Sexual size dimorphism and diet specialization in the common map turtle (*Graptemys geographica*)

by

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Abstract

Sexual size dimorphism may arise from sexual selection where one sex gains a reproductive advantage from being larger, or natural selection such as diet divergence, or both. In the common map turtle (*Graptemys geographica*), females are much larger than males, often exceeding twice their size. Extreme female-biased sexual size dimorphism has been hypothesized to be a result of natural selection for diet divergence. The goal of our study is to test the hypothesis that male and female map turtles specialize on different prey type and size. We also want to examine whether head width is a better predictor of consumed prey size. We collected fecal samples of adult females, juvenile females and adult males. Prey size can be reconstructed from mussel septa length and snail opercula length that are passed with the feces. The two sexes are consuming different prey, as well as different prey size. Females had significantly more zebra mussels in their fecal samples than males. Mollusc prey size increased with body size for females but not for males, while tricoptera prey size was independent of body size for both sexes. Residual head width is not positively related to mollusc prey type. Adult females consumed larger prey than adult males but juvenile females did not consume larger prey than same-sized males.

Introduction

Sexual dimorphism, particularly sexual size dimorphism has been observed in a large number of animal taxa (Shine 1989, Blanckenhorn 2005). Two main hypotheses, both first suggested by Darwin in 1874, have been proposed to explain the evolution of sexual size dimorphism. The first hypothesis proposes that sexual selection causes the observed differences and predicts that the relationship between body size and reproductive success differs between sexes. The result is selection favouring different body sizes at adulthood. This has proven to be an easily testable prediction and has been explored in many animal groups (reviewed by Andersson 1994 as cited by Pearson 2002). Among the most common examples is the degree to which males are larger than females in mating systems that involve male-male combat. There exists an important correlation between the intensity of male-male combat and the degree to which males exceed females in adult body size (e.g. Trivers 1976).

The second hypothesis proposes that ecological causes play an important role in the evolution of sexual size dimorphism, which may lead to sexes exploiting different ecological niches (Slatkin 1984, Shine 1989). Since ecological niches are often difficult to describe, Shine (1989) proposed the use of trophic structures (e.g. jaw width or length) as a tool to compare niche partitioning between sexes. If niche divergence has occurred, particularly through diet specialization, sexual differences in trophic structures may be a good indicator of specialization. When these structures are not sexually selected they become good candidates to test this hypothesis. Furthermore, to eliminate the simple effect of larger body sizes between the sexes, it is also important for trophic structures to be more dimorphic than body size (Shine 1989, 1991, Thom *et al*. 2004). Using these parameters, much evidence for the ecological causes of sexual size dimorphism has been

put forth (see *e.g.* Shine 1991, Temeles *et al.* 2000, Shetty and Shine 2001, Pearson *et al.* 2002, Thom 2004). Snakes have been used as a particularly good example of this phenomenon since they are gape-limited predators and maximum ingestible prey size is limited by the size of the snake's head (Shine 1991). Trophic differences can be interesting to examine in turtles since they are also, in their own way, gape limited. Many turtles are limited by the crushing strength of their jaws, which has been demonstrated through a strong correlation between prey type and head width (Lindeman 2000). Mollusc specialist, like the common map turtle (*Graptemys geographica)* have much wider heads than other species that specialize on softer prey such as insect larvae and algae (Lindeman 2000). In addition, they exhibit extreme female-biased sexual size dimorphism, where trophic structures are more dimorphic than body size (Lindeman 2000, Bulté and Blouin-Demers, unpublished data) (see Fig.1). There is no overlap of body size at adulthood but juvenile females do overlap in size with adult males, making them an interesting species with which to test for ecological causes of sexual size dimorphism.

In accordance with the ecological hypothesis we expect males and females to specialize on different prey types and different prey size. We can make the following predictions: (1) prey occurrence should differ between the sexes, (2) body size should be positively related to mollusc prey size within each sex, (3) body size should not be related to non-mollusc prey type within each sex, (4) residual head width (after the removal of the effect of body size) should be positively related to prey size and (5) juvenile females should consume larger prey than same-sized males.

Methods

Study site and data collection

This study was conducted on Lake Opinicon at the Queen's University Biological station (45º 37'N, 76º13'W). Turtles were captured from May to July 2005 using basking traps and by snorkeling near areas of aggregation. Each individual was given a unique code by drilling small holes in the marginal scutes. We measured carapace length with a forestry caliper (± 0.05m) and weight was taken on a digital scale (± 0.01g). Head width was measured twice to obtain an average using a digital caliper (± 0.01mm). We examined diet by collecting fecal samples. Turtles were kept overnight in large plastic bins partially filled with water. Water height depended on the size of the individual and never completely submerged the turtle. Dirty water was then passed through a metal coffee filter to collect solid sample and were preserved in ethanol. Adult females (n = 34), juvenile females (n = 20) and adult males (n = 32) were used for analysis.

