An Investigation of Density Dependent Feeding in *Octopus vulgaris*

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ABSTRACT

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Our experiment investigates the functional response of 12 individually housed *Octopus vulgaris* to the presentation of 3 different densities of crab. The results of this experiment indicate that *O. vulgaris* is one of few species which does not exhibit a functional response to prey density, and will consume roughly the same amount of food regardless of the amount presented. These results are in opposition to the results of many previous experiments investigating the functional responses of other species, and a few possible explanations for the unexpected results are presented.

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Introduction

The idea of density dependent predation has been heavily researched for many species, however there is a significant lack of this research in the area of octopuses and other cephalopods. In 1949, M. E. Solomon proposed that density dependent predation, predation rates which change as a result of changing prey populations, acted as a form of population control. Adding to this, C. S. Holling (1959) proposed that predators responded in two ways to prey densities, and these responses helped to control prey populations. The first response involved the predator population increasing in response to higher prey densities. This response was called the numerical response. The second response Holling proposed required individual predators to begin eating more of the prey species as a response to the prey's increased density. He called this response the functional response and described the three curves that this response could follow. A type I functional response involved a simple linear increase in amount eaten per predator in response to increases in prey density until a maximum was reached, at which point the curve would reach a plateau. This type of response was expected among filter-feeders, or for predators whose handling time of prey was negligible. A type II functional response involved a decelerating increase in predation which eventually reaches an asymptote. This response was originally described as the invertebrate response, however it has since been observed among many other species including juvenile walleyes (Czesny 2001), beavers (Fryxell 1994), least weasels (Sundell 2000), and in coyotes as a response to jackrabbit density (Bartel 2005). The third response, called a type III functional response, was described as having a sigmoid curve, which provides a haven for species at low densities and prevents localized extinctions (Holling 1959). This response was originally proposed to be a mammalian response but has since been observed in other species such as blue crabs (Seitz 2001).

Since Holling's work in 1959, the functional responses of many different species have been researched and classified as one of these three types, however it has been observed that not all species respond one of these ways. In particular, Buckner and Turnock (1965) observed the response of many species of birds to larch sawfly densities. Of these species, 26 showed some type of functional response, while 2 of them showed no response at all.

While the functional response of many species has been assessed, only one experiment has been published investigating density dependence in octopuses. In 1971, Katarina Borer investigated the effects of crab density on food intake of individually housed *Octopus briareus* Robson in the laboratory. In her research she found that *O. briareus* consistently consumed around 16% of the crabs presented. Although this is the only work to look at the effect of prey density on octopuses, it is open to criticism. Most notably, Borer included brooding female octopuses in her research. A large body of research has shown that female octopuses cease eating, or at least severely reduce intake to the point of nearly stopping altogether, shortly before they lay their eggs (Batham 1957, Brough 1965, Fisher 1923, Fox 1938, Le Souef & Allan 1933, Vevers 1961, Wells & Wells 1959, Wodinsky 1977 1978). As such, Borer's use of brooding females means that her results cannot be generalized to the population of healthy, growing octopuses. Further indicating a poor sample choice is the fact that at least some of the subjects that Borer studied lost weight during the experiment, despite being fed beyond ad lib. At the start of her experiment, the largest octopus weighed 478 gm, however at the end, it weighed only 474 gm. Because it has been shown that an octopus being fed ad lib will continuously gain weight (Walker 1970), it can be seen that at least one subject was not growing as expected. This is likely attributable to the fact that some of the octopuses were brooding, however there are other possible explanations such as illness, which could further compromise how well her findings can be generalized to the population of healthy, growing octopuses. Additional criticisms of Borer's paper came from William Van Heukelem (1976), stating that not only were the females post-spawning, but the males were too old to be used in the experiment as well. He also criticized the paper for failing to mention the effect of season, and for the water temperature being allowed to fluctuate.

As there is a critical lack of research into the presence or absence of a functional response among octopuses, and as the only research which has been conducted may not accurately reflect the population of healthy octopuses, more research is required. The experiment conducted here addressed this gap. This research was meant to investigate the effect of crab density on two species of octopus; *Octopus hummelincki*, and *Octopus vulgaris*. Additionally, in order to avoid the possible confounding effect of abnormal eating from brooding females, only young octopuses of both species were used. This research was meant to either indicate the replicability of Borer's results despite the criticisms of her study, or provide evidence indicating her results are not typical among octopuses.

For this experiment "density" was manipulated by introducing different numbers of crabs into the tanks in which individual octopuses were housed. For consistency, the crabs used in this experiment were *Uca pugnax*, as both *O. vulgaris* and *O. hummelincki* will eat this species of crab. The octopuses were exposed to densities of 15, 30, and 45 crabs, all of which are well above the number of crabs individual octopuses have been observed to eat in a 24 hour period. Every octopus was offered all of these densities in 10 day blocks in a partial latin square design. Presenting them in this design helped to control for any possible effect which order might have. The use of a partial latin square also controlled for the growth of the octopuses which occurred during the experiment. The use of 10 day blocks ensured that the number of crabs eaten was representative octopus behavior at the presented crab density and not an effect of rapidly changing densities or an unstable food supply.

Research in the area of functional response, as well as the results from Borer's (1971) research, indicates that we will most likely see a density effect of some type in the number of crabs eaten by both *Octopus hummelincki* and *Octopus vulgaris*. While the limited number of densities used in our experiment will prevent us from conclusively determining which type of response the octopuses exhibit, we will be able to find some evidence indicating whether it is a type I, II, or III. In addition, the most likely result is that as the density of crabs is increased, both species of octopus will consume higher numbers of crab, however, because of the lack of data in octopuses, we will examine the possibility of species differences in their responses.

Methods

Study species

In this experiment we used 12 juvenile *Octopus vulgaris*, purchased from Bimini, Bahamas. We also used 12 juvenile *Octopus hummelincki*, purchased in Florida. As an inclusion criterion for this experiment we required that the octopuses show no sign of optic gland secretion. This ensured the use of only juvenile octopuses, which avoided the possible confounding effect of decreased eating found among brooding females and older males.

