# Consequences of Diet Specialization for American Oystercatchers

A Thesis Submitted to the Committee on Graduate Studies in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in the Faculty of Arts and Science

Trent University, Peterborough, Ontario, Canada

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# Abstract

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American Oystercatchers (*Haematopus palliatus*) are a coastal shorebird of conservation concern, whose diets can shape their habitat space use, ecological niches, and relationship to other shorebirds. I used focal observations on foraging adults and provisioning of chicks complemented with GPS tracks of foraging movements to study diet of breeding American Oystercatchers on two barrier islands in Virginia, U.S.A. during 2022–2025. I documented the first case of diet specialization for this species, where some individuals primarily eat a single prey species, the mole crab (*Emerita talpoida*). Diet specialization was best explained by energetics, whereby traveling to forage on distant mussels (*Modiolus demissus*) cost specialists 42% more energy compared to traveling to forage on nearby mole crabs. I showed that mole crabs were an essential food source for American Oystercatchers, and organizations should protect beach habitat for mole crabs to help conserve American Oystercatchers. Second, I tested if foraging factors including diet, foraging distance, food profitability or chick provisioning rates influenced nest or brood survival. In this study system, foraging factors did not limit nest or brood survival. Instead, nest survival was driven by interannual variation in predator and storm activity and brood survival was driven by age. Third, I documented egg stripping of mole crabs in American Oystercatchers and Hudsonian Whimbrels (*Numenius hudsonicus*). Fourth, the egg stripping behavior, where American Oystercatchers remove the eggs of mole crabs and discard the carapaces, led to a facultative foraging commensalism with Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Calidris alba*) who follow American Oystercatchers to eat the discarded carapaces. By doing so, these species enhance their foraging efficiency. Fifth, I

compared the diets of male and female American Oystercatchers. In contrast to most oystercatcher species around the world, American Oystercatcher males and females show a 99% identical diet, which likely occurs due to a lower intra-species competition pressure at the study site. Sixth, I described a field technique for visually distinguishing the sexes. Using a combination of sexual dimorphism in bill color and length, back plumage color, and overall body size, males and females can be differentiated from a distance in the field.

**Keywords.—** barrier islands, breeding success, commensalism, foraging, individual specialization, GPS tracking, mole crab, sexual dimorphism, shorebird.

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# Chapter 1 – General Introduction

Optimal foraging theory dictates that individuals should forage in a way that maximizes their fitness (Pyke *et al.* 1977). Optimal foraging involves a currency (e.g., energy intake per unit time); constraints (e.g., predation risk); and a way to solve for the optimum (Schoener 1971). Optimal foraging theory involves decisions surrounding diet (which food items to eat); which foraging habitats to visit; time spent per foraging habitat; and which foraging path or strategy to adopt (Pyke *et al.* 1977).

Ecological niche theory defines the conditions where an animal lives and eats (Vandermeer 1972). The realized niche is a subset of the fundamental niche (abiotic conditions that define where a species lives, Grinnell 1924), and is occupied after the biotic conditions (animal's interactions with its environment and other species) are incorporated (Elton 1927; Bruno *et al.* 2003). Diet is a key component of the realized niche, and niche partitioning of diet through specialization on certain food resources can reduce competition and allow groups or individuals to coexist (Schoener 1974). For example, dietary niche partitioning across assemblages of multiple species of shorebirds allows thousands of shorebirds to stopover at the same site, while still meeting their migratory refueling needs (Bellefontaine and Hamilton 2023). Similarly, within Western Sandpipers (*Calidris mauri*), dietary specialization within age and sex classes reduces food competition and lets conspecifics refuel prior to spring migration (Hall *et al.* 2021).

Diet specialization, where some individuals only eat a subset of the resources available to them, can lead to different ecological niches in a population (Araújo *et al.* 2008). Populations may appear to have a generalist diet of a variety of resources, when actually different specialists make up the population (Bolnick *et al.* 2002). Individual specialization has been studied in the

context of foraging and can occur at short or long temporal scales (van de Pol *et al.* 2010; Catry *et al.* 2014).

Diet specialization is important at the level of the individual because of its potential adaptive value for foraging efficiency (van de Pol *et al.* 2010; Terraube *et al.* 2014), chick provisioning (Woo *et al.* 2008) and body condition (Durell *et al.* 2001), which can increase growth rates of young (van den Bosch *et al.* 2019) and improve chick survival (Safriel 1985; Pierotti and Annett 1990; Watanuki 1992). For example, Eurasian Oystercatcher shellfish specialists have higher body condition than worm specialists (Durell 2003), and Montagu's Harriers (*Circus pygargus*) that specialize and hunt voles (*Microtus* spp.) have higher hunting success than those with generalist diets (Terraube *et al.* 2014). For Eurasian Oystercatchers (*Haematopus ostralegus*) and Slaty-backed Gulls (*Larus schistisagus*), parents that provision chicks with a specialized diet have higher breeding success (Safriel 1985; Watanuki 1992). Similarly, White-tailed Eagles (*Haliaeetus albicilla*) that specialize and feed fish to chicks have higher breeding success but lower adult survival than those with more generalist diets (Nebel *et al.* 2023).

Diet specialization can shape a species' ecology and make some individuals more susceptible to certain environmental changes like extreme weather (van der Kolk *et al.* 2020). Eurasian Oystercatcher worm specialists have more flexibility than shellfish specialists to move to inland grassland habitat if feeding conditions are poor in intertidal areas (e.g., high water levels that inundate mudflats) (van der Kolk *et al.* 2020). Because of shellfish shortages and a 10-day cold snap, in 2012, 1,100 Eurasian Oystercatchers died in the German Wadden Sea. Most mortalities were shellfish specialists (Schwemmer *et al.* 2014).

The oystercatchers (genus *Haematopus*) are shorebirds belonging to the order *Charadriiformes* and the family *Haematopodidae* (Baker 1972; Heppleston 1973; Ahlquist 1974). *Haematopus* has distinctive bright red/orange bills that contrast with solid brown/black or pied (brown/black and white patterned) body plumage (Baker 1972; Heppleston 1973; American Oystercatcher Working Group *et al.* 2020). They are slightly sexually dimorphic but not strongly dichromatic (Baker 1974; Zwarts *et al.* 1996; Kraaijeveld-Smit *et al.* 2001; Hansen *et al.* 2009; Roodenrijs *et al.* 2024). They live primarily on coasts, and nest on either sandy or pebbly beaches or rocky shorelines (Lauro and Nol 1995b; Quintana *et al.* 2021; MacLaurin *et al.* 2026). Like many shorebirds, they have relatively low seasonal reproductive success (Nol 1985; Hazlitt and Butler 2001; Quintana *et al.* 2021; Call *et al.* 2025; Brown *et al.* 2026). *Haematopus* rely heavily on marine invertebrates for food (Hockey and Underhill 1984; Nol 1989; Hulscher 1996). Their bill morphology has evolved to be specially adapted at opening marine bivalves (Baker 1972; Swennen *et al.* 1983; Hulscher 1996). In *Haematopus*, diet is typically linked to sex (Sutherland *et al.* 1996; Lauro and Nol 1995a; Kohler *et al.* 2009; Aplin and Cockburn 2012; Rankin 2023). Diet specialization has been described for five species of birds within *Haematopus* (Sutherland *et al.* 1996; Lauro and Nol 1995a; Kohler *et al.* 2009; Aplin and Cockburn 2012; Rankin 2023), although it has not previously been documented for American Oystercatchers (*Haematopus palliatus*).

*H. palliatus palliatus* is among one of five subspecies of American Oystercatchers (American Oystercatcher Working Group *et al.* 2020). Its breeding range spans from New Brunswick and Nova Scotia, Canada to Florida, U.S.A., as well as along the Gulf Coast of the U.S. and Mexico (American Oystercatcher Working Group *et al.* 2020).

*H. palliatus palliatus* is listed as state threatened in Florida and Georgia, U.S.A. (Schulte and Simons 2015), and is considered a species of conservation concern (Clay *et al.* 2014) in other U.S. states, including Virginia. Known threats to eggs and young include predators (Sabine *et al.* 2006; Denmon *et al.* 2013; Schulte and Simons 2015; Walters *et al.* 2020) and human disturbance (Sabine *et al.* 2008; Schulte and Simons 2015; Borneman *et al.* 2016; Walters *et al.* 2020). American Oystercatchers are long-lived, often surviving 10 to 20 years (American Oystercatcher Working Group *et al.* 2020), with high adult survival (Wilke *et al.* 2017; Murphy *et al.* 2017), so conservation efforts tend to focus on improving breeding success. To protect the species, many conservation organizations in the U.S. manage the known threats of predators and human disturbance by trapping predators and limiting public access to nesting beaches (Walters *et al.* 2020; American Oystercatcher Working Group *et al.* 2020). However, previously, little was known about the role of diet at large or diet specialization in breeding success.

Chick survival appears tightly coupled to the food supply for *Haematopus* spp. (Nol 1989; Ens *et al.* 1992; Robinson *et al.* 2019; Vitale *et al.* 2022), with foraging diet, foraging distance, food profitability (food mass/handling time), and chick provisioning rates influencing fledging success (Safriel 1985; Nol 1989; Ens *et al.* 1992; Hazlitt *et al.* 2002). Oystercatcher adults feed and provision chicks bivalves and marine invertebrates from bayside mudflats, marshes, oyster reefs, and oceanside shorelines (Nol 1989). *Haematopus* spp. chicks are provisioned by adults one month past fledging (Kersten 1996). Because of this lengthy provisioning, diet has the potential to influence chick survival.

The state of Virginia in the U.S., is home to the highest concentration of breeding American Oystercatchers throughout their range (Wilke *et al.* 2005). However, since 2016, on two Virginia barrier islands, breeding productivity (chicks fledged per breeding pair) was lower

(range: 0–0.32 chicks fledged per breeding pair) than the level required to maintain the population (0.5 chicks fledged per breeding pair) (Schulte 2021), despite current management efforts to trap predators and limit recreational beach access to nesting areas with symbolic fencing. Thus, other factors like the food supply could be involved in breeding success.

This thesis started as an in-depth study of how diet might be involved in breeding success. After the second year of data collection, I noticed a subset of American Oystercatchers breeding on a barrier island in Virginia who appeared to only eat mole crabs (*Emerita talpoida*), a marine invertebrate. The principal objective of my Ph.D. dissertation developed into documenting diet specialization in American Oystercatchers, and the effects on habitat space use and reproductive success. To do this, I used a combination of behavioral observations on foraging adults and chick provisioning, along with GPS tracking of the movements of foraging birds. Through these observations, I revealed insights into other unique aspects of American Oystercatcher foraging including a specialized foraging behavior on mole crabs that supports a foraging commensalism with migratory shorebirds. I also compared the diets between the sexes. To do this, first, I verified a visual sexing technique to differentiate the sexes, using photographic methods and molecular tools.

## Thesis Objectives

The initial objective of this thesis was to:

1) Determine if foraging factors including diet, foraging distance, food profitability, or chick provisioning rates affected nest or chick survival.

As the research developed, the following objectives were identified:

2) Describe diet specialization for American Oystercatchers nesting in Virginia, U.S.A. and the reasons for its existence in this case.
3) Describe a novel foraging behavior for eating mole crabs for two species of shorebirds and postulate the circumstances leading to this behavior.
4) Document a foraging commensalism that American Oystercatchers support for Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Calidris alba*) based on their mole crab egg stripping behavior.
5) Compare the diets of male and female American Oystercatchers within the context of other oystercatcher species around the world.
6) Validate a technique for visually sexing American Oystercatchers in the field.

## Thesis Structure

In Chapter 2, I describe the first recorded instance of a group of American Oystercatchers breeding in Virginia, U.S.A. who have specialized diets and feed primarily on mole crabs. I examined if diet specialization impacted foraging efficiency, adult body condition, or chick provisioning. I test if six non-mutually exclusive mechanisms explained diet specialization including mole crab abundance, intra-species competition avoidance, kleptoparasitism avoidance, human disturbance avoidance, ecological opportunity, and/or energetics.

In Chapter 3, I examine if diet specialization had consequences for reproductive success. I included diet specialization along with other foraging factors (foraging distance, food profitability, and chick provisioning rates) in models of nest and chick survival. The model results allowed me to determine the factors limiting reproductive success on two barrier islands in Virginia, and make management recommendations for increasing breeding productivity.

Digestive bottlenecks are where individuals must take a break from feeding temporarily, so their bodies have a chance to digest the food (Kersten and Visser 1996; Zharikov and Skilleter 2003). The digestion rate model extends optimal foraging theory to incorporate digestibility of the food in foraging decisions (Verlinden and Wiley 1989; Whelan and Brown 2005). Here, individuals choose food items that maximize energy intake and minimize digestive pauses (Quaintenne *et al.* 2010). I used a digestive bottleneck context to understand why a novel egg stripping foraging technique on mole crabs occurs for two shorebird species in Chapter 4. The focus on American Oystercatchers who specialize in feeding on mole crabs introduced a novel feeding behavior surrounding mole crabs. I observed some individuals stripping the eggs from mole crabs and discarding the carapaces. Similar observations were made by a colleague in Oregon, U.S.A. with Hudsonian Whimbrels (*Numenius hudsonicus*) (S. McKeon personal communication). I synthesized our findings in Chapter 4.

Interactions between species can co-evolve to be beneficial, harmful, or neutral for both parties (Mathis and Bronstein 2020). Facilitations involve interactions where at least one party benefits (Stachowicz 2001; Bruno *et al.* 2003). Commensalism occurs if one species benefits and the other species has a net neutral effect (Mathis and Bronstein 2020). While commensalisms may be adaptive, the first step to demonstrate one is to show a non-random association between the species that benefits and the provider. For example, experimental manipulations showed that wading birds (*Egretta* spp.) nest near alligators (*Alligator mississippiensis*) to gain nest protection benefits. For alligators, the effect is neutral, since they do not necessarily eat the wading birds (Burtner and Frederick 2017). While I am unable to test for an adaptive significance of an association, I demonstrate a non-random foraging association between American Oystercatchers and two species of co-occurring shorebirds (Chapter 5). I observed that

the egg stripping of mole crabs facilitated a foraging commensalism among American Oystercatchers and migratory shorebirds who feed on the discards of mole crabs eaten by American Oystercatchers.

Niche partitioning allows for coexistence of conspecifics (Elton 1927). Most oystercatcher species show niche partitioning between the sexes where each sex has a distinctive diet (Durell *et al.* 1993; Lauro and Nol 1995a; Kohler *et al.* 2009; Aplin and Cockburn 2012). By contrast, in Chapter 6, I show that the diets of American Oystercatchers overlap between the sexes. Using focal foraging observations and published studies on other oystercatcher species, I explored why there is overlap in the diets of American Oystercatchers between the sexes while most other oystercatcher species show different diets for each sex.

To tie specific foraging behaviors to unbanded individual breeding pair members, I required a field method for sexing individuals. Traditional sexing methods rely on having the bird in hand to obtain DNA samples (Fridolfsson and Ellegren 1999) or measuring the percentage of eye flecks (Munters *et al.* 2014). In Chapter 7, I verified a visual sexing technique for American Oystercatchers that had been used by previous researchers but without rigorous genetic or morphological confirmation. The technique relied on sexual dimorphism in coloration of back plumage and bill as well as differences in bill length and overall body size. I used photographs of live birds and museum specimens to illustrate color differences between the sexes and confirmed the visually assigned field sex with the molecular sex using DNA from feathers. I used the visual sexing technique to associate diets to individuals in Chapter 2, and to examine sex-specific diets in Chapter 6.

I conclude the dissertation by discussing the conservation implications of diet specialization and future research directions.

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# Chapter 2 – Diet specialization in American Oystercatchers (*Haematopus palliatus*) breeding in Virginia, U.S.A.



An American Oystercatcher (*Haematopus palliatus*) breeding pair foraging on mole crabs and sporting GPS trackers. Photo credit: Jim Emery.

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L. A. Brown led study design, data collection and analysis, writing of the initial draft of the manuscript. E. Nol contributed to data analysis suggestions and editing drafts.

Abstract — Diet specialization in breeding American Oystercatchers (*Haematopus palliatus*) was documented on a barrier island in Virginia, U.S.A. in 2022 and 2023. Behavioral observations ($n$ = 816 observations) of adults foraging for themselves and their chicks, and GPS tracking ($n$ = 20,202 GPS fixes) identified 12 individuals that specialized feeding almost exclusively at oceanside shorelines on mole crabs (*Emerita talpoida*) (>90% of their diet). Ten generalists fed at shorelines plus bayside mudflats, eating six species of bivalves and mole crabs. Diet specialization was best explained by distance from mussels (*Modiolus demissus*), the most profitable prey species, and the energy costs of traveling to mussels. Individuals that had to travel >280 m to reach mussels specialized instead on nearby mole crabs, the second most profitable prey. Traveling to mussels would cost specialists 42% more energy than traveling to forage on mole crabs. There were no significant differences based on diet for maximum foraging distance, food profitability, adult body condition, handling time of mole crabs, chick provisioning rates or chick energy intake rates. Adults might specialize on mole crabs to conserve energy for future breeding seasons. Given this diet specialization, I recommend that American Oystercatcher conservation efforts include managing beaches for healthy mole crab populations.

**Keywords.—** conservation management, energetics, foraging, individual specialization, GPS tracking, movement ecology, niche variation, shorebird.

# Introduction

Within populations there can be a high degree of individual variation and specialization to fill different ecological niches. Niche variation in a population occurs when there are differences in resource use among individuals (Araújo *et al.* 2008). Populations that appear to be generalists and use a variety of resources can be made of different specialists (Bolnick *et al.* 2002). Diet specialists can be defined as individuals whose niche breadth is smaller than the population niche breadth (Svanbäck and Persson 2004). In other words, specialists are individuals that select a subset of resources from the total number of resources available to the population (Bolnick *et al.* 2002; Sargent 2007; Catry *et al.* 2014). Individual specialization has been studied in the context of foraging and can occur at short or long temporal scales (van de Pol *et al.* 2010; Catry *et al.* 2014). Diet specialization occurs during only part of the annual cycle for Black-tailed Godwits (*Limosa limosa*) in winter (Catry *et al.* 2014)) and female Antarctic fur seals (*Arctocephalus gazella*) once seal pups are weaned (Kernaléguen *et al.* 2015).

Diet specialization can benefit individuals because of its potential adaptive value for foraging efficiency (van de Pol *et al.* 2010), body condition (Durell *et al.* 2001), adult survival (Nebel *et al.* 2023), chick provisioning (van den Bosch *et al.* 2019), and chick survival (Safriel 1985; Pierotti and Annett 1990; Watanuki 1992; van den Bosch *et al.* 2019; Nebel *et al.* 2023). Diet specialization can arise in populations because of intra-specific competition, prey abundance, risk avoidance, human disturbance avoidance, or ecological opportunity (Caldow *et al.* 1999; Araújo *et al.* 2008; Araújo *et al.* 2011; Catry *et al.* 2014). According to the niche variation hypothesis, intra-specific competition drives diet specialization in three-spine sticklebacks (*Gasterosteus aculeatus*) (Svanbäck and Bolnick 2005; Svanbäck and Bolnick 2007). Experimental evidence indicates that increasing population density forces individual

three-spine sticklebacks to expand their diets to include additional prey species (Svanbäck and Bolnick 2007). Prey abundance drives diet specialization in individual sea otters (*Enhydra lutris*) because areas with low prey abundance are linked to individuals specializing on a smaller subset of prey types (Fujii *et al.* 2017). Even though risk avoidance could be a possible driver of diet specialization (Araújo *et al.* 2011), no studies that we have examined have documented this across taxa. Human disturbance can also shape foraging decisions in shorebirds (Goss-Custard and Verboven 1993; Burger 1994), so could theoretically drive diet specialization. In this case, birds may avoid foraging at certain habitats due to high levels of human disturbance, and instead specialize and forage on prey found at a subset of foraging habitats with low levels of human disturbance. Although, again, we know of no studies that have documented this. Variation in ecological opportunity (the diversity of resources available and accessible to individuals) can mean that some individuals have a larger set of resources available to them (broader niche width) than other individuals in the population. The broader niche width (higher ecological opportunity), allows these individuals choice to specialize on a subset of resources (Araújo *et al.* 2008), compared to individuals with fewer resources available to them that cannot afford to be choosy and must eat all available prey, resulting in a more generalist diet. Ecological opportunity has been invoked as the driving mechanism for individual specialization in diets of coyotes (*Canis latrans*) (Larson *et al.* 2020), ringed seals (*Pusa hispida*), beluga whales (*Delphinapterus leucas*) (Yurkowski *et al.* 2016), and Antarctic fur seals (Kernaléguen *et al.* 2015). For example, suburban coyotes have higher ecological opportunity because they could access both urban areas and natural lands to forage and showed more specialized diets than urban coyotes (Larson *et al.* 2020). Energetics (the energy costs to do specific activities) is an important criterion determining

foraging in shorebirds (Nol 1985), so could theoretically drive diet specialization, although, we know of no studies that have documented this.

Diet specialization has been described for five species of oystercatchers (*Haematopus* spp.) including the Eurasian (*H. ostralegus*) (Sutherland *et al.* 1996), Black (*H. bachmani*) (Rankin 2023), Sooty (*H. fuliginosus*) (Aplin and Cockburn 2012), Pied (*H. longirostris*) (Lauro and Nol 1995), and African Black Oystercatcher (*H. moquini*) (Kohler *et al.* 2009). In *Haematopus* spp. diet is also often linked to sex (Sutherland *et al.* 1996; Lauro and Nol 1995; Kohler *et al.* 2009; Aplin and Cockburn 2012; Rankin 2023). Female Eurasian Oystercatchers that specialize and feed on polychaetes tend to have longer, more pointed bills, while males that feed on bivalves tend to have shorter robust bills (Durell *et al.* 1993). In Eurasian Oystercatchers, bivalve specialists use foraging areas differently across space and time than worm specialists (van der Kolk *et al.* 2020). While Swennen *et al.* (1983) attributed diet specialization in Eurasian Oystercatchers to prey availability, in a 26-year dataset, van de Pol *et al.* (2010) failed to find support for prey abundance or intra-specific competition as the driver for diet specialization.

Despite the prevalence of diet specialization within *Haematopus*, diet specialization has not been documented in American Oystercatchers (*H. palliatus*). Diet specialization was proposed for American Oystercatchers breeding in Brazil because stable isotope analyses revealed variation among 12 breeding pairs in the diets provisioned to chicks (de Andrade Linhares *et al.* 2022), although the degree to which any individual specialized was not established. In a separate study in Brazil, also based on stable isotope analyses, American Oystercatchers showed diet variation across five sites (Gliesch *et al.* 2023). However, diet specialization was not tested for nor established in that study.

The American Oystercatcher (*H. palliatus palliatus*) breeds along the Atlantic Coast of the U.S.A. (American Oystercatcher Working Group *et al.* 2020). Adults feed and provision chicks on bivalves and marine invertebrates from bayside mudflats, marshes, oyster reefs, and oceanside shorelines (Nol 1989). Since opening bivalves takes significant time and energy, kleptoparasitism occurs, where other American Oystercatchers steal bivalve prey (Tuckwell and Nol 1997a; García and Biondi 2011). In contrast to other oystercatcher species, in American Oystercatchers, both sexes share the same diet (Brown and Nol 2024, Chapter 6). Oystercatcher species are limited to carrying single prey items to chicks (Kersten 1996). Breeding pairs can support chick growth by provisioning chicks at high rates (making many provisioning trips) (Hazlitt *et al.* 2002; Tjørve and Underhill 2009) or choosing prey items that maximize caloric energy delivered to the chicks (Safriel *et al.* 1996; de Andrade Linhares *et al.* 2022). Because of the time required to develop the musculature and bill strength to open bivalves, as well as the handling skill to correctly handle bivalves (Cadman 1980; Hand *et al.* 2010), American Oystercatcher chicks can be provisioned past the age of fledging until they are at least 60 days old, when they can forage independently (American Oystercatcher Working Group *et al.* 2020).

In 2022 and 2023 preliminary observations suggested that a subset of American Oystercatchers breeding on a barrier island in Virginia, U.S.A. appeared to only eat mole crabs (*Emerita talpoida*), a small marine invertebrate that inhabits open, high-intensity beaches. This was unusual since most individuals appeared to feed on a wide variety of bivalve prey including the Atlantic ribbed mussel (*Modiolus demissus*), hereafter referred to as mussels, the most profitable prey species (Supplementary Table S2.1). Optimal foraging theory predicts that individuals should choose the most profitable prey, all else being equal e.g., predation risk while foraging (Stephens and Krebs 1986), so mussels should have been incorporated into the diets of

all American Oystercatchers at the study site. As a follow-up, we sought to determine (1) if diet specialization on mole crabs exists in a population of American Oystercatchers breeding on two barrier islands in Virginia; (2) how foraging area use varied across space and time based on diet; (3) the adaptive value of diet specialization in terms of foraging efficiency, adult body condition, and chick provisioning; and (4) potential mechanisms explaining diet specialization. Specifically, we tested if six non-mutually exclusive mechanisms explained diet specialization including mole crab abundance, intra-specific competition avoidance, human disturbance avoidance, kleptoparasitism risk avoidance, ecological opportunity, and/or energetic costs. If mole crab abundance was the main driver of diet specialization, we predicted that mole crab abundance would be higher in areas with diet specialists than with generalists. If intra-specific competition was the main driver of diet specialization, we expected that individuals would specialize to avoid food competition with other American Oystercatchers, so specialists should distribute themselves throughout the population and be inter-mixed with generalists. If human disturbance avoidance was the main driver of diet specialization, we predicted that specialists would occur in areas without recreational access, since individuals would be free to feed on mole crabs at oceanside shorelines without being disturbed. If kleptoparasitism risk avoidance was the main driver of diet specialization, we predicted that mole crabs should be kleptoparasitized less frequently than bivalves because mole crabs have a lower food reward (wet mass mean ± SE = 2.51 ± 0.48 g, Supplementary Table S2.2) relative to other prey items like mussels (6.31 ± 1.01 g) or oysters (*Crassotrea virginica*, 3.44 ± 0.50 g). If ecological opportunity was the main driver of diet specialization, we predicted that specialists would occur in areas with access to a higher diversity of prey species that would let individuals choose mole crabs as a subset of prey to specialize on. If energetic costs were the main driver of diet specialization, we predicted that individuals would

specialize on mole crabs because that prey was the least energetically costly to travel to, due to its proximity to nests.

# Methods

## Study Area

The study islands were Assateague Island (37°51’7.2”N, 75°22’55.2”W) and Assawoman Island (37°48’3.6”N, 75°31’4.8”W), two barrier islands in Virginia, U.S.A. that are a part of Chincoteague National Wildlife Refuge. Assateague Island is divided into three management sites, Public Beach, which allows pedestrians, the Overwash, which allows over-sand vehicles and pedestrians, and the Hook, which is closed to the public during the breeding season from mid-March to mid-September (Supplementary Fig. S2.1). Assawoman Island is closed to the public during the breeding season. We collected data during the breeding season from April to August of 2022 and 2023. Assateague Island supported 20–25 breeding pairs and Assawoman Island supported 31–32 breeding pairs. Foraging habitats on both islands included oceanside shorelines with marine invertebrates such as mole crabs and coquina *(Donax varibilis*), and bayside mudflats and marshes with mussels, oysters, clams (*Mercenaria mercenaria*), and razor clams (*Tagelus plebeius* and *Ensis directus*).

## Data Collection

We investigated diet and foraging strategies in the population using behavioral data from observations on adult foraging and chick provisioning, and movement data from GPS tagged individuals. We illustrated the methods using a conceptual road map (Fig. 2.1).

# DATA COLLECTION

BANDING



GPS TAGS -
GPS TRACKING DATA &
BEHAVIOURAL OBSERVATIONS
-FORAGING ADULTS
-CHICK PROVISIONING



NO GPS TAGS -
BEHAVIORAL OBSERVATIONS
-FORAGING ADULTS
-CHICK PROVISIONING



DIET CLASSIFICATION

NEST MONITORING



PREY AVAILABILITY
& ABUNDANCE



-DISTANCE TO PREY
-ENERGETIC COSTS



**Figure 2.1.** Conceptual road map of data collection process for studying diet specialization in American Oystercatchers (*Haematopus palliatus*) at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2023.

