

## ABSTRACT

Title of Thesis: THE FORAGING HABITS AND RESULTANT  
FUNCTIONAL RESPONSE OF AMERICAN BLACK  
DUCKS

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The American black duck (*Anas rubripes*) is an outcome species for the health of the Chesapeake Bay. In order to estimate the impact that changes in black duck habitat will have on the Bay's wintering population, the relationship between black ducks and the species comprising their diets must be better understood. This study was part of a larger effort to build a comprehensive bioenergetics model for black ducks wintering in the Chesapeake Bay. Using black ducks as model species, functional response curves were created for five experimental species known to be consumed by black ducks. For each curve, three regressions representing the three types of functional response models were run. In examining the regression fits along with using biological inferences, the functional response types for each experimental species were determined to be type I for softstem bulrush seeds, type II for widgeon grass, horned pondweed, and Eastern mosquitofish, and type III for saltmarsh snails. This research was used to

determine critical foraging densities and will contribute to the bioenergetics model that will help identify areas where conservation efforts should be targeted in order to benefit black ducks and contribute to the overall health of the Chesapeake Bay.

THE FORAGING HABITS AND RESULTANT FUNCTIONAL RESPONSE  
OF AMERICAN BLACK DUCKS

By

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## Dedication

I would like to dedicate this thesis to Gilbert Mitchell. Thank you for everything you taught me through the years and for all your support. Thank you for pushing me to always do better; to be better.

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I would like to thank Dr. Alicia Berlin for all her help throughout this project. This project would not have happened without her. Also a special thanks to my advisor Dr. Patrick Kangas and additional committee members, Dr. Jennifer Murrow and Dr. Kennedy Paynter, for their invaluable guidance and advice. Furthermore, I want to thank The USGS Ecosystems Mission Area: Chesapeake Bay for funding this project, and the Woods Hole Marine Biological Laboratory for providing experimental species used in this study. Lee Karrh, Brooke Landry, and the Maryland Department of Natural Resources deserve special thanks for their generous time and assistance in helping collect SAV species. Finally, last but certainly not least, thank you to everyone at Patuxent who contributed and helped with all aspects of this project, especially Sarah Fitzgerald, Charlotte Kilchenstein, Kate McGrew, Dr. Sara Crowell, Jonathan Fiely, Alex Vidal, Sally Yannuzzi, Lizzi Bonczek, and Mark McBride.

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## INTRODUCTION

Between increasing global temperatures, rising sea levels, more extreme weather events, and subsequent complications, climate change impacts every major habitat type and plays a part in virtually all aspects of ecology. The Chesapeake Bay plays a significant role in human life, providing economic opportunities, food, and recreation. It is an important part of several commercial fisheries, such as the Maryland blue crab, and provides recreational boating, fishing, and hunting opportunities (Perry and Deller 1996). The Bay, the largest, and at one point, one of the most productive estuaries in the United States, has been substantially degraded the past several decades and is continuing to experience further degradation and constant risk of both climate and anthropogenic changes. Agricultural practices, landscape and land use changes, continued population increases, and pollution from industry and residential runoff have degraded the Bay ecosystem, decreasing its value as habitat for wildlife and for humans (Perry and Deller 1996). Sea level rise along with warming air and water temperatures are compounding the effects caused by these anthropogenic changes.

Sea-level rise and shoreline development are among the biggest threats to the Chesapeake Bay estuary and surrounding coastal wetlands (Serie 2002, Glick et al. 2008). Areas surrounding the Bay are experiencing some of the fastest increasing human population densities in the country, intensifying the problems of shoreline development. During the 50-year span between 1950 and 2000, the human population within the Chesapeake Bay watershed has doubled, increasing

from nearly eight million people to around 16 million (Ernst 2003). With this increased building and development, comes the destruction of wetlands and forests neighboring the Bay. As a quantitative reference, over 25,000 hectares of wetland surrounding the Bay was destroyed during the time span between 1955 and 1989 (Tiner et al 1994). Wetland loss is particularly impactful because of the resulting loss of the important ecosystem services they provide. Wetlands filter polluted and contaminated runoff from impermeable surfaces, agricultural lands, and residential areas before it reaches open water habitat, and also slow water flow, thereby limiting coastal erosion. The other main threat, sea-level rise, is causing both coastal areas and islands within the Bay to slowly retreat and diminish. Many Bay islands, including Smith, Bloodsworth, and Sharps have dramatically declined in surface area over the years and some are gone completely (Leatherman et al 1995, Erwin et al 2011). Additionally, Poplar Island was predicted to have been completely submerged by water by the year 2000, but was preserved by a significant restoration project started by the US Army Corp of Engineers in 1998 (Erwin et al 2007). Islands in the Bay and coastal wetlands are important habitats and nesting grounds to many species of waterfowl and water birds and to numerous other organisms (Erwin et al 1993). The effects of hunting and boating also threaten the quality of waterfowl habitat. Recreational boating and hunter activities in shallow water damage the tidal and benthic coastal ecosystems through disturbance from propeller action and wading (Kirby et al 1976). Additionally, hunting has caused lead contamination in the Bay. Although hunting with lead ammunition was outlawed in 1983, lead poisoning due to spent

ammunition is still a problem for Bay animals, particularly waterfowl (Perry and Deller 1996).

Marshes are probably the most important wetland type in the larger Chesapeake Bay ecosystem for waterfowl and numerous other species. Marshes are classified by salinity (freshwater, brackish, or salt) and by how often they are submerged by water (high or low) (Cowardin et al 1979). While the value of marshes is often underestimated by the general public, they are crucial to the long-term health of the Chesapeake Bay. Marshes, which make up about 66% of wetlands around the Bay, are highly productive (Field et al 1991). They provide many of the previously mentioned defining wetland ecosystem services, such as regulating nutrient cycles and filtering runoff before entering the Bay (Perry and Deller 1996). Marshes are highly productive and provide nutrient and food rich environment, in addition to providing cover within their vegetation for various organisms. First, the marshes of the Chesapeake Bay ecosystem were historically considered wastelands and were often among the first areas to be destroyed and built upon (Wilson et al 2007). Secondly, as sea level rises, high marshes are inundated more frequently with water. High and low marshes have distinct distributions of vegetation and animal species. Thus, species typically found in high marshes cannot survive the increased frequencies of complete submergence and must retreat to higher ground where they may be more exposed and susceptible to predation (Wilson et al 2007). Finally, an added threat specific to marshlands in the Bay is the introduction of exotic species, particularly phragmites (*Phragmites australis*) and nutria (*Myocastor coypus*) (Rice et al

2000, Wilson et al 2007). Phragmites is a fast growing plant that typically invades after a disturbance, and quickly overtakes and outcompetes a marsh's native vegetation. Most waterfowl and animal species cannot eat phragmites and the phragmites populations are generally too dense for animals to enter and use as cover or as nesting habitats. The nutria is a semi-aquatic rodent. These animals forage directly on the roots of marsh plants, accelerating erosion, and can completely transform marsh environments into mudflats in a relatively short time span (Willner et al 1979).

The Chesapeake Bay, and in particular its marsh habitats, are important to many species of birds. The Bay is a critical wintering and stopping spot along the Atlantic flyway for migrating North American waterfowl. It provides wintering grounds for a large assortment of species including, but not limited to mallards (*Anas platyrhynchos*), wood ducks (*Aix sponsa*), American black ducks, gadwalls (*Anas strepera*), teal (*Anas crecca*), hooded mergansers (*Lophodytes cucullatus*), buffleheads (*Bucephala albeola*), lesser scaup (*Aythya affinis*), ruddy ducks (*Oxyura jamaicensis*), scoters (*Melanitta spp.*), Canada geese (*Branta canadensis*), and tundra swans (*Cygnus columbianus*) (Perry and Deller 1996, Costanzo and Hindman 2015). While many of these species use the Bay as their wintering grounds, some have resident populations that live in the Bay year round. Certain species, such as Canada geese and mallards are increasing in prevalence in the Bay, but other waterfowl species are rapidly declining (Costanzo and Hindman 2015). Canada geese and mallards seem to be more adaptable and suitable to the changing environmental conditions of the Bay.

Conversely, the species in decline are apparently more sensitive to the environmental changes and presence of humans (Costanzo and Hindman 2015).

One such species of bird is the American black duck. Wintering black duck populations on the Chesapeake Bay have declined over the past few decades, and in the last ten years alone, populations have decreased by nearly 64% (Rusch et al 1989, Wilson et al 2007). Aside from habitat loss from climate change and human activities, there are other notable threats specific to black duck populations on the Chesapeake Bay. For one, black ducks have fewer potential nesting sites available due to loss of bay island and marshes as discussed earlier. As a result, nest predation by red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), crows (*Corvus spp.*), and gulls (*Larus spp.*) have become a more pronounced danger (Costanzo 2002, Haramis et al 2002, Costanzo and Hindman 2015). Another threat to black ducks is hunting, although stricter bag limit regulations were implemented in 1983 to minimize the risk (Longcore et al 2000). Hunters are now only allowed one black duck per person per day (Longcore et al 2000). Hybridization has further contributed to black duck decline. Black ducks are reproducing with other species in the *Anas* genus, most notably mallards, producing hybrids that are biochemically and structurally very similar to both parent species, yet are a separate species (Morgan et al 1976, Ankney et al 1987, Longcore et al 2000). Black ducks and mallards were once geographically isolated with black ducks mainly inhabiting east coast forests and coastal marshes, while mallards were confined to grasslands on the west coast (Brodsky and Weatherhead 1984). Mallards are more tolerant to environmental changes and

human presence, so as their range expanded eastward, they have become more prevalent while black duck populations have declined. Mallards prefer habitats further inland, but as a result of deforestation and human development, they have moved towards coastal lands, including the Chesapeake Bay (Brodsky and Weatherhead 1984). Moreover, on the Bay, thousands of captive reared mallards are released every year. In addition to being more tolerant and adaptable, mallards are reproductively superior to black ducks. After mallard hens have all been paired, the leftover males (drakes) begin pursuing black duck females (Sibley 1957). Drakes outcompete male black ducks for access to black duck females, creating hybridized offspring (Sibley 1957). If habitat degradation and hybridization continue at this rate, black ducks could risk extinction (Stotts and Davis 1960, Todesco 2016).

### Black Duck Ecology

Black ducks are a key waterfowl species in the Chesapeake Bay. Black ducks can be found all along the east coast, following the Atlantic and Mississippi flyways for their migration pathways. Their habitats range from the most northeast Canada, south to central Florida, and as far west as Iowa (Longcore et al 2000) (Figure 1). While not extensively studied, there is some evidence that black duck ranges are shifting north in response to climate change (Brook et al 2009). Within their migration range, the Bay is located at a fairly central point in terms of latitude, and is thus home to both migrant and resident populations (Longcore et al 2000) (Figure 1). Migrant populations spend their winters feeding on the Bay, at which point they migrate north to breeding grounds for the breeding

season in the spring and summer (Stotts and Davis 1960). Due to the breeding season and migration stress, food quality in wintering grounds is extremely important to survival and reproduction, further supporting the notion that habitat quality rather than quantity is crucial to wintering black ducks on the Bay (Alisauskas and Ankney 1992).

**Figure 1.** Map indicating black duck habitat range. Blue areas represent breeding grounds, orange areas represent wintering grounds, and green areas represent potential homes to year round resident populations (Longcore et al 2000).



On the Bay, black ducks utilize inland coastal areas and tidal marshes of different salinities; however, they primarily feed in saltmarsh habitats (Wilson et al 2007, Plattner et al 2010). Generalist feeders, black ducks forage on a wide



variety of food items, including vegetation (both terrestrial and aquatic), seeds, grains, insects, crustaceans, mollusks, and fish (Longcore et al 2000). Depending on the type of food, black ducks employ a variety of foraging methods. They commonly utilize filter and scooping feeding styles, usually tipping to reach food below the water's surface, but can dive for food when necessary (Longcore et al 2000).