Prey reconstruction

Three main prey types were commonly found in fecal samples: trichoptera larvae (Leptoceridae) (commonly known as caddisflies) (Milne and Milne 1980), zebra mussels (*Dreissena polymorpha*) and trap door snail (*Viviparus georgianus*) (Thompson 1998). In order to determine prey size from fecal samples, a strong relationship between structures found in the feces and prey body size must be present. Past work with zebra mussels have shown a close relationship between shell length and the internal septum, a v-shaped structure that does not easily break down and is found in the umbonal region (Prejs *et al.* 1990, Hamilton 1992, Mitchell *et al.* 1999). The trap door snail is characterized by its solid operculum (Thompson 1998), a rounded calcareous plate that closes the opening to its shell. We determined the correlations between prey body size and these structures for

both mollusc prey types. Important biases occur when determining the relationship between septum length and mussel length (Mitchell *et al.* 1998). To avoid these in the literature, we chose to determine this relationship ourselves. *V. georgianus* was collected at 3 sites of intermediate abundance (n = 30 per site) and *D. polymorpha* was collected at 4 sites of intermediate abundance (n = 45 per site). Intermediate abundance sites were chosen due to size-biases that occur at low- and high-density sites (Bulté, personal observation). Snail length and width were measured and the operculum was removed to measure length and width. Mussel length, height and width were measured and the shell was opened to measure left and right septa lengths. For both species, prey length was highly correlated with structure length ($r = 0.95$, $P < 0.0001$ and $r = 0.98$, $P < 0.0001$) for mussels and snails respectively. Septum length predicted mussel length with the following equation: mussel length = 1.07 + 8.172 (mean septa length). Snail opercula length predicted snail length with the following equation: snail length = -0.878 + 1.906 (opercula length).

Fecal samples

Fecal samples were placed in a Petri dish where all structures were identified, sorted and measured with a Zeiss stemi 2000 dissecting microscope. If individual turtles had multiple samples only one was examined. Once structures were identified they were placed on a second Petri dish on an enumerated grid. Each grid cell was assigned a number from 1 to n (n = number of structures in sample). If $n \leq 40$ all structures were measured. If $n > 40$, 25 or 0.25 of structures, whichever was largest, were randomly measured. Random numbers between 1 and n were produced by statistical software, JMP 5.0.1a. For these large samples, smallest and largest structure sizes were also measured. Structure lengths (n = 1929) were then converted to actual prey length in accordance to

the equations shown above. Fecal sample data were then merged with the turtle physical trait data and a summary table was created. Finally, maximum and minimum prey length was calculated for each prey species found in every fecal sample. This summary table also allows the calculation of prey occurrence for each functional turtle group (adult female, juvenile female and adult male).

Analysis

JMP 5.0.1a was used for all statistical analysis. Chi-square tests were used to determine if functional turtle groups (adult females, juvenile females and adult males) differed in their presence/absence of prey types. These tests were run for each prey type and were Bonferroni corrected. Regression analysis was used to test the nature of the relationship between turtle body size and the maximum and minimum size of three types of prey. Turtles that had consumed only one prey item were excluded from analysis since it did not represent a range. We also conducted an analysis of variances between functional groups on mean prey size/mean head width * 100 to determine if there existed differences in prey size once the effect of body size was removed. Regression on the residuals of head width and prey size was conducted to test if head width was positively related to prey size. An analysis of covariance was used to examine if the relationship between body size and prey size for juvenile females was steeper than for same-sized males.

Results

Contingency table analyses indicated that the occurrence of trichoptera ($\chi^2 = 2.31$, df = 2, P = 0.31) and trap door snail ($\chi^2 = 2.49$, df = 2, P = 0.29) did not differ among turtle functional groups, although the occurrence of zebra mussels did differ between groups ($\chi^2 = 15.63$, df = 2, P = 0.0004) (Fig.2). Maximum zebra mussel size increased with body size for females (r = 0.62 P < 0.001), while minimum zebra mussel size was unrelated to body size (r = 0.12, P = 0.64) (Fig.3). This relationship was not examined in males since two few males (n = 2) were found to have consumed zebra mussels. Maximum and minimum trap door snail size increased with female body size (r = 0.84, P < 0.0001 and r = 0.53, P = 0.0004 respectively) (Fig. 4a) but did not increase with male body size (r = 0.17, P < 0.44 and r = -0.26, P = 0.10 respectively) (Fig.4b). Maximum tricoptera prey size, length and width, was independent of body size for females and males (r = 0.56, $P_{\square length} = 0.07$, r = 0.19, $P_{\square width} = 0.56$, r = 0.26, $P_{\square length} = 0.07$ and r = 0.07, $P_{\square width} = 0.80$) (Fig.5a and Fig.5b).

