Snail Predation by *Hemigrapsus nudus* and *Hemigrapsus oregonensis*: Sex and Species Differences in Chela Size.

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Abstract:

The relationship between propus size and use of snails as prey in sympatric populations of *Hemigrapsus nudus* and *Hemigrapsus oregonensis* was investigated. Propal height and propal width increases with body size in a predictable manner in male and female crabs of both species. Sexual dimorphism of propal height and width relationships in both shore crabs is apparent, but there was no detectible difference in chela size between *H. nudus* and *H. oregonensis*. The lack of difference in chela size between sympatric *H. nudus* and *H. oregonensis* suggests that there is no character displacement in this trait. Both species of crabs showed a strong feeding preference for the thin-shelled gastropod *Lacuna vincta* over the thicker shelled *Littorina scutulata*, likely due to the ease of consumption. There were no differences in snail consumption rates between male and female *H. nudus* of similar propal heights, mostly due to high feeding variation among individual crabs.

Introduction:

A multitude of species coexist in the marine intertidal environment. Closely related species may be sympatric and compete for resources, such as food. Two species of shore crab, *Hemigrapsus nudus* (Dana 1851) and *Hemigrapsus oregonensis* (Dana 1851), occur in sympatry in the Salish Sea. Both species are sexually dimorphic, with the males having larger chelae. Species in sympatry may exhibit character displacement, the exaggeration of morphological or behavioral characteristics due to competition for resources (Brown and Wilson 1956). When *H. nudus* and *H. oregonensis* co-occur, *H. oregonensis* tends to be found closer to the waterand in finer sediment than the more desiccation-tolerant *H. nudus* (Sliger 1982). There is still considerable habitat overlap between these two species; the underside of a single rock may have roughly equal abundances of the two crab species (personal observation). The size of the chela may differ, which could allow the crabs to differentiate in food resource utilization.

Both species are omnivores that eat algae and small invertebrates, including snails (Behrens Yamada and Boulding 1996). The two shore crab species are known to eat *Littorina sitkana* (Philippi 1846) and *Littorina scutulata* (Gould 1849), which also occur in the rocky intertidal zone (Behrens Yamada and Boulding 1996). *Li. scutulata* moves upshore in response to the presence of *H. nudus* and crushed conspecifics, where *H. nudus* density is lower (Keppel and Scrosati 2004). This suggests that *H. nudus* represents an ecologically significant predation threat to littorines.

The thick shelled littorines are difficult prey for both *H. nudus* and *H. oregonensis* as neither crab species is a molluscivore specialists; they typically scrape or pick algae and softer invertebrates off rocks using their chelae (Behrens Yamada and Boulding 1996). Behrens Yamada and Boulding (1998) found that large *H. nudus* were capable of consuming *Li. sitkana* that were less than 8 mm in length, but had only a 37% success rate of consuming snails with lengths between 5.5-7 mm .

I sought to investigate differences in propus size between between males and females of these two crab species. The size of the propus of the chela is positively correlated with the amount of force that can be produced due to greater musculature (Behrens Yamada and Boulding 1998). A significant difference in propus size between the two species would suggest that further testing of character displacement may be warranted. A disparity in propus size to body size between male and female crabs might result in different feeding rates and shell breaking capabilities. I devised a test of preference by varying snail shell strength within the same size class. The snail species *Li. scutulata* and *Lacuna vincta* (Montagu 1803) are both in the family

Littorinidae and have similar shell shape but different shell thickness. *Lacuna vincta* has a thinner, more fragile shell and is likely to be preferred as prey by shore crabs. I also hypothesize that, if chela size is held constant, female crabs will have greater snail consumption rates than male crabs. Female crabs with claws equivalent to males have a larger body mass,are likely to have greater metabolic need, and are less easily satiated.