Black ducks were recently labeled an outcome species of the Bay ecosystem's health because of their sensitivity and susceptibility to changes, and because they live in some of the most vulnerable yet important habitats of the Bay. They also have cultural and historical importance to the community. As a result, they have become an important target for conservation and management goals. In May 2009, President Obama signed executive order 13508 which served as an attempt to help protect and restore the Bay (Federal Leadership Committee 2010). The order broadly addresses water pollution control, agricultural practices, climate change, landscape conservation, resource protection, and specifies future goals for black ducks and their habitats in the Bay. The theory is that by conserving and increasing habitat for an outcome species, such as the black duck, the general health of the Bay will subsequently benefit. The order stipulates that by 2025, black duck habitats should increase by 10% in areas within the National Wildlife Refuge System (NWR) surrounding the Chesapeake Bay (Federal Leadership Committee 2010). Additionally, by 2025, the population of wintering black ducks in the Bay should increase to a three-year average of 100,000 individuals (Federal Leadership Committee 2010). In order to reach the goals

stated in the executive order, the United States Geological Survey (USGS), Ducks Unlimited (DU), and United States Fish and Wildlife Services (USFWS), in conjunction with the Black Duck Joint Venture (BDJV) and numerous other stakeholders are collaborating to study multiple aspects of black duck ecology in order to help determine the most effective management strategies and focus conservation efforts on the highest possible quality habitats.

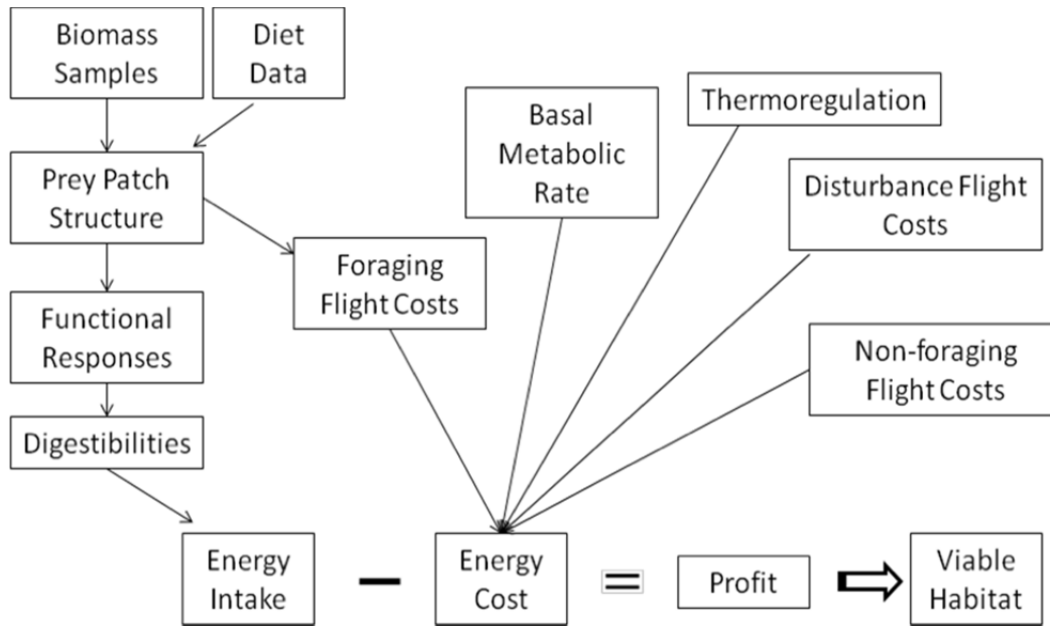
### Bioenergetics Model

Allocating protected areas for vulnerable and sensitive species is a challenging process. Often, legislators attempt to designate and protect a minimum habitat area required for the species to persist. However, that habitat must not only be of a certain size, but of good quality. Thus, conservationists must consider energetic factors in addition to resource abundance thresholds. A common practice for combining these factors is through development of bioenergetics models. Bioenergetics models calculate the energy carrying capacity of a species and help to accurately describe high quality habitats capable of supporting target population numbers.

Current knowledge of migratory and wintering waterfowl ecology suggests that availability of food for energy is the primary limiting factor of waterfowl populations (Haramis et al. 1986, Miller 1986, Conroy et al. 1989, Bergan and Smith 1993, Jeske et al. 1994). Therefore, bioenergetics models are useful tools in evaluating future habitat and harvest management goals for waterfowl species (Bishop and Vrtiska 2008, Straub 2008, Foster et al 2010).

Accordingly, a black duck bioenergetics model was adapted from a similar model created for spectacled eiders (*Somateria fischeri*) in the Bering Sea by Lovvorn et al. in 2009. Within the model, a viable habitat was classified based on its “profitability threshold” defined as the difference between total energy intake and total energy cost (Lovvorn et al 2009). If energy intake exceeded the total energy cost, then profitability was positive and the habitat was viable and should be considered of good quality. However, it is important to note that some habitats may not actually be good quality as suggested by the profitability threshold, due to various other unforeseen factors (Nolet et al 2002). In the model, energy cost was a combination of foraging activity, basal metabolic rates (BMR), and non-foraging activity costs, while energy intake was defined as a compilation of digestibility, functional response curves, and prey spatial distributions (Lovvorn et al 2009). In the black duck bioenergetics model as opposed to the eider model, diving costs and benthic food sampling were neglected. The newly adapted model is pictured in Figure 2. The following is summary of the current research status of the model components. Regarding energy costs, basal metabolic rates were researched using respirometry studies, while flight costs were estimated based on spatial analysis and observations (Jones et al 2014). As for energy intake, biomass samples and diet data were analyzed through core samples of known black duck habitats (Cramer et al 2012), in addition to analysis of contents within deceased black duck gizzards by Rawls (unpublished report). Digestibilities data were researched in terms of true metabolizable energy (TME) (Collucy et al 2015).

**Figure 2.** Outline of the black duck bioenergetics model. The specific piece of the model considered in this study is functional responses, which in conjunction with digestibilities, will eventually tie into the energy intake part of the equation (adapted from Lovvorn et al. 2009).



### Digestibility and Functional Response

Digestibility was defined as the energy content a bird consumes and is able to use. TME measures digestibility in kilocalories per gram and is calculated based on the apparent metabolizable energy (AME), corrected for the fraction of excreted non-dietary energy (Sibbald 1975, Sibbald 1976, Sherfy 1999, Collucy et al 2015).

- $AME = GE - EE$  (eqn. 1)
- $TME = [(GE * W) - (EE_f - EE_c)] / W$  (eqn. 2)

In these equations, GE represents the gross energy intake, EE is the total excreted energy loss, and W is the net mass of food intake.  $EE_f$  is the excreted energy loss of birds that had been fed using the tested food item, while  $EE_c$  is the excreted energy loss of birds that had fasted. Subtracting  $EE_c$  from  $EE_f$  corrects the AME equation to exclude the portion of energy in bird fecal and urine mater that is unrelated to intake energy (Sibbald 1975, Sibbald 1976). Previous studies support that TME is a quality of the test diet rather than a parameter varying between bird species (Sibbald 1980, Miller 1984, Hoffman and Bookhout 1985, Castro et al 1989). Consequently, TME values of different food items should be relatable among duck species, and in particular, when comparing ducks in the *Anas spp.*

Digestibilities, in conjunction with functional responses (the main focus of this study), allow for differentiation of the most energetically valuable prey items, as well as suggest probable energy carrying capacities (Wells-Berlin et al 2015). Functional response, as first coined in 1959 by C.S. Holling, is defined as predator intake rate as a function of prey density and is a central concept in describing and modeling predator-prey relationships (Rowcliffe et al 1999). Functional response models are related to the optimal foraging theory, which is used to predict the choices a consumer will make while foraging in order to maximize their net energetic gain (MacArthur and Pianka 1966, Stephens and Krebs 1986). The optimal foraging theory identifies three types of constraints, temporal, energetic, and cognitive, that limit the possible energy intake (MacArthur and Pianka 1966). Temporal constraints include search time, or the time spent traveling between prey patches looking for food, and handling time, or

the time spent pursuing, capturing, and consuming the food item. Energetic constraints are the energetic costs associated with search and handling times. Cognitive constraints are the limits of the consumer's memory and learning capacity. The optimal foraging theory can be taken a step further and separated into the prey choice model and the patch choice theory. The prey choice model depicts the decision a consumer makes when faced with the choice of stopping to forage at an existing patch or continuing its search for a different patch (Pyke et al. 1977). The patch choice theory is where the consumer must decide how long to stay in a prey patch once they have started foraging (Pyke et al. 1977). Functional response models build on the optimal foraging theory and incorporate the same constraints to help determine where the consumer can forage most efficiently by identifying the prey densities most energetically valuable to them.

Three shapes or types of functional response curves exist as a result of the constraints defined in the optimal foraging theory (Figure 3). Past studies suggest there are actually five types of functional response curves among all organisms, but types IV and V only apply to organisms at the microbial level (Andrews 1968, Sokol and Howell 1987). Unlike type I, II, and III curves, type IV and V curves are nonmonotonic, meaning they are not purely increasing or decreasing, but rather a combination (Berryman 1992, Xiao and Ruan 2001). Type IV and V relationships only occur when nutrient concentrations are at a high enough level to inhibit the growth rate of the microbe (Xiao and Ruan 2001). As type IV and V functional response curves apply only to microbial organisms, they are not considered in this study. However, type I, II, and III curves are all applicable.

Type I curves are linear, so that the rate at which prey is consumed increases proportionally to increasing prey density. A type I relationship is most commonly associated with filter feeders (Real 1977). In previous studies, a type I functional response was determined for teal (*Anas crecca*) filter feeding on rice seeds (*Oryza sativa*) (Arzel et al 2007). Type I curves were also found for brent geese (*Branta bernicla*) feeding on green algae (*Enteromorpha intestinalis* and *Ulva lactuca*) (Rowcliffe et al 1999). In these situations, predators were constrained only by search time and can be described by a linear model,  $I = aX$ , where  $I$  is the intake rate,  $X$  is the density, and  $a$  is the proportionality constant determined by the predator encounter rate of prey (Holling 1959).

Type II curves are cyrtoid shaped and are the most common predator-prey relationship, where organisms take time to capture and ingest their food (Real 1977). Type II predators are constrained by both search time and handling time (Holling 1959). The amount of food consumed per unit time initially increases linearly with density, but reaches an asymptote at higher densities, at which point the predator has reached a saturation density. Type II relationships often are representative of predators that feed on large or immotile prey (Arzel et al 2007). Type II curves were previously demonstrated by mallards feeding on varying sized pellets (Fritz et al 2001), as well as for brent geese foraging on eelgrass (*Zostera spp.*) (Charman 1979). Additionally type II predator-prey relationships are typical of diving ducks, as demonstrated in lesser scaup, white winged scoters (*Melanitta fusca*), and surf scoters (*Melanitta perspicillata*) diving for various benthic clam and mussel prey species (Richman and Lovvorn 2003, Richman and

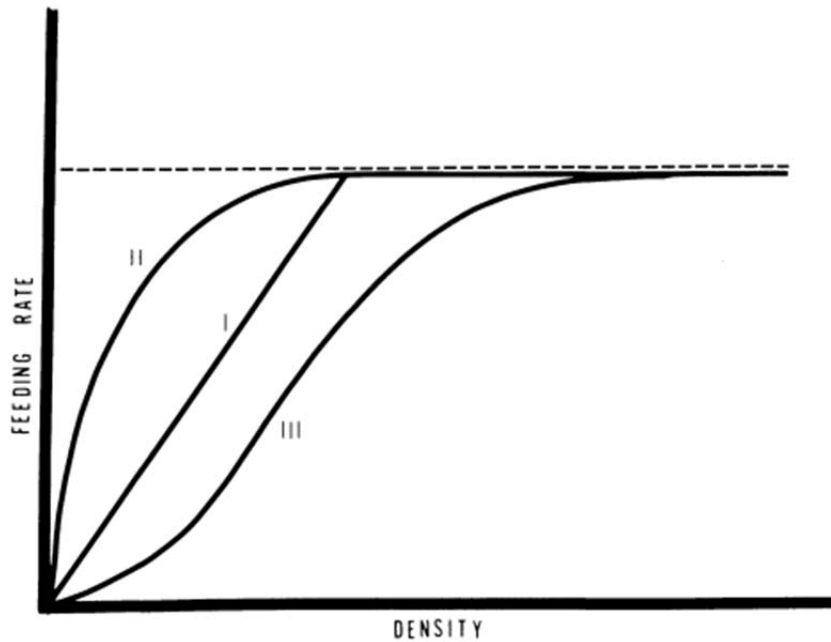
Lovvorn 2004, and Berlin 2008); and similarly in canvasbacks (*Aythya calisineria*) diving for the submerged plant wild celery (*Vallisneria americana*) (Lovvorn and Gillingham 1996). Type II curves are commonly described by the Michaelis-Menten equation. The Michaelis-Menten equation was originally developed in 1913 to describe the rate of enzyme-catalyzed reactions, but was later applied to additional rate relationships, including intake rates or functional response curves (Real 1977). The Michaelis-Menten equation is defined as  $I = aX/(b + X)$ , where  $I$  and  $X$  are the intake rate and density respectively,  $a$  is the handling time, and  $b$  is the search time (Real 1977, Berryman 1992). In this equation, the handling time ( $a$ ), represents the maximum possible intake rate regardless of density, and the search time ( $b$ ), represents the prey density at half of the maximum intake rate, which is also the inflection point of the curve (Real 1977, Berryman 1992).