*Capture and banding.* To capture American Oystercatchers, we buried leg loop carpets around nests and lured breeding pair members to the nest area for capture using wooden decoys and playback alarm calls. Upon capture, we banded individuals using standardized protocols of the American Oystercatcher Working Group (2023). We banded each bird with unique alphanumeric color-coded bands. We took standard morphometric measurements of body mass (g), unflattened wing chord length (mm), tarsus length (mm), and culmen length (mm). We calculated body condition as the unflattened wing chord length/body mass.

*GPS Tags.* For 10 individuals we also attached a GPS tag (PathTrack Ltd Nanofix® GEO + RF, 9 g) to examine fine-scale foraging movements including identification of diet. GPS tags were deployed on incubating American Oystercatcher adults at Assawoman Island ($n$ = 6) and Assateague Island, Virginia ($n$ = 4) from 16 May–2 June 2023 (Supplementary Table S2.3). We chose which individuals to tag to maximize spatial coverage across the two islands. Only a single member of a breeding pair received a GPS tag. The combined mass of the GPS tag and harness was 15 g, which was 2.5% of the average American Oystercatcher's body mass in the study population ($\bar{x}$ = 593.28 ± 8.03 g, $n$ = 36), and within the recommended limit for external tags on birds (Kenward 2000). The tag was attached 6 cm above the rump of the bird and was elevated with a 5 mm neoprene patch to prevent abrasion. The GPS tag was attached with a custom-fit leg loop harness that rested against the bird's body and above the femur/tibia, so that leg and wing movement were not impeded. The leg loop harness was made of 1.5 mm Stretch Magic™ encased in Teflon ribbon tubing (Bally Ribbon Mills). Harnesses were triple reinforced to

prevent them from coming undone. The three reinforcements included crimping the ends of the harness with leader sleeves (American Fishing Wire™ 2.69 mm 0.106" inner diameter); sewing the ends of the harness back onto themselves with nylon quilter's thread; and supergluing the ends of the harness with Loctite™ or Gorilla™ super glue. After the handling process, we monitored pairs from a distance to ensure that adults returned to incubating the nest and resuming normal activities.

Nine GPS tags were scheduled to take a GPS fix every 15 minutes during the breeding season from April to August 0400–2059 EST, using the solar-driven mode. One GPS tag was scheduled to take a GPS fix every half hour from 0000–2459 during the breeding season, so that nocturnal movements could be examined as part of a different study.

We downloaded GPS data remotely using a PathTrack Ltd base station capable of one-way remote ultra-high frequency (UHF) radio wave communication. We programmed GPS tags to attempt to connect to the base station for data download every hour. The GPS tags needed to be in clear range of the base station and in contact for 1–5 min for data to be downloaded. We placed the GPS base station on top of a dune or on a raised 2' wooden pole within 100–200 m of the nest or chick rearing area of a tagged individual and left the base station out for 24–72 h in a single location to maximize the chances that data would be downloaded. We rotated the GPS base station around the breeding areas of tagged individuals, and attempted to download data from each tagged individual every 2–3 weeks.

We processed GPS data by removing GPS fixes taken with fewer than five satellites; removing duplicate timestamps; and visually checking for outliers. We standardized sampling rates to a frequency of every 15 minutes. We used the R packages 'amt', 'move', and 'moveVis' to import and visualize the GPS data in R (Signer *et al.* 2019; Schwalb-Willmann *et al.* 2020;

Kranstauber *et al.* 2023). For all individuals, we analyzed GPS fixes during the breeding interval when individuals' movements are tied to their nest site (date individual had the GPS tag deployed on them at their nest, until the end of the last nesting attempt (nest/brood failure or date that the brood fledged at 35 days old)) (Supplementary Table S2.3).

*Nest Monitoring.* We assisted the U.S. Fish and Wildlife Service with monitoring American Oystercatcher breeding activities from 1 April–31 August in 2022 and 2023. We monitored nests two to three times per week, following the American Oystercatcher Working Group protocol (2022) which allowed us to determine nest failure dates and brood fledge or failure dates. To determine chick ages, we increased our visitation to a nest to visit every day during the scheduled three days prior to hatch, so we could visit the nest the exact day it hatched. If we were unable to be present the day a nest hatched, we gauged chick age based on the size and appearance of the chick, or by taking the median date between nest visits.

*Adult Foraging and Chick Provisioning.* We conducted 10-min observations on foraging adult American Oystercatchers. We used 10 x 42 binoculars and 60x spotting scopes to observe individuals and visually track individuals to foraging locations. During observations we recorded prey species, handling time (time from the initial dart probe when the bill is fully inserted into the substrate, until the prey is swallowed as per Tuckwell and Nol 1997b), and search time (time once a prey is swallowed, until the next handling time begins as per Tuckwell and Nol 1997b), foraging location, tidal level, band combinations, and breeding pair ID. In 2022 we used 'Otter', a voice transcription app to record handling and search time; whereas in 2023 we developed a custom timer app by using Mohler's (2023) base code, which allowed observers to record search and handling times of prey species eaten, using a timestamp on their mobile devices. We recorded metadata about foraging observations using Survey123 for ArcGIS.

We characterized each foraging observation by its foraging efficiency, using food profitability (wet food mass (g)/handling time (s)) as per Nol (1989). We used the average wet food mass for each prey species in calculations of food profitability. To determine average wet food mass, we collected a minimum of 10 individuals for each prey species, then bootstrapped the sample for 1,000 simulations to develop confidence intervals for the simulated sample estimates (Supplementary Table S2.2). We ensured that prey individuals collected represented sizes that American Oystercatchers would take by only selecting prey of sizes that corresponded to articulated (opened) bivalve shells found at foraging areas.

During chick rearing (hatch date to day 60), we conducted one-hour observations of chick provisioning. During chick provisioning observations we recorded the number of prey items fed to chicks, prey species, foraging location, and breeding pair ID. We compared chick provisioning across breeding pairs by calculating chick provisioning rates (sum of the number of prey items delivered to the brood by both pair members/number of chicks in the brood/observation duration (h)).

We also compared chick provisioning across breeding pairs based on chick energy intake rate. To do this, we first determined the caloric value for the average dry prey mass of each prey species by using published values of caloric content of dry prey mass (Armitage and Alevizon 1980; Nelson *et al.* 1996; McKinney *et al.* 2004; Hostert 2014; Witbaard *et al.* 2013). We combined these with our average wet prey mass determined in food profitability calculations described above and published values on moisture content of prey (Nelson *et al.* 1996; McKinney *et al.* 2004; Özden *et al.* 2009; Santoso *et al.* 2015; Szkoda *et al.* 2015; Zhang *et al.* 2017). This gave us the formula: kcal of dry prey mass = average prey wet mass x (100% - % moisture) x kcal/g of dry prey mass (Supplementary Table S2.4). We used the caloric content to

calculate chick energy intake rate as the kilocalories delivered to the brood by both pair members (kcal)/number of chicks in the brood/observation duration (h)).

*Diet Classification.* We used different methods to classify diets for individuals versus breeding pairs, and used different methods depending on if an individual had a GPS tag or not. For GPS tagged individuals, we classified them as specialists if individuals only visited the oceanside shoreline to feed (habitat for mole crabs and coquinas), and generalists if individuals foraged at both oceanside shorelines and bayside mudflats (habitat for mussels, oysters, clams, and razor clams). Most individuals without GPS tags were banded, so we used data from foraging observations to define specialists as individuals that only ate mole crabs, and where we had a minimum of three independent foraging observations that occurred on separate days. Some individuals that we classified as specialists also consumed a diet that contained ≤ 7% coquina*,* an ocean intertidal-dwelling bivalve. As coquina was only temporarily available for three weeks in the summer of 2022, and a few days in 2023 individuals could not incorporate this prey species regularly in their diet. We defined generalists as individuals that ate any prey species in addition to mole crabs or coquina and had a minimum of two foraging observations that occurred on separate days.

The diets of breeding pairs were classified as specialist or generalist based on foraging and chick provisioning observations. Specialist breeding pair members meant that both breeding pair members were specialists. To classify a breeding pair as specialist, we required a minimum of three observations per breeding pair, and only mole crabs or coquina could be eaten or provisioned across all observations. Generalist breeding pairs meant both breeding pair members were generalists. To classify breeding pairs as generalists, we required at least two observations per breeding pair, where any prey species other than mole crabs or coquina were eaten or

provisioned. Only one breeding pair had one pair member that was a specialist and one that was a generalist, and we excluded this pair from analysis, due to insufficient statistical power.

In addition to formal foraging observations, we further confirmed diets for individuals with our informal foraging checks. Informal foraging checks consisted of observations <10 min on each individual where we observed prey items eaten. Informal foraging checks occurred as we passed by each breeding individual during regular nest monitoring surveys and foraging observations. Assateague Island was accessible on foot or by vehicle, so each individual could be informally checked twice during each visit; once when the observer travelled the length of the island, and again when the observer returned. Assateague Island could be visited five times per week by two observers combined. Assawoman Island was more remote and only accessible on foot, so each individual could be informally checked once per visit. A single observer visited Assawoman Island three times per week to make informal foraging checks.

*Maximum Foraging Distance and Diet.* We determined the maximum foraging distance for each nest based on GPS tracking data and behavioral observations. We focused on the maximum foraging distance for each nest because generalists also ate mole crabs near nests in addition to other prey species at distant mudflats, so including all foraging distances as an average would have biased foraging distances for generalists to be lower, and obscured the energetic cost associated with traveling to distant foraging areas. For GPS tracking data, we assumed that movements were associated with foraging, since most activity when American Oystercatchers are moving corresponds with foraging (19% for foraging versus 5% for walking and <1% for territorial chases, as opposed to the ~75% of remaining activities that corresponds with non-moving behaviors (Nol 1985). We measured foraging distances during the breeding interval (either during incubation or chick provisioning), when breeding pairs are tied to their

nesting site. The breeding interval was defined as the GPS tag deployment date (tagging occurred when individuals had a nest with eggs), until the end of the last nesting attempt (date of the nest/brood failure or the date that the brood fledged at 35 days old). For the behavioral observations, a GPS location was taken for where the individual foraged and could be used in calculations of foraging distance. To measure foraging distance from the nest for both the GPS tracking data and behavioral observations, we used the Haversine method, with the R package 'geosphere', which uses the great circle method to measure the shortest distance between two points (Hijmans 2022).

*Prey Availability and Abundance.* During foraging and chick provisioning observations we noted the location where prey was obtained and the species of prey. We complemented these observations with walking the bayside habitat to record additional locations where prey was available (present). We delineated the availability for each prey species by drawing polygons or line features in ArcGIS Pro. We mapped prey availability as mole crabs, mussels, oysters, mussels and oysters, clams, and clams and razor clams. The distribution of mussels and oysters often overlapped, so we included an additional combined category of mussels and oysters on maps. Similarly, the distribution of clams and razor clams often overlapped, so we included an additional combined category of clams and razor clams on maps. We did not specifically map the distribution of coquina because of its brief availability. Although similar to mole crabs, coquina migrates along the coast with the tide (Ellers 1995), and when available could be found along the entire shoreline of Assateague Island and Assawoman Island. We counted mole crabs along the oceanside shoreline of each island in 2022 and 2023. We controlled for the tide by only sampling during falling tide and no more than two hours after low tide. For detailed methods about mole crab counts, see Supplementary Material 2.1.

*Distance to Nearest Prey.* Based on the prey availability maps, we calculated the distance to the nearest habitat for each prey species for each nest. This was done in ArcGIS Pro using the 'near' tool. The 'near' tool measures distances using Euclidean distance, which is a planar method that relies on straight lines.

*Energetic Costs.* We calculated the energetic cost of traveling one-way to the nearest mole crab habitat compared to the nearest mussel habitat for each breeding pair with a nest in 2022 and 2023 on the two study islands, and we combined this information with diet. We compared the energetic costs of traveling to mole crabs versus mussels, since mussels are the most profitable prey species and the prey that should have been included in all birds' diets at the study site. For calculations, we multiplied distance to the nearest mole crab habitat or distance to the nearest mussel habitat by the energetic cost of traveling to the prey (see Supplementary Material 2.2 for an example calculation). For mole crabs, we calculated the energetic cost of walking to the nearest mole crab habitat, since mole crabs are near nests at the study site. For mussels, we calculated the energetic cost of flying to the nearest mussel habitat, since mussels are farther from nests at the study site. We used published values from the literature for energetic costs (Nol 1985; Speakman and Bryant 1993; Linssen *et al.* 2019). We calculated energetics separately for each sex, due to reverse sexual dimorphism in body size, which leads to sex-dependent energy expenditure (Nol 1985).

*Kleptoparasitism.* In 2022 and 2023 during adult foraging and chick provisioning observations, we incidentally recorded kleptoparasitic events occurring to the focal foraging individual. Kleptoparasitism occurred if an individual's prey was stolen by another individual (Tuckwell and Nol 1997a). When this occurred, we recorded the prey species stolen and the species of the thief.

## Statistical Analysis

*Diet Composition.* To test the degree of specialization within the group of mole crab specialists relative to the group of diet generalists, we used two niche indices – total niche width and the adjusted E index from the R package 'RInSp' (Zaccarelli *et al.* 2013). Total niche width (the total number of resources used by a group) encompasses within-individual variation and between-individual variation that contributes to population niche width. Smaller total niche width values indicate groups that use fewer resources and can be considered specialists (Bolnick *et al.* 2002; Catry *et al.* 2014).

We also used the adjusted E index to test for specialization (Araújo *et al.* 2008) because this index standardizes values, so that each individual equally contributes to a population's diet specialization estimate, regardless of the number of observations made per individual. This standardization prevents many monophagous individuals that only ate one prey species from skewing the population's diet estimate towards the monophagous diet (Zaccarelli *et al.* 2013). Values close to 1 indicate diet specialization and niche partitioning, where there is high dissimilarity in diets between groups, while values close to 0 indicate high similarity in diets across groups (Araújo *et al.* 2008).

To assess if the number of observations was sufficient to classify diets, we calculated accumulation curves for prey species richness, as per Gotelli and Colwell (2001). For diet classification of individuals, we used the adult foraging observations. For diet classification of breeding pairs, we used the chick provisioning observations. We generated curves by randomizing the order of observations within individuals or breeding pairs. The curves show the cumulative number of unique prey species detected as sampling effort increases. If the curve reaches an asymptote, it indicates that a sufficient sample size was reached because additional

sampling effort does not yield observations of new prey species. If the curve does not reach an asymptote, it points towards under-sampling.

*Foraging Metrics.* We used a generalized linear mixed effects model (GLMM) statistical framework to assess how foraging metrics differed based on diet (specialist or generalist). This let us incorporate individual bird ID/breeding pair ID as a random effect to control for repeat observations on the same birds. We developed GLMMs using the 'lme4' and 'glmmTMB' packages (Bates *et al.* 2015; Mollie *et al.* 2017; McGillycuddy *et al.* 2025). We used the package 'DHARMa' (Hartig 2024) to check for fit of the residuals graphically, and test for overdispersion. We used the default GLMM distribution (gamma error distribution with a log link function) unless the model failed to converge, in which case, we used a log normal distribution. We reported model fit using the marginal $R^2$ (proportion of variance explained by the fixed effects) and conditional $R^2$ (proportion of variance explained by the fixed and random effects) from the package 'performance' (Lüdecke *et al.* 2021). We calculated the predicted means and tested for significant differences in the foraging metrics based on diet using pairwise contrast tests of the predicted means from the package 'emmeans' (Lenth 2023).

To assess if diet predicted maximum foraging distance from the nest, we used a GLMM with a log normal distribution and defined the fixed effect as diet (specialist or generalist) and random effect as breeding pair ID to account for multiple nest attempts per breeding pair. To compare if both diets met chick energy needs (chick provisioning rate or energy rate delivered to chicks), we used two GLMMs with the fixed effect as diet, random effects as breeding pair ID and chick age. For both GLMMs surrounding chick energy needs, we included chick age as a random effect to control for increasing energy needs as the chicks grew older. The GLMM for chick provisioning rate had a gamma response distribution and log-link function, while the

GLMM for energy rate delivered to chicks had a log normal distribution. To test if diet impacted mole crab handling time, we used a GLMM with a log normal distribution, and the fixed effect as diet and random effect as individual bird ID. To test for differences in food profitability between generalists and specialists, we used a GLMM with a gamma response distribution and log-link function, and defined the fixed effect as diet and random effect as individual bird ID. To test if body condition differed based on diet, we used a general linear model with gamma response distribution and log link function.

*Distribution of Diet Specialization.* We tested if intra-specific competition drove diet specialization by comparing the spatial distribution of generalists and specialists. We mapped the distribution of all nesting attempts made in 2022 and 2023 for generalist and specialist breeding pairs in ArcGIS Pro, and visually examined if specialists were distributed throughout the population and inter-mixed with generalists. To test if human disturbance drove diet specialization, we mapped the distribution of nests of generalists and specialists against the recreational use areas in ArcGIS Pro, and visually examined if specialists were located in areas without recreational access. To test if ecological opportunity drove diet specialization, we compared access to prey diversity for each diet by first calculating the distance to the nearest prey for each prey species. Then, we interpreted the distance travelled to the nearest prey habitat in relation to what distances are accessible and biologically realistic for American Oystercatchers. We considered prey within 20 km of the nest to be accessible, since GPS tracking of American Oystercatchers in North Carolina, U.S.A. shows that individuals forage up to 20 km from nests (K Goodenough personal communication).

We tested if mole crab abundance drove diet specialization by comparing the spatial distribution of generalists and specialists to mole crab abundance across the study sites. For the

2022 and 2023 data, to determine if mole crab abundance was predicted by month, year, site, or two-way interactions between each pair of predictors or a three-way interaction, we used Poisson regression models. We performed model selection for a set of nine candidate models (including the null model) using Akaike's Information Criterion corrected for small sample sizes (AIC*c*) (Akaike 1974) from the R package 'AICcmodavg' (Mazerolle 2023). The best model was considered the most parsimonious model within 2 AIC*c* units of the model with the lowest AIC*c* value (Hurvich and Tsai 1989; Burnham and Anderson 2002). This analysis was restricted to the two sites for which we had data for both years, the Hook and Overwash at Assateague Island. For the year 2022, to assess mole crab abundance across all study sites (Assawoman Island, and the Hook, Overwash, and Public Beach at Assateague Island) we used a negative binomial zero-inflated model with a log link function from the package 'pscl' (Zeileis *et al.* 2008).

The test if energetics drove diet specialization, we first tested for differences in the distance traveled to each prey species from the nest based on diet using a generalized linear model (GLM) with a gamma distribution and inverse link function, with the predictor as the interaction between diet and prey species and response variable as distance traveled. Second, we tested if a three-way interaction among the fixed effects of diet, sex, and prey species predicted energy costs using a log normal distribution GLMM, with a random effect of breeding pair ID to account for repeated observations on the same breeding pairs between study years. We conducted all analyses using R v. 4.3.1 (R Core Team 2023) and ArcGIS Pro v. 3.2 (ESRI 2011). Raw data and R scripts are available on OSF https://osf.io/dbjsh/?view_only=e6c68e949e9841d78acce7b750472cd3.

# Results

In 2022 we made 295 observations on 53 unique foraging adults and 132 observations on 21 unique breeding pairs provisioning their 36 unique chicks. In 2023 we made 126 observations on 30 unique foraging adults and 263 observations on 44 unique breeding pairs provisioning their 50 unique chicks. Over the two years, we made 680 informal foraging checks across all individuals at Assateague Island during 68 weeks of surveying, and 111 informal foraging checks on each individual at Assawoman Island during 37 weeks of surveying. Across individuals, we collected 20,202 GPS fixes (123–6,632 GPS fixes per individual, Supplementary Table S2.3).

## Diet Composition

*Individual Level.* We used 85 distinct foraging observations when a prey species was eaten across 22 individuals to determine diet composition for individual breeding adults. There were 10 generalists and 12 specialists that had an average of 4.18 ± 0.24 foraging observations per individual with a range of 3–6 foraging observations. Specialists ate two prey species (mole crabs and coquina). Coquina made up 7% of the specialist diet (Fig. 2.2). Generalists also ate mole crabs, coquina, and five other prey species: mussels, oysters, clams, and two species of razor clams. Of the 680 informal foraging checks at Assateague Island, we only observed specialists eating/provisioning chicks mole crabs and the occasional coquina. Across informal foraging checks at Assawoman Island, we observed all individuals feeding on bivalves in addition to mole crabs and coquina. Specialists occupied 15% of the niche width size (total niche width = 0.26) of generalists (total niche width = 1.79). Niche partitioning in diet occurred between generalists and specialists, with both groups generally choosing different prey species ($E_{adj}$ = 0.59, $P < 0.001$).

*Breeding Pairs.* We used 203 distinct foraging observations when a prey species was eaten or provisioned across 26 breeding pairs to determine diet composition for breeding pairs. There were 17 generalist breeding pairs and 8 specialist breeding pairs where we conducted an average of 7.96 ± 1.67 foraging observations per breeding pair with a range of 2–40 foraging observations. In total, American Oystercatcher breeding pairs in the population provisioned seven prey species to chicks, with specialist breeding pairs provisioning two prey species (mole crabs and coquina*,* and coquina made up 3% of the specialist diet), and generalist breeding pairs provisioning six prey species (mole crabs, mussels, oysters, clams, and two species of razor clams) (Fig. 2.2). Total niche width indicated that specialist breeding pairs occupied 8% of the niche width size (total niche width = 0.12) of generalist breeding pairs (total niche width = 1.56). Niche partitioning in diet occurred between generalists and specialists, with both groups generally choosing different prey species ($E_{adj}$ = 0.68, $P < 0.001$).

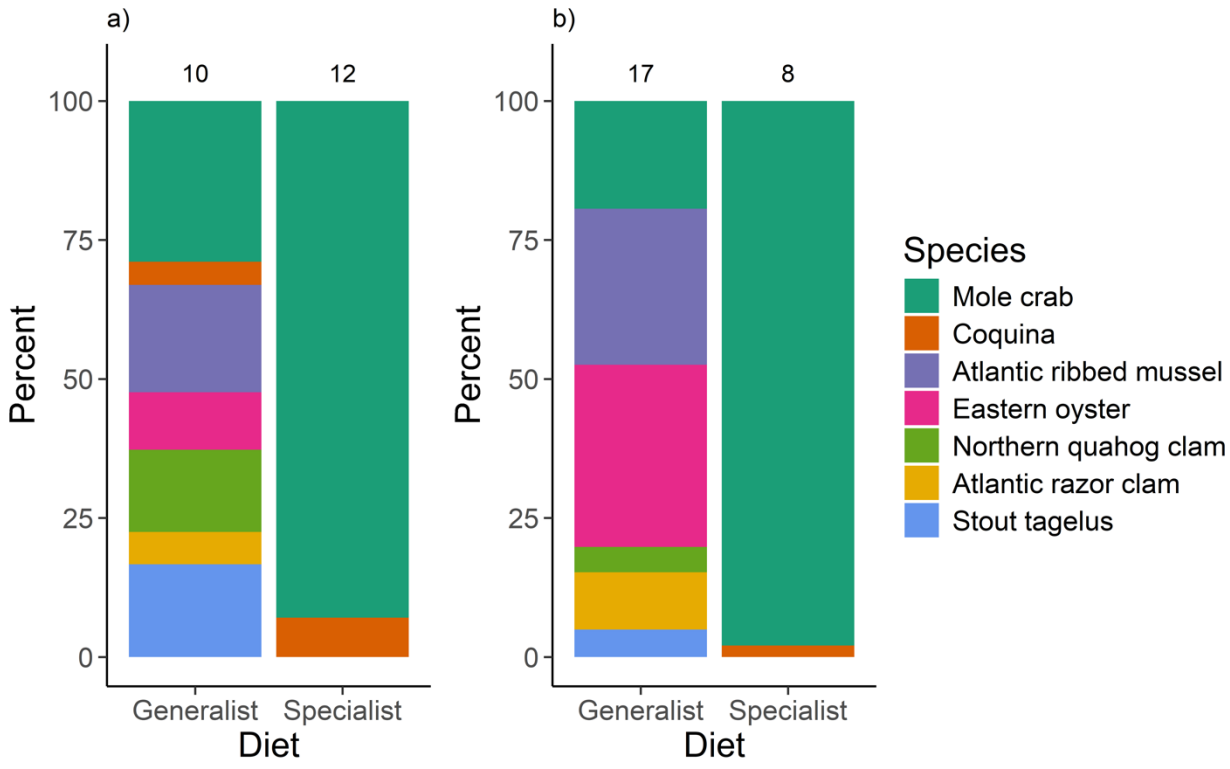



**Figure 2.1.** Diet composition for American Oystercatcher (*Haematopus palliatus*) generalist and specialist individuals at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2023 determined from a) 85 adult foraging observations (10 min duration), where where *n* represents the number of individuals, and b) 184 chick provisioning observations (60 min duration), where *n* represents the number of breeding pairs. Prey species are: mole crab (*Emerita talpoida*), coquina (*Donax varibilis*), Atlantic ribbed mussel (*Modiolus demissus*), eastern oyster (*Crassotrea virginica*), northern quahog clam (*Mercenaria mercenaria*), Atlantic razor clam (*Ensis directus*), and stout tagelus (*Tagelus plebeius*).

The accumulation curves to assess diet classification indicated that for specialists, an asymptote was reached by 2 observations, so 2 observations were sufficient criteria to classify individual specialists (Supplementary Fig. S2.2). In contrast, the curve did not reach an asymptote for generalists, which likely indicates under-sampling and an underestimation of true

diet richness for generalists. For diet classification of breeding pairs, specialists reached an asymptote at 10 observations, while generalists reached an asymptote by 23 observations, although most breeding pairs were classified based on fewer than 10 observations (Supplementary Fig. S2.2). Since the accumulation curves did not always reach an asymptote, the diet classification of individuals and breeding pairs should be interpreted conservatively. Accordingly, the results can be interpreted in a comparative framework rather than as an absolute estimate of total prey species richness in diet.

## Diet and Foraging Metrics

During breeding, across pairs on both islands, 99% of movements (19,961 of 20,202 GPS fixes) occurred within 2,000 m of the nest (Fig. 2.3, Fig. 2.4). The absolute maximum foraging distance for generalists was 16,450 m and 2,165 m for specialists. However, there was not a significant difference in the predicted median maximum foraging distance based on diet (Table 2.1, Table 2.2).

**Figure 2.3 is a video file that can be viewed at this link**
https://osf.io/wg5xb/overview?view_only=97cf9587456f4a9eb85ecb7a31a57fa2.

**Figure 2.3**. GPS-tagged American Oystercatcher (*Haematopus palliatus*) movements at Assateague Island, Virginia, U.S.A. from 19 May–31 May 2023. CEK and CEN were mole crab specialists and only fed on the oceanside shoreline. Remaining individuals were generalists and moved to bayside areas to feed. GPS data was subsetted for a portion of time to highlight the foraging strategies. A running clock shows the time represented in Eastern Standard Time.

**Figure 2.4 is a video file that can be viewed at this link**
https://osf.io/wg5xb/overview?view_only=97cf9587456f4a9eb85ecb7a31a57fa2.

**Figure 2.4.** GPS tagged American Oystercatcher (*Haematopus palliatus*) movements at Assawoman Island, Virginia, U.S.A. from 2 June–18 June 2023. All individuals were generalists

and used both bayside mudflats and oceanside shorelines to feed. GPS data was subsetted for a portion of time to highlight the foraging strategies. A running clock shows the time represented in Eastern Standard Time.

Diet did not significantly impact chick provisioning rate; energy delivered to chicks; food profitability of adults; or handling time of mole crabs, nor did diet explain much variation in the data (Table 2.1, Table 2.2, Table 2.3, Table 2.4). Similarly, there was no difference in adult body condition based on diet (specialists: predicted $\bar{x}$ = 0.44 ± SE 0.04, $n$ = 6, β = 0.03; generalists: predicted $\bar{x}$ = 0.43 ± 0.03, $n$ = 20, β = -0.85, $P$ = 0.50), and diet did not explain much variation in adult body condition (residual deviance = 0.17, null deviance = 0.18).