Study System:

All specimens were collected on San Juan Island, Washington. Two shore crabs (clade: Brachyura: Family Grapsidae), *Hemigrapsus oregonensis* and *Hemigrapsus nudus* were collected in the intertidal adjacent to the Friday Harbor Laboratories dock. These closely related crabs are morphologically similar, but can be distinguished by the presence of purple spots on the cheliped of *H. nudus* and abundant setae on the pereopods of *H. oregonensis* (Kozloff 1987). *Lacuna vincta*, in the Class Gastropoda and Family Littoridae, were collected at False Bay and Dead Man Cove. *Littorina scutulata*, in the Class Gastropoda and Family Littoridae, were collected from the rocky intertidal zone of Fourth of July Beach.

Materials and Methods:

Morphometrics

Male and females of *H. oregonensis* and *H. nudus* were measured with digital calipers (0.1 mm). Each crab was measured for carapace width, propal height and propal width. Carapace width was taken at the widest part of the carapace. Propal height was measured at the highest vertical distance along the propus. Propal width was measured perpendicular to propal height, from the left to right sides of the propus. All claw measurements were made on the left cheliped.

If there was a size disparity between the left and right claws due to regeneration of a lost claw, the crab was excluded from the study. Ratios of carapace width:propal height (CW:PH) and carapace width:propal width (CW:PW) were calculated.

Crab Feeding Preference

Three female (Fe1, Fe2, Fe3) and three male (Ma1, Ma2, Ma3) crabs of *H. nudus* with propal heights between 5-6 mm were placed in small flow-through containers. Five *L. scutulata* and five *L. vincta* with shell lengths between 4-6 mm were added to each container. The ranges of crab propal height and snail shell length were chosen based on prior studies to ensure that the crabs were capable of feeding on the hard-shelled *L. scutulata* (Behrens Yamada and Boulding 1998). *H. oregonensis* was excluded due to the rarity of female crabs of that species within the range of appropriate propal heights. After approximately 15 hours the number of *L. scutulata* and *L. vincta* consumed was counted. Three trials were conducted for each crab.

Snail Consumption by Hemigrapsus nudus

The crabs from the preference experiment were given five of each snail in each trial. After 1.5 to 3 hours the number of snails consumed was counted and converted to a consumption rate (snails consumed/hour). A total of eight feeding trials were conducted.

Statistical Analysis

For the morphometric analysis, crabs were divided into four groups based on sex and species. Standardized major axis regression was used to determine the relationship between crab morphometric parameters. Arcsin transformations were used to correct for non-normality (Sokol and Rohlf 2011). Differences in CW:PH and CW:PW were analyzed using a two-way ANOVA with factors: Sex and Species. Prey selection by *H. nudus* was analyzed using G-tests for each individual that consumed snails. An one-way ANOVA was used to determine differences in snail consumption rates by *H. nudus*.

Results:

Morphometrics:

Carapace width was a good predictor of both propal height (Figure 1, Table 1A) and propal width (Figure 2, Table 1B) in female and male *H. oregonensis* and *H. nudus*. There was less variation in the relationship between carapace width and propal height than with propal width. Due to non-normality of CW:PH and CW:PW an arcsin transformation was used. A significant effect for sex was found for both CW:PH ($F_{1, 45} = 125.6$, $p < 0.001$) and CW:PW ($F_{1, 45} = 103.81$, $p < 0.001$). There was no significant difference between *Hemigrapsus* species for CW:PH ($F_{1, 45} < 0.01$, $p = 0.983$) and CW:PW ($F_{1, 45} = 0.09$, $p = 0.764$). A significant sex*species interaction was detected for both CW:PH ($F_{1, 45}$ 4.39, $p = 0.042$) and CW:PW ($F_{1, 45} = 7.19$, $p = 0.010$). Figure 3 and 4 show the means of CW:PH and CW:PW in by sex and species respectively.

Crab Feeding Preference:

Expected values for both the number of *L. scutulata* and *L. vincta* consumed for the G-test are 0.5 multiplied by the total number of snails consumed by each individual crab. G-tests for individual *H. nudus* that eat snails were all significant at $p < 0.001$ with 1 degree of freedom (See Table 2 for statistical summary). The three crabs that did not eat either *L. scutulata* or *L. vincta* could not be tested for feeding preference.