Culture system

The octopuses were kept individually in all-glass 76 liter tanks with a closed, re-circulating water system. The tanks were connected by overflow to two external sand filters. The system was buffered by a pump-run rapid water flow chamber, and a carbon filter was used to remove color and organic contaminants from the water. Each week, 15% of the sea water was replaced with fresh sea water.

Procedure

Initially the octopuses were fed ad lib for three days. This was done to allow the subjects time to adjust to their habitats and to ensure that the stress of travel did not affect our results. This initial feeding also allowed the octopuses to be matched based on weight. After the initial settling period, the octopuses were presented with varying densities of crabs (*Uca pugnax*) in a partial latin square. The densities used for this experiment were 15, 30, and 45 crabs per tank. Each octopus was presented with each of these densities for 10 consecutive days. Each order of densities was presented to two subjects of each species.

Prior to feeding, the total mass of the crabs to be presented to each octopus was weighed and recorded. The crabs were then be introduced into the tank and left for 24 hours. After 24 hours, the remaining crabs were removed and counted, as was the remains of any crabs which had been fed upon. The mass of the remaining crabs was weighed and subtracted from the initial mass, and in this way we arrived at the amount of crab eaten, both in grams and in number. Each octopus was weighed at the beginning and end of the experiment.

At the time of this report, data for *O. hummelincki* were not available. Analysis was completed for 12 animals, believed to be *O. vulgaris*. The mean amount of crab, measured in grams, consumed by each octopus over the 10 day periods was calculated and used for statistical analysis. Amount eaten in grams was chosen for use in our analysis as it was a more precise measure of consumption than the number of crabs, which could be affected by other variables such as crab size. Means at density (irrespective of order) and during blocks 1 – 3 (irrespective of density) were analyzed. Data were analyzed using SPSS ver. 19. Repeated Measures ANOVAs were used to determine whether the number of crabs eaten varied with the different densities presented, as well as whether the mean amount consumed varied over time irrespective of density. Although the design of the experiment controls for growth, the weight of the octopuses was included in the analysis to ensure that our findings were a result of the density and not the weight of octopuses. The weight of the octopuses was controlled for by running ANCOVA and including initial weight, final weight, and weight gain as covariates.

Results

Overall mean crab consumption at each density and for each block of days can be seen in Table 1 and Figures 1 and 2. Repeated measures ANOVA indicated that there was no significant difference between the mean amounts of crab eaten at the three densities, $F = .64$ df (2, 22). Running ANCOVA to control for initial weight, final weight, and weight gain indicates that there is still no significant differences between the mean crab consumption at each density, $F = .22$ df (2, 18). Figure 1 shows the mean consumption at the three densities. Repeated measures ANOVA was also run for each block of days and indicated significant differences, $F = 31.92$ (2, 22), $p. < .001$. Figure 2 illustrates that amount of crab eaten in grams increased across sequential blocks.

Zero-order correlations were examined between the initial weight of each animal and how much it consumed during the first block of days, the final weight of each animal and how much it consumed during the last block of days, and the amount of weight gained by each animal and how much it consumed during all three blocks of days (see Tables 2 - 4). There was a significant, moderately strong positive correlation (.619, $p < .05$) between initial weight and consumption during the first block. The correlation between final weight and amount eaten during block 3 was very strong (.951, $p < .001$). The correlations between weight gain and all three blocks were each very strong, .966 for the first 10 days,

.894 for the second 10 days, and .959 for the final 10 days ($p < .001$ for all).

Discussion

These data strongly indicate that the animals used in this experiment show no functional response; their mean crab cosumption remains consistent at all prey densities. Because data for *Ocotpus hummelincki* was unavailable at the time of this paper, conclusions about the functional response of this species, or about species differences cannot be drawn. Further, conclusions drawn about the functional response of *Octopus vulgaris* may be in error, as the data analyzed may have come from a combination of both species of octopus.

The analysis also indicates that crab consumption did significantly increase as the experiment progressed, irrespective of food density. This result is not surprising, however, given the strong correlations between the different weight measurements and the amount of crab eaten. This result likely indicates, unsurprisingly, that as the animals grew larger, they ate more.

While these results point to the fact that *Octopus vulgaris* may be one of the few species that do not show a functional response, it is possible there are other reasons this response was not observed in this experiment. Alex Comfort (1956) has mentioned unpublished data about guppies (*Lebistes reticulatus*) and their relationship with the environment. The research showed that when placed in a tank a guppy will grow to the appropriate size for the tank, then cease growing. If the guppy is then placed in a larger tank, it will resume growing again, and again level off when it has reached the maximum size for its tank. This can be repeated multiple times. Other research has shown that while tank size does not significantly affect the growth or size of rainbow trout (*Onchorynchus mykiss*), trout kept in larger tanks eat significantly more than those kept in smaller tanks (Ranta 2006). It is possible that the size of the tanks used in our experiment either restricted the growth or the intake of the octopuses and was the reason no functional response was observed. The possibility also exists that our current results only reflect the plateau effect seen at very high prey densities in all three functional response types. *O. vulgaris* may show a functional response at lower crab densities, but because the densities used in this experiment were well above what they have been observed to eat under normal circumstances, the octopuses were consuming as much as they were capable of in all conditions.

Were this experiment to be repeated with both species and larger tanks for the *O. vulgaris*, the results obtained may be consistent with ours or they may be very different. Several possible results exist. The first is that *O. vulgaris* truly does not respond to density, and neither does *O. hummelincki*, and they consume the same number of crabs regardless of how many are presented. If this is the case we would expect our ANOVA results to indicate that neither density nor the species-density interaction are significant factors, while the main effect of species may still be significant. Figure 3 illustrates this response. The second possibility is that one species shows a functional response while the other does not. Within this possibility there are a couple different results we may see. It is possible that one species, either *O. vulgaris* or *O. hummelincki* will show a type I functional response, while the other shows none (see Figure 4); or we may see that one species shows a type II response, while the other shows none (see Figure 5). In either case we would expect to see that our ANOVA results would indicate that species significantly influenced the number of crabs eaten, as did density and the species-density interaction.