**Table 2.1. Log normal distribution GLMM results for the effects of diet of American Oystercatchers (*Haematopus palliatus*) on foraging metrics at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023. Coefficient estimate (*βi*), SE, and 95% CI (LCI and UCI) are presented for the fixed effect, and SD is presented for the random effects. Model fit is given as the marginal $R^2$ value (proportion of variance explained by the fixed effects) and conditional $R^2$ (proportion of variance explained by the fixed and random effects). Values are presented on a log scale.**

| Response variable | Effect | Term | *βi* | SE | LCI | UCI | SD | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Maximum foraging distance from the nest (m) | | Intercept | 6.26 | 0.20 | 5.86 | 6.65 | | |
| | Fixed | Diet (Specialist) | 0.10 | 0.35 | -0.58 | 0.78 | | 0.001 |
| | Random | Breeding pair ID | | | | | 0.35 | 0.08 |
| | | Residuals | | | | | 1.23 | |
| Chick energy intake rate (kcal/h delivered to chicks) | | Intercept | 1.34 | 0.20 | 0.95 | 1.73 | | |
| | Fixed | Diet (Specialist) | 0.23 | 0.24 | -0.23 | 0.70 | | 0.01 |
| | Random | Chick age (days) | | | | | 0.37 | 0.44 |
| | Random | Breeding pair ID | | | | | 0.65 | |
| | | Residuals | | | | | 0.86 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Mole crab (*Emerita talpoida*) handling time (s) | | Intercept | 1.73 | 0.21 | | |
| | Fixed | Diet (Specialist) | -0.14 | 0.26 | | 0.004 |
| | Random | Individual bird ID | | | 0.57 | 0.32 |
| | | Residuals | | | 0.85 | |

**Table 2.2. Predicted median, SE, and 95% CI (LCI and UCI) for the log normal distribution GLMMs testing if diet of American Oystercatchers (*Haematopus palliatus*) impacts foraging metrics at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023. The associated pairwise contrast tests are presented for the ratio of the predicted median generalist/specialist, SE, and 95% CI (LCI and UCI). For maximum foraging distance from the nest, *n* was the number of nests. For chick energy intake rate and mole crab handling time, *n* was the number of observations.**

| Response variable | Diet category | *n* | Predicted median | SE | LCI | UCI | Ratio of the predicted medians generalist/ specialist | SE | LCI | UCI |
|---|---|---|---|---|---|---|---|---|---|---|
| Maximum foraging distance from the nest (m) | Specialist | 23 | 577 | 169 | 312 | 1067 | -0.10 | 0.36 | -0.84 | 0.64 |
| | Generalist | 42 | 522 | 107 | 345 | 788 | | | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Chick energy intake rate (kcal/h delivered to chicks) | Specialist | 105 | 4.83 | 1.01 | 3.15 | 7.40 | 0.79 | 1.27 | 0.48 | 1.28 |
| | Generalist | 112 | 3.83 | 0.77 | 2.55 | 5.74 | | | | |
| Mole crab (*Emerita talpoida*) handling time (s) | Specialist | 326 | 4.88 | 0.80 | 3.47 | 6.87 | 1.15 | 0.30 | 0.67 | 1.99 |
| | Generalist | 144 | 5.64 | 1.16 | 3.68 | 8.63 | | | | |

For the associated pairwise contrast tests, if the confidence interval overlapped 1, it indicated that diet did not significantly affect the response variable.

**Table 2.3. GLMM results for the effects of diet of American Oystercatchers (*Haematopus palliatus*) on foraging metrics at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023. Coefficient estimate (*βi*), SE, 95% CI (LCI and UCI) are presented for the fixed effect, and SD is presented for the random effects. Model fit is given as the marginal $R^2$ value (proportion of variance explained by the fixed effects) and conditional $R^2$ (proportion of variance explained by the fixed and random effects).**

| Response variable | Effect | Term | *βi* | SE | LCI | UCI | SD | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| Chick provisioning rate (provisioning trips/h/chick) | | Intercept | 0.74 | 0.19 | 0.36 | 1.11 | | |
| | Fixed | Diet (Specialist) | 0.16 | 0.18 | -0.20 | 0.52 | | 0.008 |
| | Random | Chick age (days) | | | | | 0.38 | 0.49 |
| | Random | Breeding pair ID | | | | | 0.50 | |
| | | Residuals | | | | | 0.64 | |
| Food profitability (g/s) | | Intercept | -1.32 | 0.20 | -1.71 | -0.93 | | |
| | Fixed | Diet (Specialist) | 0.38 | 0.28 | -0.17 | 0.94 | | 0.06 |
| | Random | Individual bird ID | | | | | 0.48 | 0.45 |
| | | Residuals | | | | | 0.58 | |

**Table 2.4. *n* (number of observations), predicted mean, SE, and 95% CI (LCI and UCI) for the GLMMs testing if diet of American Oystercatchers (*Haematopus palliatus*) impacts foraging metrics at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023. The associated pairwise contrast tests are presented for the ratio of the predicted means generalist/specialist, SE, and 95% CI (LCI and UCI).**

| Response variable | Diet category | *n* | Predicted mean | SE | LCI | UCI | Ratio of the predicted means generalist/ specialist | SE | LCI | UCI |
|---|---|---|---|---|---|---|---|---|---|---|
| Chick provisioning rate (provisioning trips/h/chick) | Specialist | 121 | 2.45 | 0.52 | 1.62 | 3.70 | 0.85 | 0.16 | 0.59 | 1.22 |
| | Generalist | 130 | 2.09 | 0.40 | 1.43 | 3.04 | | | | |
| Food profitability (g/s) | Specialist | 44 | 0.39 | 0.08 | 0.26 | 0.59 | 0.68 | 0.19 | 0.39 | 1.19 |
| | Generalist | 31 | 0.27 | 0.05 | 0.18 | 0.39 | | | | |

For the associated pairwise contrast tests, if the confidence interval overlapped 1, it indicated that diet did not significantly affect the response variable.

## Diet Specialization Distribution

Specialists were not distributed evenly throughout the population. Instead, there was a clear demarcation at the northern end of Assateague Island where most specialists nested south of the northern end of the Overwash ($n$ = 51 nests) (Fig. 2.5), while breeding pairs nesting to the north were generalists ($n$ = 4 nests). There were a few exceptions where generalists bred at the southern end of Assateague Island at the Hook ($n$ = 8 nests), and the middle of the Overwash ($n$ = 4 nests). In comparison, all breeding pairs at Assawoman Island were generalists ($n$ = 52 nests, Fig. 2.6).




**Figure 2.5.** 2022 and 2023 American Oystercatcher (*Haematopus palliatus*) nests ($n$ = 67 nests) based on diet mapped with prey availability and distribution at Assateague Island, Virginia, U.S.A.

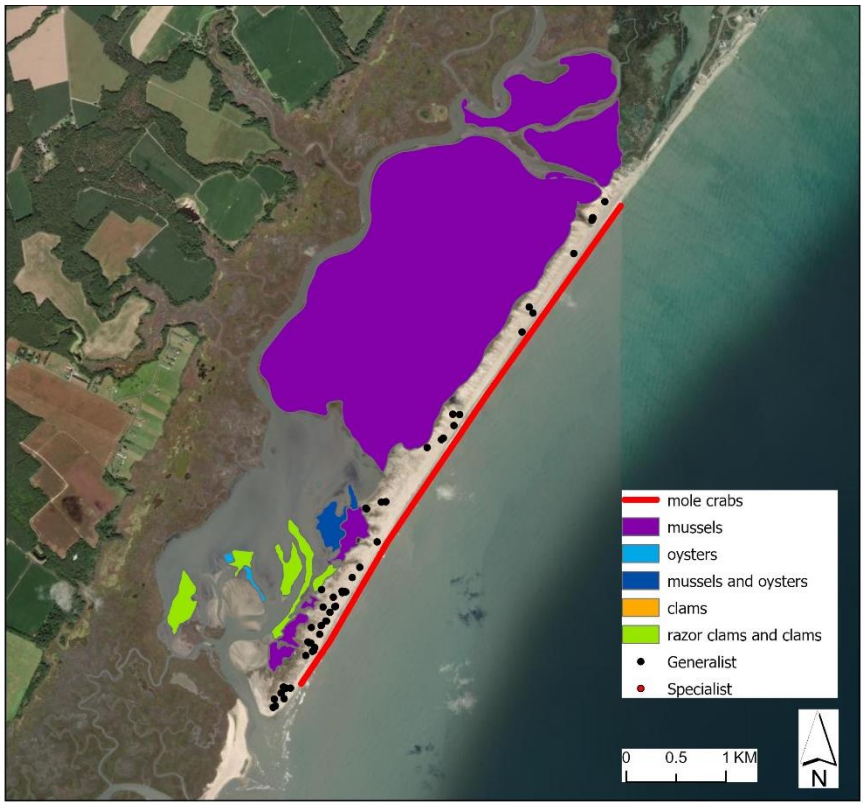



**Figure 2.6.** 2022 and 2023 American Oystercatcher (*Haematopus palliatus*) nests ($n$ = 52 nests) based on diet mapped with prey availability and distribution at Assawoman Island, Virginia, U.S.A.

The distribution of diet specialization did not correspond to the level of human disturbance (Fig. 2.7, Fig. 2.8). At Assateague Island, specialists occurred at both the Hook, which lacked human disturbance, and the Overwash, which had over-sand vehicle driving and pedestrian use. Within areas of similar human disturbance, diet varied. Both the Hook at Assateague Island and Assawoman Island lacked human disturbance but supported individuals with different diets (mostly specialists at the Hook versus generalists at Assawoman Island). Diet also varied at the Overwash, even though over-sand vehicle use was similar throughout, since vehicles were generally evenly distributed along the stretch of beach (LA Brown, unpublished data).

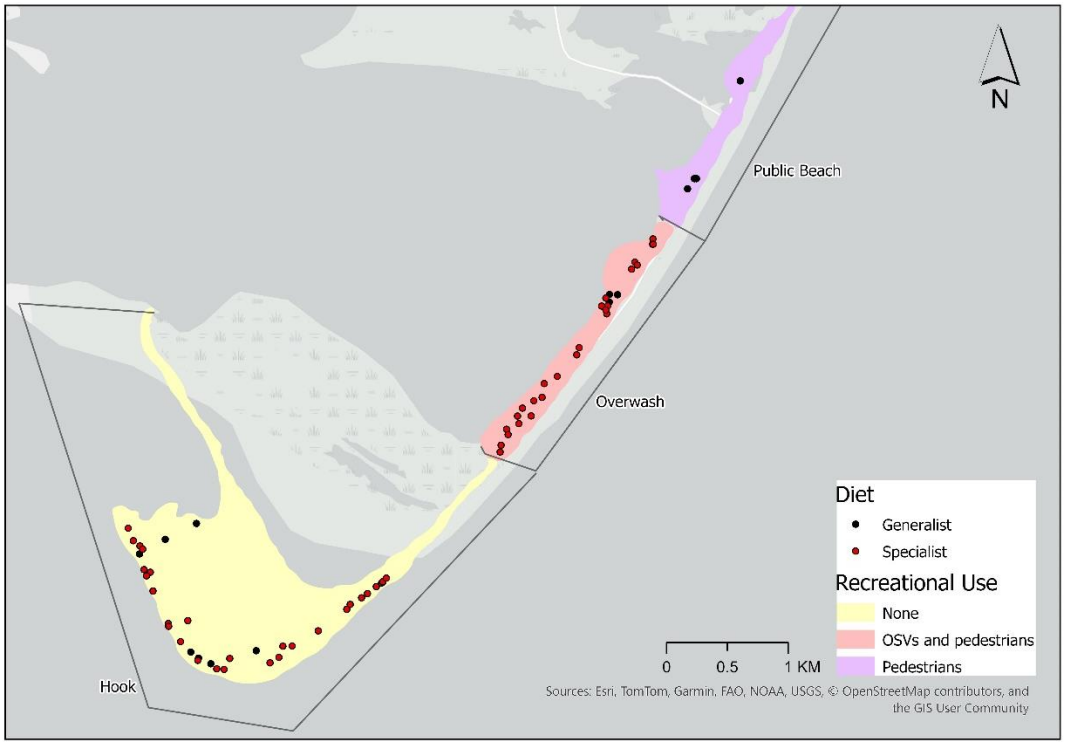



**Figure 2.7.** 2022 and 2023 American Oystercatcher (*Haematopus palliatus*) nests (*n* = 67 nests) based on diet mapped with recreational uses at Assateague Island, Virginia, U.S.A. Note that no recreational use applies to the breeding season from approximately March 15 until August 31 of each year. OSVs represent over-sand vehicle driving. In both the OSV and pedestrian use areas as well as the pedestrian use only areas, the nesting areas are closed to public access with symbolic fencing during the breeding season, so recreational use occurs in the ocean intertidal areas, where the birds forage.

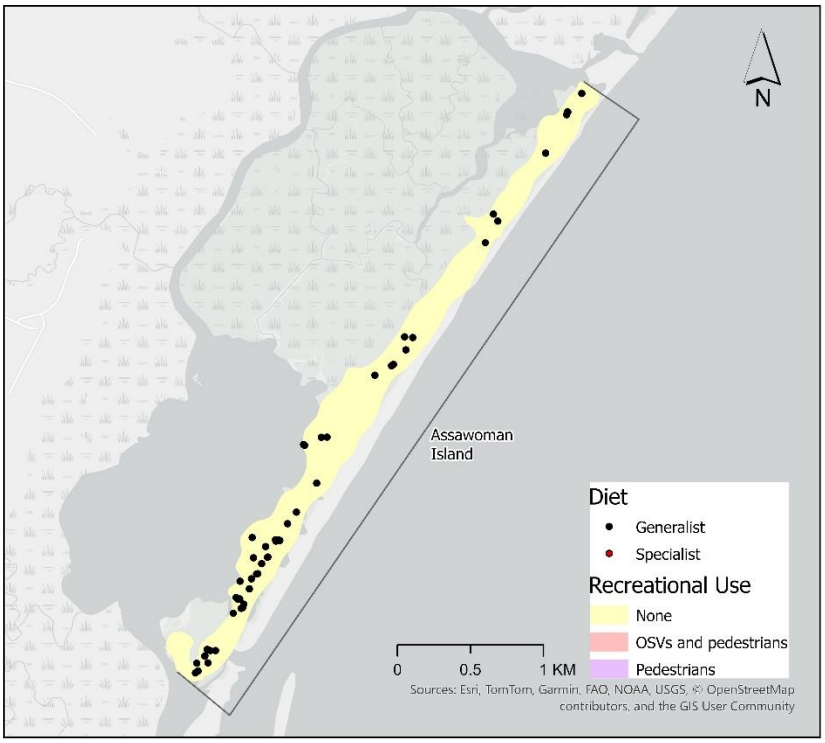



**Figure 2.8.** 2022 and 2023 American Oystercatcher (*Haematopus palliatus*) nests ($n$ = 52 nests) based on diet mapped with recreational uses at Assawoman Island, Virginia, U.S.A. The island is closed to recreational use during the breeding season from approximately March 15 until August 31 of each year.

Mole crab abundance was best explained by site (the Hook and Overwash at Assateague Island) and month in 2022 and 2023 (Supplementary Table S2.5, $R^2$ = 0.54). For 2022 and 2023, the Hook generally had higher mole crab abundance compared to the Overwash, although not significantly so. The month of July had significantly lower mole crab abundance relative to May and June (Supplementary Table S2.6, Fig. 2.9). In 2022, there were no differences in mole crab abundance across sites (Assawoman Island, or the Hook, Overwash, or Public Beach at Assateague Island) (*Adjusted* $R^2$ = 0.36, Supplementary Table S2.7, Supplementary Table S2.8, Supplementary Table S2.9).

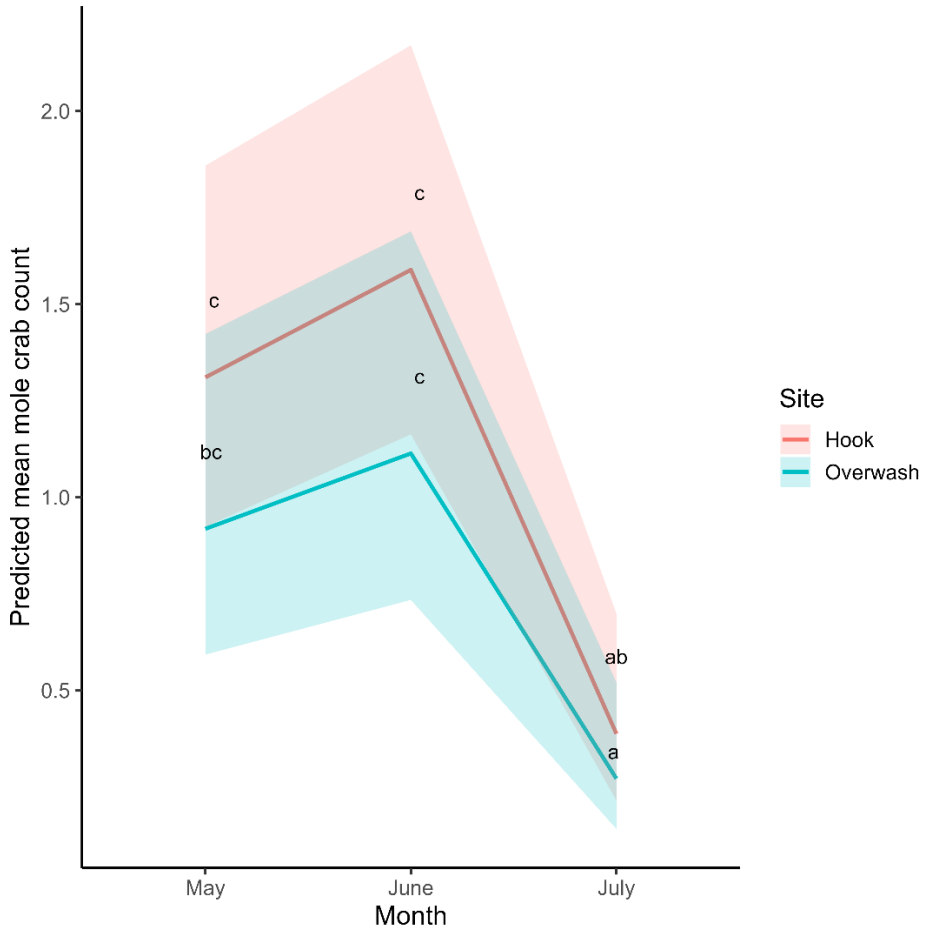



**Figure 2.9.** Predicted mean ± 95% confidence interval for mole crab (*Emerita talpoida*) abundance by site for the months of May, June, and July at Assateague Island, Virginia, U.S.A. in 2022 and 2023. $n = 35$ sampling points at the Hook and $n = 23$ sampling points at the Overwash. Different letters denote statistical significance, where the confidence intervals do not overlap.

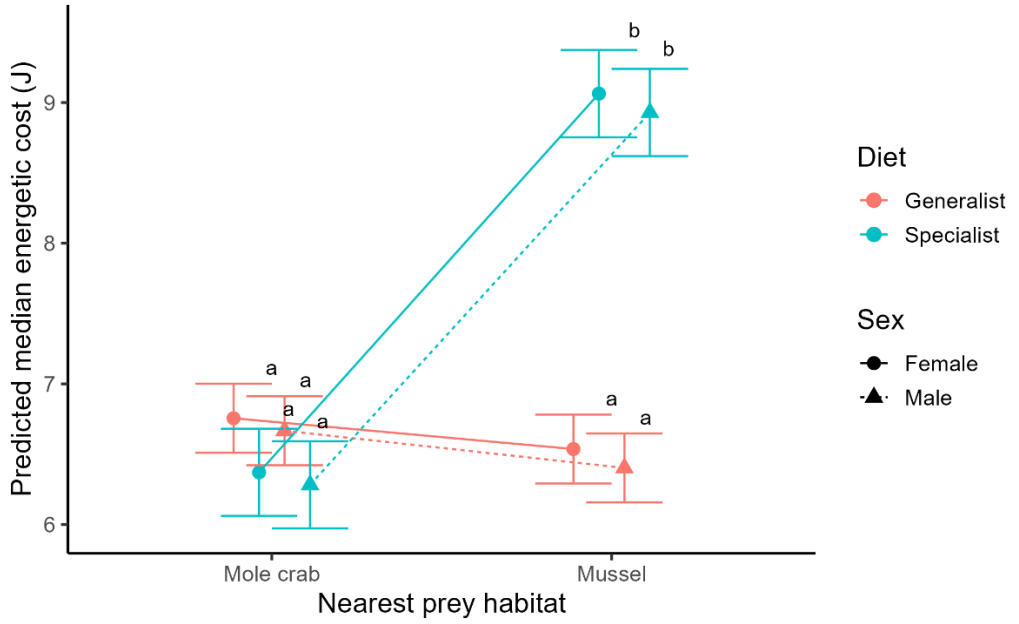



**Figure 2.10.** Predicted median ± 95% CI for the energetic costs (J) of adult American Oystercatchers (*Haematopus palliatus*) based on diet, sex, and travel to the nearest prey habitat at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023. Different letters denote statistical significance, where the confidence intervals do not overlap. Values were based on a log normal distribution GLMM testing if a three-way interaction among diet, sex, and travel to the nearest prey habitat predicted energetic costs, when accounting for repeated observations on breeding pairs between years as a random effect. Values were calculated from $n$ = 68 nests for generalists and $n$ = 51 nests for specialists.

Mussels were the most profitable prey species to eat, followed by mole crabs (Supplementary Table S2.1). The distribution of diet specialization corresponded to distance to mussels rather than other prey species (Fig. 2.5). Beyond the distance of 280 m between nests and prey, specialist breeding pairs did not travel to mudflats to feed on mussels but instead specialized on mole crabs and stayed close to nests. All specialist breeding pairs were located on the southern end of Assateague Island, where breeding pairs had to travel 4.31 times farther on

average from their nests (271–5,328 m) to reach mussels than generalists (Table 2.5, Table 2.6). In contrast all breeding pairs at Assawoman Island were generalists and had mussels within 280 m of their nests (28–278 m) (Fig. 2.6).

All pairs had access to the same number of prey species within 20 km of their nest (Table 2.6). Mole crabs were generally the closest prey to breeding pairs (within 88 m on average for specialists and within 137 m on average for generalists). Specialists nested significantly closer to mole crabs than generalists (Table 2.6). Specialists had to travel significantly farther on average than generalists to reach oysters (2.5 times farther) and razor clams (1.7 times farther, Table 2.6), but the distribution of these prey species did not correspond to the distribution of diet specialization (Fig. 2.5). There was no significant difference in the distance to clams from nests based on diet (Table 2.6). Compared to generalists, mole crab specialists faced a higher energetic cost to fly to the nearest mussel habitat versus walk to the nearest mole crab habitat (Table 2.7, Fig. 2.10). Female and male specialists expended 42% significantly more energy one-way reaching mussel habitat compared to mole crab habitat versus female generalists expended 3% less energy and male generalists expended 4% less energy one-way to reach mussel habitat compared to mole crab habitat.

## Kleptoparasitism

In 2022 and 2023 of the 816 foraging and chick provisioning observations, we only observed kleptoparasitism 11 times which was insufficient to conduct a comparison between specialists and generalists. A Ruddy Turnstone (*Arenaria interpres*), a Sanderling (*Calidris alba*), a Willet (*Tringa semipalmata*), a Great Black-backed Gull (*Larus marinus*), and an American Crow (*Corvus brachyrhynchos*) stole one mole crab each, for a total of six mole crabs. American

Oystercatchers stole three mussels from other American Oystercatchers, and Herring Gulls (*Larus argentatus*) stole two unknown prey species from American Oystercatchers.

**Table 2.5. Coefficient estimate (*βi*), SE, and 95% CI (LCI and UCI) for the GLM predicting distance (m) from the nest to the nearest prey feature for American Oystercatcher (*Haematopus palliatus*) breeding pairs based on diet at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023.**

| Term | *βi* | SE | LCI | UCI |
|---|---|---|---|---|
| Intercept | 0.0014 | 0.0002 | 0.0010 | 0.0017 |
| Mussel | -0.0000 | 0.0003 | -0.0005 | 0.0005 |
| Oyster | -0.0006 | 0.0002 | -0.0010 | -0.0002 |
| Razor clam | -0.0001 | 0.0002 | -0.0006 | 0.0004 |
| Mole crab | 0.0060 | 0.0010 | 0.0040 | 0.0079 |
| Specialist | 0.0001 | 0.0003 | -0.0005 | 0.0006 |
| Mussel:Specialist | -0.0011 | 0.0003 | -0.0017 | -0.0004 |
| Oyster:Specialist | -0.0005 | 0.0003 | -0.0011 | 0.0001 |
| Razor clam:Specialist | -0.0006 | 0.0003 | -0.0012 | 0.0001 |
| Mole crab:Specialist | 0.0040 | 0.0020 | 0.0000 | 0.0079 |

The intercept represents the diet generalist and prey species clam.

Prey species are: clams (*Mercenaria mercenaria*), mussels (*Modiolus demissus*), oysters (*Crassotrea virginica*), razor clams (*Ensis directus*), and mole crabs (*Emerita talpoida*).

**Table 2.6. Predicted mean, SE, and 95% CI (LCI and UCI) for the GLM predicting distance (m) from the nest to the nearest prey feature for American Oystercatcher (*Haematopus palliatus*) breeding pairs based on diet at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023. The associated pairwise contrast tests are presented for the difference in predicted mean distances between diet (generalists - specialists), SE, and 95% CI (LCI and UCI).**

| Prey | Diet | Predicted mean | SE | LCI | UCI | Difference in predicted means (generalists - specialists) | SE | LCI | UCI |
|---|---|---|---|---|---|---|---|---|---|
| Mussel | Specialist | 3,274.12 | 503.64 | 2,514.46 | 4,691.50 | 0.0010 | 0.0002 | **0.0007** | **0.0014** |
| | Generalist | 759.69 | 101.20 | 602.14 | 1,028.89 | | | | |
| Oyster | Specialist | 3,274.12 | 503.64 | 2,514.46 | 4,691.50 | 0.0005 | 0.0001 | **0.0002** | **0.0007** |
| | Generalist | 1,287.73 | 171.55 | 1,020.68 | 1,744.04 | | | | |
| Clam | Specialist | 698.54 | 107.45 | 536.47 | 1,000.94 | -0.0001 | 0.0003 | -0.0006 | 0.0005 |
| | Generalist | 737.84 | 98.29 | 584.83 | 999.30 | | | | |
| Razor clam | Specialist | 1,346.47 | 207.12 | 1,034.06 | 1,929.37 | 0.0005 | 0.0002 | **0.0001** | **0.0009** |
| | Generalist | 810.61 | 107.99 | 642.50 | 1,097.85 | | | | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Mole crab | Specialist | 87.93 | 13.53 | 67.53 | 126.00 | -0.0041 | 0.0020 | **-0.0080** | **-0.0001** |
| | Generalist | 136.60 | 18.20 | 108.27 | 185.00 | | | | |

For the associated pairwise contrast tests if the confidence interval overlapped is 0, it indicated that there was no significant difference in the distance to the nearest prey feature based on diet. Significant differences are bolded.

Prey species are: mussels (*Modiolus demissus*), oysters (*Crassotrea virginica*), clams (*Mercenaria mercenaria*), razor clams (*Ensis directus*), and mole crabs (*Emerita talpoida*).

**Table 2.7. Log normal distribution GLMM results for the effects of the interaction among diet of American Oystercatchers (*Haematopus palliatus*) and sex on the energetic costs (J) of traveling to forage at the nearest mole crab (*Emerita talpoida*) habitat compared to nearest mussel (*Modiolus demissus*) habitat at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023. Coefficient estimate (*βi*), SE, and 95% CI (LCI and UCI) are presented for the fixed effects, and SD is presented for the random effects. Model fit is given as the marginal $R^2$ value (proportion of variance explained by the fixed effects) and conditional $R^2$ (proportion of variance explained by the fixed and random effects). Values are presented on a log scale.**

| Effect | Term | *βi* | SE | LCI | UCI | SD | $R^2$ |
|---|---|---|---|---|---|---|---|
| | Intercept | 6.76 | 0.12 | 6.51 | 7.00 | | |
| Fixed | Diet (Specialist) | -0.38 | 0.20 | -0.78 | 0.01 | | |
| Fixed | Prey (Mussel) | -0.22 | 0.12 | -0.46 | 0.03 | | |
| Fixed | Sex (Male) | -0.09 | 0.12 | -0.33 | 0.16 | | |
| Fixed | Diet (Specialist) × Prey (Mussel) | 2.91 | 0.19 | 2.54 | 3.28 | | |
| Fixed | Diet (Specialist) × Sex (Male) | 0.00 | 0.19 | -0.37 | 0.37 | | |
| Fixed | Prey (Mussel) × Sex (Male) | -0.05 | 0.18 | -0.39 | 0.30 | | |
| Fixed | Diet (Specialist) × Prey (Mussel) × Sex (Male) | 0.00 | 0.27 | -0.53 | 0.53 | | |
| Random | Breeding pair ID | | | | | 0.56 | 0.56 |
| | Residuals | | | | | 0.73 | 0.72 |

The intercept represents the diet generalist, sex female, and prey habitat mole crab.