Snail Consumption by Hemigrapsus nudus

No significant difference in crab feeding rate (snails consumed/hour) was found ($F_{2, 21}$ = 2.52, p = 0.104) among individual *H. nudus* that fed on snails during the course of the consumption experiment (Figure 5). Fe2 ate snails at a rate of 0.59±0.53 snails/hour (variance is standard deviation), Ma1 feeding rate was 0.24±0.31 snails/hour, and Ma2 had a feeding rate of 0.80±0.38 snails/hour. Individuals Fe1, Fe3 and Ma3 did not consume any snails during the course of the experiment.

Discussion:

A few interesting patterns emerged in the morphometric analysis of *Hemigrapsus nudus* and *Hemigrapsus orogenensis*. The variance in propal height or propal width explained by carapace width was surprisingly high in female *H. nudus* with R^2 values of 0.976 found for propal height and 0.927 for propal width. Male *H. oregenensis* had the greatest variation in chela size parameters, demonstrated by R^2 of 0.693 and 0.534 for propal height and propal width respectively. The R^2 values for propal width regressed against carapace width were consistently lower than propal height regressed against carapace width across species and sexes (Table 1). In general the ability of carapace width to explain the variance in chela size parameters (i.e.: R^2 values) was greater in females of both crab species (Table 1, Figures 1 and 2). Males may have more variation in claw size due to trade-offs between claw size and factors like feeding efficiency or resource allocation. Trade-offs relating to chela size are found in fiddler crabs, which exhibit extreme sexual dimorphism. Fiddler crabs have a trade-off between the intrasexual competition and intersexual signaling functions of the dimorphic claw (Swanson et al. 2013).

This is not to say that the particular trade-offs in fiddler crabs case are analogous to that of *Hemigrapsus*, since both claws in the two shore crabs in this study are used in feeding.

Sexual dimorphism in chela size, which is readily apparent to the eye in both *Hemigrapsus nudus* and *Hemigrapsus oregonensis*, was detected statistically (Figures 3 and 4). The two-way ANOVA with factors sex and species did not show a significant species effect, suggesting that the claws of both shore crabs produce roughly the same force and are functionally equivalent (Behrens Yamada and Boulding 1998). The lack of morphological difference in the size of the chelae between the crab species removes the possibility of character displacement in the trait. It should be noted that this study was not designed to test for character displacement, but to determine if this would be an interesting question for future investigations. To make a compelling case for character displacement it is necessary to compare multiple sympatric and allopatric populations with similar abiotic and biotic conditions (Stuart and Losos 2013). Also it must be demonstrated that the trait differs due to genetic differences between sympatric and allopatric populations, that the differences between the populations are not due to species sorting, that the morphological trait is correlated to differences in resource use between the two sympatric species, and that the similar phenotype in allopatric populations compete for the same resources (Stuart and Losos 2013). The tendency of *H. nudus* to occupy the upper intertidal zone (Sliger 1987), despite considerable overlap with *H. oregonensis*, may provide enough differential resource use to prevent exclusion in sympatry. Desiccation tolerance may be a better trait to test for character displacement in these shore crabs.

H. nudus males and females clearly preferred to eat the thinner shelled *Lacuna vincta* (Table 2). During the course of the feeding preference experiment all the crabs that ate snails consumed *L. vincta* exclusively. However, one *Littorina scutuala* was eaten by *H. nudus* when determining consumption rates. The six crabs were chosen because their claws were of appropriate size to eat littorines with shell length between 4-6 mm, yet only half of the crabs ate these snails. This could be due to insufficient time to acclimate *H. nudus* to lab conditions and possibly reduced feeding associated with molting. Male snow crabs, *Chionoecetes opilio,* were shown to cease feeding 3-6 weeks before and 3-4 weeks after molting (O'Halloran and O'Dor 1988).