Type III curves are sigmoid shapes. They depict a predator-prey relationship where predators display a learning behavior, where below a certain prey threshold density the predator does not effectively utilize the available prey, as they do not come into contact with the prey often enough (Holling 1959). However, at densities above this threshold, the predator learns, then increases their intake rates until approaching the asymptote or saturation density as seen in type II curves (Holling 1959). Predators with type III relationships often feed on more motile prey and as the frequency of prey encounters increase, they either learn to position themselves better for maximal encounters or learn to hunt and handle the prey organisms more efficiently (Real 1977). These learning behaviors



have been demonstrated in many species of birds, including, but not limited, to oystercatchers (*Haematopus spp.*) (Norton Griffiths 1967), brown pelicans (*Pelecanus occidentalis*) (Orians 1969), blue herons (*Ardea herodias*) (Recher and Recher 1969), and great tits (*Parus major*) (Tinbergen 1960, Royama 1970). Organisms with type III predation curves are constrained by both search time and handling time, and also identification time (Holling 1959). A model for this type of relationship is similar to the Michaelis-Menten equation, called the Hill function, where  $I = aX^n/(b^n + X^n)$  (Real 1977, Dawes and Souza 2013). In fact, the type II equation is just a specific instance of the type III equation, where  $n$ , defined as the number of prey encounters before the predator becomes maximally efficient, is equal to 1 (Real 1977). Thus, the Hill equation will create the desired sigmoidal shape when  $n > 1$ . When differentiating between a type II and type III curve,  $n$  can be assumed to be 2, so the regression equation for type III curves used in this study is  $I = aX^2/(b^2 + X^2)$  (Real 1977, Dawes and Souza 2013).

**Figure 3.** Shapes of type I, II, and III functional response curves. (Real 1977)



#### Study Overview and Predictions

This foraging behavior study examined experimental functional response curves for American black ducks using five known species of prey at four different densities. Upon experimentally determining intake rates, the functional response curves were analyzed using three regression functions. They were first modeled with a linear regression, testing for a type I relationship. Afterward, the curves were run through two non-linear regressions based on the Michaelis-Menten and Hill model, testing for type II and III associations. Comparison of the regression  $R^2$  values determined the type of model that fit each curve best. Intake rates were also applied to pre-calculated true metabolic energy values to create metabolic energy intake rates for each prey item.

Functional response trials in waterfowl have generally been understudied (Durant et al 2003). However, given the few examples previously discussed, the

functional response curves for all experimentally tested prey species were predicted to follow a type II relationship. The tested prey species were largely immotile and thus characteristic of type II curves. While two of the species, seeds and snails, were small, they were not presented at high enough densities to enable potential filter feeding strategies. One highly motile species was used as food: fish. However, these trials still predicted a type II curve. The foraging area was thought to be small enough that even at the lowest tested prey densities, duck encounters with the fish would still not be rare enough to see evidence of a learning behavior or delayed increase in intake rate with increasing prey density. Results from this study are an important piece of the black duck bioenergetics model, which will ultimately be used in determining the best quality habitat to focus conservation efforts.

## METHODS

Trials were conducted at the seaduck research colony at the U.S. Geological Survey's Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland. Trials used captive black ducks hatched in 2012 at the colony. The lineage of black ducks at PWRC originated from two pairs donated by the Sylvan Heights Bird Park in Scotland Neck, North Carolina. The individuals used in this study were F2 generation descendants from the original pairs. Ducks were housed in outdoor 3.7m x 4.3m enclosed pens, each containing a round 3m diameter pond. Ducks were fed Mazuri Seaduck Diet ® *ad libitum*. All procedures involving black ducks in this study were approved by the Patuxent Wildlife Research Center Animal Care and Use Committee (ACUC) (no. 2011-11) and the

University of Maryland Institutional Animal Care and Use Committees (IACUC) (no. 880409-1).

Ducklings were hatched and raised by people rather than by their mothers or other ducks and handled constantly to become accustomed to human presence. They were exposed to operant conditioning, using mealworms as positive reinforcement and a clicker as a secondary re-enforcer. The conditioning was used to help ducklings become acclimated to the environments in which they would complete trials. Ducklings were regularly exposed to a large, blue 1.83m x 0.91m x 0.91m fiberglass tank and a wooden 1m x 1m x 7cm box where trials were conducted (Figures 4 and 5). Based on observations during preliminary training, five ducks, consisting of three males and two females, were chosen for the study.

Trials were conducted using five different prey items at four different prey densities. The five food items included widgeon grass (*Ruppia maritima*), horned pondweed (*Zannischellia palustris*), softstem bulrush seed (*Scirpus validus*), eastern mosquitofish (*Gambusia holbrooki*), and saltmarsh snails (*Melampus bidentatus*). Food species were chosen based on previous research and was a good representation of the range of organisms that black ducks usually feed on in the Chesapeake Bay. Widgeon grass, horned pondweed, and saltmarsh snails are well-documented food items for black ducks (Costanzo and Malecki 1989, Cramer 2009, Eichholz and Yerkes 2010, Plattner et al 2010, Cramer et al 2012), while softstem bulrush seeds are a common food for many species of dabbling ducks and are often targeted in management goals (Hindman and Stotts 1989). Additionally, in a previous study, all but fish were identifiable in the gizzards of

deceased black ducks. Rawls (unpublished report) found that out of a total of 131 analyzed black duck gizzards, widgeon grass was found 39.7% of the time, marking the most commonly found species overall, while horned pondweed, saltmarsh snails, and softstem bulrush seeds were found in 1.53%, 5.34%, and 0.76%, respectively, of samples. Eastern mosquitofish were not identified in gizzards because unlike the other prey items chosen, fish are more completely digested and have no outer shell; however, they are still a well-known prey choice of black ducks (Costanzo and Malecki 1989, Longcore et al 2000, Cramer 2009, Eichholz and Yerkes 2010).

Experimental densities were determined based on rough estimates during field observations or based on previous research (Table 1). The densities were chosen to be representative of ranges from lower to higher than typically found in nature. Horned pondweed, widgeon grass, and Eastern mosquitofish densities were estimated based on observations made in the field during collection. Saltmarsh snail densities were determined with the help of researchers at the University of Delaware familiar with snail distributions in saltmarshes. Finally, bulrush seed densities were modeled after ranges used in previous research at PWRC.

A randomized schedule was used to designate a bird and density for each trial. Each bird was assigned a number one through five and each density assigned a number one through four. Using a random number generator, one bird and one treatment were selected. Regardless of the type of food or density being used, each trial followed the same basic steps. The trial birds fasted approximately

fifteen hours before the trial. Shortly before the trial began, the weight or number of prey items corresponding to that trial's listed density was measured and placed into the tank or box setup. Next, the trial bird was transferred to the testing apparatus with a one square meter area space available to forage. This signified the start of the trial. All trials were video recorded using a GoPro camera (GoPro, San Mateo, California) placed above the foraging area. After one hour, the duck was removed from the trial area and returned to its home pen, with full access to their normal food. The remaining prey items were then collected from the testing apparatus and measured. Birds were closely monitored through the trial process for any signs of distress or illness, in which case the trial was immediately stopped and if necessary, the bird received medical treatment from the research center's wildlife veterinarian.

**Figure 4.** Setup for water substrate trials.



**Figure 5.** Setup for mud substrate trials.



*Ruppia maritima* and *Zannischellia palustris*

Both widgeon grass and horned pondweed are types of submerged aquatic vegetation (SAV) and were collected in the field with the help of the Maryland Department of Natural Resources (DNR). Widgeon grass was collected along the St. Charles River in Maryland near Piney Point. Horned pondweed was collected along the Severn River in Annapolis, Maryland. Once obtained, the SAV was stored in environmental chambers kept around 45 degrees Celsius, and in water of approximately equal salinity to that of the water the grasses were found in.

SAV trials were conducted in water substrate within the large blue tank (Figure 4). The tank was filled with water to a one-foot depth, and part of the tank was blocked off so that each duck only had access to feed in a one square meter area. The bottom of the tank was lined with a layer of rocks and pebbles in an

attempt to emulate a more natural environment. An aerator and aquarium pumps were used in the open side of the tank to increase circulation and aeration in the water. Before and after each trial, grass was collected and the wet weight was recorded.

### *Scirpus validus*

Softstem bulrush seeds were ordered from ERNST seeds (Meadville, PA). Unlike SAV and fish trials, bulrush seeds were presented to the ducks in a mud substrate. Seeds were scattered in a layer of mud and water one to two inches deep, within a one square meter wooden box (Figure 5). Mud was collected from ponds around the research center and washed through a series of sieves in order to remove any organic compounds. This ensured that during trials, the only food available to the ducks were seeds. The sieves used were numbers 18 and 35, corresponding to 1.00 and 0.500 mm openings respectively, for the initial cleaning and then additionally number 25, corresponding to a 0.71 mm opening, for isolating only seeds after the trial was finished. Upon washing and sieving, remaining seeds were dried, sorted, and weighed to determine the remaining mass and thus the amount each duck consumed.

### *Gambusia holbrooki*

Eastern mosquitofish were collected in ponds around the Patuxent Wildlife Research Center using minnow traps and nets. Once trapped, they were kept in a large fish tank at the colony and fed commercial fish food twice a day. As with the SAV trials, fish trials were conducted in the blue tank setup (Figure 4). The tank was again blocked off, allowing the ducks to forage in a one square



meter area. The number of fish was measured as number of individuals as opposed to mass.

*Melampus bidentatus*

Saltmarsh snails were ordered from the Marine Biological Laboratory (Wood’s Hole, MA). Upon arrival, they were kept in a fish aquarium lined with moist organic matter and fed lettuce. Similarly to the fish trials, snail densities were determined using number of individuals rather than biomass. Additionally, like seeds, snail trials were conducted in mud substrate within the wooden box (Figure 5). Mud was collected and cleaned as described under the seed methods. However, larger number 10 sieves were used, rather than the smaller number 25 sieves. The numbers of remaining snails were counted at the end of each trial to determine how much each duck consumed.

**Table 1.** Specific densities tested for each prey item.

	<i>R. maritima</i> (grams)	<i>Z. palustris</i> (grams)	<i>S. validus</i> (grams)	<i>G. holbrooki</i> (individuals)	<i>M. bidentatus</i> (individuals)
<b>Density #1</b>	100	100	10	10	10
<b>Density #2</b>	600	600	20	30	30
<b>Density #3</b>	1100	1100	30	50	50
<b>Density #4</b>	1600	1600	40	100	100

Video footage was analyzed for time spent foraging while in the apparatus. In a successful foraging event, time started when the duck’s bill entered the water or mud and ended upon removal of their bill. These times were

summed together to find the aggregate foraging time of that trial. Following video analysis, each duck's intake rate was calculated as the amount of food consumed divided by the time spent foraging. Functional response curves were created for each food item, plotting intake rate as a function of density. Curves were fitted with a linear regression, followed by two non-linear regressions (Donnelly and Phillips 2001). The two non-linear models used were the Michaelis-Menten equation and the Hill equation. Each regression was run using the SAS procNLIN procedure with the Marquardt method to estimate the handling time coefficient or maximal intake rate (a) and search time coefficient or density where the intake rate is half of the maximum value (b) (ProcNLIN, SAS Institute 2003) (Lovvorn and Gillingham 1996, Richman and Lovvorn 2003, Richman and Lovvorn 2004, Wells-Berlin 2008, and Schafer 2008). Coefficients of determination ( $R^2$ ) were compared for each regression to determine which model was the best fit for each curve (Juliano and Williams 1987, Lundberg 1988).  $R^2$  values were calculated using corrected sum of squares (Motulsky and Ransnas 1987). All individual data points were used in each regression and  $R^2$  calculation to ensure the best possible accuracy of estimates (Juliano and Williams 1987). When  $R^2$  values between two models were nearly equal, biological relevance of estimated parameters was examined to differentiate the better model (Lundberg 1988, Fritz et al 2001, Durant et al 2003). This process was repeated for intake rates based on biomass consumed per second, and number of individuals eaten per second. Biomass values for fish and snail trials had to be converted from number of individuals, as the number of snails and fish were used during these trials rather than mass. The

conversion factor used for snails was calculated by averaging 10 sets of 10 snails to find the average mass of one individual snail. The average mass of saltmarsh snails was calculated as 0.056 g/individual. As for determining the conversion factor for eastern mosquitofish, the mass was estimated using primary literature. A mass of 0.29 g/individual was used, as found in a study on western mosquito fish (*Gambusia affinis*) (Chipps and Wahl 2004). This was accepted as an appropriate mass, as western mosquitofish are very similar in size and weight to the eastern mosquitofish used in this study. The size of western mosquitofish in the age class measured by Chipps and Wahl (2004) were also comparable to the size of eastern mosquitofish used in this study.