While our current research indicates that *O. vulgaris* does not show a functional response, the preponderance of research in this field shows that most animals do, therefore if this experiment were repeated in more ideal circumstances it is possible that both species, *O. vulgaris* and *O. hummelincki,* would show a functional response, and their consumption will be influenced by the number of crabs presented to them. In this situation we would expect our ANOVA results to indicate that density is significant, while both species and the species-density interaction may or may not be significant, depending on the response types the two species exhibit. If both species show the same type, either type I or type II, again species and the species-density interaction may or may not be significant. These responses can be seen in Figures 6 and 7. However, if the species exhibit different responses, one showing a type I and the other a type II, then our ANOVA results would indicate that both species and the interaction would be significant (see Figure 8).

While including only three different densities in this experiment does not allow us to determine with certainty whether a functional response is type I, II, or

III, pairwise t-tests could be used to give us some indication of the type. The tests would compare the mean number of crabs eaten when presented with 15 crabs to the mean number eaten when presented with 30, and the mean number of crabs eaten when presented with 30 to the mean number eaten when presented with 45. The octopuses may respond to density in any of Holling's (1959) three different response curves, however the type I response, a linear response, is unlikely to be seen if this experiment is repeated. The type I functional response is most often seen among filter feeders and predators who hunt by touch (Woodsworth 1976). Key to this curve is that the handling time of the prey is very low, and so the predator does not have to spend much time eating the prey after it has been caught; the predator's time is spent hunting, not consuming the prey.

The type III functional response is also unlikely to be seen in a replication of this experiment. A type III functional response is most common when prey switching occurs (Smith 1998). Since the octopuses in this experiment will only be presented with one type of prey, there will be no opportunity for prey switching, making this response unlikely. Future research which offers multiple prey choices could investigate whether density affects prey switching among these species. Because a type I and type III response are nearly indistinguishable using only three different densities, we would expect that if the response were either of these types, then both t-tests would indicate significant differences.

The response curve most likely to be seen during a replication of the experiment is type II. Type II responses are most often formed when there is substantial handling time of a prey item. With this type of response, as prey density increases, the time the predator spends hunting is reduced, and the time spent consuming prey item is increased (Holling 1959b). As the prey density continues to increase, the predator approaches a maximal point where all of their time is spent consuming the prey, and none is spent hunting. Increases in density beyond this point no longer lead to increases in consumption. As the consumption of crabs does require some time and effort on the octopuses part, this is the curve we are most likely to see.

In the case of a type II functional response it is possible that the t-test comparing the mean number of crabs eaten at densities of 15 and 30 will be significant, while the difference between the mean number of crabs eaten at densities of 30 and 45 will be non-significant, indicating the the increase of prey consumed had decelerated or leveled off. However, if the true maximum number of crabs eaten has not been reached in this experiment, the differences between all of the densities may be significant, regardless of response type.

Of interest is also the mechanism which causes a functional response. In the literature it is described as a result of increasing encounter rates; the predator does not have to spend as much time searching for prey at higher densities as it does at lower densities and therefore is able to consume more prey (Holling 1959). This certainly adequately explains the phenomenon in the wild, however it can be witnessed even within the lab. In the smaller environments used in experiments (i.e., tanks or cages), it can often be assumed the predator is always aware of any prey that is within its enclosure. In these instances the predator must only cross it's enclosure to catch it's prey, there is no real time spent searching, and it can be said that the encounter rate is near infinite. While this is not a likely scenario in nature, functional responses can be observed even in situations such as this (Borer 1971, Czesny 2001, Jones 2003, Mattila 1998). While most of these experiments were not conducted using octopuses, they were conducted in settings similar to this experiment, indicating there may be a mechanism other than encounter rate at work, otherwise the predators would eat until they are sated, then stop, and at all densities they should reach satiety after consuming approximately the same amount of prey. So why, when presented with increased densities, do the predators consume more before reaching satiation?

One possible explanation comes from neurotransmitters; specifically neuropeptide Y. NPY is a well studied neurotransmitter and is very strongly associated with appetite and feeding. Increased secretion of NPY within the paraventricular nucleus has shown a correlation with increased appetite (Kalra 1991). Injections of NPY have caused feeding and drinking behavior in rats (Stanley 1985), and the strength of the response increases as the dosage of the injection increases (Ida 1999). Injections of NPY have even caused feeding and drinking behaviors in previously sated rats (Kalra 1988, Stanley 1985).

Neuropeptide Y is normally secreted at regular intervals, just prior to scheduled feeding times (Kalra 1991), however it has also been shown that NPY is released in response to stimuli, and the amount of NPY released varies in response to the strength of the stimulus (Zhu 2011). Therefore, if the presentation of higher prey densities is a stronger stimulus than lower densities, it would follow that the predator would have elevated levels of NPY when presented with higher densities, and would consume more prey before reaching satiety.

While research does not indicate that the octopus produces Neuropeptide Y, in 2002, Hirohumi Suzuki *et al* discovered a neuropeptide Y-like substance (later named neuropeptide F) within *Octopus vulgaris*. Since then, neuropeptide F has been shown to be the invertebrate form of neuropeptide Y, and to cause the same behavioral changes (Nässel 2011). This explanation could easily be tested by a follow-up study which measures the levels of NPF in octopuses in response to varying prey densities.