It was my original intention to test for sex differences in consumption rates, but this was not possible as I could not collect many crabs of the appropriate claw size for gastropod feeding and many of the crabs I did collect did not feed. There were no statistically significant differences in consumption rates (snails eaten/hour) among the three feeding *H. nudus*. These individuals had highly variable feeding rates, mostly due to trials in which the crab did not feed. Sylvia Behrens Yamada and Elizabeth Boulding (1998) found that *H. nudus* consumed 1.8 *Littorina. sitkana*/individual crab/day. In my study crabs fed on 13.03 *Lacuna vincta*/individual crab/ day. The greater consumption rate in my study is likely due to the easily breakable shells of *La. vincta*.

The findings of this study suggest that there is no potential for character displacement of chela size in the sympatric *H. nudus* and *H. oregonensis*. This leaves the question of species co-occurrence open to other possibilities. *H. nudus* has a strong preference for *La. vincta*, but it seems as if there have been no studies that show predation on *La. vincta* in the field. It should be noted that *H. nudus* and *La. vincta* usually occupy different portions of the intertidal and may have little contact with each other, unlike the relationship between *H. nudus* and *Li. scutulata*. There is some potential for overlap in the winter when *La. vincta* migrates up shore. Although no differences in consumption rates between male and female *H. nudus* were found, this might be due to logistical issues surrounding the experimental design and little replication. Future studies should include more crabs, the exclusion of non-feeding crabs, and trial periods with longer time intervals. Additionally, any subsequent study should utilize multivariate and geometric morphometric methods to quantify claw shape instead of using ratios, as two similar ratios may have different shape.

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Table 1: SMA regressions of carapace width and propus measures.

A) The relationship between carapace width and propal height. x is carapace width and y is propal height. B) The relationship between carapace width and propal height. x is carapace width and y is propal width.

A

	N	SMA Regression Carapace Width vs Propal Height	R^2
Female *H. nudus*	13	y = 0.273*x - 0.678	0.976
Male *H. nudus*	13	y = 0.311*x - 1.385	0.868
Female *H. oregonensis*	9	y = 0.351*x - 0.833	0.894
Male *H. oregonensis*	14	y = 0.39*x - 1.149	0.693

B

	N	SMA Regression Carapace Width vs Propal Width	R^2
Female *H. nudus*	13	y = 0.157*x - 0.386	0.927
Male *H. nudus*	13	y = 0.209*x - 1.288	0.859
Female *H. oregonensis*	9	y = 0.175*x + 0.037	0.724
Male *H. oregonensis*	14	y = 0.244*x - 0.688	0.534

Table 2: Size and prey preference in *H. nudus*.

Size parameters of experimental *Hemigrapsus nudus* and number of prey consumed in 24 hour intervals (three trials). Crabs Fe1, Fe3, and Ma3 did not feed on snails and were not testable (NT) for preference.

Individual	Carapace Width (mm)	Propal Height (mm)	Number of *Lacuna vincta* consumed	Number of *Littorina scutulata* consumed	G	p-value
Fe1	23.6	5.9	0	0	NT	
Fe2	23.1	5.5	15	0	20.8	$p < 0.001$
Fe3	20.6	5	0	0	NT	
Ma1	19.1	5.4	14	0	19.4	$p < 0.001$
Ma2	18.4	5.4	15	0	20.8	$p < 0.001$
Ma3	20.1	6	0	0	NT	