# Discussion

Two distinct foraging strategies exist on the two Virginia barrier islands -- mole crab specialists and generalists. Specialists ate almost exclusively mole crabs at oceanside shorelines, while generalists showed the typical American Oystercatcher feeding strategy of eating seven prey species including mole crabs and six bivalve species at bayside mudflats and oceanside shorelines (Schulte and Simons 2015). Generalists follow optimal foraging theory, where individuals choose the highest profitable food item, the mussel, to maximize energy intake and minimize costs (Stephens and Krebs 1986; Araújo *et al.* 2008). In comparison, specialists forgo feeding on mussels, and instead specialize on the second most profitable prey, the mole crab.

Both diets appeared to be equally effective strategies at meeting the nutritional needs of American Oystercatcher chicks, since the number of chick provisioning trips and chick energy intake rates were similar for each diet. In comparison, a 15-year study on Thick-billed Murre (*Uria lomvia*) shows that specialists provision chicks at lower rates then generalists, but this does not affect the number of chicks fledged (Woo *et al.* 2008). In contrast, Herring Gull (*Larus argentatus*) habitat specialists along the Belgian Coast, are better able to provision their chicks, since specialists travel shorter distances and forage in smaller areas, and this leads to faster chick growth rates than generalists (van den Bosch *et al.* 2019).

There were no significant differences in mole crab handling time, food profitability, or body condition based on diet. In contrast, Eurasian Oystercatchers differ in body condition based on diet (Durell *et al.* 2001), and bivalve specialists have faster prey handling times and achieve higher food profitability than worm specialists (van de Pol *et al.* 2009). Furthermore, Eurasian Oystercatchers that are experimentally forced to specialize on bivalves, improve their prey handling times and food profitability (Wanink and Zwarts 1996). However, differences in adult

foraging efficiency do not result in differences in adult survival for Eurasian Oystercatchers (van de Pol *et al.* 2009).

## Mechanisms Explaining Diet Specialization

Diet specialization was best explained by distance to mussels and the energetic costs of traveling to mussels, rather than prey abundance, kleptoparasitism avoidance, intra-specific competition, human disturbance avoidance, or ecological opportunity. Mole crab abundance did not appear to drive diet specialization. The Hook of Assateague Island supported the most diet specialists but had similar mole crab abundance as other sites (Assawoman Island, and Overwash and Public Beach at Assateague Island) in 2022. By contrast, in 2023, the Hook had higher mole crab abundance than the Overwash. If mole crab abundance was the main driver of diet specialization, we would have expected the Hook to have had higher mole crab abundance across all sites in 2022, which it did not. We lacked sufficient data to find support for kleptoparasitism avoidance as a driver of diet specialization; although with our limited sample size, mole crabs were the top stolen prey species. This would suggest that mole crabs are a highly sought after prey species and would not support the hypothesis that individuals specialize on mole crabs to avoid kleptoparasitism. We also failed to find support for intra-specific competition driving diet specialization, since specialists were not inter-mixed throughout the populations on both islands. Instead, there was a clear distinction in the distribution of specialist and generalist breeding pairs. Specialist breeding pairs only nested on the southern end of Assateague Island, while north of that and at Assawoman Island breeding pairs were generalists. Human disturbance avoidance did not explain diet specialization because if recreational use prevented individuals from foraging exclusively on oceanside shorelines, individuals at Assawoman Island, whose nesting areas are closed to the public, should also have specialized on mole crabs, which they did not.

Additionally, most individuals at the Overwash of Assateague Island had specialist diets, despite over-sand vehicle driving and pedestrians. Furthermore, if diet specialization were driven by a lack of human disturbance, one would expect American Oystercatchers at other closed areas to the public to also have specialist diets. However, to date, diet specialization has only been described at Assateague Island, and a generalist diet is the normal diet of American Oystercatchers throughout their range (American Oystercatcher Working Group *et al.* 2020). Ecological opportunity did not explain diet specialization because individuals of both diets had the same number of prey species available to them. Thus, specialists did not have higher ecological opportunity that led individuals to specialize on mole crabs as a subset of available prey species. For both diets, all individuals could have accessed mussels, the most profitable prey species found on the two study islands. Specialists could have flown 280–5,328 m one-way (560–10,656 m round-trip) to reach mussels, which is within the foraging range of American Oystercatchers (up to 16 km, based on the GPS tracking data in the present study). But, individuals that had to travel more than 280 m from nests (one-way) to reach mussels opted instead to forage closer to nests and specialize on mole crabs, the second most profitable prey species. Traveling to forage on mussels cost specialists 42% more energy compared to traveling to forage on mole crabs. Most barrier islands in the state of Virginia have adjacent mudflats backing onto beach nesting habitat where American Oystercatchers can forage on mussels and other bivalve species. However, the south end of Assateague Island has a unique habitat configuration, which does not have adjacent mudflats nor the associated food sources. The habitat configuration which impacts the distance to mussels, and hence the energetic cost to travel to mussels is the most likely driver of diet specialization for American Oystercatchers that nest here.

Adults might specialize on nearby mole crabs to conserve energy for future breeding seasons. American Oystercatchers are long-lived, typically reaching at least 10 years old (American Oystercatcher Working Group *et al.* 2020). Adults also have a high survival rate of 0.91 (Wilke *et al.* 2017). The long-lived nature of these birds might favor investing in adult survival and future reproductive effort over current reproductive effort.

## Future Studies

Since specialists were spatially clustered in one area, this might suggest that mole crab diet specialization is a learned behavior. Future research could examine if (a) diet specialization spreads throughout the population and (b) if mole crab specialists remain specialists year-round or remain specialists across years, as diet specialization can change across temporal scales (Baert *et al.* 2021). It is unknown at the study islands if mole crab abundance in the winter is sufficient to support mole crab specialists, or if specialists must migrate to follow mole crabs. The trophic polymorphism hypothesis states that individuals migrate to follow seasonally available food resources (Chapman *et al.* 2011) and has been supported with Black Oystercatchers (Rankin 2023). For Black Oystercatchers in Alaska, U.S.A. and British Columbia, Canada, the propensity to migrate increases with specialization on limpets (greater proportion of limpets in the diet), since limpets are only seasonally available (Rankin 2023). Future studies could test if the trophic polymorphism hypothesis explains partial migratory behavior in American Oystercatchers in Virginia.

## Conservation Management Implications

The importance of oyster reefs as a food supply for American Oystercatchers is well-established (Tuckwell and Nol 1997b; Brush *et al.* 2017), and management to conserve American Oystercatchers reflects this knowledge. Millions of dollars from the Deepwater Horizon oil spill

have been spent on oyster reef restoration projects to benefit American Oystercatchers (Farell *et al.* 2016; Frederick *et al.* 2016; Shaffer *et al.* 2019; Copertino *et al.* 2022). The existence of American Oystercatchers that specialize on a diet of mole crabs supports considering prioritizing beach management to maintain mole crab populations, in areas with diet specialists. This would have the added benefit of helping other migratory shorebirds that also rely on mole crabs during stopovers, like the U.S. federally threatened Red Knots (*Calidris canutus*), Ruddy Turnstones, Sanderlings, and Willets (Connors *et al.* 1981; Howe 1982; Dinsmore 1994; Aju *et al.* 2019; Baker *et al.* 2020; Macwhirter *et al.* 2020; Nettleship 2020).

Mole crab population management may involve balancing human recreational use of beaches and beach renourishment with mole crab abundance. The abundance of marine invertebrates dwelling in the ocean intertidal zone, including mole crabs, can be reduced by pedestrian and off-road vehicle traffic (Schlacher *et al.* 2016) as well as fishermen who collect them for bait. Additionally, beach renourishment can depress mole crab abundance (*Emerita analoga*) for up to four months (Wooldridge *et al.* 2016). Conservation organizations may want to consider reducing human disturbance, restricting bait collection, and timing beach renourishment to minimize impacts to benthic infauna consumed by breeding and migratory shorebirds.

## Conclusion

We provide the first evidence of diet specialization in American Oystercatchers. Mole crab diet specialization in American Oystercatchers was best explained by differences in the foraging distance from mussels and higher energetic costs of traveling to mussels. Individuals might specialize on mole crabs to conserve energy. This research supports considering managing

beaches for mole crab populations in areas with diet specialists to help conserve the foraging habitat of American Oystercatchers.

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# Supplementary Materials

**Supplementary Table S2.1. Mean ± SE food profitability (g/s) for American Oystercatcher (*Haematopus palliatus*) prey species at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2022 and 2023.**

| Prey Species | *N* | Wet mass (g) | Mean handling time (s) | SE handling time (s) | Mean food profitability (g/s) | SE food profitability (g/s) |
|---|---|---|---|---|---|---|
| Atlantic ribbed mussel | 177 | 6.31 | 92.65 | 56.38 | 0.86 | 0.11 |
| Mole crab | 1,761 | 2.51 | 22.80 | 1.33 | 0.45 | 0.01 |
| False angel wing clam | 65 | 2.26 | 13.89 | 1.49 | 0.31 | 0.04 |
| Northern quahog clam | 62 | 1.82 | 29.38 | 5.61 | 0.29 | 0.05 |
| Stout tagelus | 19 | 4.96 | 48.66 | 11.51 | 0.28 | 0.06 |
| Coquina | 182 | 0.32 | 2.86 | 0.22 | 0.18 | 0.01 |
| Eastern oyster | 80 | 3.44 | 38.05 | 4.64 | 0.17 | 0.02 |
| Atlantic razor clam | 23 | 1.95 | 40.55 | 8.94 | 0.10 | 0.03 |

Food profitability was calculated as the wet mass (g)/handling time (s). Note that details about how wet mass was obtained for food profitability calculations can be found in Supplemental Table S2.2.

Species scientific names are:
Atlantic ribbed mussel (*Modiolus demissus*)

Mole crab (*Emerita talpoida*)
False angel wing clam (*Petricolaria pholadiformis*)
Northern quahog clam (*Mercenaria mercenaria*)
Stout tagelus (*Tagelus plebeius*)
Coquina (*Donax varibilis*)
Eastern oyster (*Crassotrea virginica*)
Atlantic razor clam (*Ensis directus*)

**Supplementary Table S2.2. Bootstrapped wet masses (g) of American Oystercatcher (*Haematopus palliatus*) prey collected in 2022 at Assateague Island and Assawoman Island, Virginia, U.S.A. LCI and UCI represented the 95% confidence interval.**

| Species | *N* | Mean | SE | LCI | UCI |
|---|---|---|---|---|---|
| Atlantic ribbed mussel | 19 | 6.31 | 1.01 | 4.33 | 8.27 |
| Mole crab | 24 | 2.51 | 0.48 | 1.58 | 3.45 |
| False angel wing clam | 25 | 2.26 | 0.17 | 1.94 | 2.59 |
| Northern quahog clam | 10 | 1.82 | 0.15 | 1.53 | 2.10 |
| Eastern oyster | 19 | 3.44 | 0.50 | 2.49 | 4.44 |

Species scientific names are:
Atlantic ribbed mussel (*Modiolus demissus*)
Mole crab (*Emerita talpoida*)
False angel wing clam (*Petricolaria pholadiformis*)
Northern quahog clam (*Mercenaria mercenaria*)
Eastern oyster (*Crassotrea virginica*)

**Supplementary Table S2.3. GPS tagged American Oystercatchers (*Haematopus palliatus*), bands, breeding island, number of GPS fixes, and duration of tag data collection during the breeding interval at Assateague Island and Assawoman Island, Virginia, U.S.A. in 2023.**

| Bands | Island | Diet | GPS fixes | Tag data duration during the breeding interval |
|---|---|---|---|---|
| CEN | Assateague | Specialist | 861 | 5/17/2023—5/30/2023 |
| CEK | Assateague | Specialist | 3,367 | 5/17/2023—7/5/2023 |
| CAT | Assateague | Generalist | 3,223 | 5/18/2023—7/11/2023 |
| CEM | Assateague | Generalist | 1,388 | 5/17/2023—6/6/2023 |
| CCE | Assawoman | Generalist | 523 | 6/2/2023—6/19/2023 |
| CAY | Assawoman | Generalist | 123 | 6/2/2023—6/5/2023 |
| CKT | Assawoman | Generalist | 1,612 | 5/21/2023—6/21/2023 |
| CCK | Assawoman | Generalist | 554 | 6/2/2023—6/21/2023 |
| CAP | Assawoman | Generalist | 6,632 | 5/21/2023—6/28/2023 |
| CEJ | Assawoman | Generalist | 1,949 | 5/16/2023—7/14/2023 |

The breeding interval was defined as the GPS tag deployment date (tagging occurred when individuals had a nest with eggs), until the end of the last nesting attempt (date of the nest/brood failure or the date that the brood fledged at 35 days old).

**Supplementary Table S2.4. Energy content for the mean dry mass (kcal) of American Oystercatcher (*Haematopus palliatus*) prey species.**

| Species | Wet mass (g) | % Moisture | Energy content of dry mass (kcal/g) | kcal of dry mass |
|---|---|---|---|---|
| Atlantic ribbed mussel | 6.31 | 88.6[a] | 4.38[a] | 3.15 |
| Mole crab | 2.51 | 74.9 [b] | 3.60[c] | 2.27 |
| Northern quahog clam | 1.82 | 87.5[a] | 3.98 [a] | 0.91 |
| Stout tagelus | 4.75[d] | 56.86 [e] | 1.05 [e] | 2.16 |
| Coquina | 0.32 | 84.67[f] | 2.26 [c] | 0.11 |
| Eastern oyster | 3.44 | 80.55[g] | 3.70[h] | 2.48 |
| Atlantic razor clam | 1.95[i] | 83.00[j] | 4.70g[k] | 1.56 |

Letters denote citations. Wet mass is average wet mass of prey collected from Assateague Island and Assawoman Island, Virginia in 2022, unless listed with a letter. Calories in an individual average sized prey item for the oystercatcher was calculated using the formula: kilocalories of dry prey mass = wet mass x (100 % - % moisture) x kcal/g of dry mass.

Species scientific names are:
Atlantic ribbed mussel (*Modiolus demissus*)
Mole crab (*Emerita talpoida*)
Northern quahog clam (*Mercenaria mercenaria*)
Coquina (*Donax varibilis*)
Eastern oyster (*Crassotrea virginica*)
Atlantic razor clam (*Ensis directus*)

References are as follows:
a: McKinney 2004
b: Santoso *et al.* 2015. The only available moisture data was for a similar species to *Emerita talpoida*, *Emerita emeritus.*
c: Armitage and Alvezian 1980
d: Yussepone *et al.* 2020
e: Nelson 1996
f: Özden *et al.* 2009
g: Zhang 2017
h: Hostert 2014
i: Swennen *et al.* 1985. Citation provided the ash free dry mass, and we calculated wet mass using the known ash free dry mass value from the source and moisture from Szkoda *et al.* 2015. Wet mass = dry mass/(100% - moisture %)
j: Szkoda *et al.* 2015
k: Witbaard *et al.* 2015

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**Supplementary Table S2.5. AIC*c* model selection results for candidate Poisson regression models predicting mole crab (*Emerita talpoida*) abundance based on site (Assawoman Island, and the Hook, Overwash, and Public Beach at Assateague Island, Virginia, U.S.A.), month, year, and their interactions in 2022 and 2023. The best model (site + month) was the most parsimonious within two AIC*c* units of the model with the lowest AIC*c*.**

| Model Predictors | *K* | AIC*c* | ΔAIC*c* | Model likelihood | *wi* | Log likelihood | Cumulative *wi* |
|---|---|---|---|---|---|---|---|
| Site + Month + Year + Site x Year + Month x Year + Month x Site | 14 | 1,271.04 | 0.00 | 1.00 | 0.82 | -620.91 | 0.82 |
| Site*Month*Year | 13 | 1,274.09 | 3.05 | 0.22 | 0.18 | -623.52 | 1.00 |
| Site + Month | 7 | 1,298.78 | 27.74 | 0.00 | 0.00 | -642.23 | 1.00 |
| Site + Month + Year | 4 | 1,356.71 | 85.66 | 0.00 | 0.00 | -674.30 | 1.00 |
| Month | 6 | 1,380.24 | 109.20 | 0.00 | 0.00 | -684.00 | 1.00 |
| Month + Year | 3 | 1,417.09 | 146.05 | 0.00 | 0.00 | -705.51 | 1.00 |
| Site | 5 | 1,551.59 | 280.55 | 0.00 | 0.00 | -770.71 | 1.00 |
| Site + Year | 2 | 1,609.54 | 338.50 | 0.00 | 0.00 | -802.75 | 1.00 |

| **Model Predictors** | ***K*** | **AIC*c*** | **ΔAIC*c*** | **Model likelihood** | ***wi*** | **Log likelihood** | **Cumulative *wi*** |
|---|---|---|---|---|---|---|---|
| Year | 4 | 1,618.37 | 347.33 | 0.00 | 0.00 | -805.13 | 1.00 |

Where *K* was the number of parameters; AIC*c* was the Akaike information criterion corrected for small sample sizes; ΔAIC*c* was the change in AIC*c* information score from the model with the lowest AIC*c*; model likelihood was the probability of the observed data; *wi* was individual model weight and was the proportion of the predictive power included in the model out of all possible candidate models; log likelihood was the natural logarithm of the model likelihood; and cumulative *wi* was the sum of the individual model weights.

**Supplementary Table S2.6. Poisson regression model coefficient estimates (*βi*), SE, 95% confidence intervals (LCI and UCI), Z values, and *P* values for mole crab (*Emerita talpoida*) abundance predicted by site and month at Assateague Island, Virginia, U.S.A in 2022 and 2023.**

| Term | *βi* | SE | LCI | UCI | Z | *P* |
|---|---|---|---|---|---|---|
| Intercept | 0.27 | 0.13 | 2.04 | 0.04 | 0.01 | 0.53 |
| Overwash | -0.36 | 0.16 | -2.16 | 0.03 | -0.68 | -0.03 |
| June | 0.19 | 0.16 | 1.18 | 0.24 | -0.13 | 0.51 |
| July | -1.22 | 0.25 | -4.87 | 0.00 | -1.71 | -0.73 |

The intercept represents the site as the Hook, and month of May.

**Supplementary Table S2.7. Zero-inflated negative binomial model with a log-link function, coefficient estimate (*βi*), SE, 95% CI (LCI and UCI), Z value, and *P* value for 2022 mole crab (*Emerita talpoida*) abundance predicted by site at Assateague Island (Hook, Overwash, Public Beach) and Assawoman Island, Virginia, U.S.A.**

| Site | *Bi* | SE | LCI | UCI | Z | *P* |
|---|---|---|---|---|---|---|
| Intercept (Hook) | 1.00 | 1.76 | -2.44 | 4.44 | 0.57 | 0.57 |
| Overwash | 0.13 | 1.33 | -2.47 | 2.73 | 0.10 | 0.92 |
| Public Beach | -0.09 | 0.92 | -1.90 | 1.71 | -0.10 | 0.92 |
| Assawoman Island | -1.12 | 0.61 | -2.31 | 0.07 | -1.84 | 0.07 |

**Supplementary Table S2.8. *n* (number of cylinder cores), predicted mean, SE, and 95% CI (LCI and UCI) for the zero-inflated negative binomial model with a log-link function that predicted mole crab (*Emerita talpoida*) abundance by site at Assateague Island (Hook, Overwash, Public Beach) and Assawoman Island, Virginia, U.S.A. in 2022.**

| Site | *n* | Predicted mean | SE | LCI | UCI |
|---|---|---|---|---|---|
| Hook | 50 | 2.72 | 4.77 | 0.09 | 84.96 |
| Overwash | 20 | 3.09 | 2.05 | 0.84 | 11.33 |
| Public Beach | 50 | 2.47 | 2.34 | 0.39 | 15.85 |
| Assawoman Island | 60 | 0.89 | 1.17 | 0.07 | 11.72 |

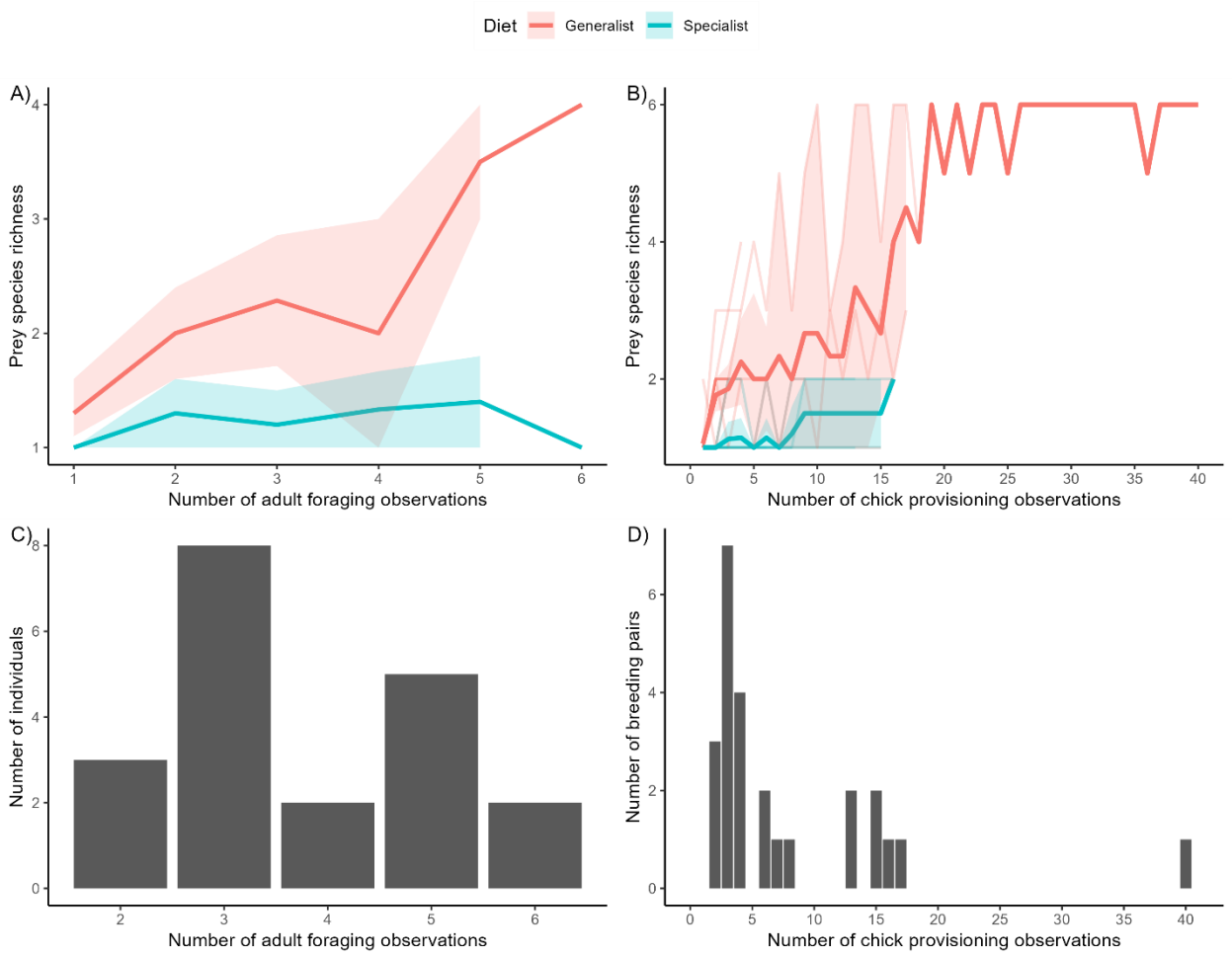
**Supplementary Table S2.9. Pairwise contrast tests for the ratio of the predicted means between sites, SE, and 95% CI (LCI and UCI) for the zero-inflated negative binomial model with a log-link function predicting mole crab (*Emerita talpoida*) abundance by site at Assateague Island (Hook, Overwash, Public Beach) and Assawoman Island, Virginia, U.S.A. in 2022.**

| Contrast | Ratio of the predicted means | SE | LCI | UCI |
|---|---|---|---|---|
| Hook / Overwash | 0.88 | 1.17 | 0.03 | 26.56 |
| Hook / Public Beach | 1.10 | 1.01 | 0.10 | 11.67 |
| Hook / Assawoman Island | 3.06 | 1.86 | 0.64 | 14.54 |
| Overwash / Public Beach | 1.25 | 0.80 | 0.24 | 6.54 |
| Overwash / Assawoman Island | 3.48 | 3.23 | 0.32 | 37.82 |
| Public Beach / Assawoman Island | 2.78 | 1.53 | 0.68 | 11.47 |

Note that if the confidence interval overlapped 1, there was no significant difference in mole crab abundance.




**Supplementary Figure S2.1.** Map of the study area barrier islands in Virginia, U.S.A. The two barrier islands are located on the mid-Atlantic eastern coast on the Delmarva Peninsula, and are considered a part of Chincoteague National Wildlife Refuge. Assateague Island is divided into three sites, the Hook, Overwash, and Public Beach. Assawoman Island is 10 km southwest of Assateague Island.




**Supplementary Figure S2.2.** Accumulation curves of prey species richness (mean ± 95% confidence interval) consumed in the diet of American Oystercatchers (*Haematopus palliatus*) at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2023 in relation to observation effort. Plot A) relates to observations of foraging adults that were used to classify diets of individuals. Plot B) relates to observations of chick provisioning that were used to classify diets of breeding pairs. Note that the confidence intervals appear to truncate prior to the maximum number of observations in both plots due to a low sample size with a large number of observations. For some specialists, prey species richness was >1 because of the presence of coquina in the diet. Plot C) shows the number of individuals whose diets were classified with a

certain number of foraging observations on adults. Plot D) shows the number of breeding pairs whose diets were classified with a certain number of chick provisioning observations.

**Supplementary Material 2.1 – Mole crab count (*Emerita talpoida*) methods**

In 2022 we counted mole crabs in early May and late July at each kilometer of oceanside beach on Assateague Island and Assawoman Island. Since mole crabs are most active during falling tide (Forward *et al.* 2005), we surveyed during falling tide, no more than two hours after low tide (K. Gieder, 2012, unpubl. data). At each sampling site, we counted mole crab abundance in a 50 m stretch of oceanside shoreline, with five sampling points spaced 10 m apart in the 50 m stretch. On Assateague Island the number of sampling sites was 18 at the Hook, 9 at the Overwash, and 15 at Public Beach; whereas on Assawoman Island we had 18 sampling sites spaced equidistantly across the island. We made three counts in the lower, middle, and upper portion of the swash zone. Three meters separated each of the swash zones, since this scale best represents mole crab abundance (Schoeman *et al.* 2014). The lower swash zone occurred where the leading edge of the waves ebbed. Portions of the swash zone were considered relative rather than absolute locations since the swash zone was defined by the tides. We used a 11.43 cm diameter x 15.24 cm height sediment core cylinder for counts.

Since mole crab abundance can change throughout the summer based on the breeding schedule and recruitment of mole crabs (Diaz and Costlow 1987), we increased our mole crab sampling effort in 2023 to count mole crabs at the beginning of each month in May, June, and July. Mole crabs were only counted on Assateague Island at the Hook and Overwash. Mole crabs were counted every 100 m at a single sampling point (Hook: $n$ = 35 sampling points, Overwash: $n$ = 23 sampling points). Three counts were made in the lower, middle, and upper portions of the swash zone. We used the same-sized sediment core cylinder as in 2022.

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## Supplementary Material 2.2 - Energetic cost of moving to the nearest mole crab habitat compared to mussel habitat for specialists and generalists

On the two study islands, for each breeding pair with a nest, we calculated the energetics of traveling to the nearest mole crab habitat versus traveling to the nearest mussel habitat. We performed calculations separately for each sex, since sex affects the energetic cost of moving, given that females are larger in body size than males (Brown and Nol 2024). Below, is an example calculation for a male mole crab specialist.