In order to examine the curves energetically, biomass intake rates were converted to metabolizable energy intake rates using TME values (Table 2). TME values were determined via a literature review. After curves were analyzed in terms of energetic intake, evaluations of the energetic quality of food items were taken one step further and used to estimate the hypothetical total amount of food necessary and total foraging time a black duck would need to undergo in order to meet their energetic demands. This was completed using an estimation of daily energy expenditure from a previous study of a twenty-four hour black duck energy budget, weighted to account for diurnal and seasonal patterns (Jones et al 2014). Black ducks were predicted to spend about 1,244.25 kilojoules per bird per day (Jones et al 2014). From the daily energy output, in conjunction with TME estimates measured in kJ/g, the mass, and when applicable, the number of prey individuals needed each day to meet the energy requirement were calculated.

Next, the total foraging time required to consume that amount of prey was found by incorporating intake rates determined via the curves produced by this study. The specific intake rates used in the calculation correlated to the densities at the critical threshold, meaning the selected intake rates represented the minimum prey intake in an energetically valuable area. Intake rates were then combined with the already calculated amount of food black ducks would need to consume per day to compute the amount of time the ducks would ideally need to forage on a daily basis (Table 7).

**Table 2.** True metabolizable energy (TME) values for each prey species.

<b>Food Species</b>	<b>TME (kcal/g)</b>	<b>Predator Species</b>	<b>Source</b>
<i>R. maritima</i>	1.10	<i>A. rubripes</i>	Coluccy et al 2015
<i>Z. palustris</i>	1.10	<i>A. rubripes</i>	Used same value as <i>R. maritima</i>
<i>M. bidentatus</i>	0.99	<i>A. rubripes</i>	Coluccy et al 2015
<i>S. validus</i>	0.77	<i>A. platyrhynchos</i>	Hoffman and Bookhout 1985
<i>F. mummichog</i>	3.66	<i>A. rubripes</i>	Coluccy et al 2015

Other analyses included testing for seasonal and gender differences in intake rates was performed using analysis of covariance (ANCOVA). ANCOVA analyses were also used to detect differences between the functional response curves of each prey item and each individual bird. Tests were considered significant at the 5% level, and all analyses were completed using SAS (ProcMIXED, SAS Institute 2003).

## RESULTS

For each prey species' functional response curves, the three regressions showed very similar and sometimes nearly identical fits as described by their  $R^2$  values (Table 3 and 4). To compensate, biological and ecological criteria were considered before inferring the most probable type of functional response model. After considering the biological relevance for each scenario in conjunction with the  $R^2$  values, the most likely functional response types for each prey item were type II for *R. maritima* and *Z. palustris*, type I for *S. validus*, type II for *G. holbrooki*, and type III for *M. bidentatus* (Table 3 and 4). A number of other nonlinear and polynomial models were tested, but none showed  $R^2$  values greater than the models discussed above.

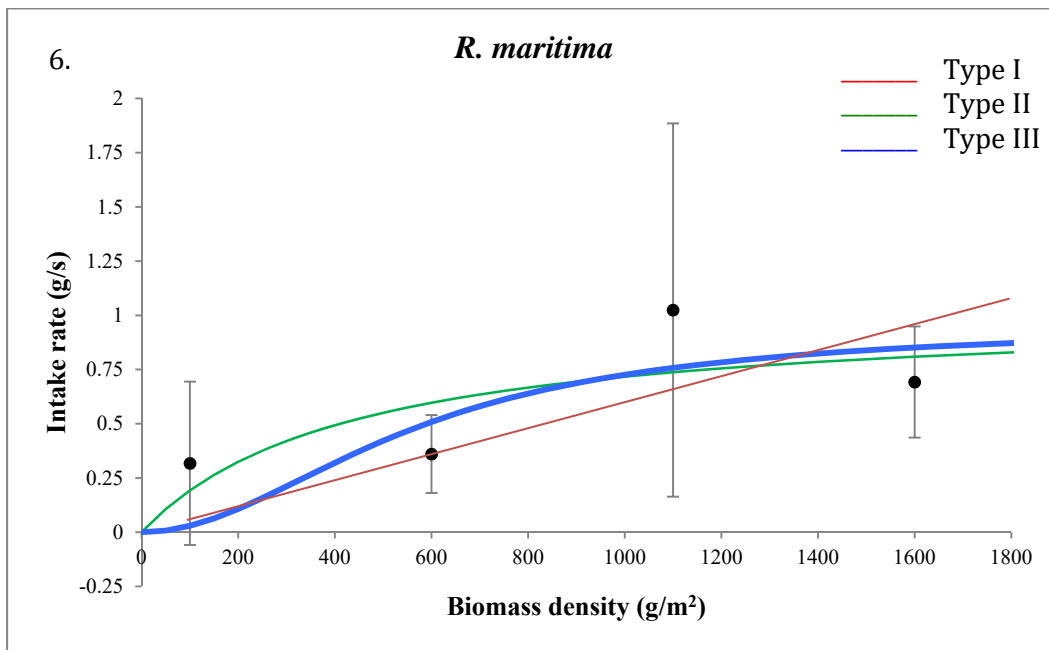
In modeling the potential type II relationship for *S. validus*, the nonlinear regression with the Michaelis-Menten equation was not possible. The results of the SAS procNLIN procedure revealed that the Hessian matrix of this model was singular, meaning the second derivative does not exist as a result of the parameters being collinear (SAS institute 2003). In summary, the nonlinear regression for a type II model for this prey item could not be concluded because it estimated a linear rather than nonlinear relationship. The type III regression, however, was successfully estimated and produced meaningful parameter results.

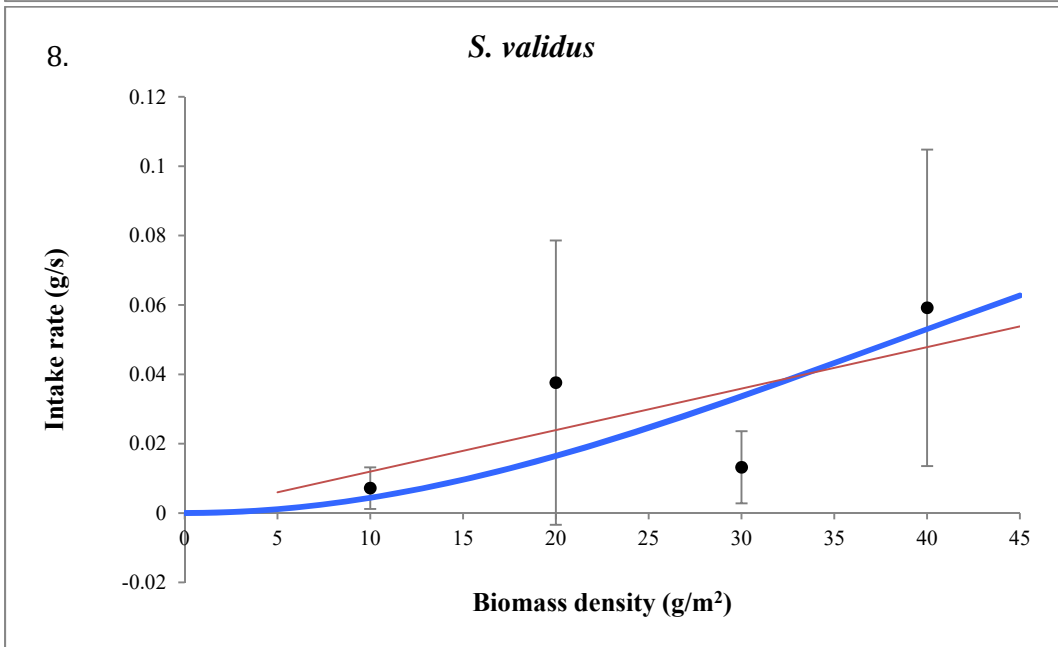
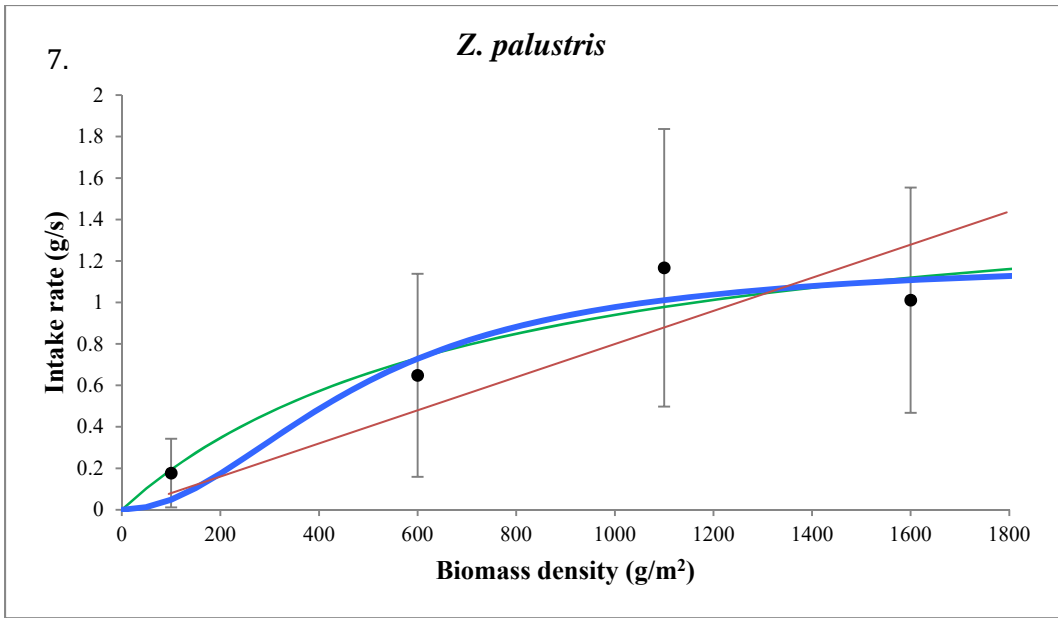
Based on the TME data from Table 2, biomass intake rates measured in grams consumed per second (Figure 6-10 and Table 4) were converted to energetic intake rates in units of kilocalories per second and graphed as a function of biomass density (Figure 13-18). Analysis of fit for metabolizable energy curves

in addition to the estimated equations and parameters are presented in Table 6. Based on these energy intake curves, *R. maritima* and *Z. palustris* provide the highest energy gains, while *M. bidentatus* provide the lowest metabolizable energy to the ducks (Figures 13-18).