Female head width was unrelated to consumed zebra mussel maximum length (r = -0.04, P = 0.89) (Fig.6a) or consumed trap door maximum length (r = 0.05, P = 0.85) (Fig.6b).

When the effect of body size was removed, functional groups differed in the maximal size of trap door size consumed (r = 0.93, $F_{2,47} = 11.34$, P < 0.0001), a comparison among the three groups showed that adult females consumed larger prey than adult males but not significantly larger prey than juvenile females (Fig.7). Juvenile females did not consume larger prey than same-sized males ($F_{1,1} = 0.08$, P = 0.78) (Fig.8)

Discussion

Our results provide support for the hypothesis that male and female map turtles specialize on different prey type and size. The three functional groups: adult females, juvenile females and adult males, had distinct relationships with each prey type. One exception is the frequent presence of trap door snails in fecal samples of all functional groups. This commonality is most likely due to high abundance and large size distribution of this species, which enables turtle functional groups to consume individuals of different sizes. Though sexes did not differ in the occurrence of trichoptera larva (Leptoceridae) within fecal samples, a distinct trend was observed. Leptoceridae casings were found in 50% of adult male and juvenile female samples but were only present in 33% of adult female samples. This softer, presumably easier to consume prey, seems more important in the diets of smaller individuals. Leptoceridae emergence occurs in June and July (Bulté and Gravel, personal observation) which causes significant changes in prey availability, having important effects on the diets of all three groups. We plan to look at these months and examine the possible shift in diet that occurs during the entire active season.

The most noteworthy difference among the functional groups was the presence of zebra mussels in the diet of females, a prey which is nearly absent in male samples (Fig.2). Though a previous study has shown that captive-reared map turtles may feed on this invasive species of molluscs (Serrouya, 1995), our study is among the first to describe its occurrence in nature. Zebra mussels were most often found in adult female fecal samples (45.5%), though juvenile females had a similar amount (40.0%). Only 6.25% of males had zebra mussels in their fecal samples. We find further support that *G. geographica* females are more molluscivorous than males (Lindeman 2000). There was

no relationship between body size and number of septa found in the fecal samples (result not shown), indicating that adult females do not consume more mussels than juvenile females. Interestingly, juvenile females of equal carapace length to adult males consumed zebra mussels while males could not or did not (Fig.2). Morphological differences may play an important role since juvenile females have relatively wider heads than same-sized males (Fig.1). In map turtles, head width is highly correlated to alveolar surface, the area used for crushing prey (Lindeman 2000). If zebra mussels are difficult to crush, this morphological difference may explain why juvenile females can include zebra mussels in their diet and males cannot. Tucker *et al*. (1997) showed that shell strength was the most important factor deterring diamondback terrapins (*Malaclemys terrapin*) from consuming mud snails, which are abundant in their habitat and are of same size as other gastropods included in the turtle diet. Moreover, in many reptiles, aspects of head size can be a better indicator of bite force than body size (Herrel and O'Reilley 2005).

Although fecal samples enable us to examine certain aspects of prey occurrence, it is an imperfect method to compare relative importance of prey in diet since structures, particularly septa, may be crushed and thus overlooked. Mussels and other invertebrates leave distinct carbon and nitrogen signatures, thus the ideal method would compare the relative importance of prey with the use of isotopes (Bulté and Blouin-Demers, unpublished data).

The relationship between maximal and minimal mollusc type prey size and turtle body size differed between the sexes, while the relationship between softer prey and body size did not. As predicted, consumed trichoptera larvae (Leptoceridae) size was unrelated to body size for either sex. Furthermore, males and females did not differ in size of prey consumed (Fig.5a and Fig.5b). This confirms that turtle body size is insignificant in

relation to consumption of this prey, though it seems somewhat more important in the diets of smaller individuals (adult males and juvenile females) than larger individuals (adult females) (Fig.2). Maximum zebra mussel length consumed was significantly and positively related to female body size while minimum length showed an insignificant positive relationship. Larger females are able to crush and consume more challenging prey since mussel shell strength increases exponentially with size (Tucket *et al* 1997). They also continue to consume small sized prey. The same pattern was found between trap door snails and female body size. Larger females are able to consume larger snails but continue to consume small prey. In fact, they seem to include larger snails faster then they exclude smaller snails (Fig.4a), which is made obvious by the great variance in minimal prey size. Thus, the range of consumable snail size increases with body size for females, though the degree to which they are selecting different prey sizes is unclear. We plan to examine prey availability in our study site to tease out the effect of choice. Overall, males show a dissimilar trend. Maximum and minimum consumed snail lengths were unrelated to male body size. Surprisingly, larger males seemed to consume the smallest and largest snails (Fig.4b). The trend for increased variance in larger turtles seems to also apply to males. The difference in strength of relationships between prey size and body size for the two sexes may be explained by the strength of selection on trophic structures. Lindeman (2000) has shown that differences in diets that are associated with relative head width are more evident in females than in males, thus males have not specialized to consume large and hard to crush prey. Why females have been able to do this remains unclear. One possible explanation relates to energy balances. Many ectothermic females must increase in size to increase their fertility (i.e. lay more eggs) (Shine 2005), thus large reproductive females may require more energy for growth