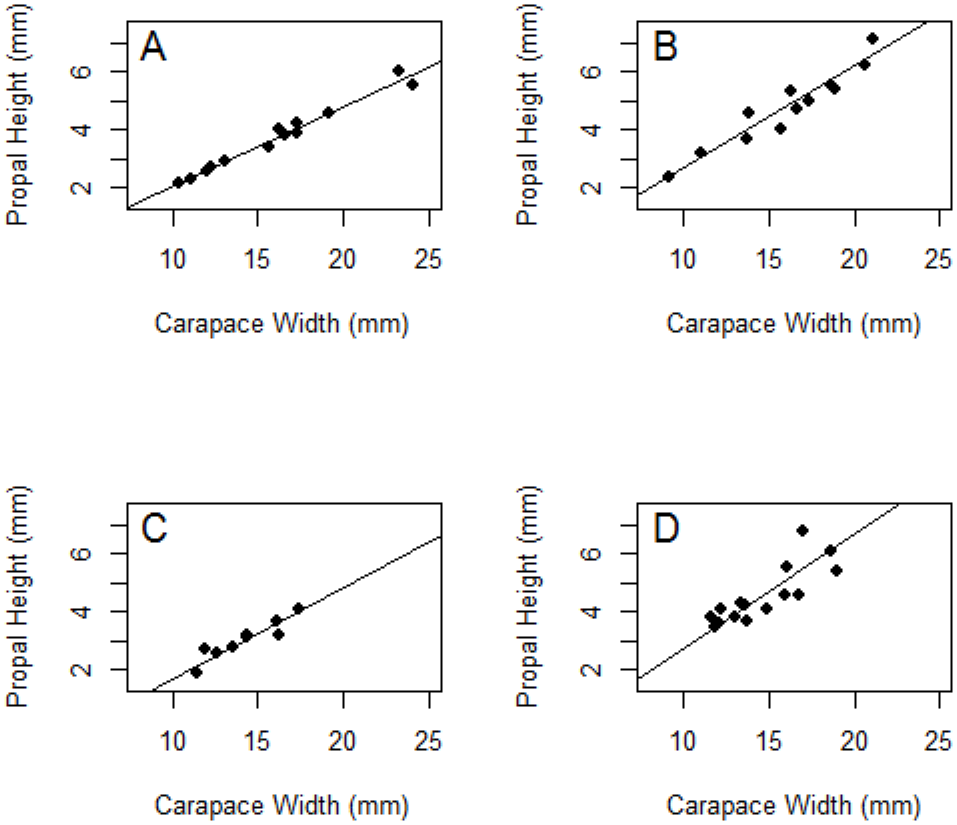

Figure 1: Relationship of carapace width and propal height in *Hemigrapsus*. Line of best fit from SMA regression. See Table 1A for descriptive statistics. A) Female *H. nudus*. B) Male *H. nudus*. C) Female *H. oregonensis*. D) Male *H. oregonensis*.