In support of this explanation is a qualitative observation from this experiment. The densities presented to the octopuses were well beyond the amount any could eat in a given 24 hour period, so each day several crabs remained alive in the octopus tanks. At the same time every day, the remaining crabs were removed from the tank to be counted. When new crabs were introduced into the tanks, the octopuses would immediately attack and pull as many crabs as could fit under their webbing. While it seems odd that the octopuses would ignore the old crabs in their tanks but immediately attack the new crabs, Kalra's (1991) research goes a long way toward explaining it. The crabs were removed and replaced at the same time every day; Kalra's research indicates that just prior to the introduction of the new crabs, the octopuses would begin secreting increased amounts of NPF, causing them to pounce on their prey as soon as they were introduced.

Another possible explanation for density dependent feeding comes from Optimal Foraging Theory. According to Roger Mellgren (1984), when foraging at several patches of food, the subject will remain at a given patch until there is a certain number of prey items left in the patch, at which point the subject will move to the next patch. This number is called the Leftover Constant, and should be the same at each patch in a given environment. However, this number will vary with certain changes, such as the difficulty in traveling between patches, and the risk that the subject will be preyed upon by another predator.

If the Leftover Constant is the determining factor in density dependent feeding, then in our experiment we could treat each daily trial as a single patch, and each different day as a different patch. According to the Leftover Constant, we would then expect to find that the amount eaten varies as a function of how many crabs above and beyond the Leftover Constant are presented. We would expect that each day, the number of crabs remaining within the tank would not vary significantly, regardless of the density which had been presented. In this case, we would not see the type II functional response we would predict, but the linear type I functional response.

These two explanations, neuropeptide F and the Leftover Constant, are not necessarily mutually exclusive. It is possible that the Leftover Constant is simply the number of prey items remaining in the tank at which point satiety outweighs the strength of the stimulus, and the subject ceases consumption. If this is the case, then the Leftover Constant does not contribute further to our explanation of functional response, however it does provide a way for us to predict the number of prey items that will be eaten at a given density.

Before we can address the question of the underlying mechanism of functional responses, we must first conduct the research to determine with more accuracy what response can be seen in octopuses. For a subject which has been extensively researched in other species, there is a significant lack of research among octopuses and other cephalopods. We must first obtain data on the subject which is more generalizable than the one experiment which has been conducted. The experiment we conducted was somewhat limited in its scope and serves only as a first step into investigating the density dependent feeding of octopuses. Further, replication of this study to ensure the accuracy of the results in needed. The use of only three different densities does not allow the response type to be determined with any confidence. Using only three densities, a type I and type III response are indistinguishable, and if a maximum intake is not reached in the experiment, a type II response may be indistinguishable as well. Further, as the crabs were only replaced every 24 hrs, the density within the tanks was not be steady. It is possible that with constant replacement of the eaten crabs different results would be obtained. Replication of this experiment in a more natural setting may also yield beneficial results. Additionally, conducting a similar experiment using different prey species could lead to different responses in the predators. This experiment is only the first step toward better understanding the feeding behavior of octopuses.

Following this experiment, future research can investigate more fully just what exactly is the nature and cause of density dependent feeding.

Table 1
Descriptive Statistics for Amount of Crab Eaten in Grams, Across Octopuses (n = 4 per group), in 10 Day Periods

	Mean	Std Dev	Min	Max
Mean Crab Eaten Per Day at Density 15	9.21	4.01	4.28	16.43
Mean Crab Eaten Per Day at Density 30	9.40	3.30	5.30	14.20
Mean Crab Eaten Per Day at Density 45	10.07	4.31	5.36	19.36
Mean Crab Eaten Per Day During Days 4 - 13	7.90	3.04	4.28	14.14
Mean Crab Eaten Per Day During Days 14 - 23	9.54	3.69	5.62	16.39
Mean Crab Eaten Per Day During Days 24 - 33	11.23	4.13	7.07	19.36

Table 2
Zero-Order Correlation Between Initial Weight and Crab Eaten in Grams During Days 4 – 13

	Initial Weight	Crab Eaten During Days 4 - 13
Initial Weight	1	.619*
Crab Eaten During Days 4 - 13		1

*p < .05

Table 3
Zero-Order Correlation Between Final Weight and Crab Eaten in Grams During Days 24 – 33

	Final Weight	Crab Eaten During Days 24 - 33
Final Weight	1	.951*
Crab Eaten During Days 24 - 33		1

*p < .001

Table 4

Zero-Order Correlations Between Weight Gained and Crab Eaten in Grams During Each Block of Days

	Weight Gained	Crab Eaten During Days 4 - 13	Crab Eaten During Days 14 - 23	Crab Eaten During Days 24 - 33
Weight Gained	1	.966*	.894*	.959*
Crab Eaten During Days 4 - 13		1	.907*	.975*
Crab Eaten During Days 14 - 23			1	.942*
Crab Eaten During Days 24 - 33				1