and reproduction than adult males. One way to fulfill these requirements is to consume larger, more energetic prey. To examine this question it would be very interesting to compare energetic content of different prey types and sizes. If metabolic rates were known, we could determine if females consume large prey because they must or because they can.

Though adult females consume larger prey than adult males, it is unclear whether juvenile females can do the same (Fig.8). The relationship between body size and maximum prey length does not differ between these two groups (Fig.7) but Fig.8 shows an interesting pattern. Adult females consume prey that represents a surprising 53 % of their head width, juvenile females consume prey that represents 38 % of their head width and adult males maximal prey length represents only 29% of their head width. Thus, juvenile females have close to a 10 % advantage. An interesting question to examine is whether or not this is biologically significant. It is plausible that consuming slightly larger prey gives juvenile females a competitive advantage over adult males (Thom *et al.* 2004), giving them additional energy for growth and maturation.

Contrary to our prediction, there was no significant relationship between maximal prey size and residual female head width (effect of body size removed) (Fig.6a and Fig.6b). Females with relatively wider heads were unable to consume larger prey than other females. On its own, body size explains 50 % of the variability in maximal prey length and seems to be the most important factor. Head size dimorphism gives females an advantage over males (intersexual) but not over other females (intrasexual).

In conclusion, we found that male and female map turtles do specialize on different prey type and prey size, showing that ecological divergence may play an

important role in the extreme female-biased sexual size dimorphism present in this species.

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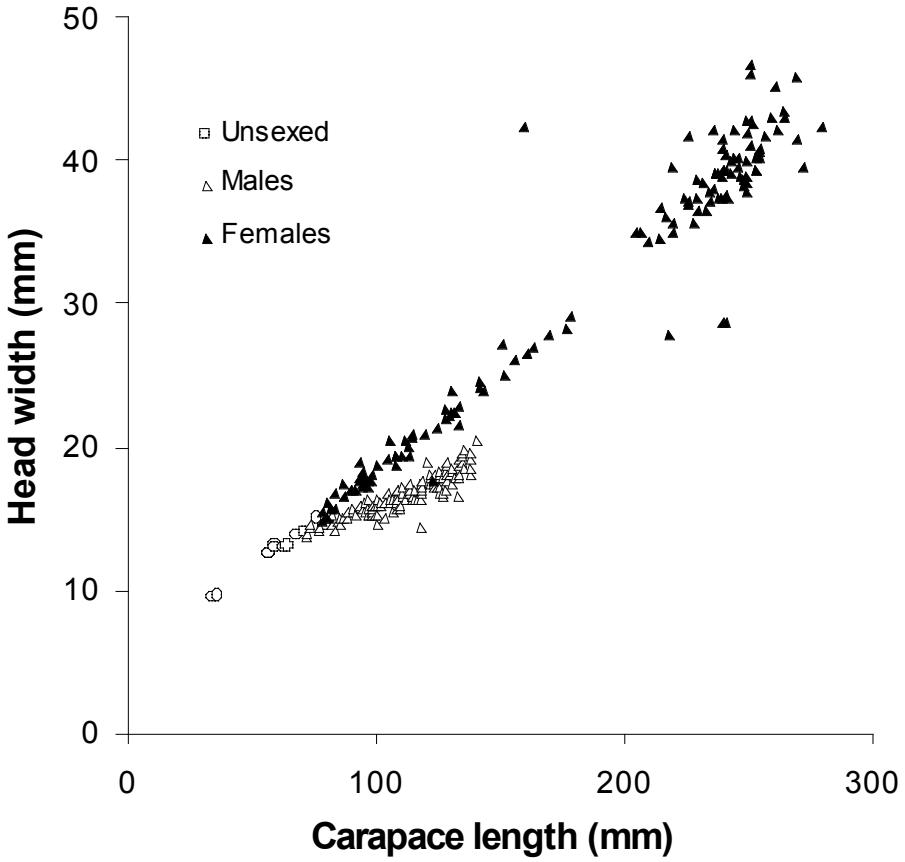