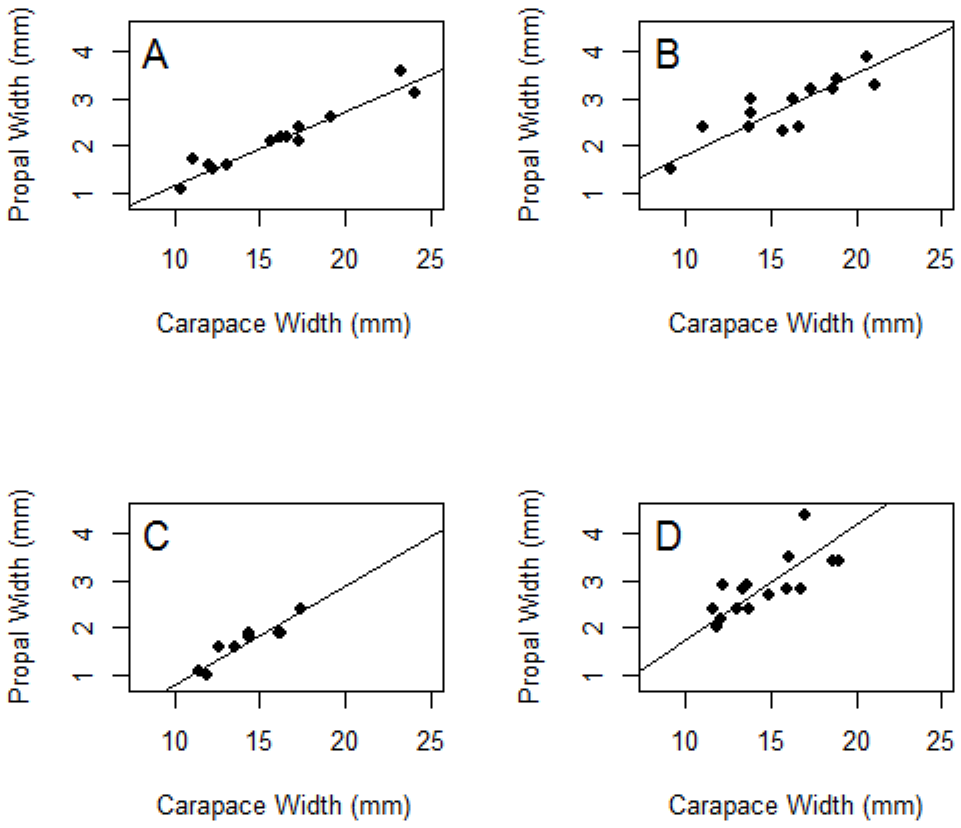

Figure 2: Relationship of carapace width and propal width in *Hemigrapsus*.

Line of best fit from SMA regression. See Table 1B for descriptive statistics. A) Female *H. nudus*. B) Male *H. nudus*. C)Female *H. oregonensis*. D) Male *H. oregonensis*.