*p < .001

Figure 1

Mean Amount of Crab Consumed in Grams at Each Density

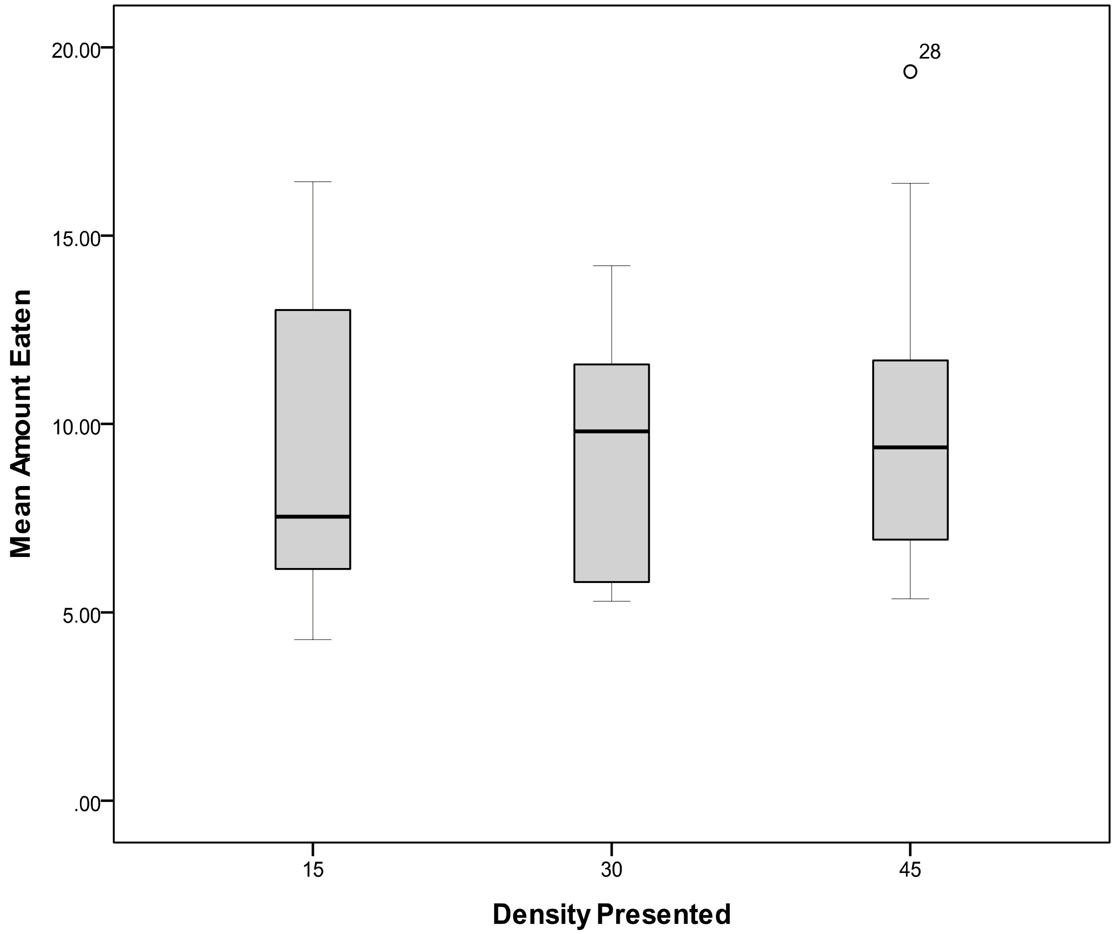


Figure 2

Mean Amount of Crab Consumed in Grams During Each Block of Days

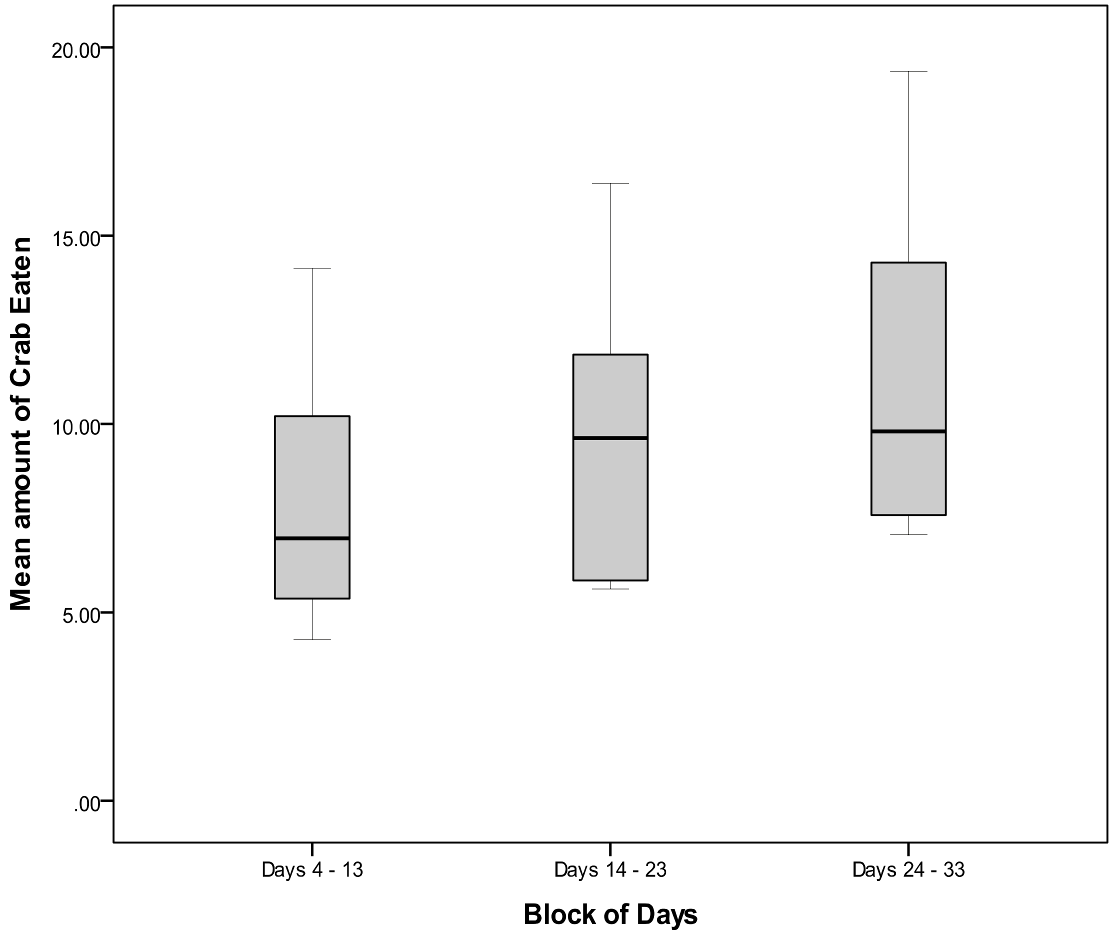


Figure 3

Projected Results: No Functional Response in O. vulgaris *and* O. hummelincki