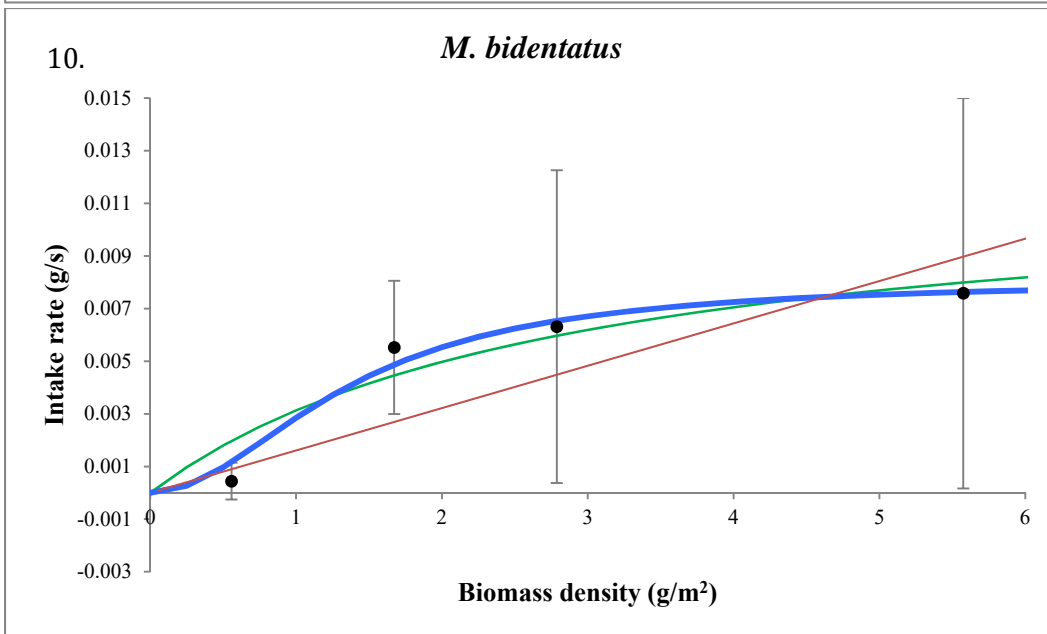
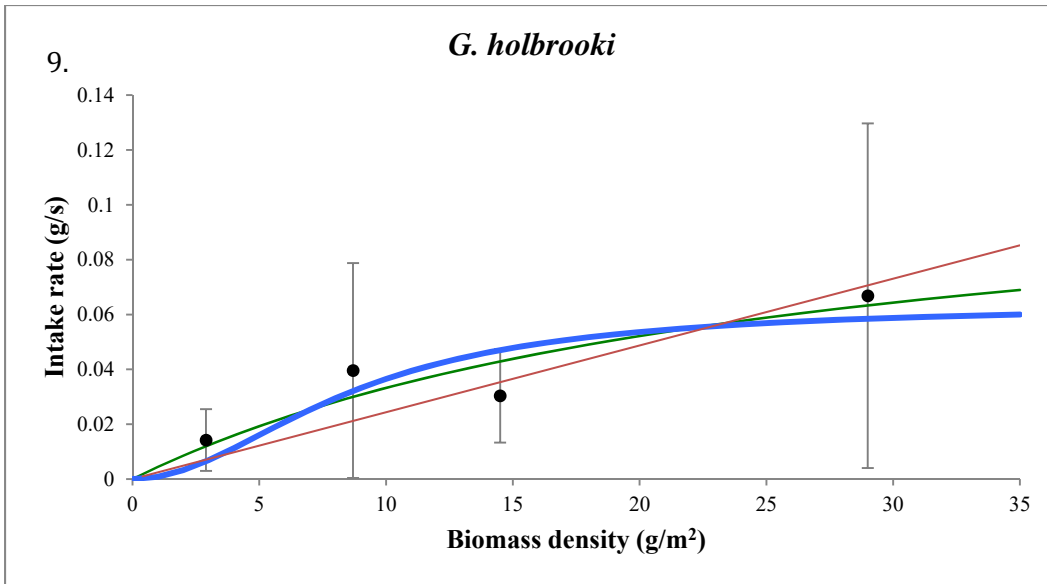
All overall model fits were significant (Table 3, 4, and 5). However, there was a great deal of variation as indicated by the error bars. Regressions and  $R^2$  calculations were performed on all data points, while in the graphs only the average intake rates at each density were shown. Calculated  $R^2$  values ranged from 0.177 to 0.379 (Table 3, 4, and 5). Satisfactory  $R^2$  values in previous functional response research on various organisms, including waterfowl, were found to vary widely. Curves were considered an acceptable representation of the data when  $R^2$  values ranged anywhere from 0.3 to 0.9 (Dale et al 1994, Donnelly and Phillips 2001, Fritz et al 2001, Pitt and Ritchie 2002, Schenk and Bacher 2002, Richman and Lovvorn 2003, Richman and Lovvorn 2004, Arzel et al 2007, Berlin 2008, Robinson and Merrill 2012, Murray et al 2013).

**Figures 6-10.** Functional response curves using biomass measures. Data shows the mean intake rate (g/s) of the five birds tested as a function of prey density (g), with error bars of +/- one standard deviation. Each curve was fit to a linear regression representing a type I predator prey relationship (red), as well as two nonlinear regressions. The two nonlinear models were the Michaelis-Menten equation demonstrating a type II curve (green) and Hill equation for a type III curve (blue). Goodness of fit measures and parameter estimates for each curve listed in Table 4.





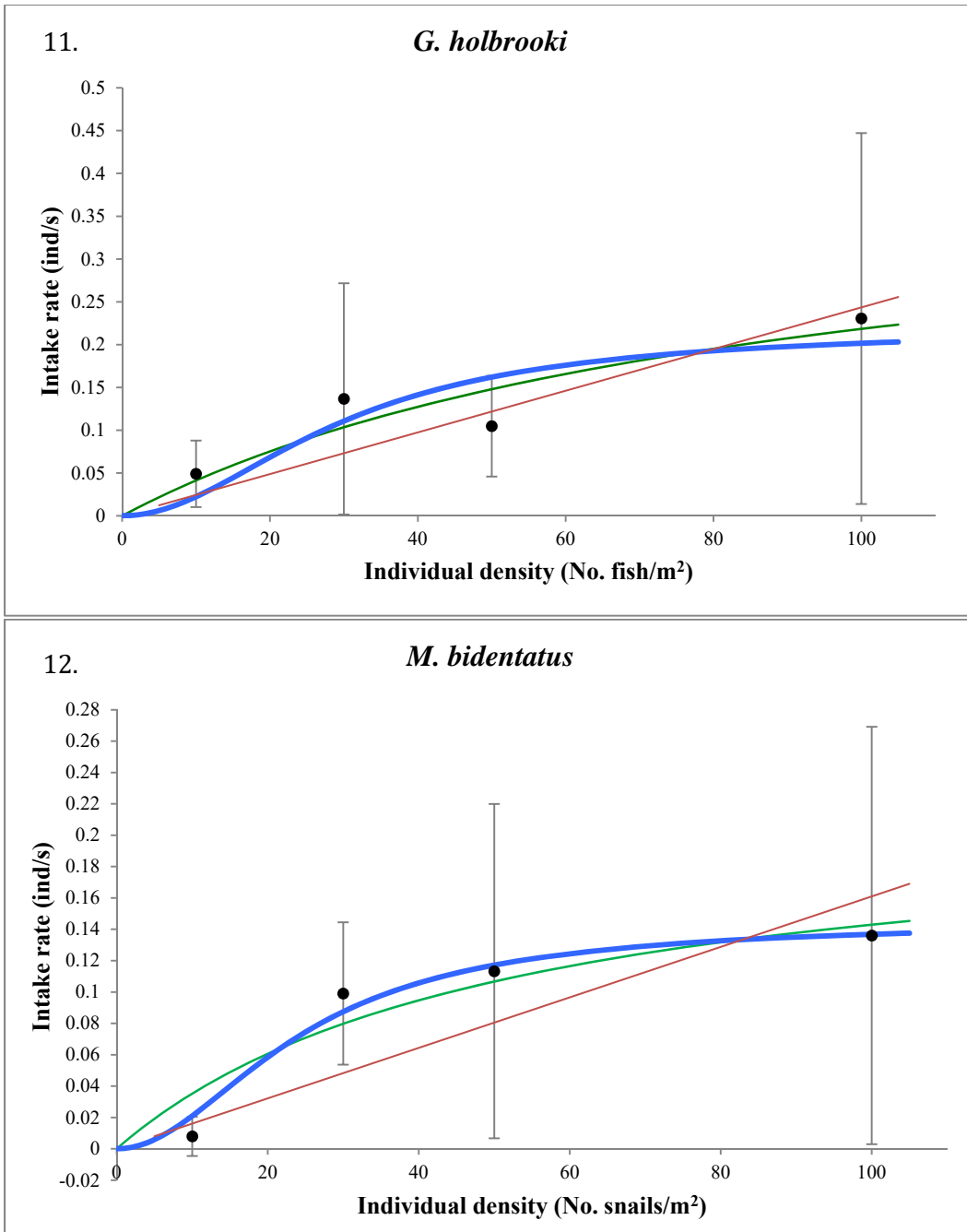




**Table 3.** Linear and nonlinear regression model fits and parameter estimates for each prey item. Parameters and goodness of fit values calculated using separate data points for each bird, rather than averages. Type II model parameters for *S. validus* estimated to be linear, thus no meaningful equation could be derived.

Prey Species	Model	R <sup>2</sup>	Equation	(F, p-values)
<i>R. maritima</i>	Type I	0.0499	$I = 0.0006X$	(26.8, <0.0001)
	Type II	0.379	$I = 1.03X/(434.8+X)$	(15.04, 0.0001)
	Type III	0.378	$I = 0.96X^2/(564.1^2+X^2)$	(14.22, 0.0002)
<i>Z. palustris</i>	Type I	0.279	$I = 0.002X$	(50.22, <0.0001)
	Type II	0.379	$I = 1.64X/(748.9+X)$	(29.05, <0.0001)
	Type III	0.378	$I = 1.21X^2/(487.9^2+X^2)$	(28.98, <0.0001)
<i>S. validus</i>	Type I	0.177	$I = 0.001X$	(20.48, 0.0002)
	Type II	NA	NA	NA
	Type III	0.166	$I = 0.20X^2/(67.29^2+X^2)$	(9.43, 0.0016)
<i>G. holbrooki</i>	Type I	0.167	$I = 0.002X$	(24.85, <0.0001)
	Type II	0.194	$I = 0.12X/(26.36+X)$	(12.45, 0.0004)
	Type III	0.161	$I = 0.06X^2/(8.62^2+X^2)$	(11.63, 0.0006)
<i>M. bidentatus</i>	Type I	0.187	$I = 0.002X$	(22.43, 0.0002)
	Type II	0.245	$I = 0.01X/(2.86+X)$	(12.59, 0.0004)
	Type III	0.269	$I = 0.008X^2/(1.36^2+X^2)$	(13.3, 0.0003)

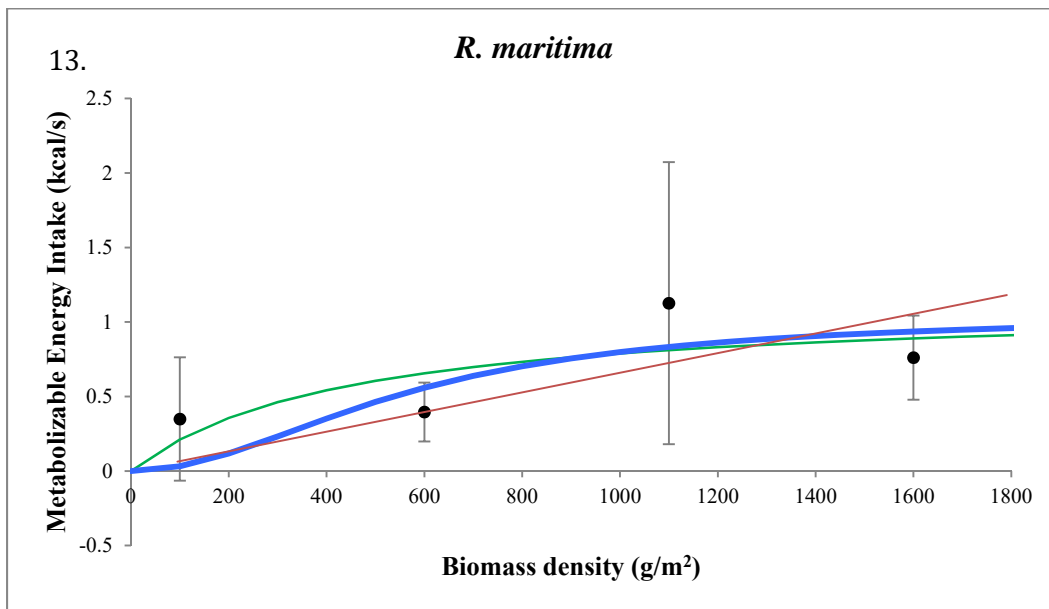
**Figures 11 and 12.** Functional response curves using number of individuals for intake and density measures. Each curve was fit to a linear regression representing (red), as well as two nonlinear regressions (type II – green) and (type III – blue). Goodness of fit measures and parameter estimates for each curve listed in Table 5.