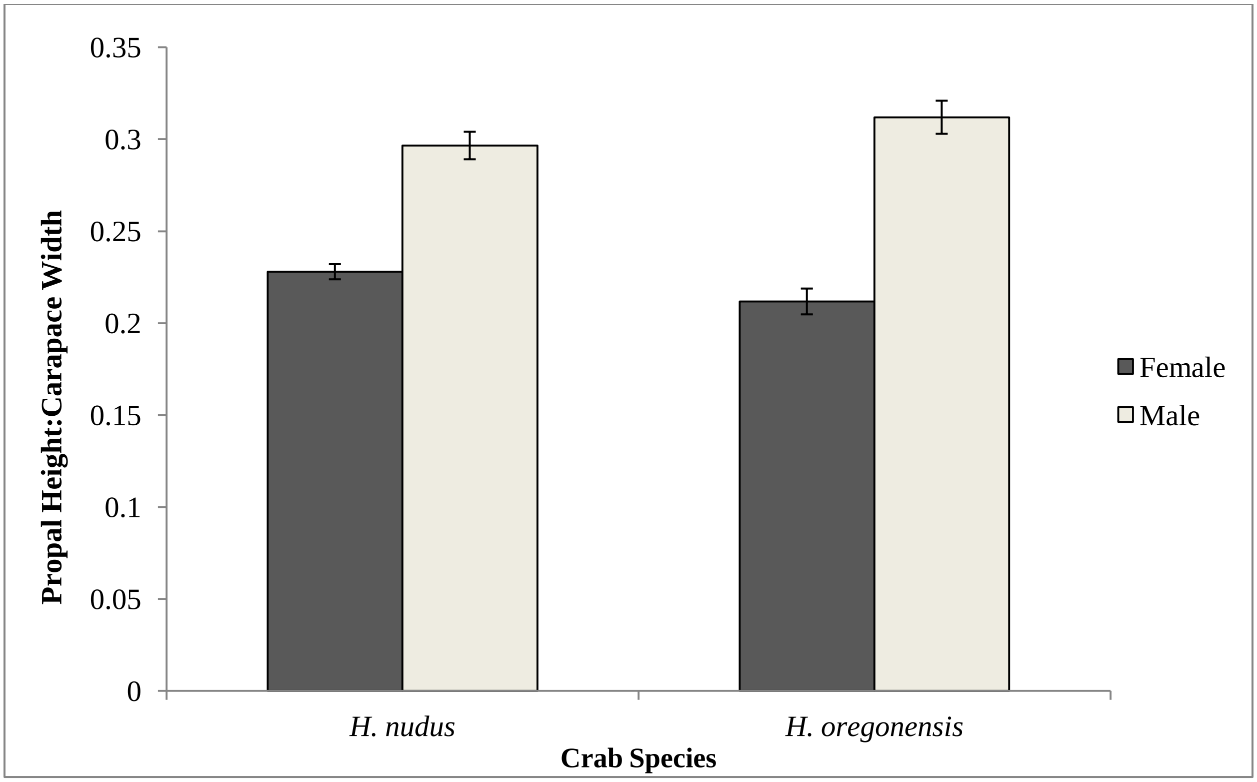

Figure 3: Differences in propal height:carapace width ratio between sex and species.

The sex factor was statistically significant (F = 125.6. $p < 0.001$), while the species factor was insignificant (F > 0.01, p = 0.983). There was a significant interaction (F = 4.39, p = 0.042). Error bars represent standard error of the mean.

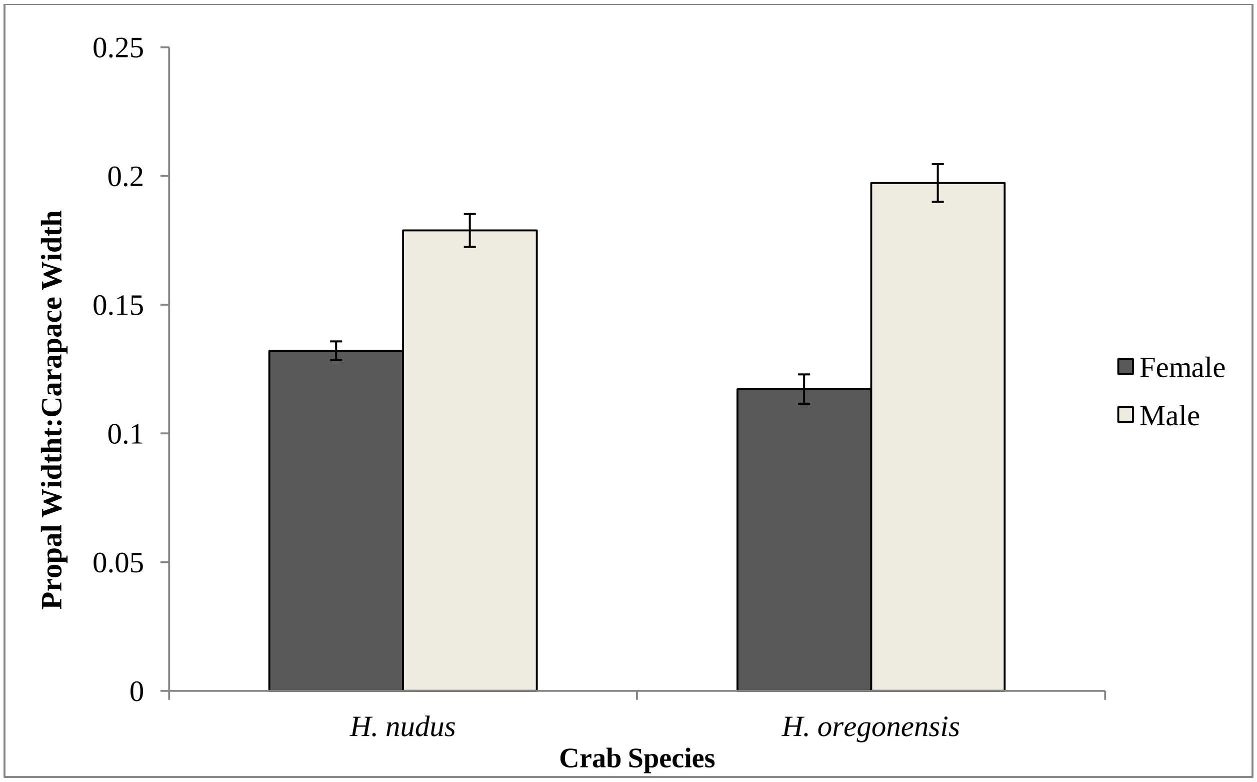

Figure 4: Differences in propal width:carapace width ratio between sex and species.

