $P < 0.001$) with females having wider ($F_{1,41} = 70.64$; $P < 0.001$) and taller ($F_{1,41} = 49.50$; $P < 0.001$) heads as well as longer lower jaws ($F_{1,41} = 11.75$; $P = 0.001$), and a greater head volume ($F_{1,41} = 56.37$; $P < 0.001$). Residual bite forces were also larger in females compared to males ($F_{1,41} = 43.11$; $P < 0.001$).

A stepwise multiple regression run on the morphometric data for all individuals retained a significant model ($R^2 = 0.99$; $P < 0.001$) with head width ($\beta = 0.87$) and the in-lever for jaw closing ($\beta = 0.13$) as the only significant predictors. Thus, animals with wider heads and longer jaw closing in-levers bit harder. Finally, an ANCOVA with head width as covariate no longer detected differences in bite force between males and females ($F_{1,40} = 0.002$; $P = 0.96$) of *M. terrapin* showing that males and females do not differ in bite force for a given head width. This was compared by an ANOVA performed on the residuals of a regression of bite force on head width ($F_{1,41} = 0.026$; $P = 0.87$).

Interspecific differences in bite force and head dimensions

A MANCOVA with carapace length as covariate detected significant differences between species for males (Wilks' lambda = 0.08; $F_{5,9} = 20.23$; $P < 0.001$). Subsequent univariate ANCOVAs with carapace length as a covariate further showed that differences were significant for most head dimensions (head length: $P < 0.001$; head height: $P < 0.001$; lower jaw length: $P = 0.005$) as well as bite force ($P = 0.032$) with male *M. terrapin* having larger heads and greater bite forces than male *T. scripta* (Fig. 1). Head width was, however, not different between males of both species ($P = 0.33$). For females significant differences between species were also detected (Wilks' lambda = 0.30; $F_{5,41} = 19.03$; $P < 0.001$) with differences being bite force ($P < 0.001$) and all head dimensions (head length: $P < 0.001$; head width: $P < 0.001$; lower jaw length: $P = 0.02$) except head height ($P = 0.93$). Female *M. terrapin* had bigger heads and larger bite forces for a given carapace length (Fig. 1). Finally, an analysis performed for juveniles of both species also detected significant differences (Wilks' lambda = 0.14; $F_{5,18} = 20.23$; $P < 0.001$). However, differences between species were significant only for head length ($P < 0.001$), lower jaw length ($P = 0.041$), and bite force ($P = 0.01$) with juvenile *M. terrapin* having longer heads and higher bite forces. Differences in species for all sex and age classes remained when using head width as a covariate in the analyses ($F_{1,83} = 27.71$; $P < 0.001$; see Fig. 1b) with *M. terrapin* biting harder than *T. scripta* for a given head width.

Diet and prey hardness

A total of 12 species of prey items were found to make up the majority of the diet (Table 2). Although the most important prey items by mass for large and medium-sized females were *Macoma balthica* (Baltic tellin) and *Geukensia demissa* (ribbed mussel), in small females *Geu. demissa* and *Gemma gemma*