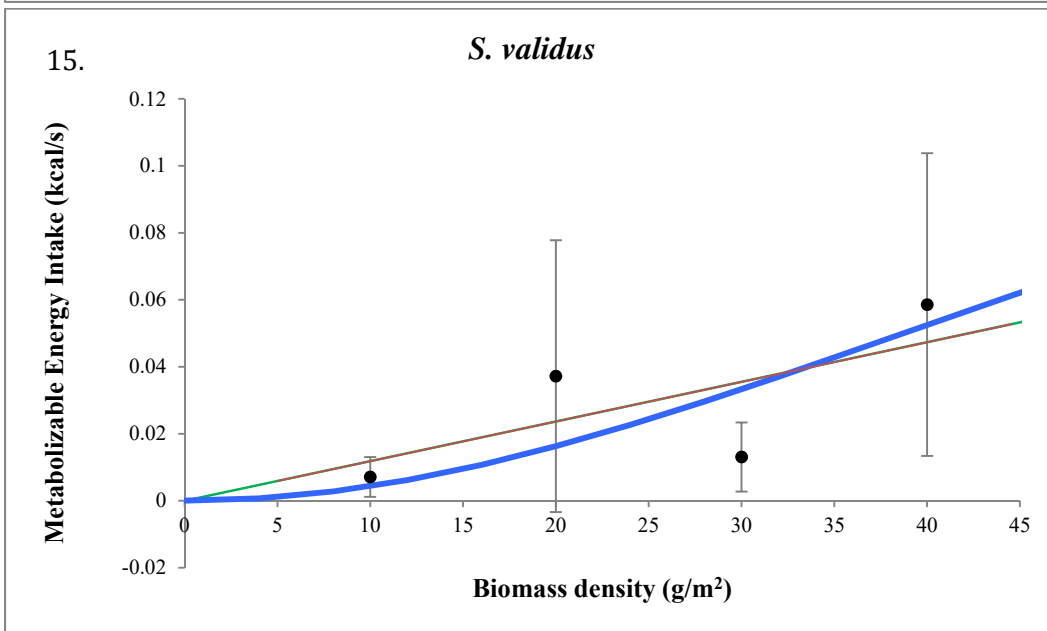
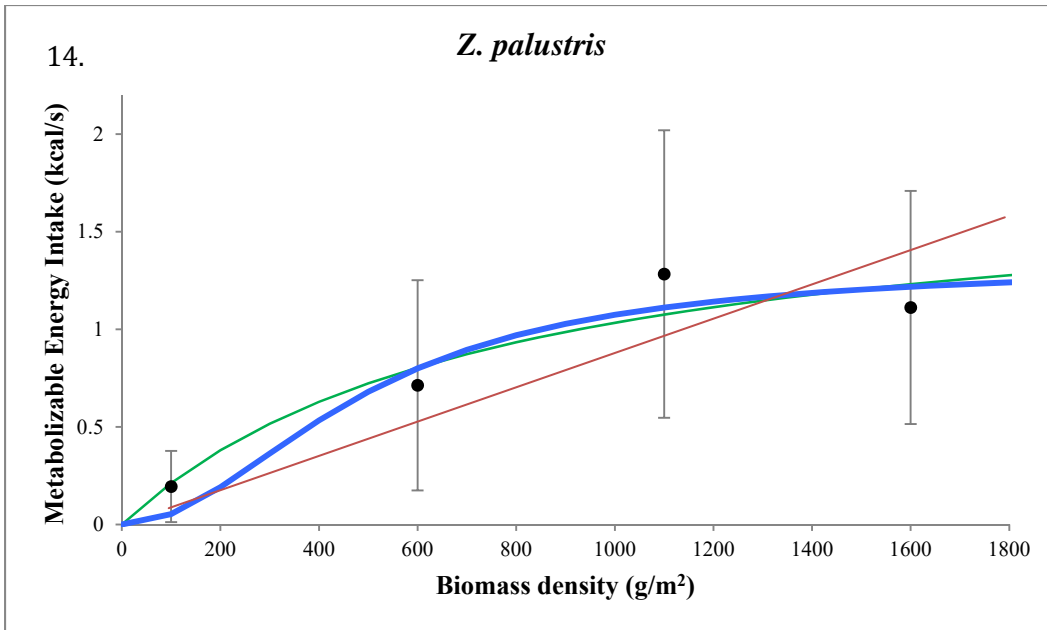


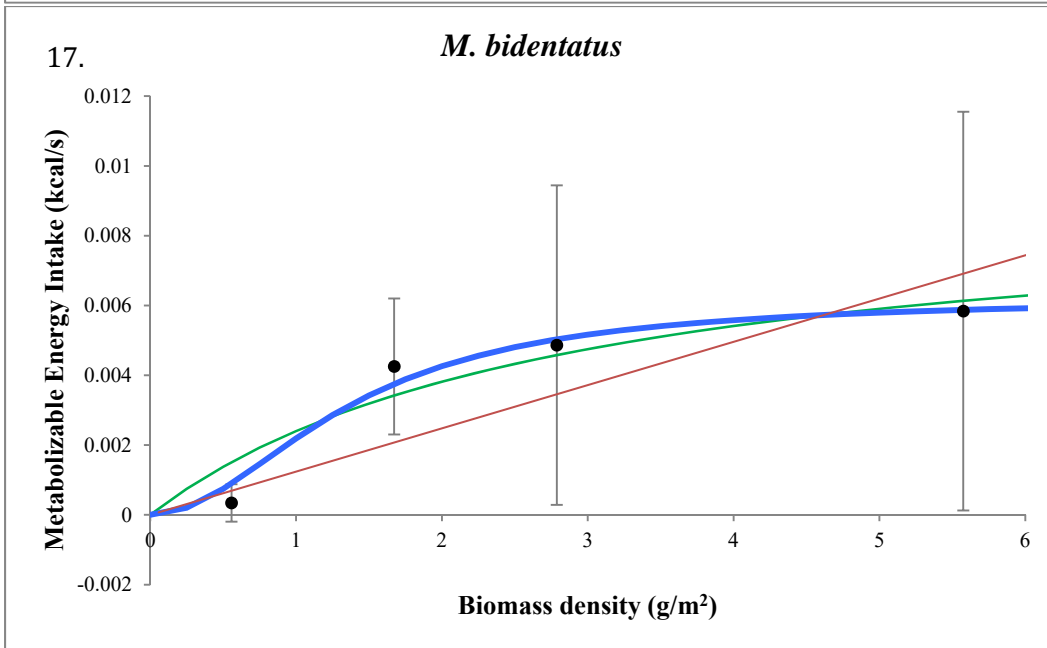
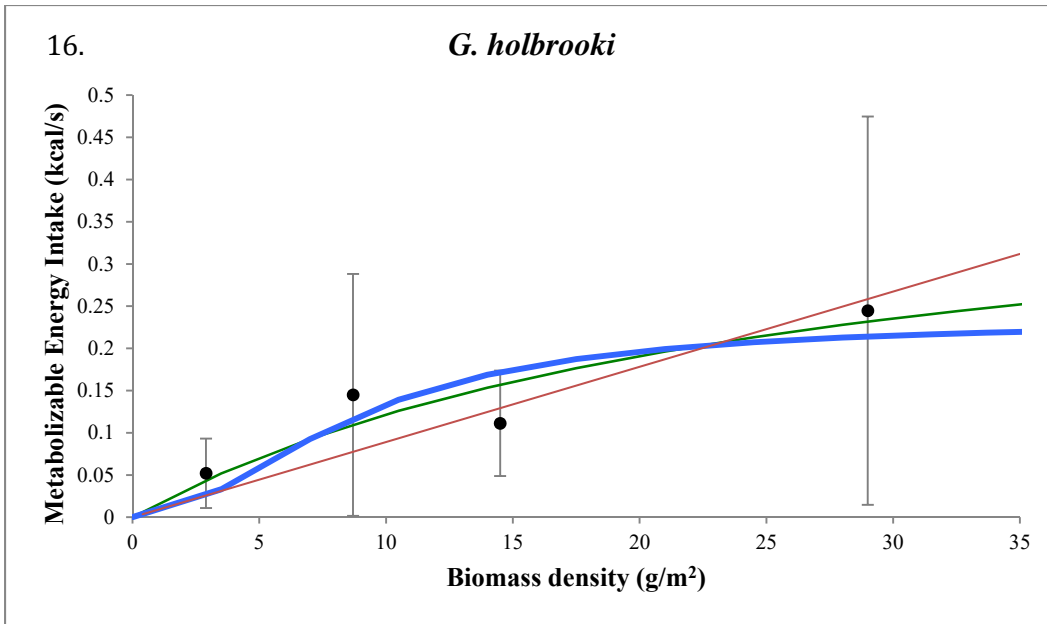
**Table 4.** Linear and nonlinear regression model fits and parameter estimates for *G. holbrooki* and *M. bidentatus*, measured as number of individuals rather than mass. All overall model fits were significant.

<b>Prey Species</b>	<b>Model</b>	<b>R<sup>2</sup></b>	<b>Equation</b>	<b>(F, p-values)</b>
<i>G. holbrooki</i>	Type I	0.167	$I = 0.002X$	(24.85, <0.0001)
	Type II	0.193	$I = 0.42X/(90.88+X)$	(12.45, 0.0004)
	Type III	0.161	$I = 0.22X^2/(29.71^2+X^2)$	(11.63, 0.0006)
<i>M. bidentatus</i>	Type I	0.187	$I = 0.002X$	(22.43, 0.0002)
	Type II	0.244	$I = 0.22X/(51.39+X)$	(12.59, 0.0004)
	Type III	0.269	$I = 0.14X^2/(24.32^2+X^2)$	(13.3, 0.0003)

**Figures 13-17.** Functional response curves using energetic measures. Data shows the mean intake rate (g/s) of the five birds tested as a function of prey density (g), with error bars of +/- one standard deviation. Each curve was fit to a linear regression representing a type I predator prey relationship (red), as well as two nonlinear regressions. The two nonlinear models were the Michaelis-Menten equation demonstrating a type II curve (green) and Hill equation for a type III curve (blue). Goodness of fit measures and parameter estimates for each curve listed in Table 6.







**Table 5.** Linear and nonlinear regression model fits and parameter estimates for metabolized energy intake for each prey item. Parameters and goodness of fit values calculated using separate data points for each bird, rather than averages. Type II model for *S. validus* parameters estimated to be co-linear, thus no meaningful equation could be derived.

Prey Species	Model	R <sup>2</sup>	Equation	(F, p-values)
<i>R. maritima</i>	Type I	0.0499	$I = 0.0007X$	(26.8, <0.0001)
	Type II	0.193	$I = 1.13X/(434.9+X)$	(15.04, 0.0001)
	Type III	0.112	$I = 1.05X^2/(564.1^2+X^2)$	(14.22, 0.0002)
<i>Z. palustris</i>	Type I	0.279	$I = 0.0009X$	(50.17, <0.0001)
	Type II	0.379	$I = 1.81X/(751.2+X)$	(29, <0.0001)
	Type III	0.377	$I = 1.33X^2/(489^2+X^2)$	(28.92, <0.0001)
<i>S. validus</i>	Type I	0.177	$I = 0.001X$	(20.49, 0.0002)
	Type II	NA	NA	NA
	Type III	0.164	$I = 0.20X^2/(67.48^2+X^2)$	(9.44, 0.0016)
<i>G. holbrooki</i>	Type I	0.167	$I = 0.009X$	(24.85, <0.0001)
	Type II	0.193	$I = 0.44X/(26.36+X)$	(12.45, 0.0004)
	Type III	0.161	$I = 0.23X^2/(8.62^2+X^2)$	(11.63, 0.0006)
<i>M. bidentatus</i>	Type I	0.187	$I = 0.001X$	(22.44, 0.0002)
	Type II	0.245	$I = 0.009X/(2.87+X)$	(12.59, 0.0004)
	Type III	0.267	$I = 0.006X^2/(1.36^2+X^2)$	(13.3, 0.0003)



Black ducks were estimated to spend about 1,244.25 kilojoules per bird per day (Jones et al 2014). In further evaluating the energetic quality of the food items used in this study, this previously predicted energy output of black ducks was used in conjunction with the half maximum energy intake rate (Figures 13-17, Table 5), in order to calculate the theoretical total amount of food necessary and total foraging time a black duck would need to undergo in order to meet their energetic demands. Black ducks would need to spend just under ten minutes a day feeding on SAV, approximately twenty minutes eating fish, nearly fifty minutes foraging seeds, and over 26 hours foraging snails in order to meet their daily energy demands (Table 6).

**Table 6.** Steps in the calculation of total daily foraging time needed for each prey species assuming a daily energy expenditure of 1,244.25 kJ/bird/day.