The sex factor was statistically significant ($F_{1,45}$ = 103.8. $p < 0.001$), while the species factor was insignificant ($F_{1,45}$ = 0.09, $p = 0.764$). There was a significant interaction ($F_{1,45}$ = 7.19, p = 0.01). Error bars represent standard error of the mean.

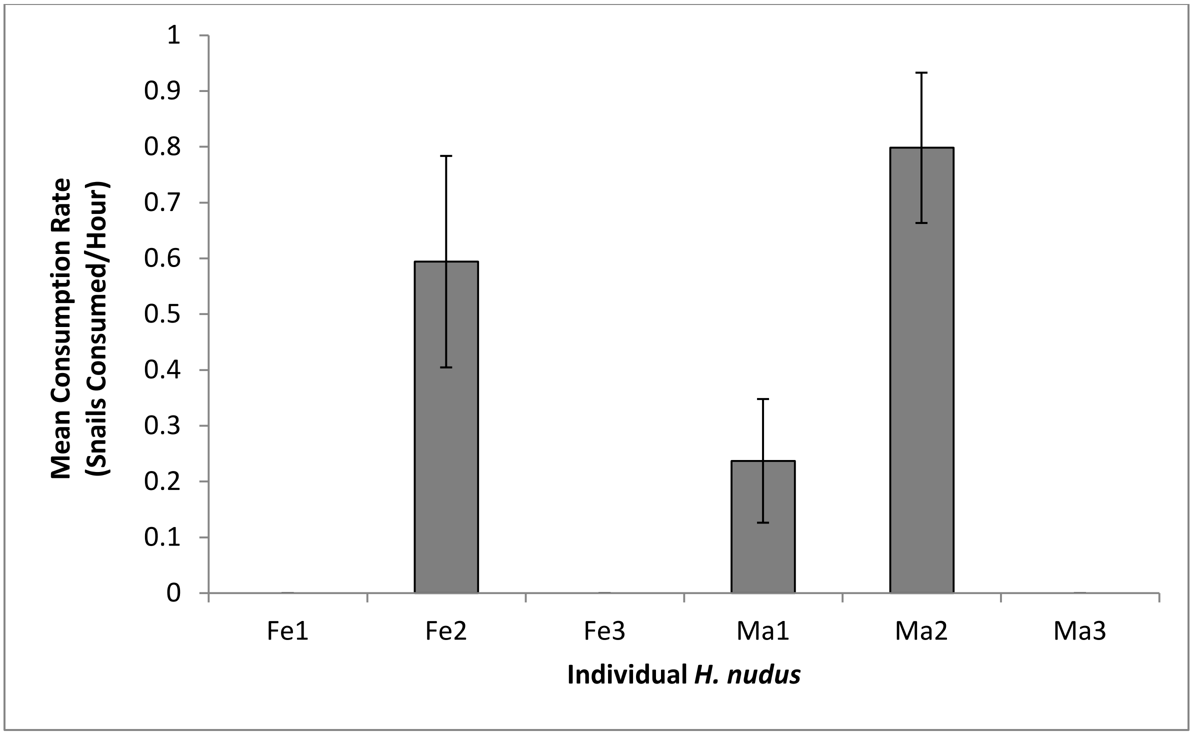

Figure 5: Consumption rates by individual *H. nudus*.

Mean consumption rates (n = 8 trials) of 3 female (Fe1 to Fe3) and 3 male (Ma1 to Ma3) *H. nudus*. Crabs Fe1, Fe3, and Ma3 did not consume snails. The individuals that eat snails did not differ in their consumption rates ($F_{2,21} = 2.52$, $p = 0.104$). Error bars represent standard error of the mean.