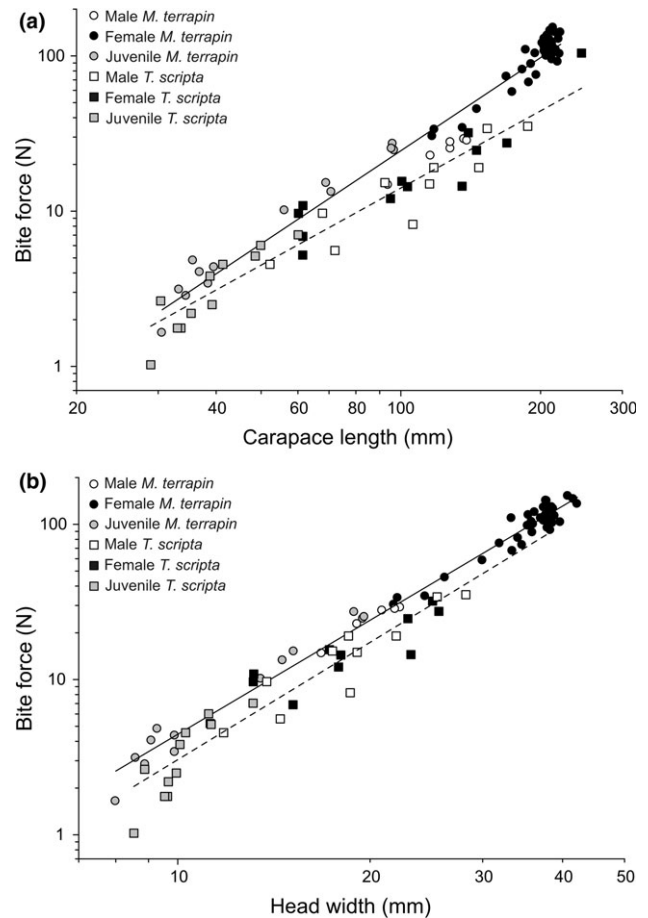


Figure 1 Scatter plot illustrating the relationships between (a) carapace length and bite force and (b) head width and bite force for *Malaclemys terrapin* (regression line) and *Trachemys scripta* (dashed regression line). *Malaclemys terrapin* always has greater bite forces than *T. scripta*. Note the log axes.

(amethyst gem clam) were the dominant prey (Table 2). In males, the dominant prey by mass were *Littorina saxatilis* (rough periwinkle) and *G. gemma* (Table 2). Although large and medium-sized females also frequently consumed *Ilyanassa obsoleta* (mud snail), these prey were less common in small females and males. Plant matter was also commonly consumed in all groups but in low volume (Table 2). Additionally, small amounts of blue mussel *Mytilus edulis*, razor clam *Ensis directus*, unidentified barnacle fragments, mantis shrimp *Squilla empusa* and small rocks (<2 mm) were also found.

A total of 23 mud snails (*I. obsoleta*), 8 periwinkles (*L. saxatilis*) and 20 coffee bean snails (*Melampus bidentatus*) were crushed to determine the force needed to fracture the items. Mud snails ranged in size from 10.6 to 19.4 mm and required forces ranging from 24.1 N to over 240 N to be crushed. Periwinkles ranged in size from 2.7 to 6.6 mm and required forces of 4 N to 15.1 N to be crushed. Coffee bean snails ranged in size from 3.2 to 11.7 mm and required forces of 1 N to 39.1 N to be crushed (Fig. 2). Forces tended to increase with

Table 2 Diet for males, small females, medium females and large females of *Malaclemys terrapin*

	Large females (N = 37)		Medium females (N = 14)		Small females (N = 11)		Males (N = 37)	
	%weight	% occ.	%weight	% occ.	%weight	% occ.	%weight	% occ.
<i>Ilyanassa obsoleta</i>	7.93	15.79	9.97	17.14	1.19	12.50	2.16	9.16
<i>Littorina saxatilis</i>	1.52	3.29	2.04	4.29	5.05	8.33	27.87	13.74
<i>Gemma gemma</i>	3.31	11.18	8.93	11.43	32.66	14.58	33.87	15.27
<i>Mya arenaria</i>	7.99	7.24	6.40	8.57	16.87	4.17	2.60	3.82
<i>Macoma balthica</i>	48.75	9.21	25.17	8.57	3.88	4.17	1.02	3.82
<i>Geukensia demissa</i>	22.86	10.53	30.45	10.00	26.45	8.33	5.98	9.92
<i>Hydrobia</i> sp.	0.02	3.95	1.65	4.29	2.28	12.50	12.45	9.16
Crabs	6.40	15.13	13.67	12.86	2.60	8.33	4.61	9.92
Plant matter	0.71	17.76	1.24	15.71	4.88	20.83	3.02	19.08
<i>Melampus bidentatus</i>	0.05	0.66	0.31	1.43	3.69	2.08	5.76	3.05
Fish	0.19	3.29	0.13	2.86	0.43	4.17	0.65	2.29
<i>Crepidula</i> sp.	0.27	1.97	0.04	2.86	0.00	0.00	0.01	0.76

Indicated are the % weight and the % occurrence (% occ.) of each prey item in the diet. In bold are represented the two most important prey groups for each sex/size class.