1) Energetic cost to walk one-way to the nearest mole crab habitat

*Input values:*

- Distance to mole crabs is 88 m (current study)
- Estimated straight line walking speed (excluding pecking and probing) is 1 m/s (approximately 50% of observed mean maximum walking speed of 1.9 m/s reported for Eurasian Oystercatchers by Speakman and Bryant (1993))
- Energetic cost of walking for an American Oystercatcher is 331 kJ/14 h (Nol 1985)

2a) Convert kJ/14 h to J/s

(331 kJ/14 h) / 14 h = 23.64 kJ/h

(23.64 kJ/h) / (3600 s/h) = 0.006 kJ/s

0.006 kJ/s x 1,000 J/kJ = 6.57 J/s

Energetic cost of walking is 6.57 J/s

2b) Calculate energy spent walking one-way to the nearest mole crab habitat

[88 m / (1 m/s)] x 6.57 J/s = 578.16 J

3) Energetic cost to fly one-way to the nearest mussel habitat

*Input values:*

- Distance to mussels is 3,274 m (current study)
- Flight speed for a Eurasian Oystercatcher is 12 m/s (Linssen *et al.* 2019)

- Energetic cost of flight is 1,759 kJ/14 h (Nol 1985)

3a) Convert kJ/14 h to J/s

(1,759 kJ/14 h) / 14 h = 125.64 kJ/h

(125.64 kJ/h) / (3600 s/h) = 0.03 kJ/s

0.03 kJ/s x 1,000 J/kJ = 34.90 J/s

Energetic cost of flying is 34.90 J/s

3b) Calculate energy spent flying one-way to the nearest mussel habitat

[3,274 m / (12 m/s)] x 34.90 J/s = 9,527.70 J

4) Compare flying to nearest mussel habitat to walking to nearest mole crab habitat

(9,527.7 J - 578.16 J)/578.16 J x 100% = 1,548%

*Conclusion:* Flying to the nearest mussel habitat takes 1,548% more energy than walking to the nearest mole crab habitat for a male mole crab specialist.

We repeated calculations for each breeding pair with a nest. The respective distance to the nearest mole crab habitat or mussel habitat was included for each breeding pair with a nest. For female breeding pair members, we substituted the energetic cost of walking for an American Oystercatcher as 362 kJ/14 h (Nol 1985) and the energetic cost of flight as 2,012 kJ/14 h (Nol 1985).

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# Chapter 3 – Temporal not foraging factors affect reproductive success for American Oystercatchers (*Haematopus palliatus*) on two barrier islands in Virginia, U.S.A.



One-day-old American Oystercatchers (*Haematopus palliatus*) chicks brooded by adult. Photo credit: Ken King.

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L. A. Brown led study design, data collection and analysis, writing of the initial draft of the manuscript, and revisions of the manuscript with input from co-authors. K. Oliver contributed to data collection, field supervision, research coordination, and logistics. K. Holcomb contributed to research coordination and logistics. E. Nol contributed to study design, data analysis suggestions, and editing drafts.

Abstract.—Barrier islands in Virginia, U.S.A. support the most breeding American Oystercatchers (*Haematopus palliatus*) throughout their range; however reproductive success remains low. This study focused on how the food supply might influence reproductive success on two barrier islands in coastal Virginia. From 2022–2024, 821 observations were made on foraging adults and brood provisioning to assess food profitability, distances to foraging areas, diets of breeding pairs, and brood provisioning rates. Two hundred fifty-four nests were monitored, 102 of which hatched 215 chicks. Overall, foraging factors did not affect breeding success at the study site. Instead, daily nest survival was best explained by year. Interannual variation in predator and storm activity determined hatching success. In 2024, a lack of storm overwash and limited predator activity led to higher hatching success compared to 2023 and 2022 when nor'easters flooded nests and there was high nest predator activity by foxes, avian predators, and ghost crabs. Daily brood survival was best explained by age, where daily survival decreased with age. Older chicks tended to be of larger body size and hide less from predators, which likely increased their predation risk. Efforts to control predators and increase nesting habitat elevation can support American Oystercatcher reproductive success.

**Keywords.—** breeding performance, brood survival, diet specialization, foraging, individual specialization, nesting success, predation, overwash, shorebirds

# Introduction

The American Oystercatcher (*Haematopus palliatus*) is an obligate coastal bird that nests on beaches and in adjacent coastal marshes of the U.S. Atlantic Coast (American Oystercatcher Working Group *et al.* 2020). The American Oystercatcher is a species of conservation concern (Clay *et al.* 2014) and is listed as state threatened in Georgia and Florida (Schulte and Simons 2015). American Oystercatchers inhabit a complex marine ecosystem with multiple factors contributing to the breeding success including the food supply, predation, storm overwash, and human disturbance (Nol 1989; Schulte and Simons 2015; Vitale *et al.* 2022).

Brood survival is tightly connected to the food supply for *Haematopus* spp. (Nol 1989; Ens *et al.* 1992; Robinson *et al.* 2019; Vitale *et al.* 2022). *Haematopus* spp. provide biparental care, where both adults provision broods (Nol 1989). Because of the handling skills and musculature required to successfully open bivalve prey (Kersten 1996; Hand *et al.* 2010), *Haematopus* spp. chicks must be provisioned one month past the age of fledging until they are 60 days old and can forage for themselves (Kersten 1996). This lengthy provisioning period means that factors affecting foraging including the distance to the foraging area from the nest, brood provisioning rates, diet, and food profitability (food mass/handling time) can influence fledging success (Safriel 1985; Nol 1989; Ens *et al.* 1992; Hazlitt *et al.* 2002).

The state of Virginia in the U.S.A. has the highest concentration of breeding American Oystercatchers throughout their range (Wilke *et al.* 2005). On two barrier islands in Virginia, from 2016–2021, breeding productivity (chicks fledged per breeding pair) was lower (range: 0–0.32 chicks fledged per breeding pair) than the level required to maintain the population and balance adult mortality (0.5 chicks fledged per breeding pair) (Walters *et al.* 2020). Assateague Island and Assawoman Island, Virginia, U.S.A. are managed by the U.S. Fish and Wildlife

Service as a part of Chincoteague National Wildlife Refuge. Current management efforts include predator trapping and closing nesting areas to human disturbance. Despite current management efforts, breeding productivity remained low, so other factors like the food supply could be involved. Our aim was to understand the role of the food supply on American Oystercatcher breeding productivity at Assateague Island and Assawoman Island. Specifically, we investigated how food profitability, distance to the foraging area, diet, and brood provisioning rates might impact nest and brood survival.

# Methods

## Study Area

The study was conducted on Assateague Island (37° 51’ 7.2” N, 75° 22’, 55.2” W; 753 ha) and Assawoman Island (37°, 48’, 3.6” N, 75°, 31’, 4.8” W; 129 ha) in coastal Virginia, U.S.A. We collected data during the American Oystercatcher breeding season from April to August of 2022–2024. From 2022–2024, Assateague Island supported 20–26 breeding pairs and Assawoman Island supported 26–32 breeding pairs. Our study population consisted of banded breeding birds with unique alphanumeric coded leg bands, so breeding pairs were distinguishable from one another. We regularly banded adults, so that at least one breeding pair member was banded (Table 3.1). Breeding pair members tend to spend time together, so if one adult was banded, the pair was distinguishable (L. A. Brown unpublished data). We also recognized distinct breeding pairs based on their location, since American Oystercatchers are highly territorial and defend nesting territories (Nol 1985).

**Table 3.1. American Oystercatcher (*Haematopus palliatus*) breeding productivity (chicks fledged per breeding pair) from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A.**

| Year | Island | Breeding pairs | Breeding pairs with at least one banded adult | Breeding pairs with two unbanded adults | Nesting density (nests/hectare) | Nests laid | Hatched nests | Hatched chicks | Broods that fledged at least one chick | Chicks fledged | Chicks fledged per breeding pair |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2022 | Assateague Island | 20 | 5 | 15 | 0.07 | 52 | 5 | 9 | 3 | 5 | 0.25 |
| 2023 | Assateague Island | 25 | 21 | 4 | 0.04 | 33 | 14 | 31 | 7 | 9 | 0.36 |
| 2024 | Assateague Island | 26 | 22 | 4 | 0.04 | 33 | 19 | 46 | 10 | 16 | 0.62 |
| 2022 | Assawoman Island | 31 | 8 | 23 | 0.33 | 43 | 22 | 45 | 4 | 5 | 0.16 |
| 2023 | Assawoman Island | 32 | 28 | 4 | 0.39 | 50 | 19 | 33 | 5 | 9 | 0.28 |
| 2024 | Assawoman Island | 29 | 26 | 3 | 0.33 | 43 | 23 | 51 | 11 | 24 | 0.83 |

Note that nests laid includes initial nests and re-nests.

The two islands are 10 km apart and provide nesting habitat for American Oystercatchers consisting of sand-shell substrate and sparse to no vegetation. On both islands, nesting areas are closed to the public during the breeding season (mid-March–end of August). Both islands experience similar weather patterns with nor'easters and hurricanes occurring in late summer and into the fall (McPherran *et al.* 2021). Foraging habitats on both islands include oceanside shorelines with marine invertebrates including Atlantic mole crabs (*Emerita talpoida*), and bayside mudflats and marshes with natural populations of Atlantic ribbed mussels (*Modiolus demissus*), eastern oysters (*Crassotrea virginica*), northern quahog clams (*Mercenaria mercenaria*), and Atlantic razor clams (*Tagelus plebeius* and *Ensis directus*), as well as commercially seeded populations of eastern oysters and northern quahog clams (Fig. 3.1 and Fig. 3.2). Assateague Island supports breeding pairs that feed primarily on Atlantic mole crabs from oceanside beaches, as well as breeding pairs that have a generalist diet of Atlantic mole crabs and bivalves including Atlantic ribbed mussels, eastern oysters, northern quahog clams, and Atlantic razor clams. Assawoman Island only has breeding pairs with a generalist diet. For the two islands, both adults of a breeding pair had the same diet in all cases, except for one pair on Assateague Island where one adult had a specialist diet and the other had a generalist diet (Brown and Nol 2026, Chapter 2).

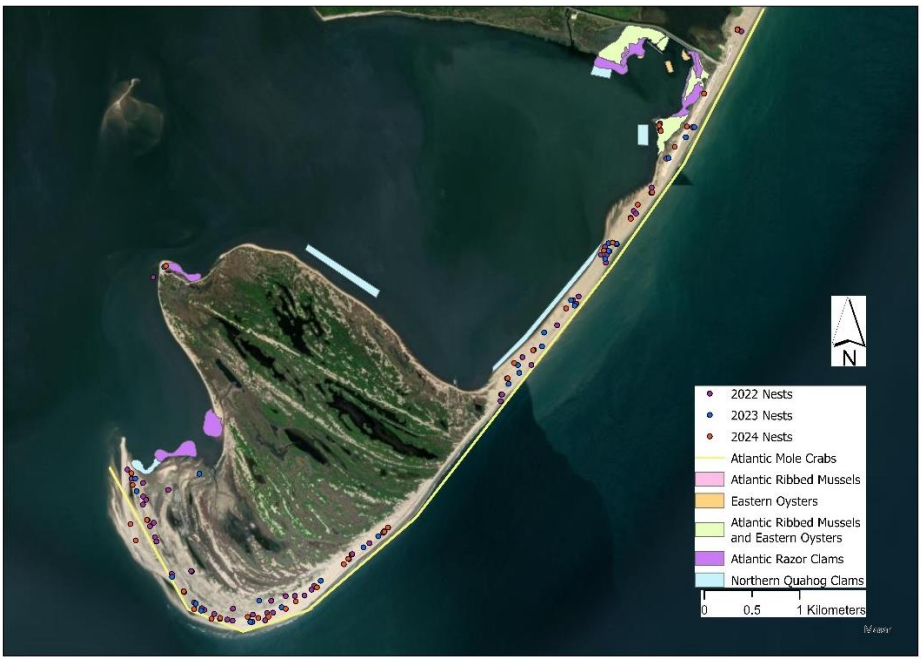



**Figure 3.1.** 2022–2024 American Oystercatcher nests and prey distribution at Assateague Island, Virginia, U.S.A.




**Figure 3.2.** 2022–2024 American Oystercatcher nests and prey distribution at Assawoman Island, Virginia, U.S.A.

On both islands, Chincoteague National Wildlife Refuge contracts the U.S. Department of Agriculture to trap mammals prior to and during the breeding season. The main predators include red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), crows (American Crows (*Corvus brachyrhynchos*) and Fish Crows (*Corvus ossifragus*)), gulls (*Larus spp.*), Peregrine Falcons (*Falco peregrinus*), and Atlantic ghost crabs (*Ocypode quadrata*). In 2023 only, due to changes in staffing levels, the U.S. Fish and Wildlife Service set up Reconyx™ and Browning™ game cameras at some nests to capture predation events. The U.S. Fish and Wildlife Service programmed game cameras to take three photos 30 sec apart after being motion activated. We used the number of trapped predators by the U.S. Department of Agriculture and the number of depredated nests to indirectly assess predator activity. Across years, the U.S. Fish and Wildlife Service made more predator trapping requests and trapping effort on Assateague Island (3,469 nights and 88 days) than on Assawoman Island (200 nights and 16 days) (Table 3.2).

## Data Collection

*Nest Monitoring.* We assisted the U.S. Fish and Wildlife Service with monitoring American Oystercatcher breeding activities from April 1–August 31 from 2022–2024. American Oystercatchers typically laid 1–3 eggs per clutch, and re-nested up to two times within a breeding season if initial nests failed (Nol *et al.* 1984). Incubation takes 27 days (American Oystercatcher Working Group *et al.* 2020). For determining nest initiation dates, we typically knew the exact date because we found nests during egg-laying before clutch completion. If a nest was found after clutch completion, we calculated the nest initiation date by counting backwards from the hatch date. We visited nests 2–3 times per week until nests hatched/failed and recorded the number of eggs and GPS coordinates for the nest. To determine hatch dates, we used actual hatch dates, ages of the chicks, or the median (middle) date between two nest visits. We

attributed nest failures to overwash, predation, abandonment, infertility, or unknown cause of failure. We defined overwash as when wrack (organic material defining the high tide line) was located above the nest site. We determined predation from unique tracks and signs around the nest, and we used game camera photos. For the game cameras, if a predator was captured in a photo and the eggs disappeared later that day without other discernible causes, we attributed the nest failure to predation. We defined nest abandonment as unhatched nests that passed their hatch dates and were no longer incubated. We checked eggs from abandoned nests for infertility by checking the yolk content. If an egg had a bloody yolk, it indicated no fertilization.

We monitored broods 1–3 times per week until all chicks fledged (reached 35 days old) or were lost from a brood and recorded the number and age of chicks during each visit. We considered the brood as fledged if the breeding pair fledged at least one chick. Chicks from a brood are kept as one unit with both parents typically watching over the brood, unless one parent is off defending the territory or foraging (L. A. Brown unpublished data). Most chicks disappear for unknown reasons (Schulte and Simons 2015). We were able to attribute chick mortality to predation if a depredation event was directly observed.

*Foraging Metrics.* We used a combination of behavioral observations of foraging and brood provisioning behaviors as well as GPS tracking data to measure foraging variables for each breeding pair, including diet, food profitability, distance to the foraging area, and brood provisioning rate. For behavioral observations, we used 10 × 42 binoculars and 60× spotting scopes to observe a foraging adult from a breeding pair for 10 minutes or brood provisioning for one hour using focal animal sampling (Altmann 1974). Observations on foraging adults occurred throughout incubation and chick rearing until chicks fledged. Brood provisioning observations occurred from the time chicks hatched until they fledged. We timed our observations to occur

during falling and low tide when foraging habitat is most available. We rotated which breeding pairs/nests we visited, so that we could make observations on foraging adults 1–3 times per week for each breeding pair throughout the months of April to August. We made brood provisioning observations 2–3 times per week for each brood from the hatch date to fledging at day 35. We usually stationed ourselves to do observations from a tall dune, where we could simultaneously see the nesting area and foraging area(s) of a focal breeding pair. This let us continuously track a focal breeding pair and tie specific foraging behaviors to them. During adult foraging observations and brood provisioning observations we recorded the identity of the breeding pair, prey species eaten/provisioned, prey handling time (time from the initial dart probe when the bill is fully inserted into the substrate, until the prey is swallowed) (Tuckwell and Nol 1997), and foraging location. We determined breeding pair ID based on the unique bands of the breeding pair members, foraging location, and brood age. Foraging behaviors could be tied to a pair even when one adult was unbanded because pair members tend to forage together in similar locations (L. A. Brown unpublished data). To identify the breeding pair when both pair members were unbanded, we relied on the territoriality of American Oystercatchers, where breeding pair members tend to stay near nests to defend territories (Nol 1985). In this way, we associated the nest/brood location to the closest unbanded pair that was defensive/territorial, and then we continuously watched that pair during the observation to tie individual foraging behaviors to them. We used prey handling times to calculate food profitability as wet food mass (g)/handling time (s), as per (Nol 1989). We had determined wet food mass by collecting sizes of individuals of each prey species that American Oystercatchers would take (their shells were opened) and measuring the wet mass. Average wet mass ± SE for each prey species was Atlantic mole crab: 2.51 ± 0.48 g, $n$ = 19, Atlantic ribbed mussel: 6.31 ± 1.01 g, $n$ = 19, eastern oyster: 3.44 ± 0.50 g,

*n* = 19, northern quahog clam: 1.82 ± 0.15 g, *n* = 10. We calculated a brood provisioning rate for each breeding pair as the sum of the number of prey items delivered to the brood by both pair members/observation duration (h).

*GPS Tracking.* In 2023 and 2024, we deployed 12 GPS tags (PathTrack Ltd Nanofix® GEO + RF, 9 g) on American Oystercatcher breeding adults on Assawoman Island (*n* = 6 in 2023, *n* = 1 in 2024) and Assateague Island, Virginia (*n* = 4 in 2023, *n* = 1 in 2024) (Supplementary Table S3.1). To distinguish individuals, we banded birds with black Darvic bands that had unique alphanumeric codes. A single member of a breeding pair received a GPS tag. We attached GPS tags to birds using leg loop harnesses made of Teflon ribbon (Bally Ribbon Mills). The GPS tag sat above the bird's rump and was elevated with a 5 mm neoprene patch to prevent abrasion. We strengthened the Teflon harnesses by inserting 1.5 mm Stretch Magic™ inside the Teflon, and then crimped, glued, and sewed the harness ends onto the harness. The GPS tag and harness mass was 15 g. We recaptured individuals after one year to remove GPS tags.

In 2023, we programmed 9 GPS tags to take a GPS fix every 15 minutes during the breeding season from April to August 0400–2059 EST, using the solar-driven mode. One GPS tag was scheduled to take a GPS fix every half hour from 0000–2459 during the breeding season, so that nocturnal movements could be examined as part of a different study. In 2024, we programmed 2 GPS tags to take a GPS fix every 15 minutes from April to August 0400–2059 EST. We downloaded GPS data remotely using Bluetooth with a PathTrack Ltd base station. We rotated the GPS base station across nests of tagged individuals to download data from each individual every 2–3 weeks.

**Table 3.2. Predator take and trapping effort by the U.S. Department of Agriculture at Assateague Island and Assawoman Island, Virginia, U.S.A. from January 1–September 30 in 2022, 2023, and 2024.**

| | Predators trapped | | | | | Trapping effort | |
|---|---|---|---|---|---|---|---|
| | Red fox (*Vulpes vulpes*) | Raccoon (*Procyon lotor*) | Opossum (*Didelphis virginiana*) | Fish Crow (*Corvus ossifragus*) | American Crow (*Corvus brachyrhynchos*) | Trapping nights | Trapping days |
| Assateague Island | | | | | | | |
| 2022* | 25 | 13 | 0 | 0 | 3 | 1,149 | 34 |
| 2023 | 20 | 8 | 0 | 2 | 0 | 1,034 | 24 |
| 2024 | 25 | 17 | 0 | 3 | 0 | 1,286 | 30 |
| Assawoman Island | | | | | | | |
| 2022 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2023 | 1 | 0 | 0 | 0 | 0 | 112 | 7 |
| 2024 | 1** | 0 | 2 | 0 | 0 | 88 | 9 |

* No trapping requests were made for Assawoman Island in 2022.

** 1 Red fox was found as roadkill in late May at the south end of Wallops Island (the island immediately north of Assawoman Island). After this roadkill event, no red fox signs were reported.

We processed GPS data by removing GPS fixes taken with fewer than five satellites; removing duplicate timestamps; and visually checking for outliers. We used the R packages 'amt', 'move', and 'moveVis' to import and visualize the GPS data in R (Signer *et al.* 2019; Schwalb-Willmann *et al.* 2020; Kranstauber *et al.* 2023).

*Diet Classification.* We used different methods to classify individual's diets based on whether they had a GPS tag or not (Brown and Nol 2026, Chapter 2). We used Bolnick *et al.*'s (2002) definition of specialists as individuals that select a subset of resources from the total number of resources available to the population. For individuals without a GPS tag, we used data from foraging observations to define specialists as individuals who primarily ate Atlantic mole crabs (>90% of their diet) with a small allowance for Coquina (*Donax varibilis*) (<10% of their diet), another ocean intertidal-dwelling invertebrate (Brown and Nol 2026, Chapter 2). Coquina was only temporarily available for three weeks in the summer of 2022, and a few days in 2023,

so individuals did not incorporate this prey species regularly in their diet. We defined generalists as individuals who ate any prey species in addition to Atlantic mole crabs or Coquina, including Atlantic ribbed mussels, eastern oysters, northern quahog clams, and Atlantic razor clams (Brown and Nol 2026, Chapter 2). For GPS tagged individuals, we classified diet based on movements to foraging habitat. Specialists only visited the oceanside shoreline to feed, and generalists foraged at both the oceanside shoreline and bayside mudflats (Brown and Nol 2026, Chapter 2). We defined breeding pairs as a specialist if both breeding pair members were specialists, and generalist if either breeding pair member was a generalist. Across both islands, we classified breeding pairs as having a generalist diet for 84 nests and 44 broods, and as having a specialist diet for 63 nests and 21 broods (Supplementary Table S3.2).

*Foraging Distance from the Nest.* We used a combination of behavioral observations and GPS tracking data to determine distance to the foraging area from the nest. Even though American Oystercatcher chicks are precocial and mobile after hatching (American Oystercatcher Working Group *et al.* 2020), chicks tend to stay near the nest, so we used the nest as a proxy to measure foraging distances. For individuals lacking a GPS tag, we used the behavioral observations to assess foraging distance. Based on the foraging and brood provisioning observations, we delineated feeding areas by drawing polygons around meaningful units of the foraging habitat with the software ArcGIS Pro v. 3.2 (ESRI 2011), as per Brown and Nol (2024). We then calculated the centroid of each feeding area in ArcGIS Pro, from which we measured foraging distance from the nest. For each observation, we measured foraging distance whenever a unique breeding pair member visited a unique foraging area. For example, in one observation, a breeding female might visit three separate foraging areas and a breeding male might visit one foraging area. For GPS tagged individuals, we measured distance to the foraging area from the

nest by first distinguishing foraging movements from other movements based on when the movement occurred during the tidal cycle. Most foraging activity occurs during falling tide (one to five hours after high tide) and low tide (one hour on either side of low tide) (L. A. Brown unpublished data), so we filtered movements as foraging if they occurred during falling or low tide. We obtained tidal time information from the nearest NOAA tidal gauge station (8630413 for Assateague Island and 8630440 for Assawoman Island). For both the behavioral observations and GPS data, we measured the distance between a foraging location and the nest, using the Haversine method, with the R package 'geosphere' (Hijmans 2022).

## Statistical Analysis

We calculated breeding productivity from 2022–2024 and assigned the cause of failure to each nest when possible. We developed two separate survival models using the program 'RMark' (Laake 2022). Each model generally contained the same pairs throughout the study period (Table 3.1). To examine daily nest survival from incubation to hatching or nest failure, we developed a model considering all nests (effective sample size = 2,561 nest days). To examine daily brood survival to fledging or brood loss, we developed a model considering only nests that hatched (effective sample size = 3,223 nest days). RMark used a generalized linear model (GLM) approach with a logistic-exposure link function to model daily survival rates as a function of foraging and temporal covariates (Rotella *et al.* 2004). Prior to including predictors in candidate models, we tested for collinearity among our predictors using Pearson's correlation test for sets of continuous predictors, biserial correlation tests for sets of categorical and continuous predictors, and chi-square tests for sets of categorical predictors. For daily nest survival we tested if daily nest survival was predicted by diet of the breeding pair (generalist or specialist), distance to the foraging area from the nest, and/or food profitability. For each nest, we averaged distance to the foraging area from the nest and food profitability across the observations. For daily brood

survival, we tested if daily brood survival was predicted by diet, distance to the foraging area from the nest, and/or brood provisioning rate (number of prey items delivered per hour). For each brood, we averaged distance to the foraging area from the nest and brood provisioning rate across the observations. We did not include island as a predictor in either model because island and diet strongly corresponded to one another, since Assawoman Island only supported birds with generalist diets (Supplementary Table S3.2).

We used a multi-step modeling approach as per Schulte and Simons (2015). In Stage 1 of modeling, we tested if linear and quadratic time and age effects and year should be retained as predictors. If the 95% confidence interval overlapped zero, the predictor was uninformative according to Arnold (2010) and dropped from the model. For informative predictors, we reported the model coefficients (β). In Stage 2 of modeling, we moved forward with the best model from Stage 1 and added the foraging variables. If year was an informative predictor in Stage 1, we tested for two-way interactions between year and foraging predictors in candidate models. We also tested for year-specific effects by analyzing the data separately for each year. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC*c*). We considered all models ≤ 2 ΔAIC*c* to be competitive (Burnham and Anderson, 2002).

We calculated daily survival rate and period survival for nests and broods for the null model and significant predictors of the top model. We defined period survival for nests as survival until hatching (27 days after incubation) (American Oystercatcher Working Group *et al.* 2020). We defined period survival for broods as survival until fledging (35 days after hatching) (American Oystercatcher Working Group *et al.* 2020). We performed statistical analyses in R v. 4.3.1 (R Core Team 2023). Codes and data used in the analysis are available at https://osf.io/dmk4e/?view_only=6b85b45054414663bb54b64278278a9b.

## Results

From 2022–2024 across both islands we monitored 254 nests, 40% ($n$ = 102 nests) of which hatched 215 chicks. Of the 102 broods, 39% ($n$ = 40 broods) fledged at least one chick, and 32% of chicks ($n$ = 68 chicks) fledged in total (Table 3.1). Breeding productivity peaked in 2024 for both islands with breeding productivity exceeding the goal of 0.5 chicks fledged per breeding pair in 2024 but not in 2023 or 2022 (Table 3.1). In daily survival models, we included 147 nests and 65 broods that had foraging data for every predictor. From 2022–2024 across both islands and all breeding pairs, we made 339 observations of foraging adults and 482 observations of brood provisioning. Summary statistics for each foraging predictor are presented in Table 3.3.

**Table 3.3. Summary statistics for foraging predictors of American Oystercatchers (*Haematopus palliatus*) breeding at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024.**

| Reproductive stage | Variable | *n* | Min | Max | Mean | SE |
|---|---|---|---|---|---|---|
| Incubation | Food profitability (g/s) | 131 | 0.01 | 1.81 | 0.42 | 0.03 |
| Incubation | Foraging distance from the nest (m) | 137 | 38.95 | 1,618.13 | 286.30 | 23.66 |
| Pre-fledging | Foraging distance from the nest (m) | 76 | 38.95 | 1,058.88 | 235.03 | 18.75 |
| Pre-fledging | Provisioning rate (number of prey items delivered to a brood per hour) | 71 | 0.90 | 15.00 | 4.27 | 0.39 |

For reproductive stage, incubation was defined as the duration when breeding pairs had a nest with eggs, and pre-fledging was defined as the time when chicks hatch at day 0 until day 34 (the day prior to fledging). Variables are presented in units per breeding pair. To best represent the foraging data based on the largest sample size, *n* represented the number of nests or broods for which we had foraging data, and could include some nests/broods with partial foraging data (only data for one but not all of the foraging predictors).