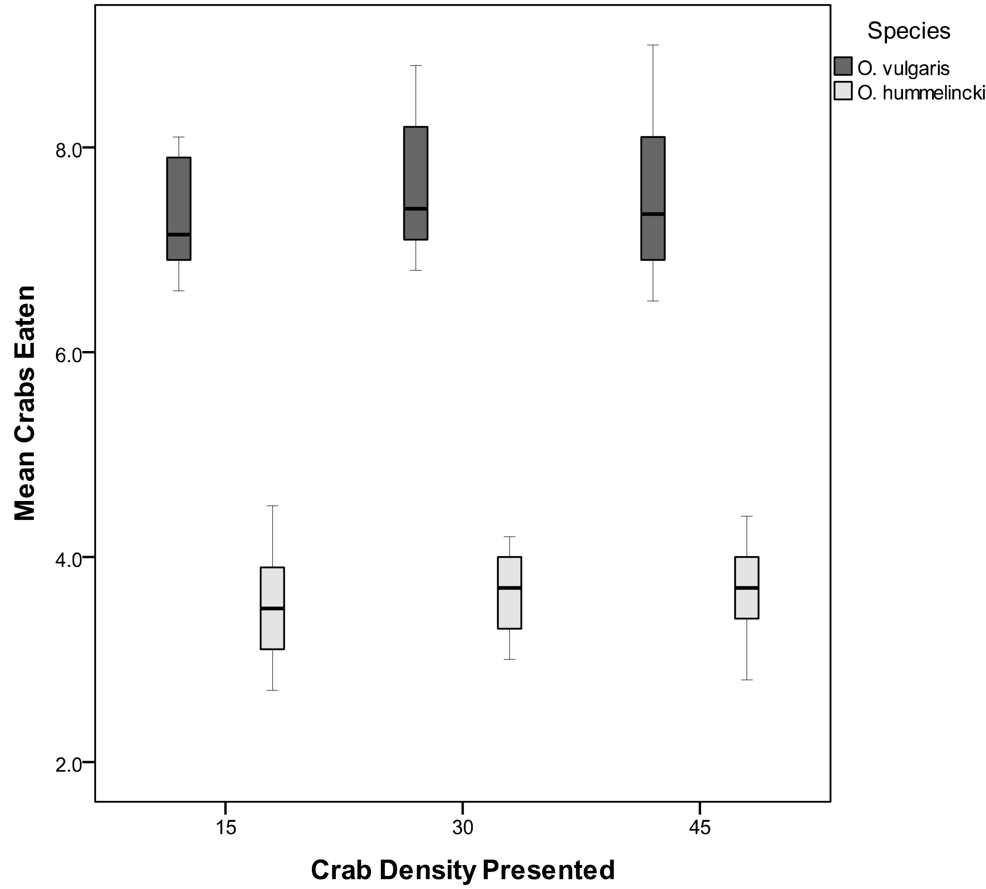


Figure 4
Projected Results: No Functional Response in O. vulgaris*, Type I Response in* O. hummelincki

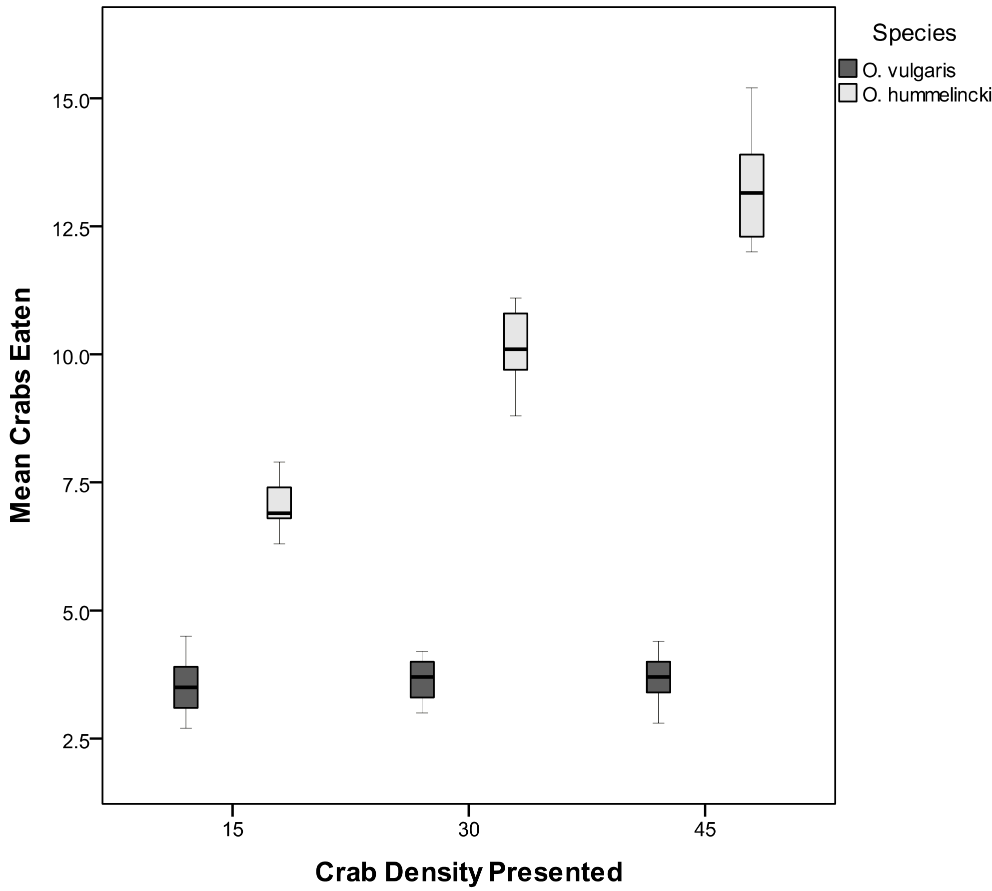


Figure 5

Projected Results: No Functional Response in O. vulgaris*, Type II Response in* O. hummelincki