Prey spp.	TME (kcal/g)	Converted TME (kJ/g)	Daily energy requirement (KJ/bird/day)	Daily prey mass requirement (g/bird/day)	Daily prey individuals requirement (#individuals/bird/day)	Prey intake rates (g/sec)	Time needed to consume required prey mass (sec/bird/day)
<i>R. maritima</i>	1.10	4.60	1244.25	270.35	-	0.51	525.51
<i>Z. palustris</i>	1.10	4.60	1244.25	270.35	-	0.82	328.91
<i>S. validus</i>	0.99	4.14	1244.25	300.39	-	0.10	2959.48
<i>G. holbrooki</i>	3.66	15.31	1244.25	81.25	280.18	0.06	1344.12
<i>M. bidentatus</i>	0.77	3.22	1244.25	386.21	6896.64	0.004	95596.92

Based on the pattern of each residual plot, the data was log transformed before ANCOVA tests were performed. Potential gender effects were tested and found to have no significant effects on the amount of prey consumed for all prey species (*R. maritima*:  $F=0.02$ ,  $p=0.8820$ ; *Z. palustris*:  $F=0.37$ ,  $p=0.5515$ ; *S. validus*:  $F=0.56$ ,  $p=0.4629$ ; *G. holbrooki*:  $F=0$ ,  $p=0.9971$ ; *M. bidentatus*:  $F=4.16$ ,  $p=0.2902$ ). Likewise, seasonal effects also had no significant impact on prey consumed (*R. maritima*:  $F=1.62$ ,  $p=0.2196$ ; *S. validus*:  $F=0.75$ ,  $p=0.3967$ ). No trials were conducted during the spring breeding season, and only *R. maritima* and *S. validus* were tested over the course of more than one season (both fall and winter). The other three prey species, *Z. palustris*, *G. holbrooki*, and *M. bidentatus*, were entirely tested in the summer and accordingly were not tested for seasonal effects. Because gender and season did not cause significant variation, all functional response data could be combined and analyzed together.

As expected, amount consumed and intake rate differences between prey species as a whole were significantly different ( $F=36.83$ ,  $p<0.0001$ ;  $F=37.35$ ,  $p<0.0001$ ). However, in comparing each individual prey species, ANCOVA tests showed some varying results. Each prey type is inherently different, so it's reasonable to expect their intakes to be significantly different, with the exception of *R. maritima* and *Z. palustris*. These are both SAV species and showed no significant difference in either amount consumed or intake (Table 7). Conversely, the other prey combinations do show significant differences. *R. maritima* and *Z. palustris* have decidedly different intake rates from each of the other three species (Table 7). Likewise, *M. bidentatus* and *G. holbrooki* also differ in all three

categories (Table 7). In the final two prey combinations, *S. validus* differs from *M. bidentatus* only in terms of energy intake, while *S. validus* differs from *G. holbrooki* both in amount consumed and energy intake, but not mass intake (Table 7).

**Table 7.** Results from ANCOVA tests between prey species. The table displays the F and p-values from each test for the amount of prey consumed in grams, the intake rate in grams per second, and the metabolizable energy intake rates in kilocalories per second.

<b>Prey combination</b>	<b>Mass consumed</b>	<b>Mass intake rate</b>	<b>Metabolizable energy intake rate</b>
<i>R. maritima</i> - <i>Z. palustris</i>	(0.01, 0.9280)	(0.23, 0.6340)	(0.18, 0.6732)
<i>R. maritima</i> - <i>S. validus</i>	(74.68, <0.0001)	(40.72, <0.0001)	(43.80, <0.0001)
<i>R. maritima</i> - <i>G. holbrooki</i>	(19.95, <0.0001)	(39.93, <0.0001)	(12.71, 0.0010)
<i>R. maritima</i> - <i>M. bidentatus</i>	(69.17, <0.0001)	(78.09, <0.0001)	(108.5, <0.0001)
<i>Z. palustris</i> - <i>S. validus</i>	(71.96, <0.0001)	(47.89, <0.0001)	(49.72, <0.0001)
<i>Z. palustris</i> - <i>G. holbrooki</i>	(19.60, <0.0001)	(51.01, <0.0001)	(16.86, 0.0002)
<i>Z. palustris</i> - <i>M. bidentatus</i>	(70.27, <0.0001)	(99.47, <0.0001)	(108.89, <0.0001)
<i>S. validus</i> - <i>G. holbrooki</i>	(23.27, <0.0001)	(1.76, 0.1925)	(14.77, 0.0004)
<i>S. validus</i> - <i>M. bidentatus</i>	(1.79, 0.1903)	(2.94, 0.0959)	(4.43, 0.0432)
<i>G. holbrooki</i> - <i>M. bidentatus</i>	(30.17, <0.0001)	(15.18, 0.0005)	(51.75, <0.0001)

## DISCUSSION

### Sources of Variation

As noted in previous functional response experiments, the results of this study should be treated with caution as trials were conducted in an experimental rather than field based setting (Abrams 1982). Historically, functional response tests have been conducted both using field-based observations and using experimental testing with no real indication to which is better. That being said, a recent comparison was conducted, suggesting that experimentally determined functional response data is more accurate (Dujins et al 2015). One cited problem of field-based observations is that they often lack both high and low prey density data, since high density areas are rare and low densities are avoided by the forager (Dujins et al 2015). Additionally, in the field, intra and interspecific interactions can lead to interference causing underestimated intake rates (Dujins et al 2015). While the more accurate technique for measuring intake rates, experimental settings still have their shortcomings. Captive ducks may not be as eager to forage as they would in the wild since they know they will be fed. Starvation is never a risk for them. Similarly, because the ducks are raised in captivity, they are not naturally familiar with the selected prey items. They must grow accustomed to what and how to eat. This issue presented itself during snail trials. Because snails were not part of the captive diet as a duckling, it was difficult to teach and entice the ducks to forage for and consume snails. If this study were repeated, the ducks should be fed each prey item as regularly as possible, starting at a young age.

As indicated by the large error bar on each curve, individual intake rates were highly variable. As a result, the models were limited in their quality by the variance in the data and the calculated  $R^2$  values were relatively low. Trials need to be further analyzed using more birds. Additionally, the  $R^2$  values between potential functional response models did not clearly reveal the best fitting model. In order to more definitively distinguish between type II and type III functional response classifications, additional lower densities need to be tested. These additional densities would allow for the detection of the characteristic lag in intake rate increase at low prey availabilities, representative of the learning curve that defines a type III predator prey relationship. Further tests of higher densities would also be worthwhile. By including additional trials for higher prey availabilities, the saturation points of all three types of curves would be more evident.

### Functional Response

Functional response and intake rates are an important piece of population ecology when trying to model and manage specific species or habitats and are an essential part of predator-prey relationships. While intake rates have been extensively studied in mammals, little is known about intake rates in waterfowl for species of ducks, geese, and swans, also known as *Anitidae spp.* (Durant et al 2003). This study specifically focused on developing functional response curves for black ducks. The resulting functional response curves for each of the five selected prey species showed varying results, as follows.

*R. maritima* and *Z. palustris*

Response curves for both tested SAV species showed approximately equal  $R^2$  values, representing goodness of fit, for the type II and III models (Figures 6 and 7, Table 4). The type I fit, however, was substantially lower for both prey items (Table 4). Upon consideration of biological criteria related to both prey species and the functional response types (Lundberg 1988), the most appropriate model selected for each was the type II equation. This functional response relationship was chosen because it is the most common for herbivores feeding on vegetation (Fritz et al 2001, Durant et al 2003). The parameters of the type II models estimated for these species reveal some ecologically important information. In the Michaelis-Menten equation ( $I = aX/(b+X)$ ), the first parameter (a) represents the maximum intake rate independent of prey density, while the second parameter (b) is the prey density when the intake rate is half the maximum rate (Real 1977, Berryman 1992). The prey density determined from b is also an estimate for the critical density threshold for that prey species (Richman and Lovvorn 2003, Richman and Lovvorn 2004, Wells-Berlin 2008). This density has important management implications. Densities at or above the critical density threshold are considered valuable for the predator, but densities below this threshold are not beneficial and the predator will likely leave in search of more densely available prey. In the *R. maritima* model equation ( $I = 1.03X/(434.8+X)$ ) the maximum intake rate was 1.03 g/s, while the critical density threshold was 434.8 g/m<sup>2</sup> (Table 3). As for *Z. palustris* ( $I = 1.64X/(748.9+X)$ ), the maximum intake rate was predicted as 1.64 g/s, and the critical density was 748.9 g/m<sup>2</sup>

(Table 4). When considering management options for black duck habitats, designated protected areas containing SAV species should have *R. maritima* and *Z. palustris* at densities of at least 434.8 and 748.9 g/m<sup>2</sup> respectively in order to be useful for black ducks.

In conservation and management involving SAV species, other dynamics should be considered as well. Bay and seagrasses, otherwise known as SAV, are diverse and were once extremely abundant in the Bay. Some of the native species in the Chesapeake Bay include widgeongrass (*R. maritima*), wild celery (*Valisneria americana*), redhead grass (*Potamogeton perfoliatus*), and several species of pondweeds (*Potamogeton spp.*) (Haramis 1991). One exotic SAV species of note is *Hydrilla vericillata*, which is growing in abundance in the Potomac River and has been shown to both help increase water quality and provide a food source to various waterfowl species (Erwin 1996). SAV beds are an important food source for wintering waterfowl as well as a summer brood rearing habitat for resident waterfowl. SAV abundance on the Bay has dramatically declined since the late 1960's (Kemp et al 1983). Densities were at a historic low in 1984 and have rebounded somewhat since then, especially along the Severn and Magothy Rivers, but distributions are still patchy and relatively sparse (Erwin and Beck 2007, Orth et al 2010). In a worldwide assessment of seagrass abundance, global trends showed an accelerated decline the past decade with current estimated loss rates of about 7%, which is comparable to decline rates seen in other well documented threatened habitats such as mangroves, coral reefs, and tropical rainforests (Waycott et al 2009). Some of the factors



contributing to SAV decline are sediment and nutrient input into the Bay, resulting in reduced light penetration and hypoxic conditions (Kemp et al 1983, Kemp et al 2005, Diaz and Rosenberg 2008, Orth et al 2010), dredging, overfishing, and exotic species (Jackson et al 2001, Williams 2007). The foraging activities of the invasive mute swan (*Cygnus olor*) are particularly detrimental to SAV populations (Erwin and Beck 2007). Declining SAV beds have also led to habitat and distribution changes in waterfowl and water birds (Terborgh 1989, Haramis 1991, Perry and Deller 1995, Erwin 1996, Lynch 2001, Erwin and Beck 2007). Two well-documented cases of waterfowl species that have been negatively impacted by SAV decline in the Bay involve redhead and canvasback ducks. In the 1950's, redhead and canvasback duck wintering populations were prevalent on the Bay. Around 80,000 redheads and over 250,000 canvasback, corresponding to over half of the entire North American wintering population inhabited the Bay (Phillips 2001). Populations of both species plummeted with the coinciding SAV decline in the 1960's. As of 1980, redhead population levels on the Bay were below 1,000 individuals and have not recovered, as many of these individuals shifted their range to winter in North Carolina instead (Phillips 2001). Canvasback ducks, on the other hand, have recovered slightly to nearly 50,000 individuals wintering on the Bay today (Phillips 2001). Canvasbacks were able to rebound by changing their predominant food source from SAV species to small clams (Perry and Uhler 1988). While never officially documented, it is conceivable that wintering black duck populations on the Bay have encountered similar problems. It is possible that like redhead and canvasbacks, black duck

declines could be related to SAV declines and the associated lower water quality and increased sedimentation. The historically declining trends and current SAV status as well as resulting waterfowl habitat and distributional changes in response need to be considered when considering protecting habitat areas for black ducks, containing SAV species.

#### *S. validus*

Response curves for the type II model could not be determined (Table 4). The parameters for the Michaelis-Menten equation regression were linearly related, and consequently, no meaningful estimates could be made. Of the other two models, the type I regression showed a slightly better fit than type III (Figure 8, Table 4). Type I functional response curves are indicative of filter feeding methods in waterfowl (Arzel et al 2007); therefore, biologically, a type I relationship between black ducks and seeds is plausible. When filter feeding, ducks create a flow of water through their mouth and out their lamellae. This type of feeding favors medium sized seeds (1-10 mm<sup>3</sup>) (Gurd 2006, Brochet et al 2012). Larger seeds impede the flow of water, and smaller seeds cannot be contained by the lamellae (Gurd 2006, Brochet et al 2012). *S. validus* seeds are classified as a medium sized seed. The type I equation for seeds as displayed in Table 4 is  $I = 0.001X$ . There is no maximum intake rate indicated by the equation, but it is inherently known that at some point the duck will become saturated and no longer increase their consumption rate. Additionally, there is no critical density threshold indicated by this model. In a type I relationship, intake rate is

independent of density, so there is no density level below which seeds would no longer be a useful food source.