## Nest Survival

The candidate set of models for nest survival in Stage 2 of modeling included the predictors of diet, food profitability, and year. We considered diet and food profitability as distinct possible predictors, since they were not significantly correlated with one other ($t_{145}$ = 0.27, $P$ = 0.79, $r$ = 0.02, 95% CI[-0.14, 0.18]). We dropped distance to the foraging area as a possible predictor from the set of candidate models because distance to the foraging area was significantly associated with diet ($t_{145}$ = 2.52, $P$ = 0.01, $r$ = 0.20, 95% CI[0.04, 0.35]). Year was the top predictor of daily nest survival among temporal variables (Supplementary Table S3.3), so we retained year in Stage 2 of modeling.

Even though diet and food profitability appeared in models within two AIC*c* units of the top ranked model, the top and most parsimonious model only included the predictor year (Table 3.4), and year was an informative predictor ($\beta_{Year}$ = 2.935 ± SE 0.165, 95% CI [2.613, 3.258]). Thus, the food variables were not important predictors of daily nest survival. A separate analysis also indicated there were no year-specific effects of diet or food profitability on daily nest survival. For each study year, the null model was the top model (Supplementary Table S3.4).

Daily nest survival increased from 2022–2024 (Table 3.5). Interannual variation in predator and storm activity contributed to yearly differences in nest survival (Fig. 3.3 and Fig. 3.4). Predation and overwash were the leading causes of nest failure on both islands across years, with predation causing 49% of the 142 nest failures, overwash causing 33% of nests failures, abandonment causing 4% of nest failures, infertility causing 1% of nest failures, and unknown reasons causing 13% of nests failures.

**Table 3.4. Year best predicted American Oystercatcher (*Haematopus palliatus*) daily nest survival during incubation from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A.**

| Model | *K* | AIC*c* | ΔAIC*c* | $w_i$ | Deviance |
|---|---|---|---|---|---|
| S(~Year) | 3 | 557.770 | 0.000 | 0.432 | 551.760 |
| S(~Year + Diet) | 4 | 559.126 | 1.356 | 0.219 | 551.110 |
| S(~Year + Food Profitability) | 4 | 559.647 | 1.877 | 0.169 | 551.631 |
| S(~Year + Diet + Food Profitability) | 5 | 561.033 | 3.263 | 0.085 | 551.010 |
| S(~Year + Diet + Year * Diet) | 6 | 561.571 | 3.801 | 0.065 | 549.538 |
| S(~Year + Food Profitability + Food Profitability * Year) | 6 | 563.495 | 5.725 | 0.025 | 551.462 |
| S(~Year + Diet + Diet * Year + Food Profitability + Food Profitability * Year) | 9 | 567.484 | 9.714 | 0.003 | 549.414 |
| S(~Null - intercept only) | 1 | 568.687 | 10.917 | 0.002 | 566.685 |

Where *K* represented the number of parameters; AIC*c* represented the Akaike information criterion corrected for small sample sizes; ΔAIC*c* represented the change in AIC*c* information score from the top model; $w_i$ (model weight) represented the proportion of the predictive power included in the model out of all possible candidate models; and deviance represented the amount of variation in the data that is explained by the model.

Definition of foraging predictors include: diet (specialist or generalist), and food profitability (prey mass in g/handling time of prey in s).

**Table 3.5. American Oystercatcher (*Haematopus palliatus*) daily and period nest survival during incubation increased with year at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024.**

| | | Daily survival | | | Period survival | | |
|---|---|---|---|---|---|---|---|
| Year | *n* | Estimate | SE | 95% CI | Estimate | SE | 95% CI |
| 2022 | 57 | 0.950 | 0.008 | 0.932, 0.963 | 0.247 | 0.055 | 0.148, 0.361 |
| 2023 | 48 | 0.972 | 0.005 | 0.959, 0.981 | 0.464 | 0.069 | 0.327, 0.591 |
| 2024 | 42 | 0.982 | 0.004 | 0.971, 0.989 | 0.619 | 0.074 | 0.458, 0.746 |
| Null - intercept only | 147 | 0.969 | 0.003 | 0.962, 0.975 | 0.428 | 0.040 | 0.348, 0.505 |

Period survival was the probability that a nest survived until hatching at day 27. *n* represented the number of nests. The null model represented the overall daily and period nest survival rate for all nests across years and islands.

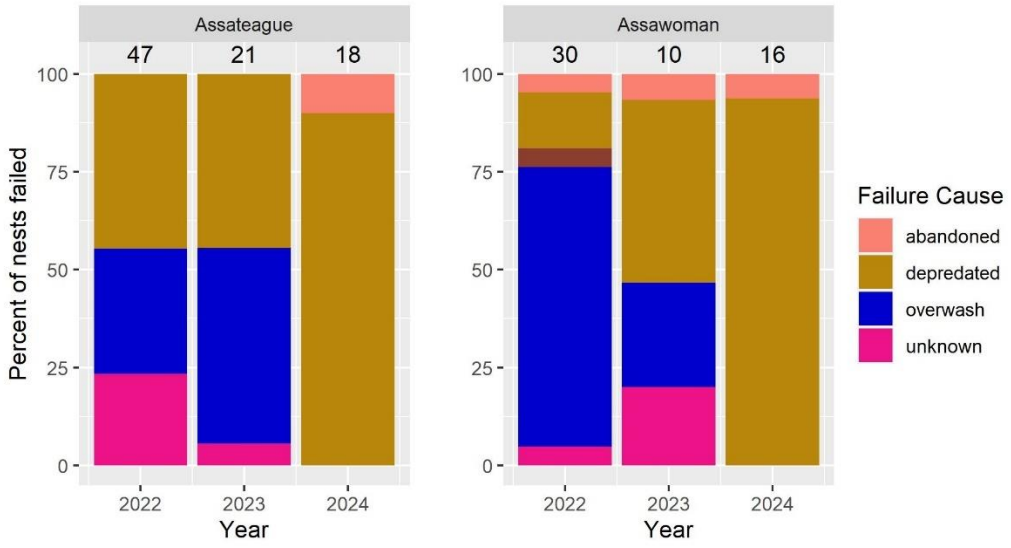



**Figure 3.3.** Percent of nests failed based on failure cause for American Oystercatchers on Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024. Labels above each bar represent the total number of nests.

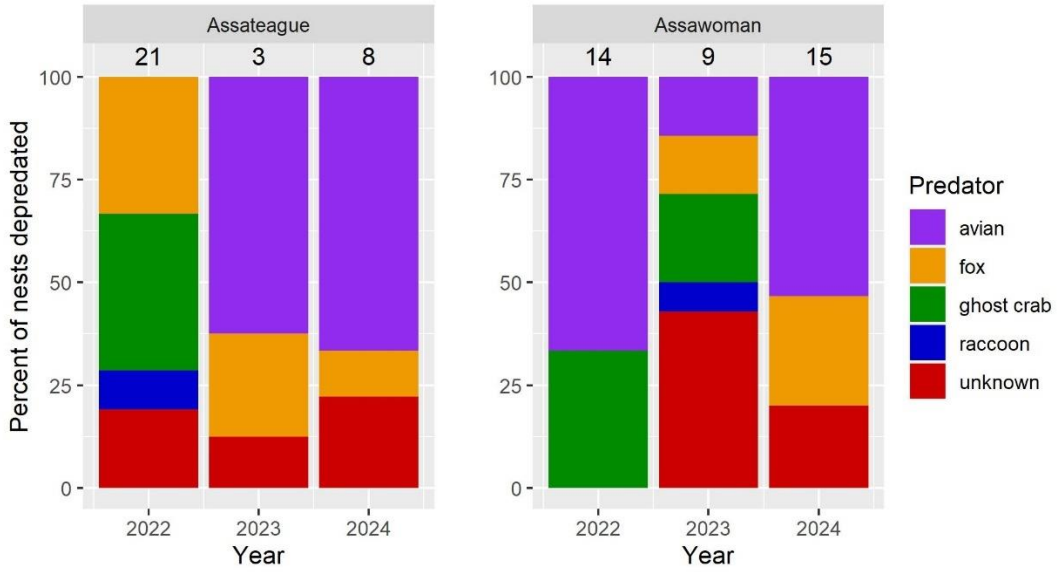



**Figure 3.4.** Percent of depredated American Oystercatcher nests by different predators on Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024. Labels above each bar represent the total number of nests.

On Assateague Island, red foxes were the leading trapped nest predator ($n$ = 75 of 121 trapped predators), followed by raccoons ($n$ = 38), and crows ($n$ = 8). On Assawoman Island, the U.S. Department of Agriculture trapped one red fox in 2023 and two Virginia Opossums in 2024. After a red fox died as roadkill in late May of 2024, we stopped observing red fox signs on Assawoman Island and all remaining nests hatched.

In 2022, a single nor'easter over Mother's Day weekend (May 5–8, 2022), and high tide events in mid-June and mid-July meant that overwash caused 32% of the 47 nest failures on Assateague Island and 71% of the 21 nest failures on Assawoman Island (Fig. 3.3). In 2023, overwash from four storms and high tide events in early May, late May, early June, and late June contributed to 50% of the 18 nest failures on Assateague Island and 27% of the 30 nest failures on Assawoman Island. In 2024, a lack of storms meant that no nests failed due to overwash on either island that year.

## Brood Survival

The candidate set of models for brood survival included the predictors of diet, distance to the foraging area, and brood age. There was no collinearity among the predictors (Supplementary Table S3.5). Thus, we proceeded with all predictors in Stage 2 of modeling. A linear term for brood age was an informative predictor in the top model among temporal variables of daily brood survival, so we retained brood age in Stage 2 of modeling (Supplementary Table S3.6).

Neither diet nor distance to the foraging area were important predictors of brood survival. The top model for daily brood survival contained the predictors of brood age and diet (Table 3.6). Mole crab specialist diets showed higher daily brood survival rates than generalist diets (Supplementary Fig. S3.1), although diet was not an informative predictor ($\beta_{\text{Diet specialist}}$ = 0.89 ± SE 0.51, 95% CI [-0.10 to 1.88]). Only brood age was an informative predictor ($\beta_{\text{Brood age}}$ = -0.06

± SE 0.01, 95% CI [-0.08 to -0.04]). Daily brood survival decreased as chicks aged (Fig. 3.5). In 2022, the cause of chick mortality was unknown in all cases except for three avian depredation events witnessed by observers. Two 3-week old chicks were killed by Great Black-backed Gulls (*Larus marinus*) on Assawoman Island, and one 7-day old chick was killed by a Peregrine Falcon on Assateague Island. We speculate that Great Black-backed Gulls took additional chicks on Assawoman Island in 2022 because 2–5 week old chicks kept disappearing from Assawoman Island in the same area as the two witnessed chick depredation events, and a Great Black-backed Gull was frequently observed attacking broods. There were no signs of other sources of depredation, nor major storms when the 2–5 week old chicks were disappearing from Assawoman Island. In 2023 and 2024, we did not witness any direct chick depredation events. Overall daily survival rate of broods across years and islands for the null model was 0.992 ± SE 0.002, 95% CI [0.989, 0.995], $n$ = 65 broods with a period survival until fledging as 0.763 ± 0.041, 95% CI [0.670, 0.833].

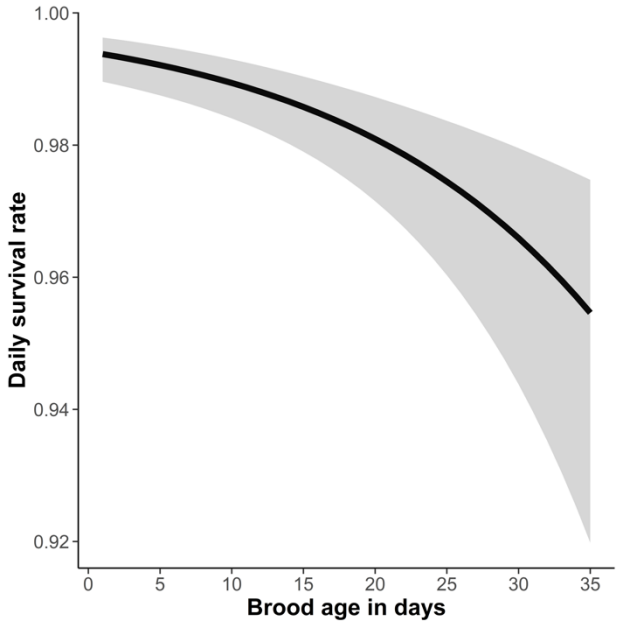



**Figure 3.5.** American Oystercatcher (*Haematopus palliatus*) daily brood survival rate decreased with age at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024. Shading represents the 95% CI.

**Table 3.6. Brood age best predicted American Oystercatcher (*Haematopus palliatus*) daily brood survival from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A.**

| Model | *K* | AIC*c* | ΔAIC*c* | $w_i$ | Deviance |
|---|---|---|---|---|---|
| S(~Brood age + Diet) | 3 | 214.86 | 0.00 | 0.28 | 208.85 |
| S(~Brood age + Diet + Distance) | 4 | 215.43 | 0.57 | 0.21 | 207.41 |
| S(~Brood age) | 2 | 216.45 | 1.60 | 0.13 | 212.45 |
| S(~Brood age + Diet + Brood provisioning rate) | 4 | 216.74 | 1.88 | 0.11 | 208.73 |
| S(~Brood age + Distance) | 3 | 216.85 | 2.00 | 0.10 | 210.85 |
| S(~Brood age + Diet + Distance + Brood provisioning rate) | 5 | 217.41 | 2.55 | 0.08 | 207.39 |
| S(~Brood age + Brood provisioning rate) | 3 | 218.36 | 3.50 | 0.05 | 212.35 |
| S(~Brood age + Distance + Brood provisioning rate) | 4 | 218.62 | 3.76 | 0.04 | 210.61 |
| S(~Null - intercept only) | 1 | 246.66 | 31.81 | 0.00 | 244.66 |

Where *K* represented the number of parameters; AIC*c* represented the Akaike information criterion corrected for small sample sizes; ΔAIC*c* represented the change in AIC*c* information score from the top model; $w_i$ (model weight) represented the proportion of the predictive power included in the model out of all possible candidate models; and deviance represented the amount of variation in the data that was explained by the model.

Definition of foraging predictors include: diet (specialist or generalist); distance (foraging distance from the nest during pre-fledging); and brood provisioning rate (number of prey items delivered to a brood per hour).

Of the predictors, only brood age was informative. All foraging predictors were uninformative because their confidence intervals overlapped with zero.

## Discussion

Foraging factors did not limit breeding success of American Oystercatchers at two barrier islands in Virginia. Instead, variation in hatching success was best explained by annual variation in depredation and overwash from the storms/high tide events, and fledging success was most affected by age. Fledging success was similar for breeding pairs regardless of diet. This contrasts with Eurasian Oystercatchers (*Haematopus ostralegus*) at Skokholm Island off the Irish Sea that provision chicks with worms and arthropods and have three times higher fledging success compared to breeding pairs that provision chicks with limpets (Safriel 1985). Similarly, Slaty-backed Gulls (*Larus schistisagus*) in Japan that provision young with seabirds, have higher fledging success than breeding pairs that provision young with fish or marine invertebrates (Watanuki 1992). Herring Gulls (*Larus argentatus*) in Newfoundland, Canada that specialize on blue mussels (*Mytilus edilus*) also have higher hatching and fledging success than any other diet because blue mussels provide essential nutrients (calcium and sulfonated amino acids), which aid in bone development and growth (Pierotti and Annett 1990). Our findings that diet did not impact fledging success is consistent with Thick-billed Murres (*Uria lomvia*), where brood survival is similar for breeding pairs that specialize provisioning chicks with rare fish species and breeding pairs that provision multiple fish species (Woo *et al.* 2008). In a similar fashion, Brown Skuas (*Stercorarius antarcticus*) have similar brood survival regardless of diet, even though breeding pairs that provision birds to chicks have chicks with higher body condition than breeding pairs that provision fish (Votier *et al.* 2004).

Without sufficient prey or provisioning, chicks can die from starvation. American Oystercatcher chicks in Florida have died of starvation because of severe declines in oyster abundance (Vitale *et al.* 2022). Schulte and Simons (2015) also reported that 27% of American

Oystercatcher chicks died from starvation or exposure in North Carolina. For Black Oystercatchers (*Haematopus bachmani*), broods with lower energy intake rates have lower brood survival (Robinson *et al.* 2019). While we did not assess chick body condition directly, we did not find any emaciated chicks on either island across of the three years of the study, and we did not attribute any known chick mortality to starvation. This suggests that food was probably not a limiting factor at either island.

Contrasting with previous studies (Nol 1989; Ens *et al.* 1992; Schulte and Simons 2015) distance to the foraging area was not important for brood survival in our study. In the 1980s in Virginia, distance to the foraging area was important to American Oystercatcher fledging success because foraging proximity reduced time spent away from broods and facilitated increased vigilance over broods, which reduced predation risk of chicks (Nol 1989). Additionally, American Oystercatchers in North Carolina with sound side foraging access have higher fledging success than breeding pairs without sound side foraging access (Schulte and Simons 2015). Similarly, Eurasian Oystercatchers that have foraging grounds adjacent to their nesting areas have 3.5 times greater fledging success than breeding pairs with distant foraging grounds because foraging proximity promotes increased vigilance over broods and higher brood provisioning rates (Ens *et al.* 1992). In our study, brood provisioning rates do not differ based on diet (L. A. Brown unpublished data), so brood provisioning is unlikely to underly a possible relationship with brood survival based on the distance to the foraging area. As for predation risk explaining the possible link between brood survival and distance to the foraging area, even when both parents loafed within 5 m of chicks and were vigilant against predators, we watched a Great Black-backed Gull take a chick from the parents. In our study area, where avian predators are the top predator of chicks, distance to the foraging area might be less important for brood survival

than in areas where mammals are the top predators of chicks. It may be that adults close to nests discourage mammalian predators but not avian predators.

We expected that breeding pairs with higher food profitability should be more efficient foragers, which would facilitate their return to the nest sooner, and reduce predation risk of nests, therefore increasing nest survival. However, similarly to Nol (1989), food profitability did not impact nest survival. Food profitability is independent of searching time for prey, so even if individuals are efficient foragers, prey could be widely distributed across the landscape, so individuals might spend more time searching for food and wind up spending a similar time away from the nest.

At our site, hatching success seemed to be most influenced by stochasticity in predator activity and storms. Our findings are consistent with other studies in Virginia (Denmon *et al.* 2013) and North Carolina (Schulte and Simons 2015; Walters *et al.* 2020) that identify predators and overwash from storms as two of the top limiting factors for American Oystercatcher breeding success. In our study, the year 2023 had higher hatching success relative to 2022, and this corresponded with a decrease in predator activity in 2023, which might have been linked to differences in hurricane activity. Hurricane Ian struck the area in October of 2022 and could have removed nest predators for the 2023 nesting season (Schulte and Simons 2016). In 2024, American Oystercatchers experienced high hatching success due to favorable weather from a lack of strong storms, removal of a depredating red fox, and no Atlantic ghost crab depredation.

In our study, brood survival decreased with age, which is consistent with American Oystercatchers in Florida. In Florida, insufficient food resources caused older chicks to have lower survival than younger chicks (Vitale *et al.* 2022). In our study, where food did not appear to be a limiting factor, older chicks seemed to experience a higher risk of depredation due to

chicks > 3 weeks old seeming to seek cover less when avian predators flew overhead (L. A. Brown, pers. obs.). This observation is consistent with age-dependent chick hiding behavior in Mountain Plovers (*Charadrius montanus*) (Sordahl 1991). Older American Oystercatcher chicks are also of larger body size and would provide a bigger food reward for predators. In our study, gulls typically attacked and depredated chicks that were at least two weeks old. In contrast, Laughing Gulls (*Leucophaeus atricilla*) in Texas attacked and depredated American Oystercatcher chicks younger than two weeks old (Anderson 2014), and in North Carolina, younger American Oystercatcher experience lower survival because younger chicks are less mobile and have more difficulty evading predators (Schulte and Simons 2015).

## Management Recommendations

Since long-term studies are better able to detect multi-year dynamics of prey populations, we note that food might be a limiting factor for American Oystercatcher populations elsewhere, and that the management recommendations presented here are appropriate for this study site, based on a small number of years. Predators and overwash remain the top threats for American Oystercatcher breeding success at our study site. Once depredating red foxes were trapped and removed from our study islands, hatching success increased. As in our study islands, other studies have reported high levels of fox depredation (Schulte 2012) and found increased hatching success after trapping (McGowan 2004). Simply counting trapped animals may not reflect true predation rates, since one red fox can depredate all nests on one of our study islands in a single night. More game cameras monitoring nests could better quantify the threat of nest predation at our study site. We reiterate that continued investment in predator control efforts are important to maintain American Oystercatcher breeding success.

Gull harassment or lethal management programs have been attempted to increase reproductive success of shorebirds, but most programs seem to have little to no efficacy (Harris and Wanless 1997; Olijnyk and Brown 1999; Keane 2002). It is more difficult to manage gull predation when gulls are not nesting in the area, as is the case on Assawoman Island. Removal of 18 gulls that specialize in feeding on terns did not reduce *Sterna* spp. chick depredation because other gulls in the population replaced them (Donehower *et al.* 2007). So far, there do not seem to be any existing cost-effective strategies for reducing gull depredation of American Oystercatcher chicks. Before beginning a campaign against gulls, future research could quantify how problematic gull depredation of shorebird chicks is by identifying the percent composition that shorebird chicks make up in gull diets using behavioral observations of foraging gulls, stomach content analysis, and DNA barcoding of fecal samples.

As climate change increases storm frequency and intensity and sea levels rise (Lee *et al.* 2023), nest flooding will become a greater problem. We echo the management recommendation of Vitale *et al.* (2022) that efforts which increase beach elevation like beach renourishment should help reduce nest losses to overwash. One simple way to increase elevation might be to place used car tires on beaches. In 2022, one breeding pair on Assateague Island nested in a car tire that was partially buried in the sand. When storms occurred the nest in the tire remained dry, even though nests surrounding it were flooded.

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# Supplementary Materials

**Supplementary Table S3.1. GPS tag details for American Oystercatchers (*Haematopus palliatus*) at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024.**

| Bands | Diet | Island | GPS fixes |
|---|---|---|---|
| CEK | Specialist | Assateague | 6,758 |
| NAN | Specialist | Assateague | 1,276 |
| CEN | Specialist | Assateague | 902 |
| CEM | Generalist | Assateague | 6,907 |
| CAT | Generalist | Assateague | 5,279 |
| CKT | Generalist | Assawoman | 5,631 |
| CAY | Generalist | Assawoman | 3,925 |
| CCK | Generalist | Assawoman | 3,723 |
| CAP | Generalist | Assawoman | 3,516 |
| CEJ | Generalist | Assawoman | 2,644 |
| KX | Generalist | Assawoman | 1,509 |
| CCE | Generalist | Assawoman | 522 |

**Supplementary Table S3.2. Frequency of American Oystercatcher (*Haematopus palliatus*) nests and broods based on diet and island from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A.**

| | Diet | Island | *n* |
|---|---|---|---|
| Nest | Specialist | Assateague Island | 63 |
| | Generalist | Assateague Island | 31 |
| | Specialist | Assawoman Island | 0 |
| | Generalist | Assawoman Island | 53 |
| Brood | Specialist | Assateague Island | 21 |
| | Generalist | Assateague Island | 5 |
| | Specialist | Assawoman Island | 0 |
| | Generalist | Assawoman Island | 39 |

**Supplementary Table S3.3. Year was the top temporal predictor for American Oystercatcher (*Haematopus palliatus*) daily nest survival during incubation from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A. Year was retained as a predictor in Stage 2 of modeling.**

| Model | *K* | AIC*c* | ΔAIC*c* | $w_i$ | Deviance |
|---|---|---|---|---|---|
| S(~Year) | 3 | 557.77 | 0.000 | 0.979 | 551.76 |
| S(~Nest age + I(Nest age$^2$)) | 1 | 567.30 | 9.53 | 0.008 | 565.30 |
| S(~Null - intercept only) | 1 | 568.69 | 10.92 | 0.004 | 566.69 |
| S(~Nest age) | 2 | 569.30 | 11.53 | 0.003 | 565.30 |
| S(~Time) | 2 | 570.69 | 12.92 | 0.002 | 566.68 |
| S(~Nest age + Time) | 3 | 571.12 | 13.35 | 0.001 | 565.11 |
| S(~Nest age + I(Nest age$^2$) + Time) | 3 | 571.12 | 13.35 | 0.001 | 565.11 |
| S(~Time + I(Time$^2$)) | 3 | 572.60 | 14.83 | 0.001 | 566.59 |
| S(~Nest age + Time + I(Time$^2$)) | 4 | 573.06 | 15.29 | 0.000 | 565.04 |
| S(~Nest age + I(Nest age$^2$) + Time + I(Time$^2$)) | 4 | 573.06 | 15.29 | 0.000 | 565.04 |

Where *K* represented the number of parameters; AIC*c* represented the Akaike information criterion corrected for small sample sizes; ΔAIC*c* represented the change in AIC*c* information score from the top model; $w_i$ (model weight) represented the proportion of the predictive power included in the model out of all possible candidate models; and deviance represented the amount of variation in the data that was explained by the model.

**Supplementary Table S3.4. Foraging factors did not affect American Oystercatcher (*Haematopus palliatus*) daily nest survival during incubation in 2022, 2023, or 2024 at Assateague Island and Assawoman Island, Virginia, U.S.A. The null model was the top model in every study year.**

| Year | Model | *K* | AIC*c* | ΔAIC*c* | $w_i$ | Deviance |
|---|---|---|---|---|---|---|
| 2022 | S(~Null - intercept only) | 1 | 236.09 | 0.00 | 0.40 | 234.09 |
| 2022 | S(~Diet) | 2 | 236.47 | 0.38 | 0.33 | 232.45 |
| 2022 | S(~Food profitability) | 2 | 238.03 | 1.94 | 0.15 | 234.02 |
| 2022 | S(~Diet + Food profitability) | 3 | 238.46 | 2.36 | 0.12 | 232.42 |
| 2023 | S(~Null - intercept only) | 1 | 196.37 | 0.00 | 0.52 | 194.36 |
| 2023 | S(~Diet) | 2 | 198.22 | 1.86 | 0.21 | 194.21 |
| 2023 | S(~Food profitability) | 2 | 198.37 | 2.01 | 0.19 | 194.36 |
| 2023 | S(~Diet + Food profitability) | 3 | 200.24 | 3.87 | 0.08 | 194.21 |
| 2024 | S(~Null - intercept only) | 1 | 125.32 | 0.00 | 0.49 | 123.31 |
| 2024 | S(~Diet) | 2 | 126.89 | 1.57 | 0.22 | 122.88 |
| 2024 | S(~Food profitability) | 2 | 127.10 | 1.78 | 0.20 | 123.08 |
| 2024 | S(~Diet + Food profitability) | 3 | 128.81 | 3.49 | 0.09 | 122.78 |

Where *K* represented the number of parameters; AIC*c* represented the Akaike information criterion corrected for small sample sizes; ΔAIC*c* represented the change in AIC*c* information score from the top model; $w_i$ (model weight) represented the proportion of the predictive power included in the model out of all possible candidate models; and deviance represented the amount of variation in the data that was explained by the model.

**Supplementary Table S3.5. Foraging predictors were not correlated with one another for American Oystercatcher (*Haematopus palliatus*) brood survival at Assateague Island and Assawoman Island, Virginia, U.S.A. 2022–2024.**

| Predictor 1 | Predictor 2 | *t* | df | *P* | *r* | LCI | UCI |
|---|---|---|---|---|---|---|---|
| Distance | Brood provisioning rate | -1.83 | 63 | 0.07 | -0.22 | -0.44 | 0.02 |
| Distance | Diet | 0.41 | 63 | 0.69 | 0.05 | -0.20 | 0.29 |
| Brood provisioning rate | Diet | 1.48 | 63 | 0.14 | 0.18 | -0.06 | 0.41 |

LCI and UCI represent the lower and upper 95% confidence interval. For the continuous predictors of distance and brood provisioning rate, statistical values were calculated using Pearson's correlation test, else for the other combination of predictors, the statistical values were calculated using biserial correlation tests.

Definition of foraging predictors include: diet (specialist or generalist); distance (foraging distance from the nest during pre-fledging); and brood provisioning rate (number of prey items delivered to a brood per hour).