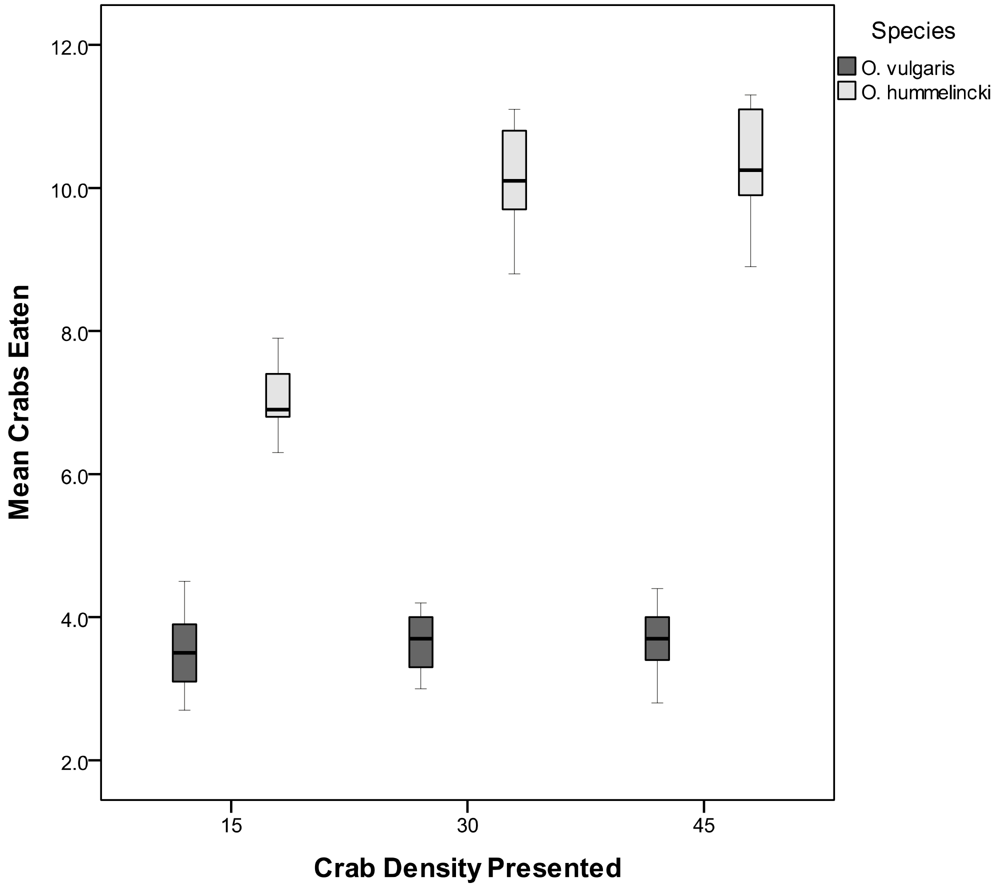


Figure 6

Projected Results: Type I Response in O. vulgaris *and* O. hummelincki

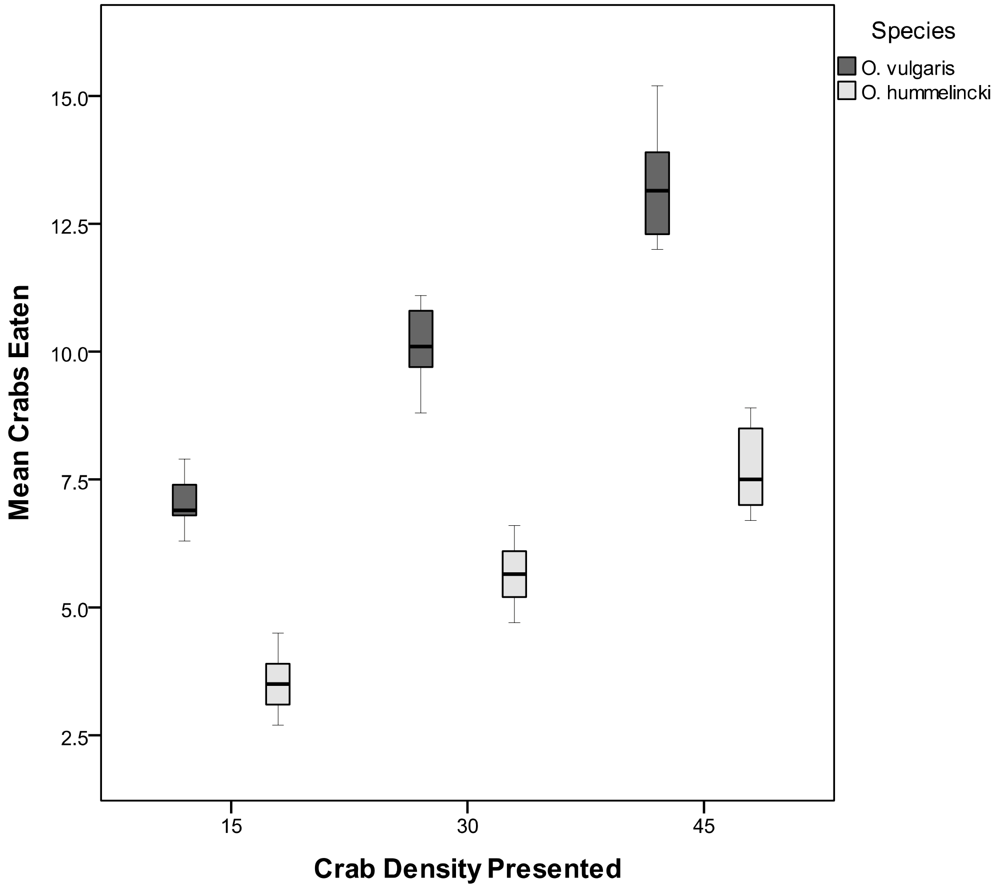


Figure 7

Projected Results: Type II Response in O. vulgaris *and* O. hummelincki