Figure 1. Relationship between body size and head width in the common map turtle (*Graptmeys geographica*), showing differences between the sexes. Adapted from Bulté and Blouin-Demers, unpublished data

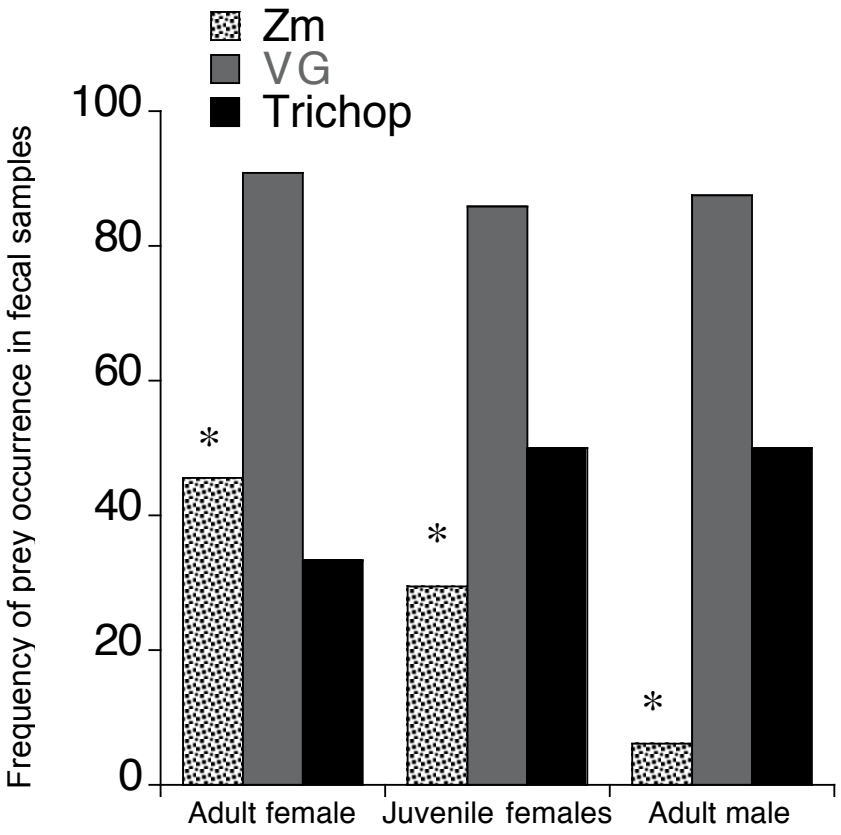

Figure 2. Frequency of prey occurrence in fecal samples Zm = zebra mussels, VG = trap door snail and Trichop = trichoptera, * indicates $p < 0.005$

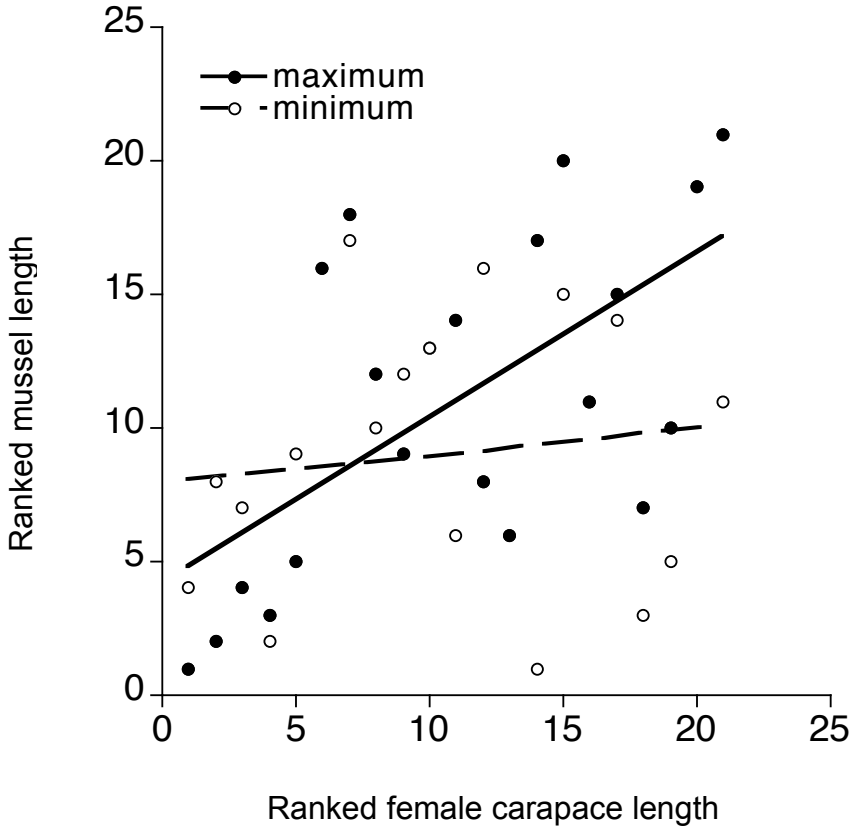

Figure 3. Ranked maximum and minimum zebra mussel length consumed as a function of female carapace length (n =21)