shell width for periwinkles, coffee bean snails and mud snails (Table 3). A total of four fiddler crabs (*Uca pugilator*), one green crab (*Carcinus maenas*) and six mud crabs (*Panopeus* sp., *Eurypanopeus* sp. or *Dyspanopeus* sp.) ranging in carapace sizes of 8.0–34.2 mm were crushed. The maximum force required to crush any crab was 32.9 N, but the majority required forces of <10 N. The force required to crush a crab increased with both carapace length and the length of the first claw (Table 2). The maximum forces required to crush ribbed mussels (*Geu. demissa*) and oysters (*Crassostrea virginica*) were 160 N and 29.9 N respectively (Fig. 2). Mussels (N = 14) ranged in length from 28.2 to 92.6 mm, while the oysters (N = 20) ranged in length from 4.1 to 18.1 mm. Although the dimensions of the oysters were strongly

correlated with the forces needed to crush them, no correlations between the dimensions of the mussels and their crush force were detected (Table 2).

Discussion

Our results show that male and female *M. terrapin* differ in head size and shape with females having larger heads than males. This difference in head size results in differences in bite force with females biting harder than males for a given carapace length as observed in other durophagous species (Bulté *et al.*, 2008a). However, when taking into account the difference between the sexes in head width, the differences in bite force between the sexes were no longer significant suggesting that the sexes differ only in relative head size but not, for example, muscle architecture (Pfaller *et al.*, 2011). From a comparative perspective, our results showed that *M. terrapin* has a significantly larger head than the closely related generalist *T. scripta* (Cagle, 1950; Clark & Gibbons, 1969). This suggests evolutionary divergence in durophagous specialists resulting in the evolution of larger heads (see also Lindeman & Sharkey, 2001; Herrel *et al.*, 2002; Herrel & O'Reilly, 2006). Moreover, our results show that the larger heads resulted in larger bite forces in *M. terrapin* compared to *T. scripta*. However, even when taking into account variation in head width, the principal determinant of bite force in *M. terrapin* together with the in-lever for jaw closing, *M. terrapin* still bit harder than the generalist *T. scripta*. This suggests that the evolution of higher bite forces does not only involve the evolution of larger and specifically wider heads, but also implies changes in the biomechanics of the lever system, and/or the muscle architecture and physiology (Herrel & O'Reilly, 2006). Given the importance of the jaw in-lever as a determinant of bite force in *M. terrapin* differences in the lever system of the jaws likely contribute to the observed differences in bite force when correcting for head width. However, differences in jaw muscle architecture or physiology may also play an important role in driving the observed differences between

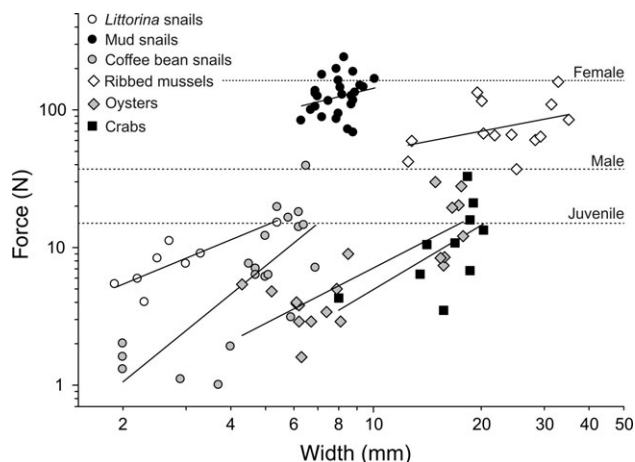


Figure 2 Plot of prey width versus the force needed to crush them. Superimposed are the mean bite forces measured for female, male and juvenile *Malaclemys terrapin*. Although females are capable of crushing most prey they encounter, prey such as mud snails and ribbed mussels may not be accessible to most males and juveniles. Note the log axes.