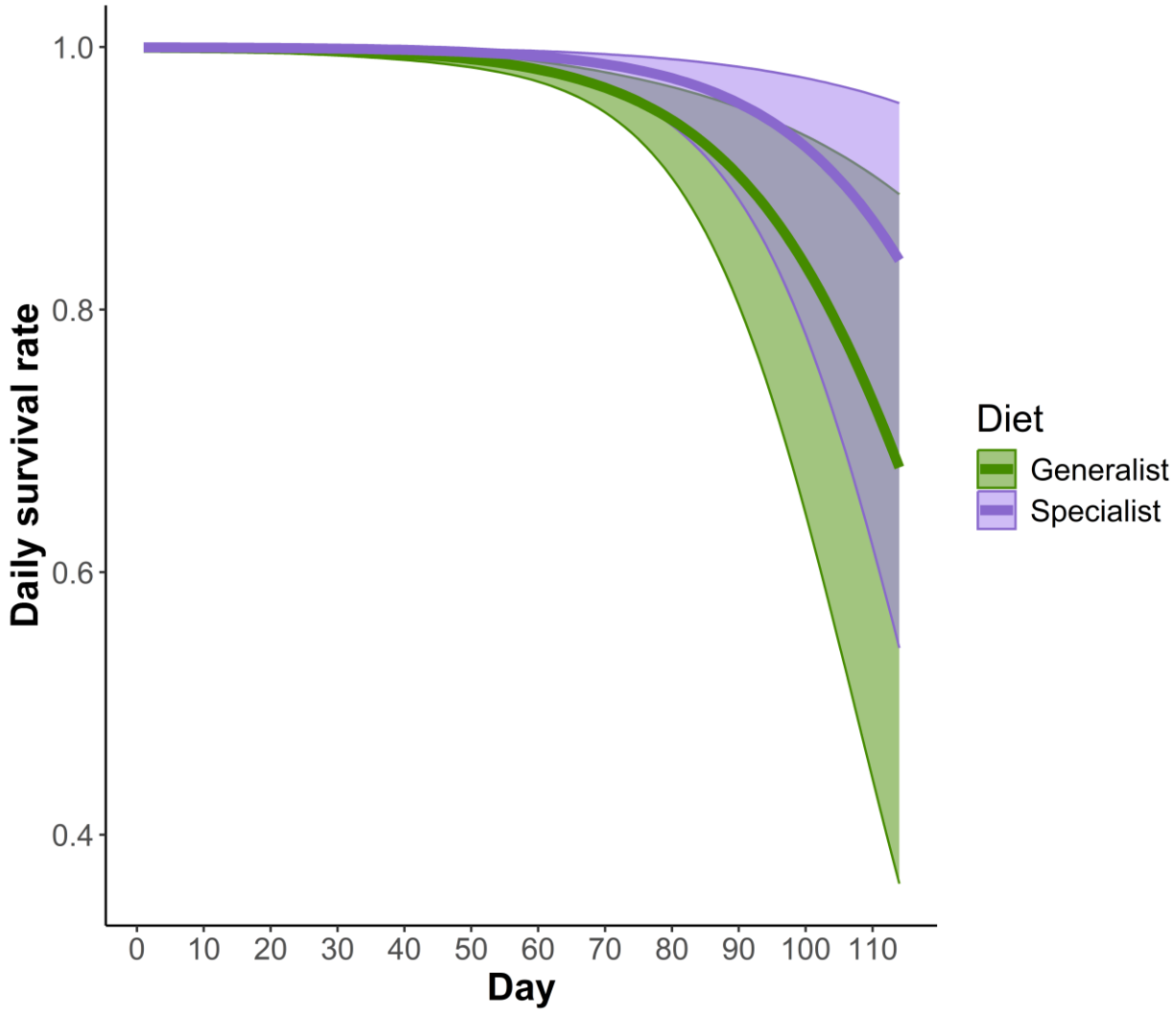
**Supplementary Table S3.6. Brood age was the top temporal predictor for American Oystercatcher (*Haematopus palliatus*) daily brood survival from 2022–2024 at Assawoman and Assateague Island, Virginia, U.S.A. Brood age was retained as a predictor in Stage 2 of modeling.**

| Model | *K* | AIC*c* | ΔAIC*c* | $w_i$ | Deviance |
|---|---|---|---|---|---|
| S(~Brood age + Time + I(Time$^2$)) | 4 | 208.89 | 0.00 | 0.37 | 200.88 |
| S(~Brood age + I(Brood age$^2$) + Time + I(Time$^2$)) | 4 | 208.89 | 0.00 | 0.37 | 200.88 |
| S(~Brood age + Time) | 3 | 211.21 | 2.31 | 0.12 | 205.20 |
| S(~Brood age + I(Brood age$^2$) + Time) | 3 | 211.21 | 2.31 | 0.12 | 205.20 |
| S(~Time + I(Time$^2$)) | 3 | 216.16 | 7.27 | 0.01 | 210.15 |
| S(~Brood age) | 2 | 216.45 | 7.56 | 0.01 | 212.45 |
| S(~Brood age + I(Brood age$^2$)) | 2 | 216.45 | 7.56 | 0.01 | 212.45 |
| S(~Time) | 2 | 219.33 | 10.44 | 0.00 | 215.33 |
| S(~Year) | 3 | 246.27 | 37.38 | 0.00 | 240.26 |
| S(Null - intercept only) | 1 | 246.66 | 37.77 | 0.00 | 244.66 |

Where *K* represented the number of parameters; AIC*c* represented the Akaike information criterion corrected for small sample sizes; ΔAIC*c* represented the change in AIC*c* information score from the top model; $w_i$ (model weight) represented the proportion of the predictive power included in the model out of all possible candidate models; and deviance represented the amount of variation in the data that was explained by the model.

Of the predictors, only brood age was informative. Linear and quadratic time were uninformative predictors because their confidence intervals overlapped with zero.

**Supplementary Figure S3.1. Mole crab (*Emerita talpoida*) special diets had higher daily brood survival rates than generalist diets for American Oystercatchers (*Haematopus palliatus*) from 2022–2024 at Assawoman and Assateague Island, Virginia, U.S.A. Even though diet appeared in the top model predicting daily brood survival (lowest AIC, see Table 3.6), diet was not an informative predictor, since its confidence interval overlapped with zero.**



# Chapter 4 – Stripping eggs from large mole crabs (*Emerita* spp.): a feeding strategy in migratory Hudsonian Whimbrels (*Numenius hudsonicus*) and breeding American Oystercatchers (*Haematopus palliatus*)




An American Oystercatcher (*Haematopus palliatus*) captures a mole crab (*Emerita talpoida*).

Photo credit: Michael Forgues.

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L. A. Brown and S. McKeon equally contributed to study design, data collection and analysis, writing of the initial draft of the manuscript, and revisions of the manuscript. E. Nol contributed to revisions of the manuscript.

Abstract.—Many shorebirds experience digestive bottlenecks, where they can intake energy at faster rates than they can process it, which forces individuals to take digestive pauses during foraging. Some individuals selectively strip soft-bodied parts of invertebrate prey and leave the exoskeleton uneaten to increase prey digestibility. Here we describe migratory Hudsonian Whimbrels (*Numenius hudsonicus*) in Oregon, U.S.A., and breeding American Oystercatchers (*Haematopus palliatus*) in Virginia, U.S.A., stripping and eating eggs from mole crabs (*Emerita* spp.), and explore the relationship between size of the prey and this behavior. We also examined the prevalence of egg stripping in American Oystercatchers and whether it was associated with diet. Hudsonian Whimbrels stripped eggs from 41 Pacific mole crabs (*Emerita analoga*) 41 times. About 10% of Atlantic mole crabs (*Emerita talpoida*) (64 of 554) had their eggs stripped by 11 American Oystercatchers. Both American Oystercatchers and Hudsonian Whimbrels targeted larger mole crabs for egg stripping. Egg stripping did not significantly increase prey handling time for American Oystercatchers, nor was it associated with diet specialization. The low prevalence of egg stripping might be explained by individual prey preferences or the satiation state of individuals. Hudsonian Whimbrels and American Oystercatchers appear to follow the digestive rate model of foraging, where they minimize cumulative foraging time by selecting easily digestible mole crab eggs. Highly digestible and nutrient-rich mole crab eggs may help to drive energetically intensive migratory and breeding behaviors in shorebirds.

**Keywords.—** digestion rate model, digestive bottleneck, foraging preference, marine invertebrate, mole crabs, shorebird.

# Introduction

Optimal foraging theory, which includes the contingency model, predicts that individuals should maximize food profitability (food mass/handling time), given the predation risk, searching time, and handling time for food (Stephens and Krebs 1986). However, the contingency model does not account for digestive constraints. Digestion can limit consumption if an individual can intake energy at a higher rate than it can be processed (Jeschke *et al.* 2002). These digestive bottlenecks force individuals to pause feeding to digest food (Kersten and Visser 1996; Zharikov and Skilleter 2003). The digestion rate model incorporates digestibility into foraging decisions, where individuals choose food items that maximize their energy intake while minimizing digestion time (Verlinden and Wiley 1989; Whelan and Brown 2005). In this way individuals can minimize cumulative foraging time by minimizing digestive pauses (Quaintenne *et al.* 2010). The digestion rate model has been used to explain shorebird foraging behavior (Quaintenne *et al.* 2010).

For shorebirds who consume marine invertebrates, 50–90% of the invertebrate can be inorganic and indigestible (Zwarts and Blomert 1990). One way to increase digestive efficiency is to strip the soft-bodied edible parts of invertebrates and to discard the exoskeleton (Zwarts and Blomert 1990). Red Knots (*Calidris canutus*) who only eat the flesh and organs of bivalves achieve higher energy intake rates than those who swallow bivalves with the shell (Karasov and McWilliams 2005). Eurasian Whimbrels (*Numenius phaeopus* spp.) in Mauritania and Brazil have also been reported to eat only the flesh of fiddler crabs (*Afruca* spp.) and to discard the chelae (Zwarts and Blomert 1990; Fedrizzi *et al.* 2016).

The strength of selection to only eat the flesh/organs of prey can be tempered by prey size, prey abundance, satiation, and kleptoparasitism risk (Zwarts and Blomert 1990, Zwarts and Dirksen 1990, Fedrizzi *et al.* 2016, Gommer *et al.* 2018, Morales-Torres *et al.* 2023). For

Eurasian Whimbrels, as the size of the fiddler crab increases, the amount of indigestible material in their chelae increases, and leads to increased selectivity for flesh removal (Zwarts and Blomert 1990; Fedrizzi *et al.* 2016). Additionally, when fiddler crabs are less abundant, Eurasian Whimbrels only discard the exoskeleton 20% of the time, compared to 40% of the time when fiddler crabs are abundant (Zwarts and Blomert 1990). For Crab Plovers (*Dromas ardeola*), as their stomachs fill up with food, individuals switch from choosing the highest profitable prey, white spot sentinel crab (*Macrophthalmus sulcatus*), to selecting the most digestible prey, African blue swimming crab (*Portunus segnis*) (Gommer *et al.* 2018). When individuals are surrounded by others who might steal their food, prey items might be chosen based on quick handling times to minimize the risk of kleptoparasitism, instead of chosen based on their digestibility (Tuckwell and Nol 1997a; Morales-Torres *et al.* 2023).

Mole crabs (*Emerita* spp.) are anomuran crustaceans that serve as a staple food for many migrating and breeding shorebirds (Dinsmore *et al.* 1998, Peterson *et al.* 2000, Nettleship 2020, Fedrizzi and Carlos 2023; Brown *et al.* 2026; Chapter 2). Mole crabs are found on both the Pacific and Atlantic Coast of the United States, with the Pacific Coast having the Pacific mole crab (*Emerita analoga*) and the Atlantic Coast having the Atlantic mole crab (*Emerita talpoida*) (Efford 1969; Diaz 1980). Both species of mole crabs are wash zone specialists on sandy beaches, and frequently the most common intertidal crustacean at the beach (Efford 1969). Breeding aggregations can be dense, with numbers reaching 6,000 animals per square meter in some areas (Efford 1965). Females only begin producing eggs when they are reproductively mature and of large size (in Bogue Banks, North Carolina, the smallest female Atlantic mole crab bearing eggs was 14.1 mm in carapace length; Diaz 1980). Large females carry masses of up to 5,000 orange eggs underneath the folded abdomen (Efford 1970). Females can produce multiple

clutches within a breeding season (late winter to early fall) and the number of ovigerous (egg-bearing) females peaks in late summer (Diaz 1980).

Two shorebird species that feed on mole crabs are Hudsonian Whimbrels (*Numenius hudsonicus*) and American Oystercatchers (*Haematopus palliatus*) (Fedrizzi 2008, Morales-Torres *et al.* 2023; Brown *et al.* 2026; Chapter 2). Hudsonian Whimbrels are long-distance migrants that move along the Pacific Coast of the Americas from their breeding grounds in the Arctic to their wintering grounds in South America (Johnson *et al.* 2016; Skeel and Mallory 2020). Hudsonian Whimbrels in North America have a generalist diet that includes invertebrates such as *Emerita* spp., burrowing crabs, molluscs (Morales-Torres *et al.* 2023), berries (MacKay 1892; Montevecchi and Tuck 1987), and flowers (Mallory 1981). Eurasian Whimbrels experience digestive bottlenecks, where they can consume food at 2–3 mg of ash-free dry mass per second, but because of digestive pauses, the maximum crude intake rate is 1 mg of ash-free dry mass per second (Zwarts and Dirksen 1990).

American Oystercatchers in North America breed along the Atlantic Coast from Maine to Florida and over to the Gulf Coast of Texas (American Oystercatcher Working Group *et al.* 2020). American Oystercatchers consume bivalves and other marine invertebrates (Nol 1985, Fedrizzi 2008), with some breeding American Oystercatchers in Virginia specializing on Atlantic mole crabs (>90% of the diet is mole crabs, as opposed to most American Oystercatchers that eat a variety of prey including marine invertebrates and multiple bivalve species) (Brown *et al.* 2026, Chapter 2). Oystercatcher species experience digestive bottlenecks (Kersten and Visser 1996). Eurasian Oystercatchers (*Haematopus ostralegus*) can ingest food 4 times faster than they can process it, with a maximum processing ability of 1,067 kJ in a single day and up to 80 g of food storage in their esophagus (Kersten and Visser 1996).

The present study was motivated by field observations of Hudsonian Whimbrels and American Oystercatchers stripping the eggs from mole crabs. In mid-July of 2017, in Oregon, we observed 3 Hudsonian Whimbrels extract Pacific mole crabs from shallow water and place them on the sand upside down. Hudsonian Whimbrels removed and ate the eggs from the Pacific mole crabs, and left behind the majority of each mole crab, including its carapace. Hereinafter, we refer to this behavior as egg stripping. Of shorebirds and gulls present in the area at the time of study, only Hudsonian Whimbrels were seen handling mole crabs in this way. We also found several female Pacific mole crabs exposed on the sand and in pooled water; they were all moribund (injured, incapacitated, and stripped of eggs). The size of these moribund female Pacific mole crabs seemed large in comparison to the many thousands of free-moving individuals of both sexes in the area. Beside several moribund crabs were tracks that matched Hudsonian Whimbrels. In the summer of 2022, in Virginia, we observed several breeding American Oystercatchers stripping the eggs from Atlantic mole crabs. The American Oystercatchers sometimes ingested the eggs themselves and sometimes provisioned eggs to their chicks. The American Oystercatchers left the carapaces of the Atlantic mole crabs as discards. We explored if egg stripping by Hudsonian Whimbrels or American Oystercatchers adhered to a digestion rate model.

## Methods

As a result of these preliminary observations we sought to describe mole crab egg stripping behavior in Hudsonian Whimbrels and American Oystercatchers. For both shorebirds, we examined the size of mole crabs when egg stripping occurred. For American Oystercatchers, we also explored (1) the prevalence of egg stripping behavior in the population; (2) handling time to strip mole crabs of eggs compared to whole ingestion; and (3) if egg stripping was associated with mole crab diet specialization. Since only reproductively mature larger female

mole crabs can bear eggs (Diaz 1980) and larger females carry more eggs (Efford 1970), we predicted that Hudsonian Whimbrels and American Oystercatchers would target stripping eggs from larger mole crabs. Since egg stripping is an additional step in food handling, we expected that handling time would increase when American Oystercatchers stripped eggs from mole crabs versus ingesting them whole. Since some individual American Oystercatchers specialize on feeding on mole crabs (Brown *et al.* 2026), we explored if the specialists performed egg stripping more than generalists.

## Study System

The study area for migratory Hudsonian Whimbrels was a 3.2 km stretch on South Beach, Oregon, U.S.A. (44°36′46.0″N, 124°02′51.7″W). South Beach is a sandy beach where migratory Hudsonian Whimbrels forage along the oceanside shoreline on prey such as the Pacific mole crab. We collected data on Hudsonian Whimbrels in July of 2017. Hudsonian Whimbrels seen at the study area were not banded.

The study area for breeding American Oystercatchers comprised two barrier islands in Virginia, U.S.A.: Assateague Island (37°51′07.2″N, 75°22′55.2″W) and Assawoman Island (37°48′03.6″N, 75°31′04.8″W). Both barrier islands have sandy beaches, which the American Oystercatchers nest on, and oceanside shorelines adjacent to beach nesting areas, where individuals can forage on Atlantic mole crabs. We collected data during the 2022 breeding season from April to August. Assateague Island supported 20 breeding pairs and Assawoman Island supported 31 breeding pairs. All breeding pairs had nearby access (<150 m from nest) to oceanside shorelines containing Atlantic mole crabs. Breeding American Oystercatchers at the study area are a part of ongoing behavioral studies, so many individuals are banded (~60% of the breeding population).

## Data Collection

*Hudsonian Whimbrels.* To compare with the observed female Pacific mole crabs that were found moribund in 2017, we haphazardly sampled an equal number of ovigerous female Pacific mole crabs from the surrounding intertidal area by hand. We used mole crab carapace length (length from the rostrum to the end of the carapace) as a measure of total size. We used calipers to measure the carapaces of moribund and ovigerous female mole crabs.

*American Oystercatchers.* We conducted 10 min observations on foraging adult American Oystercatchers, as per Altmann (1974) and Nol (1985). We used 10×42 binoculars and 60× spotting scopes to observe individuals. During observations we recorded (1) if American Oystercatchers stripped eggs from mole crabs or ingested them whole; (2) handling time (time from the initial dart probe when the bill is fully inserted into the substrate, until the prey is swallowed; Tuckwell and Nol 1997b); (3) search time (time once a prey is swallowed, until the next handling time begins; Tuckwell and Nol 1997b); (4) foraging area location; (5) individual band combinations; and (6) individual sex based on sexual dimorphism in body size, bill color, and mantle color (Chapter 7). For each mole crab, we estimated carapace length as a fraction of the foraging American Oystercatcher's bill length (e.g., one-eighth, one-quarter, one-third, or one-half of the bill length), similarly to Tuckwell and Nol (1997b). Because males and females have different bill lengths (Nol 1985), we multiplied mean bill length (for the bird's sex) by the prey size measured relative to the bill length, to calculate actual prey size. We used the values of average male and female bill length (Brown and Nol 2024, Chapter 6).

During chick rearing (hatch date to day 60), we conducted 1 h observations of chick provisioning 2 or 3 times per week for each brood. During chick provisioning observations, we recorded the number of prey items fed to chicks, prey species, foraging area location, and identity of the breeding pair.

We classified diets for individuals and breeding pairs based on behavioral observations and GPS tracking data. We considered individuals as mole crab specialists if they ate only Atlantic mole crabs after three focal observations, with a small allowance for *Donax varibilis* (<15% of diet is *Donax varibilis*). Generalists were individuals who ate multiple prey species in addition to mole crabs and *Donax varibilis.*

## Statistical Analysis

*Hudsonian Whimbrels.* We ran a two-way Wilcoxon test to test for a difference in size between moribund and live ovigerous female Pacific mole crabs.

*American Oystercatchers*—We ran one-tailed Mann-Whitney *U*-tests to look at (1) if larger Atlantic mole crabs were stripped of eggs compared to swallowed whole, and (2) if handling time increased when Atlantic mole crabs were stripped of eggs compared to swallowed whole. We used a chi-square test to see if there was an association between diet specialization and Atlantic mole crab egg stripping. We conducted all analyses using R 4.3.1 (R Core Team 2023).

# Results

## Hudsonian Whimbrels

We found 41 moribund female Pacific mole crabs whose eggs had been stripped. When egg masses were removed from Pacific mole crabs, individuals were frequently injured and disabled. Moribund female Pacific mole crabs were significantly larger (mean ± SE = 27.70 ± 0.73 mm, $n = 41$) than live ovigerous females captured on the beach (23.18 ± 1.01 mm, $n = 41$, $W = 479$, $P = 0.002$).

## American Oystercatchers

In 2022, we made 133 observations on adult American Oystercatchers who ate 554 Atlantic mole crabs and 39 observations of adults provisioning chicks 142 Atlantic mole crabs.

Of the 25 breeding pairs who ate or provisioned Atlantic mole crabs, 11 individuals from 11 distinct breeding pairs stripped eggs from Atlantic mole crabs. An individual Atlantic mole crab had a ~10% chance of having its eggs stripped when preyed on by an American Oystercatcher (stripped eggs comprised 11.6% of Atlantic mole crab prey items eaten by adults [64 of 554], and 9.2% of Atlantic mole crab prey items offered to chicks [13 of 142]).

Atlantic mole crabs stripped of eggs were significantly larger (carapace length: mean ± SE = 18.17 ± 0.59 mm, $n$ = 70 Atlantic mole crabs) compared to those whose entire body was consumed (16.33 ± 0.41 mm, $n$ = 492 Atlantic mole crabs, $W$ = 22495, $P < 0.001$). The minimum threshold size of Atlantic mole crabs whose eggs were stripped was 8.92 mm. There was no significant difference in handling time based on whether the eggs were stripped from Atlantic mole crabs (mean ± SE = 14.12 ± 1.13 s, $n$ = 25 Atlantic mole crabs) or if the Atlantic mole crabs were ingested whole (16.78 ± 1.65 s, $n$ = 354 Atlantic mole crabs; $W$ = 5705.5, $P$ = 0.99). There was no significant association between mole crab diet specialization and stripping eggs from Atlantic mole crabs ($\chi^2_1 = 0.12$, $P$ = 0.73).

## Discussion

Egg stripping of *Emerita* spp. was recorded for migratory Hudsonian Whimbrels in Oregon and breeding American Oystercatchers in Virginia. Both species targeted larger mole crabs for egg stripping. There was a 10% probability that an individual Atlantic mole crab would have its eggs stripped by an American Oystercatcher. Egg stripping did not significantly increase handling time compared to swallowing prey whole for American Oystercatchers. Egg stripping was not associated with the diet specialization that we observed in American Oystercatchers. Similarly to our study, American Oystercatchers in Brazil remove and ingest the eggs plus the abdomen from mole crabs (*Emerita brasiliensis*) greater than 17 mm in carapace length, but smaller mole crabs are swallowed whole (Fedrizzi 2008).

Both Hudsonian Whimbrels and American Oystercatchers appear to follow the digestive rate model and use egg stripping as an efficient foraging strategy, probably due to digestive constraints. *Emerita* spp. are high in protein and fatty acids (Haq *et al.* 2018), and their eggs may be more digestible and richer in lipids than whole prey. Eggs of *Portunus sanguinolentus* (Portunidae, Brachyura), a different species of crustacean, are 60% protein, 21% lipids, and 8% carbohydrates (Sounndarapandian and Shankar Dey 2008). A similar nutrient composition (17% lipids and 7% carbohydrates; Schreibman and Zarnoch 2009) is found for the eggs of Atlantic horseshoe crabs (*Limulus polyphemus*), a chelicerate arthropod that fuels migrations for Red Knots and Ruddy Turnstones (*Arenaria interpres*) (Tsipoura and Burger 1999). The higher digestibility of eggs relative to whole prey could explain why some individuals strip eggs. Egg stripping occurs in other avian taxa, such as Boat-tailed Grackles (*Quiscalus major*), which consume crayfish (*Cambarus*) eggs (McIlhenny 1937). Egg stripping may be more prevalent than recorded because it might be difficult to detect when prey species bear eggs internally.

Interestingly, only 10% of mole crabs captured by American Oystercatchers had their eggs stripped, despite the supposed higher digestibility of eggs and that egg stripping does not significantly add prey handling time. Two possible explanations for why egg stripping of mole crabs is not more prevalent could be (1) individual variation in prey preference and/or (2) the satiation state of individuals. Zwarts and Blomert (1990) showed that some Eurasian Whimbrels are choosy and only eat portions of their prey. This could apply to American Oystercatchers as well.

Since egg stripping was equally likely across American Oystercatchers regardless of diet specialization, this suggests that egg stripping is a flexible foraging strategy given the satiation state of the individual. Crab Plovers switch from preying on the most profitable food items at the

start of feeding when their stomachs are empty, to preying on more digestible food items later in feeding as their stomachs fill up (Gommer *et al.* 2018). We hypothesize that a similar strategy is occurring with American Oystercatchers. Future studies could run a cafeteria style experiment to identify the threshold satiation point at which individuals might switch strategies from maximizing food profitability over the short-term (whole mole crab ingestion) to maximizing energy intake in the long-term by choosing more digestible items (stripping eggs from mole crabs). Additionally, the digestive pauses between when individual mole crabs have their eggs stripped or are ingested whole could be quantified to determine the digestive constraints imposed by whole prey ingestion compared to only egg ingestion. Mole crab eggs appear to provide an easily digestible calorie-rich food resource that may help drive the transglobal migrations and intense breeding behaviors of shorebirds.

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Chincoteague National Wildlife Refuge Research and Monitoring Special Use Permits #22-006, and Trent University's Animal Care Committee Animal Care Use Approval #27856.

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# Chapter 5 – American Oystercatchers (*Haematopus palliatus*) support a foraging commensalism for Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Calidris alba*)



Sanderling (*Calidris alba*) following after an American Oystercatcher (*Haematopus palliatus*) eating a mole crab (*Emerita talpoida*). Photo credit: Nicole Ball.

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L. A. Brown led study design, data collection and analysis, writing of the initial draft of the manuscript, and revisions of the manuscript with input from co-authors. T. MacLaurin, E.

Levine-Barnoff, and S. Banerjee contributed to data collection, and revisions of the manuscript. E. Nol contributed to study design and revisions of the manuscript. The idea for the interaction between Ruddy Turnstones and Sanderlings first came from observations by students in a field course taught by E. Nol.

Abstract.— We documented a facultative foraging commensalism that American Oystercatchers (*Haematopus palliatus*) support for Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Calidris alba*) during their spring and fall migrations through coastal Virginia, U.S.A. Some breeding American Oystercatchers strip eggs from mole crabs (*Emerita talpoida*) and then discard the carapaces and remaining flesh. We made 179 observations of Ruddy Turnstones and Sanderlings following American Oystercatchers, to eat discarded carapaces. More Ruddy Turnstones ($\bar{x}$ = 2.48 ± 0.29 (SE)) and Sanderlings (4.64 ± 1.24) followed a foraging American Oystercatcher in spring than in fall (Ruddy Turnstones: 1.25 ± 0.25, Sanderlings: 3.67 ± 0.62), perhaps reflecting pressure to minimize stopover duration and refuel quickly to reach the breeding grounds. American Oystercatchers supported a stronger foraging commensalism for Ruddy Turnstones, who increased mole crab consumption by 15 times in the presence of an egg-stripping American Oystercatcher, compared to an increase of 1.4 times for Sanderlings. Ruddy Turnstones were more aggressive foragers, pursuing egg-stripping American Oystercatchers, while Sanderlings opportunistically took nearby discards. Mole crab egg stripping by American Oystercatchers provides an easily accessible food source that supplements diets of Ruddy Turnstones and Sanderlings.

**Keywords.—** diet specialization, *Emerita talpoida,* foraging strategies, *Haematopus,* kleptoparasitism, mixed-species associations, mixed-species flocks, mole crabs, shorebirds, stopover ecology

# Introduction

Many waterbirds readily form mixed-species feeding associations (Amat 1990; Davis Jr. 2003; Davis Jr. 2007; Hamza and Selmi 2016; Gutiérrez and Soriano-Redondo 2018). Feeding associations might form to increase foraging efficiency (Gutiérrez and Soriano-Redondo 2018), or reduce costs associated with finding food (Amat 1990). Feeding associations can negatively impact others if kleptoparasitism (stealing food) occurs (Tuckwell and Nol 1997) or have a neutral effect if commensalism occurs (one individual benefits from the foraging activities of a host without negatively affecting the host) (Amat 1990; Mathis and Bronstein 2020). Feeding associations can also range from obligate (required because it makes up a critical component of the diet) to facultative (not necessary because it is one of a few diet components but occurs opportunistically) (Macdonald *et al.* 2012).