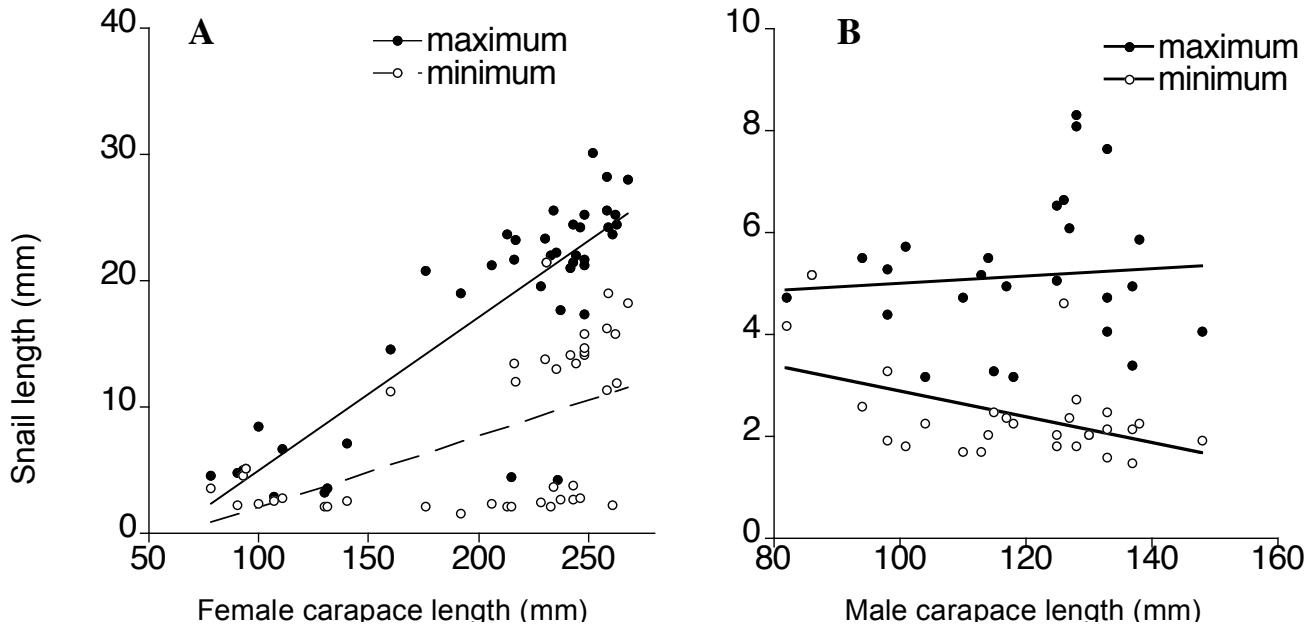

Figure 4. Maximum and minimum trap door snail length consumed as a function of **(a)** female carapace length (n = 38) and **(b)** male carapace length (n = 25)