As with SAV prey species, other elements must be considered. Specifically, waterfowl have an added ecological relationship with seeds. Waterfowl, and in particular, dabbling ducks, are important vectors for seed dispersal of not only wetland, but also terrestrial plants (Soons et al 2016). Seeds are most commonly transported internally, post digestion, also called endozoochory (Brochet et al 2010). Duck digestive systems are adapted to optimize calorie intake per unit time, as opposed to the quantity of food intake per unit time, as a result, full digestion often does not occur, allowing seeds to survive the digestion process and remain viable (Van Leeuwen et al 2012). During digestion, the gizzard, containing soft and hard particles also known as grit, grind food into smaller fragments for digestion (Soons et al 2016). Most plant material are unlikely to survive this process, but seeds, especially small to medium sized (<1 mm<sup>3</sup> and 1-10 mm<sup>3</sup>), often pass through relatively unscathed (Soons et al 2016). Black ducks' role in seed dispersal is a crucial step in plant life cycles, as it is needed to help maintain genetic diversity, as well as allow for migration, colonization, and range expansion of otherwise immobile plants.

#### *G. holbrooki*

Response curves showed the best fit was the type II functional response model, although types I and III were not materially lower (Figures 9 and 11, Table 4 and 5). From a biological perspective, a type II curve is logical. Fish trials were unlikely to show a type I relationship, as filter feeding is not an option. Likewise,

a type III curve is also not expected because even at the lowest densities, black duck encounter rates of fish would not be rare enough that the ducks would be required to relearn how to hunt the fish. As shown in Table 4 and 5, the model that best represented fish functional response trials was  $I = 0.129X/(26.36+X)$  for biomass and  $I = 0.42X/(90.88+X)$  for number of individuals. Using these equations, the predicted maximum possible intake rates of fish were 0.12 g/s and 0.42 fish/sec. The critical foraging thresholds estimated by the type II model were 26.36 g/m<sup>2</sup> or 90.88 fish/m<sup>2</sup>. When conserving known habitats of mosquitofish, efforts should be aimed towards areas where fish can be found at densities near 91 fish per square meter in order to best help black ducks.

*M. bidentatus*

Response curves for snails were the only prey item in this study best represented by a type III functional response curve (Figures 10 and 12, Tables 4 and 5). Although the type II R<sup>2</sup> was not considerably lower, a type III relationship between the ducks and snails is presumptive from a biological perspective. The lowest snail densities (ten snails within a one square meter area of mud) resulted in very low encounter rates between the ducks and snails. Such rare encounters are indicative of the learning curve dynamic expected in a type III predator-prey relationship (Royama 1970, Tinbergen 1960). To model a type III relationship, a nonlinear regression of the Hill equation was fit to the data. The estimated equations for the snail functional response curves were  $I = 0.008X^2/(1.36^2+X^2)$  for biomass and  $I = 0.14X^2/(24.32^2+X^2)$  for number of individuals (Table 4 and 5). Because the Hill equation uses the same parameters as the Michaelis-Menten

equation, the estimated maximum intake rates of snails were 0.0081 g/s or 0.14 snails/s, and the critical density thresholds were 1.36 g/m<sup>2</sup> and 24.32 snails/m<sup>2</sup>. According to results of this study, wetland areas receiving management consideration as black duck habitats should have available snail densities of at least 24 snails per square meter in order for the habitat to be deemed valuable.

Similarly, to their relationships with seeds, ducks can be an important dispersal vector for snails. While waterfowl transport of free-living animal species is not sufficiently researched and often still only anecdotal, there is support and evidence for ducks as dispersal vectors of invertebrates, primarily snails (van Leeuwan and van der Velde 2012, van Leeuwan 2012). On their own, snails can only actively travel a few kilometers per year, but with the help of waterfowl, their range increases tremendously (Kappes et al 2011). Bird transport helps to explain the wide distribution and rapid spread of snails, especially when considering colonization by exotic snail species (Alonso and Castro-Diez 2008, van Leeuwan 2012). Snail colonization is of special interest to people because they are vectors of many human and livestock parasites (Morley 2008). Unlike seeds, which are primarily dispersed by waterfowl internally or via endozoochory (Brochet et al 2010), snails can undergo endozoochory, but are also a likely candidate for ectozoochory or external dispersal (Boag 1986). During ectozoochory, snails can either attach passively or actively and the attachment can persist anywhere from a few hours to a couple days (van Leeuwan and van der Velde 2012). During transport, snails are able to survive despite low levels of desiccation (van Leeuwan and van der Velde 2012). External attachment

primarily occurs in the feathers of the bird, but the snails can also attach to the bird's legs and bill (van Leeuwan and van der Velde 2012). Such attachment is possible due to the low mass of the snail in concurrence with the high contact area available on the shell, and can occur while the duck is amongst snail-infested vegetation (van Leeuwan and van der Velde 2012). Snails are able to float on the water's surface, so they can attach away from vegetation as well (Bimler 1976). As for, internal transport, snails go through a similar process as already discussed regarding seed dispersal. The same adaptations that help snails survive in variable, and sometimes, harsh wetland environments, also help them survive digestion. Their shell helps provide protection from being crushed in addition serving as a barrier against digestive enzymes (van Leeuwan 2012). Furthermore, their small size helps them more easily pass through digestion and take advantage of the energy vs. quantity trade-offs of duck digestive systems (van Leeuwan 2012). More research is needed on a wider range of dabbling duck and aquatic snail species, for both ectozoochoric and endozoochoric modes of dispersal, but snail transport via duck vectors is likely a more common form of dispersal than previously realized.

### Metabolizable Energy

Functional response curves provide data on intake rates and resource abundance, but give no insight into prey quality or energy content. While there is some evidence that food abundance is actually a more important indicator of waterfowl use than nutritional or energetic values (Euliss and Harris 1987, Euliss

et al 1991), energetic intake is still a necessary consideration and a large part of the black duck bioenergetics model.

Theoretically, birds should select for prey items of better quality or value, meaning prey species that offer higher energy gains. For instance, preferential prey selection has been demonstrated by changes in prey choice in response to seasonal changes affecting the energetic demands placed on waterfowl (Miller 1987). While prey preference works in theory, there are often other influences, such as extreme weather or geographical barriers that deter birds from searching for highest possible quality foods, and instead, prompt them to settle for food types that require less energy expenditure (Jorde et al 1984). Predators and birds with access to higher food availability will be more selective in the type and quality of prey they consume, while predators in more food-limited environments will be less picky. Nonetheless, food quality was examined as part of this study in order to gain insight into the energetic value of each prey species. As described earlier, energetic value was examined by combining functional response results with a measure of metabolizable energy called the true metabolizable energy values (TME). While not used in this study, it is important to mention another commonly used measure for metabolizable energy called the assimilation energy (AE) (Richman and Lovvorn 2003, Richman and Lovvorn 2004, Wells-Berlin 2008, Schafer 2008, Lovvorn et al 2009, Wells-Berlin 2015). Like TME, AE measures the energy a predator gains upon consumption as a function of energy gained and lost through excretion and urine. AE is used in many other functional

response analyses similar to this study. In fact, as mentioned earlier, AE values are a key part of the research from which the entire black duck study is modeled.

The metabolizable energy intake curves created in this study suggest that of the five tested food items, SAV species are significantly the most energetically valuable prey to black ducks, although not statistically different from each other (Figure 13 and 14, Table 6). The same TME estimate was used for both SAV species, so it's not possible through this study, but it would be interesting to see how the relative value of *Z. palustris* would change in relation to *R. maritima* after being calculated with its own specific TME value. Additionally, although these were the only two SAV species used, it would be noteworthy to compare the energetic value of other common Bay grass species. The next most valuable prey item was *G. holbrooki* (Figure 16, Table 6). *G. holbrooki* had the highest TME value of any other prey item tested in this study; however, due to their high mobility and consequently higher handling times, the fish were still less valuable overall as compared to the SAV species. The final two prey items demonstrated much lower energy gains for the ducks than the fish and grasses, though as already discussed, these two species have added ecological interactions with black ducks aside from a purely predator prey relationship. *S. validus* was more valuable than *M. bidentatus*, but still exhibited the second lowest metabolic intake rate of all tested species (Figure 15, Table 6). *Scirpus spp.*, as a whole, have been shown to produce uniformly low metabolizability values (Sherfy 1999), yet are still considered a staple in black duck diets and are typically targeted in waterfowl management plans (Hindman and Stotts 1989). Finally, the lowest quality prey



item, *M. bidentatus* (Figure 17, Table 6), provide low energetic gains, similar to snails, but are also consistently included in black duck diets (Costanzo and Malecki 1989, Cramer et al 2009, Cramer et al 2009, Eichholz and Yerkes 2010, Coluccy et al 2015). *M. bidentatus* are highly abundant along the Bay and can sometimes exceed densities of several thousand per square meter (Heitkamp and Zemella 1988, Gittenberger et al 2004, Anders et al 2009, Cadee 2011). They also have relatively thin and easily digestible shells (Coluccy et al 2015). Such easy capture and digestibility may be part of the reasoning behind black ducks so often foraging for snails with so little energy gain in return.

When the energetic quality of food items in this study were further analyzed and the hypothetical total amount of food required and total foraging time a black duck would need to undergo in order to meet their energetic demands were calculated (Table 7), the SAV species were once again portrayed as the most superior quality food item, while snails were clearly the least energetically valuable prey. Based on the calculations, black ducks would need to spend under ten minutes eating SAV as compared to the over twenty six hours needed for consuming snails in order to meet their daily energetic demands (Table 7). These calculations suggest that snails alone should not be enough to sustain black ducks. However, black ducks are opportunistic and generalist feeders, and unlike the trials in this study, black ducks in natural environments are not limited to only one type of prey. Black ducks will feed on whatever prey are available, and will simultaneously forage for multiple prey species. It is also important to note that TME values are purely measures of energy content and do not address nutritional

values, such as lipid and protein content of prey items (Sherfy 1999). Further research should be conducted to examine the nutritional aspects of the prey species used in this study. Accordingly, snails, although not enough on their own, cannot be discounted as an important prey species.

### Management Implications and Continued Research

Eventually, the results of this study will be used in determining specific habitats to conserve in order to help manage wintering black duck populations within the Chesapeake Bay watershed. Black ducks are considered an outcome species of the Bay. Consequently, in theory, as a byproduct of increasing black duck populations and their habitats, the overall health of the Bay will also benefit. This study is a specific piece of a much larger overarching bioenergetics project. Thus, while black duck functional response curves are an important contribution of otherwise missing information, our results cannot be extrapolated beyond giving information on foraging behavior. Functional response and metabolic energy intake cannot be used in determining or inferring prey preference. Additionally, intake rates do not given any insight into competition interactions. Black ducks were the only consumer species tested. While results of this study suggest that SAV is the most valuable food choice, black ducks may be wholly or partially excluded from patches by competitively superior waterfowl species that also depend heavily on SAV consumption. If this is the case, the predicted benefits of SAV management for black ducks could be severely overestimated. As with competition, functional responses do not address prey distribution. Trials simulated foraging in a single prey patch. Accordingly, the tested individuals

were not required to make decisions associated with the previously discussed optimal foraging theory and prey choice model. The potential impacts and related costs of competition for access to food and patchy or scattered prey distributions need to be considered before a complete understanding of black duck conservation and management can be obtained.

The functional response trials conducted in this study give us information about optimal prey densities for black ducks. The critical foraging densities concluded in this study were 749 g/m<sup>2</sup> for *R. maritima*, 435 g/m<sup>2</sup> for *Z. palustris*, 26 g/m<sup>2</sup> or 91 fish/m<sup>2</sup> for *G. holbrooki*, and 1.4 g/m<sup>2</sup> or 24 snails/m<sup>2</sup> for *M. bidentatus*. *S. validus* did not have a critical density as a result of having a linear relationship between intake rate and prey density. The densities determined in this study should be considered in future management decisions concerning black ducks and their environments, and should be incorporated into the black duck bioenergetics model.

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