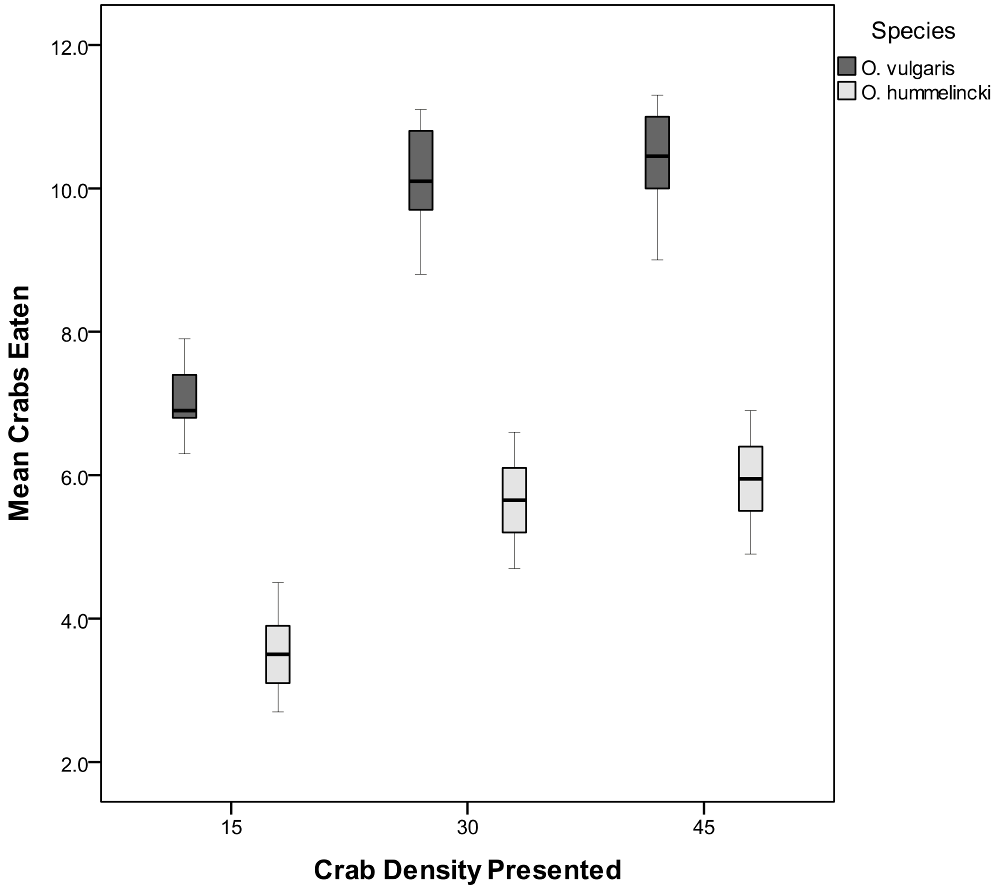
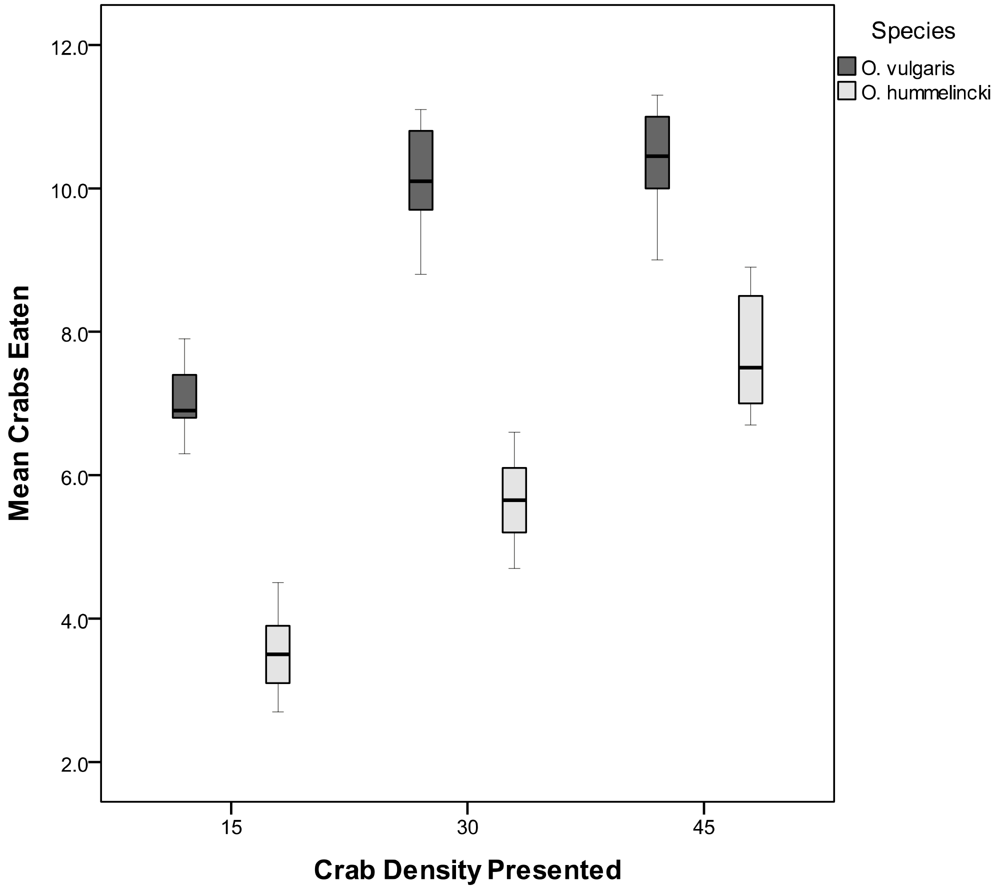


Figure 8

Projected Results: Type I Response in O. hummelincki*, Type II Response in* O. vulgaris



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