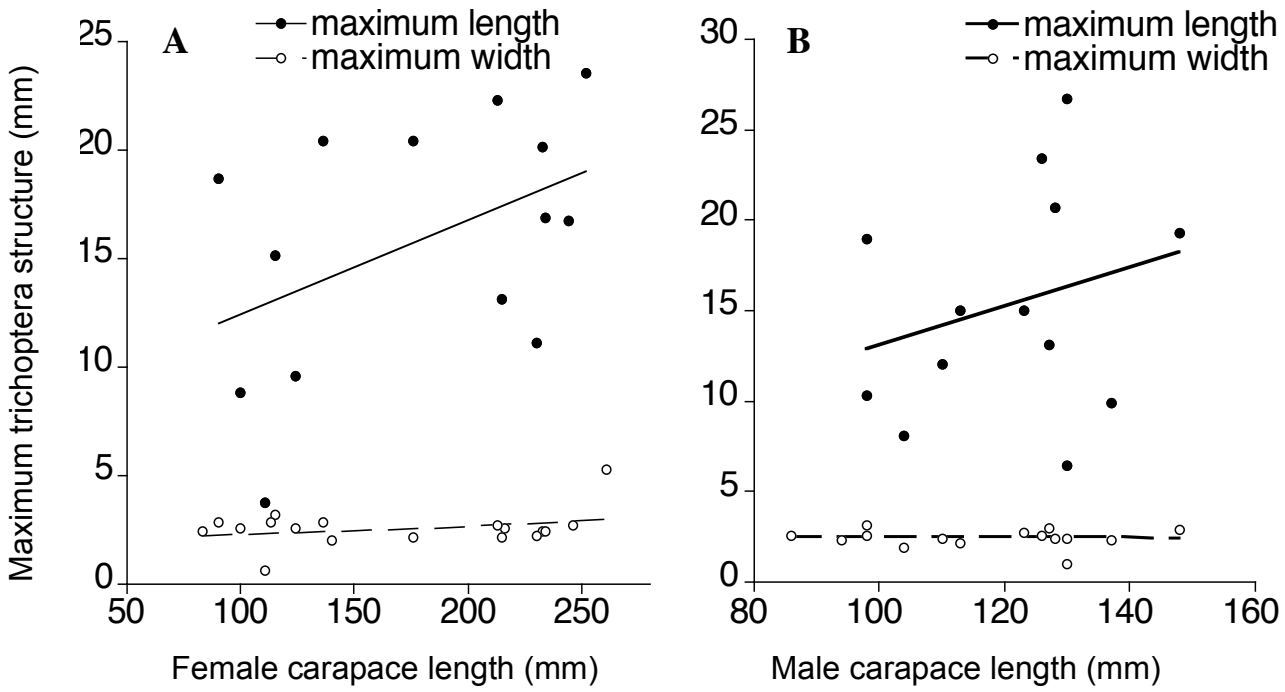

Figure 5. Maximum trichoptera length and width as a function of **(a)** female carapace length (n = 13) and (**b)** male carapace length (n = 14)

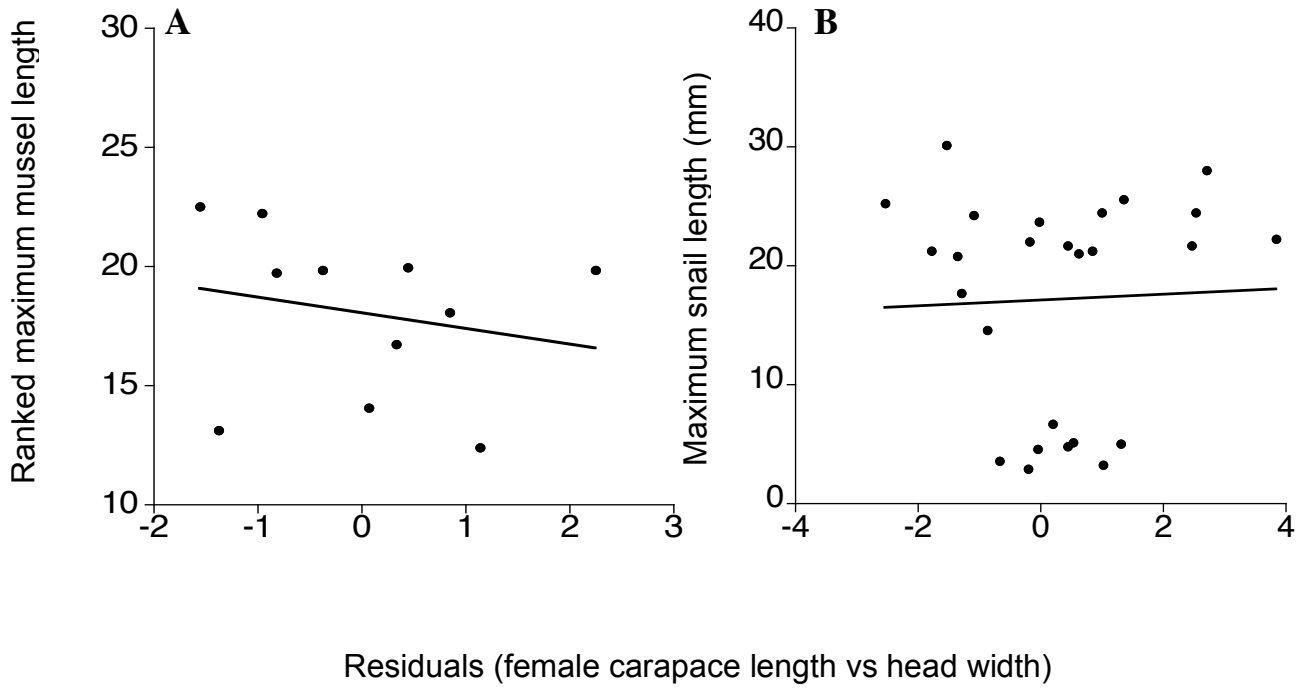

Figure 6 (a) Ranked maximum zebra mussel length consumed as a function of female residual head width (n =11) and maximum snail length as a function of residual head width (n = 26)