Table 3 Regressions describing the relationship between prey dimensions and crush strength

	<i>r</i>	<i>P</i>
Rough periwinkle <i>Littorina saxatilis</i> (<i>N</i> = 8)		
Snail height (mm)	0.81	0.015
Snail width (mm)	0.82	0.013
Operculum height (mm)	0.76	0.028
Operculum width (mm)	0.91	0.002
Mud snail <i>Ilyanassa obsoleta</i> (<i>N</i> = 23)		
Snail height (mm)	0.32	0.13
Snail width (mm)	0.44	0.037
Operculum height (mm)	−0.09	0.72
Operculum width (mm)	0.14	0.58
Mass (g)	0.42	0.056
Coffee bean snails <i>Melampus bidentatus</i> (<i>N</i> = 20)		
Snail height (mm)	0.82	< 0.001
Snail width (mm)	0.79	< 0.001
Mass (g)	0.79	< 0.001
Oysters <i>Crassostrea virginica</i> (<i>N</i> = 20)		
Shell length (mm)	0.69	= 0.001
Shell width (mm)	0.80	< 0.001
Shell height (mm)	0.71	< 0.001
Mass (g)	0.82	< 0.001
Ribbed mussels <i>Geukensia demissa</i> (<i>N</i> = 14)		
Shell length (mm)	0.44	0.16
Shell width (mm)	0.48	0.12
Shell height (mm)	0.52	0.08
Mass (g)	0.48	0.11
Crabs (<i>N</i> = 11)		
Carapace length (mm)	0.64	0.045
Carapace width (mm)	0.61	0.064
Claw 1 length (mm)	0.78	0.008
Claw 1 height (mm)	0.33	0.35

Bold values indicate significant relationships between prey dimensions and the force needed to crush them.

species. For example, it has been shown that positive allometric increase in bite force during ontogeny in the turtle *Sternotherus minor* is facilitated by changes in both muscle size and the degree of muscle pennation (Pfaller *et al.*, 2011). Such differences between species likely also involve differences in muscle architecture in addition to differences in muscle size, yet this remains to be tested. Given that the differences between species are already significant in juveniles, our data suggest that whatever anatomical differences exist, they must already be present in juveniles allowing them to exploit hard prey common in their environment.

Our results suggest that females are capable of crushing all types of prey measured, including the hardest mud snails and ribbed mussels, and these are also consumed more frequently, especially in large and medium-size females (Table 2). The force needed to crush mud snails may, however, limit males to exploit them as a dietary resource as suggested previously (Tucker *et al.*, 1997). The high bite forces in females thus allow them to access resources like mud snails and ribbed mussels, not as readily available to males. Juveniles are even more strongly constrained in their diet with neither mud snails nor ribbed mussels likely being potential food items. These

data parallel those for other durophagous species like map turtles characterized by a strong sexual dimorphism in head size, shape, and diet (Lindeman, 2000, 2006a,b). In these turtles a dimorphism in bite force also exists allowing females to eat harder snails than males (Bulté *et al.*, 2008a,b). Finally, bite force in map turtles seems to be directly limiting resource use in females given the strong correspondence between *in vivo* bite force and the hardness of the largest snail recovered in the diet (Bulté *et al.*, 2008a,b). The close match between bite force and prey size and hardness demonstrated for turtles and other vertebrates (Herrel *et al.*, 2001, 2006; Aguirre *et al.*, 2003; Herrel & O'Reilly, 2006; Bulté *et al.*, 2008a,b; De León *et al.*, 2014) suggests that bite force may indeed be directly limiting resource use and that this performance trait is fitness relevant.

Our results demonstrate significant dimorphism in head size and shape in a durophagous turtle resulting in differences in bite force ultimately underlying differences in diet. Although our results do not allow us to discriminate between the energy intake hypothesis and niche divergence due to intersexual competition, they clearly illustrate how the larger heads and bite forces of females provide them access to harder and larger prey providing both energetic benefits and likely reducing inter-sexual competition given the clear differences in proportion by which dietary resources are consumed by both sexes. Our results do unambiguously show, however, how the evolution of head shape dimorphism may allow males and females to consume different prey. The direct link between bite force and the access to novel or exclusive resources may pave the way for durophagous species like *M. terrapin* to evolve pronounced head shape divergence between the sexes (Lindeman & Sharkey, 2001). Additional comparative studies are needed to quantitatively test whether durophagous species in general show a greater amount of head size and shape dimorphism compared to other species as well as the broader evolutionary implications of our study.

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