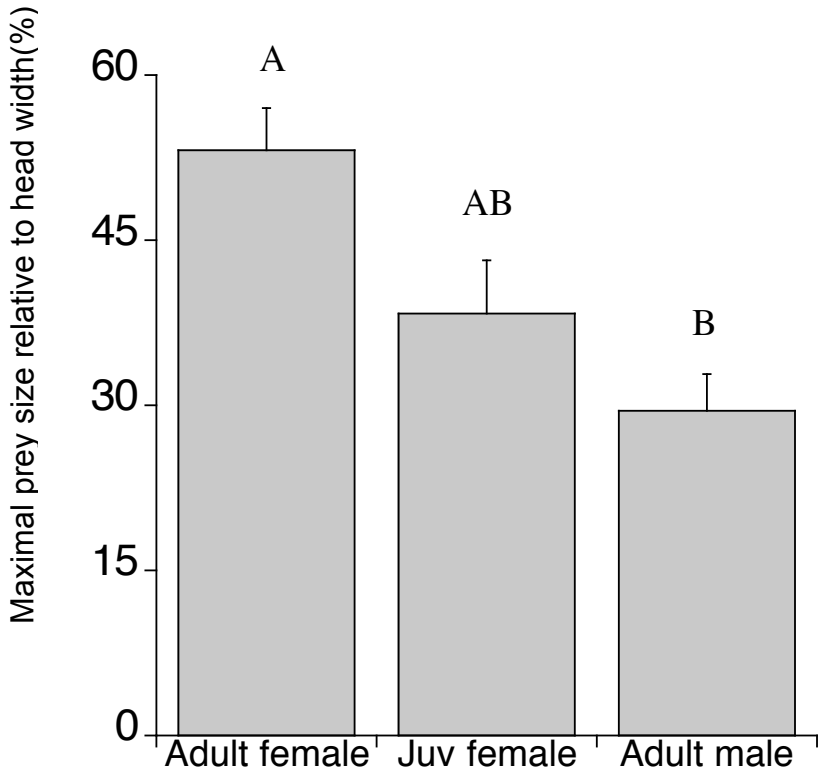

Figure 7. Maximal snail size relative to head width as a function of sex, A is different from B ($p < 0.05$

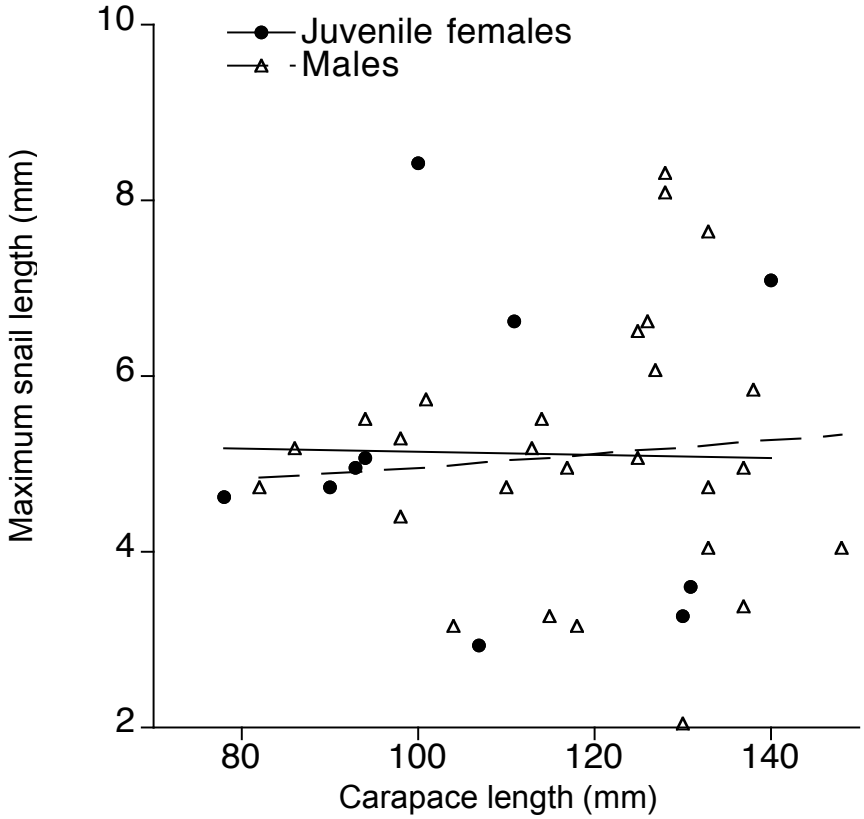

Figure 8. Relationship between maximum snail length consumed and carapace length for juvenile females (n = 10) and adult males (n = 27)