American Oystercatchers (*Haematopus palliatus*) are coastal shorebirds of conservation concern (Clay *et al.* 2014). Their diet includes mole crabs (*Emerita talpoida*), an ocean intertidal-dwelling invertebrate among a range of bivalve prey (Brown and Nol 2026, Chapter 2). When foraging on mole crabs, some breeding American Oystercatchers strip and consume the nutrient-rich eggs (Brown *et al.* 2025, Chapter 4), which leaves the carapaces of mole crabs with their remaining flesh in the body and the legs as discards. These discarded mole crabs present an easily accessible food source for other shorebirds.

Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Calidris alba*) are shorebirds who stopover in coastal United States to refuel during their migrations (Tucker *et al.* 2022). Both species feed on marine invertebrates, including mole crabs (Dinsmore *et al.* 1998; Peterson *et al.* 2000; Nettleship 2020), and are opportunistic foragers (Petracci 2002; Vahl *et al.* 2005). In Brazil, both species follow American Oystercatchers to eat discarded gill remnants of true crabs

(Brachyura) (Fedrizzi 2008), and in Argentina, Sanderlings follow American Oystercatchers to eat discarded yellow clams (*Mesodesma mactroides*) (Petracci 2002). Similarly, in Florida, U.S.A., Sanderlings follow Ruddy Turnstones to eat prey that Ruddy Turnstones expose in the wrack (Davis Jr. 2003).

In coastal Virginia, USA, we observed that after an American Oystercatcher stripped eggs from mole crabs, a flock of Ruddy Turnstones and Sanderlings followed behind the American Oystercatcher to eat the discarded mole crabs (Fig. 5.1). We tested if American Oystercatchers might support a foraging commensalism for Ruddy Turnstones and Sanderlings. No such relationship had been described among these three species that involves foraging on mole crabs. We quantified a facultative foraging commensalism among American Oystercatchers, Ruddy Turnstones, and Sanderlings using focal foraging observations from two perspectives: the American Oystercatcher and the benefiting species (Ruddy Turnstones and Sanderlings). We used observations on American Oystercatchers stripping eggs from mole crabs to quantify the number of shorebirds involved in the foraging commensalism. We used observations on Ruddy Turnstones and Sanderlings to record if following an American Oystercatcher stripping eggs from mole crabs increased their consumption rate.

# Methods

## Study Area

The study was conducted at Assateague Island, Virginia, U.S.A. (37° 51’ 7.2” N, 75° 22’, 55.2” W). Assateague Island is a part of a chain of barrier islands in Virginia that are designated as a protected area for migratory shorebirds by the Western Hemisphere Shorebird Reserve Network (The Nature Conservancy 2024). The island supports nesting habitat of breeding American Oystercatchers, protected within the Chincoteague National Wildlife Refuge. We made

observations along a 6.8 km stretch of oceanside intertidal beach that supported 22 breeding pairs of American Oystercatchers in 2025.

## Data Collection

We collected data from May 8–June 3 and July 25–September 10, 2025 to capture the spring and fall migration, respectively, of Ruddy Turnstones and Sanderlings. We used 5-min focal sampling as per Altmann (1974) to quantify and characterize the commensalism. We rotated between focally sampling an American Oystercatcher, Ruddy Turnstone, or Sanderling, since we could only continuously watch the foraging behavior of one individual at a time. When a foraging American Oystercatcher was the focal species, we counted the maximum number of Ruddy Turnstones and Sanderlings within 5 m of it, over 5 min, while the American Oystercatcher stripped eggs from mole crabs. This let us determine how many Ruddy Turnstones and Sanderlings might benefit from an American Oystercatcher. Based on our observations, we chose a 5 m radius because this was the distance that we observed shorebirds following foraging American Oystercatchers. When a Ruddy Turnstone or Sanderling was the focal individual, we recorded the number of mole crabs that Ruddy Turnstones, or Sanderlings obtained and ate as discards or captured by themselves, as well as other prey species eaten. We balanced making focal observations on Ruddy Turnstones and Sanderlings when an American Oystercatcher stripping eggs from mole crabs was present versus absent, so that we could compare mole crab consumption rates. We used 60x spotting scopes and 10 x 42 binoculars for observations.

Integrated within our regular nest monitoring for American Oystercatchers, we typically walked or drove a four-wheel drive vehicle along the study area's beach 2–3 times per week. If we saw an American Oystercatcher foraging on mole crabs, we stopped to do a focal observation. Ideally, we did a set of three observations, one focused on the American

Oystercatcher, one for a randomly chosen Ruddy Turnstone, and one for a randomly chosen Sanderling. Ruddy Turnstones and Sanderlings at the study site were unbanded, so observations on spatially segregated individuals were considered distinct and unique. We made a maximum of a single observation per individual Ruddy Turnstone and Sanderling in each condition (presence or absence of a foraging American Oystercatcher). Observations tended to occur at falling tide when mole crabs come to the surface of the sand to feed themselves and are more readily available for consumption by American Oystercatchers (L. A. Brown unpublished data). We recorded the GPS location of the observation to attempt to account for factors that might vary spatially and impact foraging habitat use including mole crab abundance, beach width and slope, and recreational access. For Sanderling observations, since we were aware that Ruddy Turnstones are aggressive foragers (Vahl *et al.* 2005) and suspected that they might kleptoparasitize mole crabs from Sanderlings, we recorded the maximum number of Ruddy Turnstones within 5 m of the focal Sanderling to test whether there was a numerical response between Ruddy Turnstones and Sanderlings.

## Statistical Analysis

We used summary statistics to quantify the number of Ruddy Turnstones and Sanderlings following a foraging American Oystercatcher during the spring and fall migration. To test if Sanderlings and Ruddy Turnstones ate more mole crabs when American Oystercatchers were present, we used a general linear model (Poisson family with a log link function) with the predictor as the interaction between the presence of a feeding American Oystercatcher (present or absent) and species (Sanderling or Ruddy Turnstone), and the response variable as the total number of mole crabs eaten (number of discarded mole crab carapaces obtained and the number of mole crabs that the focal individual obtained themself). We were unable to include location or

the number of Ruddy Turnstones within 5 m of Sanderling in models due to overparameterization and models not converging.

To examine if the presence of a foraging American Oystercatcher changed the total prey consumption rate (number of discarded mole crab carapaces + the number of mole crabs that the focal individual obtained on their own + number of other prey species eaten) for a Ruddy Turnstone or Sanderling, we tested if Sanderlings and Ruddy Turnstones ate more total prey when American Oystercatchers were present, using a zero-inflated negative binomial model because in many observations neither Ruddy Turnstones nor Sanderlings captured any prey. The model predictor was the interaction between the presence of a foraging American Oystercatcher and species, and the response variable was the total number of prey eaten.

We developed the Poisson regression model in base R, and zero-inflated negative binomial model with the R package 'pscl' (Zeileis *et al.* 2008). For each model, we report the $R^2$ (proportion of variance that the predictors explained) using the 'performance' package (Lüdecke *et al.* 2021) and calculated the estimated marginal means from the model using the R package 'emmeans' (Lenth 2023). We checked the residuals for model fit using diagnostics with the package 'DHARMa' (Hartig 2024). We performed all statistical analyses in R v. 4.3.1 (R Development Core Team 2023). R data and scripts are available at OSF https://osf.io/qbhk6/overview?view_only=7adb97fe600b45e99c674e5e54676a4c.

# Results

In spring, a foraging American Oystercatcher had an average of 2.48 ± SE 0.29 (max = 5) Ruddy Turnstones and 4.64 ± SE 1.24 (max = 28) Sanderlings within 5 m of it ($n$ = 31 observations). In fall, a foraging American Oystercatcher had an average of 1.25 ± SE 0.25 (max = 2) Ruddy Turnstones and 3.67 ± SE 0.62 (max = 15) Sanderlings within 5 m of it ($n$ = 52

observations). For Ruddy Turnstones, we made $n = 35$ observations when American Oystercatchers were present and $n = 54$ observations when American Oystercatchers were absent. For Sanderlings, we made $n = 47$ observations when American Oystercatchers were present and $n = 43$ observations when American Oystercatchers were absent. Across all focal foraging observations, Ruddy Turnstones ate 93 mole crab discards from American Oystercatchers, and 9 mole crabs and 317 other prey items on their own. For Ruddy Turnstones, other prey species consisted of coquina (*Donax varibilis*) and Atlantic horseshoe crab (*Limulus polyphemus*) eggs and their carcasses. Additionally, Ruddy Turnstones ate Coleoptera and Isoptera that washed up in the wrack line (marine debris). Across all focal foraging observations, Sanderlings ate 87 mole crab discards from American Oystercatchers, and 28 mole crabs and 46 other prey items on their own. For Sanderlings, other prey species consisted of polychaetes, amphipods, and coquina. A foraging Sanderling had an average of 0.60 ± SE 0.10, max = 5 Ruddy Turnstones within a 5 m radius.

A significant interaction between the presence of an American Oystercatcher stripping eggs from mole crabs and species accounted for 64% of the variation in the predicted mean number of mole crabs eaten ($R^2_{Nagelkerke} = 0.64$, Table 5.1). Both Sanderlings and Ruddy Turnstones obtained significantly more mole crabs (primarily discards) when an American Oystercatcher was present, and Ruddy Turnstones benefited more than Sanderlings. Ruddy Turnstones obtained 15 times more mole crabs when an American Oystercatcher was present as compared to when they were absent (Fig. 5.2). Sanderlings obtained 1.4 times more mole crabs when an American Oystercatcher was present as compared to when they were absent. When American Oystercatchers were absent, Ruddy Turnstones ate 70% fewer mole crabs than Sanderlings.

A significant interaction between the presence of an American Oystercatcher stripping eggs from mole crabs and species accounted for 66% of the variation in the predicted mean number of total prey eaten ($R^2 = 0.66$, Table 5.2). The presence of a foraging American Oystercatcher reduced the total number of prey that Ruddy Turnstones ate by 46% (Fig. 5.2). By contrast, the presence of a foraging American Oystercatcher increased the total number of prey that Sanderlings ate by 13%. In the absence of American Oystercatchers, Sanderlings ate 75% fewer total prey compared to Ruddy Turnstones (Fig. 5.2). The higher total prey count eaten by Ruddy Turnstones compared to Sanderlings was driven by ingestion of coquina by some individuals (>6 coquina for some observations).

**Figure 5.1 is a video, so should be viewed by clicking the provided link**

https://osf.io/wg5xb/overview?view_only=97cf9587456f4a9eb85ecb7a31a57fa2.

**Figure 5.1.** Video illustrating the foraging commensalism among American Oystercatchers (*Haematopus palliatus*), Ruddy Turnstones (*Arenaria interpres*), and Sanderlings (*Calidris alba*) at Assateague Island, Virginia, U.S.A.

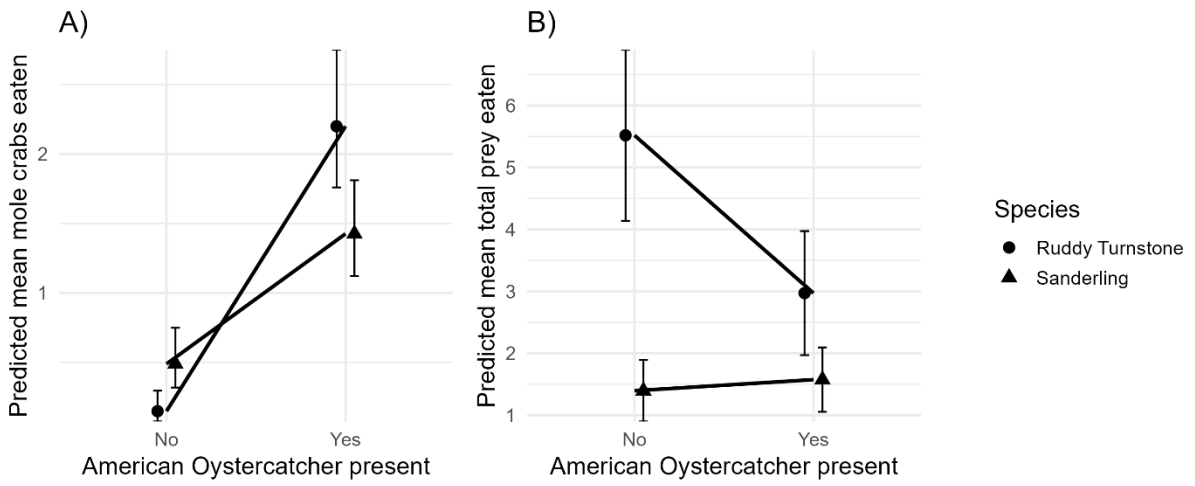



**Figure 5.2.** A) Predicted mean mole crabs (*Emerita talpoida*) eaten and B) total prey eaten by Ruddy Turnstones (*Arenaria interpres*) (*n* = 89) and Sanderlings (*Calidris alba*) (*n* = 90) in the presence or absence of an American Oystercatcher (*Haematopus palliatus*) stripping eggs from mole crabs at Assateague Island, Virginia, U.S.A. in 2025. Error bars represent the 95% confidence interval.

**Table 5.1. Poisson regression model estimates (*β*), SE, and 95% confidence interval (CI) for the predicted number of mole crabs (*Emerita talpoida*) eaten by Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Calidris alba*) in the presence or absence of a foraging American Oystercatcher (*Haematopus palliatus*) at Assateague Island, Virginia, U.S.A. in 2025.**

| Model term | *β* | SE | CI |
|---|---|---|---|
| Intercept | -1.91 | 0.35 | -2.69, -1.29 |
| Presence of an American Oystercatcher stripping eggs from mole crabs | 2.70 | 0.37 | 2.03, 3.51 |
| Species Sanderling | 1.19 | 0.42 | 0.42, 2.07 |
| Presence of an American Oystercatcher stripping eggs from mole crabs x Species Sanderling | -1.63 | 0.45 | -2.56, -0.78 |

The intercept represents the absence of a feeding American Oystercatcher and the species Ruddy Turnstone.

**Table 5.2. Zero-inflated negative binomial model estimates (*β*), SE, and 95% confidence interval (CI) for predicting the total number of prey eaten by Ruddy Turnstones (*Arenaria interpres*) and Sanderlings (*Calidris alba*) in the presence or absence of a foraging American Oystercatcher (*Haematopus palliatus*) at Assateague Island, Virginia, U.S.A. in 2025.**

| Model term | *β* | SE | CI |
|---|---|---|---|
| Intercept | 1.71 | 0.13 | 1.46, 1.96 |
| Presence of an American Oystercatcher stripping eggs from mole crabs | -0.62 | 0.21 | -1.04, -0.20 |
| Species Sanderling | -1.37 | 0.22 | -1.81, -0.94 |
| Presence of an American Oystercatcher stripping eggs from mole crabs x Species Sanderling | 0.74 | 0.33 | 0.10, 1.38 |

The intercept represents the absence of a feeding American Oystercatcher and the species Ruddy Turnstone.

## Discussion

American Oystercatchers that strip eggs from mole crabs and discard the carapaces support a facultative foraging commensalism with Ruddy Turnstones and Sanderlings. By following American Oystercatchers, Ruddy Turnstones and Sanderlings increase the number of mole crabs eaten (primarily discards) over what they achieve while foraging on their own. Ruddy Turnstones appear to benefit more from following American Oystercatchers than Sanderlings do, in part because there are fewer of them following each American Oystercatcher. Both Ruddy Turnstones and Sanderlings seem to rely on American Oystercatchers more for foraging during the spring compared to the fall, which might be related to different seasonal migration strategies.

Increased consumption rates stemming from a foraging commensalism have also been reported for Ruddy Turnstones and Sanderlings that follow American Oystercatchers to eat discarded true crabs (Fedrizzi 2008), Sanderlings that follow American Oystercatchers to eat discarded Yellow Clams (Petracci 2002), and Sanderlings that follow Ruddy Turnstones to eat prey that Ruddy Turnstones expose in the wrack (Davis Jr. 2003). Frequent observations of other species benefiting from American Oystercatcher foraging may be because American Oystercatchers often leave parts of their bivalve prey uneaten. Among other examples of commensalism, Wilson's Phalaropes (*Steganopus tricolor*) who associate with Chilean Flamingos (*Phoenicopterus chilensis*) gain higher foraging success from the Chilean Flamingos that stir up water and help bring prey to the surface (Gutiérrez and Soriano-Redondo 2018). Similarly, Brown Pelicans (*Pelecanus occidentalis*) follow Double-crested Cormorants (*Phalacrocorax auritus*) to retrieve fish left in the wake of the cormorants (Davis Jr. 2007).

Following American Oystercatchers for mole crab discards might be energetically advantageous for Ruddy Turnstones and Sanderlings. Both shorebird species obtained more mole

crabs when an American Oystercatcher was present. Sometimes an increase in prey abundance is not equivalent to an increase energetically, if mole crab discards are less nutrient-rich. However, here, an increase in the number of mole crabs likely improves the energetic value for Ruddy Turnstones and Sanderlings, since only larger female mole crabs are gravid, stripped of eggs, and discarded by American Oystercatchers (Brown *et al.* 2025, Chapter 4). We observed both migrating species but primarily Ruddy Turnstones stand and wait to take discarded mole crab carapaces. Although this waiting behavior reduced total prey consumption for Ruddy Turnstones, the discarded mole crab carapaces from American Oystercatchers are large (carapace length mean ± SE: 18.17 ± 0.59 mm; Brown *et al.* 2025, Chapter 4) and provide a high food reward compared to the mole crabs Ruddy Turnstones captured themselves. We also noticed that larger mole crabs tend to bury themselves deeper in the sand (L. A. Brown unpublished data), so might only be readily accessible for American Oystercatchers who have long bills (in Virginia, U.S.A. females: $\bar{x}$ = 89.17 ± SE 0.59 mm, males $\bar{x}$ = 83.8 ± 0.8 mm, Brown and Nol 2024, Chapter 6) compared to Sanderlings (in New Jersey, U.S.A. females: $\bar{x}$ = 26.5 ± 0.2 mm, $n$ = 20; males: $\bar{x}$ = 25.2 ± 0.4 mm, $n$ = 14, Castro *et al.* 1992) and Ruddy Turnstones (in low Arctic, Canada females: $\bar{x}$ = 24.2 ± 0.2 mm, $n$ = 40; males: $\bar{x}$ = 23.5 ± 0.1 mm, $n$ = 67, Nettleship 2020).

There was a slightly stronger foraging commensalism between American Oystercatchers and Ruddy Turnstones than between American Oystercatchers and Sanderlings, which might stem from differences in aggression, dominance, and the inherent foraging strategy of each species. Ruddy Turnstones are aggressive foragers who frequently kleptoparasitize prey from conspecifics and other species (Vahl *et al.* 2005; Vahl *et al.* 2007). If a mole crab was discarded by an American Oystercatcher, Ruddy Turnstones typically beat Sanderlings to the discard or stole the discard directly from Sanderlings more often than Sanderlings won or kept the discard.

Ruddy Turnstones regularly pursued and followed an American Oystercatcher that was stripping eggs from mole crabs. Generally, a Ruddy Turnstone only switched to foraging for itself or left to seek out another American Oystercatcher foraging on mole crabs, if an American Oystercatcher started a digestive break (paused foraging for > 2 min). In contrast, Sanderlings tended to take the opportunity of eating a nearby discarded mole crab, but less frequently went out of their way to follow an American Oystercatcher. Instead, Sanderlings continued to forage for mole crabs themselves more than Ruddy Turnstones, as evidenced by the higher number of mole crabs that Sanderlings obtained on their own, in the absence of an American Oystercatcher. In this way, American Oystercatchers appeared to reduce the foraging effort for Ruddy Turnstones but not for Sanderlings. Even though there was a stronger feeding commensalism between American Oystercatchers and Ruddy Turnstones, fewer Ruddy Turnstones followed foraging American Oystercatchers compared to Sanderlings because Ruddy Turnstones occur in smaller flocks (often 1–2 and up to 6 individuals) than Sanderlings (often 10–100 individuals) at the study site, and Ruddy Turnstones were aggressive to each other and excluded others from the immediate area.

Flock sizes following American Oystercatchers could also be related to seasonal differences in migration. During spring migration, both Ruddy Turnstones and Sanderlings relied more heavily on American Oystercatchers for food, as evidenced by higher numbers of them following an American Oystercatcher foraging on mole crabs. This might reflect different migration strategies during pre-breeding spring migration versus post-breeding fall migration. In spring, Arctic breeding shorebirds like Ruddy Turnstones and Sanderlings minimize migration duration to reach the breeding grounds in time to breed (Farmer and Wiens 1999; Nilsson *et al.* 2013; Duijns *et al.* 2019). This can be accomplished by rapidly refueling during stopovers

(Atkinson *et al.* 2007). Following an American Oystercatcher for food could increase mass gain rates for Ruddy Turnstones and Sanderlings. Because of the temporal pressure during the spring, more birds tend to migrate in the same temporal window, resulting in larger migration flocks (O'Reilly and Wingfield 1995), which could lead to more shorebirds following an American Oystercatcher. In contrast, in the fall, time pressures and fitness consequences to migrate are relaxed, with species minimizing the energy it takes to migrate (Farmer and Wiens 1999; Zhao *et al.* 2017). This results in an extended fall migration, with fewer birds migrating simultaneously, so flock sizes can be smaller, and refueling stops more frequent and longer in duration (O'Reilly and Wingfield 1995; Hedenström and Alerstam 1997). This could manifest as fewer Ruddy Turnstones and Sanderlings following foraging American Oystercatchers in the fall.

The small increase in the total number of prey that Sanderlings ate when an American Oystercatcher was present compared to absent might be a byproduct of American Oystercatchers selecting foraging sites with higher prey abundance. Suitable mole crab habitat overlaps with habitat for other ocean intertidal prey like coquina (Leber 1982), so Sanderlings and American Oystercatchers might select similar foraging habitat but target different prey species. While we tried to account for spatial variation in prey abundance through the proxy of observation location, we were unable to do so because of limited statistical power. In the future, additional observations of the commensalism behavior, or stratifying sampling in areas of known high versus low prey abundance, might allow the addition of prey abundance as a covariate.

Overall, mole crabs are an energy-rich food source (Haq *et al.* 2018) that could strongly motivate Ruddy Turnstones and Sanderlings to follow foraging American Oystercatchers to easily access this food. Future research might investigate how the foraging commensalism impacts stopover duration and body condition. To carry out such a study, all species involved in

the foraging commensalism would need to be individually identified, with some Ruddy Turnstones and Sanderlings co-existing in areas with American Oystercatchers that forage for mole crabs and strip the eggs from them, while others lack this. Additionally, the proportion of mole crabs in the diets of Ruddy Turnstones and Sanderlings could be quantified through fecal samples and DNA metabarcoding. This information could serve as an initial step to get at the role that American Oystercatchers play in fueling the long-distance migrations of these species.

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# Chapter 6 – Diet overlaps between the sexes in breeding American Oystercatchers



Parent American Oystercatchers (*Haematopus palliatus*) provisioning chicks. Photo credit: Lyn A. Brown.

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L. A. Brown led study design, data collection and analysis, writing of the initial draft of the manuscript, and revisions of the manuscript. E. Nol contributed to editing drafts.

Abstract.— Sexual dimorphism in bill size can lead to sex-specific foraging strategies. All 12 extant species of oystercatchers (*Haematopus*) have sexually dimorphic bills, and most oystercatcher species show intersexual niche partitioning in diet, where males and females eat different prey species in different proportions. Intersexual niche partitioning in diet has not been examined in American Oystercatchers (*Haematopus palliatus*). This study tested for intersexual niche partitioning in diet in a population of American Oystercatchers breeding on two barrier islands in coastal Virginia, U.S.A. in 2022 and 2023. Diet composition, prey size selection, and foraging areas were compared between the sexes ($n$ = 31 males and $n$ = 28 females). Unlike other oystercatcher species, male and female American Oystercatcher diets overlapped by 99%. Both sexes took similar-sized prey across the seven prey species and shared use of 59% of feeding areas. Previous studies on other oystercatcher species may have found intersexual niche partitioning in diet because of highly competitive environments due to high population density or low prey availability. In contrast, the present study in Virginia barrier islands that found diet overlap between the sexes may be due to a low competitive environment from low breeding densities and sufficient prey abundance.

**Keywords.—** niche partitioning, niche utilization theory, intersexual competition, reverse sexual dimorphism, foraging strategies, coastal Virginia, shorebirds, *Haematopus*

# Introduction

Diet specialization in a population can develop if some individuals select a subset of resources from the total number of resources available to the population (Bolnick *et al.* 2002). Factors driving diet specialization may include inter- and intra-species competition, prey abundance and ecological opportunity (Svanbäck and Bolnick 2007; Bolnick *et al.* 2010; Araújo *et al.* 2011). The underlying basis for diet specialization can come from differences in feeding morphology (Selander 1966).

The niche utilization theory posits that differences in bill morphology between the sexes can lead to different foraging niches (Selander 1966). Sexual dimorphism in bill size is prevalent in shorebirds (Nebel and Thompson 2011). All 12 extant species of oystercatchers (*Haematopus spp.*) (Winkler *et al.* 2020) display reverse sexual dimorphism in bill size, where females have longer bills than males (Baker 1972; Nol 1985; Durell *et al.* 1993; Lauro and Nol 1995; Kohler *et al.* 2009; Aplin and Cockburn 2012; Roodenrijs 2023). The niche utilization theory has been supported for a number of shorebirds (Catry *et al.* 2014; Hall *et al.* 2021) including most oystercatcher species (Durell *et al.* 1993; Lauro and Nol 1995; Kohler *et al.* 2009; Aplin and Cockburn 2012; Table 6.1). Across oystercatcher species, females with longer, pointy bills are better suited for softer-bodied prey, while males with their shorter, robust and blunt bills are better suited for harder-shelled prey (Hulscher and Ens 1992; Lauro and Nol 1995; Durell 2003; Aplin and Cockburn 2012).

American Oystercatchers (*Haematopus palliatus*) are a species of conservation concern with the eastern U.S. population estimated to be 14,735 ± 320 individuals (Schulte 2023). Barrier islands in Virginia, U.S.A. host the highest concentration of breeding American Oystercatchers throughout their range (Wilke *et al.* 2005); however breeding populations have declined here

since 2016 (Wilke 2021). As part of an ongoing investigation into why the breeding population in Virginia is declining, we studied the role of diet.

**Table 6.1. Summary of oystercatcher studies finding intersexual niche partitioning or niche overlap in diet.**

| Species | Location | Niche Part-itioning | N | Method | Niche index | Findings | Source |
|---|---|---|---|---|---|---|---|
| Sooty Oystercatcher | New South Wales, Australia | Y | 4 males and 3 females | Foraging observations and bill lengths measured | Horn's index | Most prey species are eaten exclusively by one sex. | Aplin and Cockburn 2012 |
| Sooty Oystercatcher | Furneaux Islands, Tasmania Australia | Y | 11 males and 12 females | Foraging observations and bill lengths measured | Manly's alpha index | Females take softer-bodied prey, while males take harder-bodied prey. | Lauro and Nol 1995 |
| Pied Oystercatcher | Furneaux Islands, Tasmania Australia | Y | 9 males and 11 females | Foraging observations and bill lengths measured | Manly's alpha index | Females take softer-bodied prey, while males take harder- bodied prey. | Lauro and Nol 1995 |
| Eurasian Oystercatcher | Exe Estuary, United Kingdom | Y | 29 adults and 19 juveniles | Foraging observations and bill lengths measured | Descriptive analysis | Five out of six females had pointed bills, while all males had chisel- shaped bills. 70% of worm feeders were female, while 90% of mussel hammerers were male. | Durell *et al.* 1993 |

| Species | Location | Niche Part-itioning | N | Method | Niche index | Findings | Source |
|---|---|---|---|---|---|---|---|
| African Oystercatcher | Marcus Island, South Africa | Y | 2 breeding pairs | Foraging observations | Correspon-dence analysis | There was a 20% difference in the proportion of limpets taken by each sex. | Hockey and Underhill 1984 |
| African Oystercatcher | Southeast coast of South Africa | Y | 5 breeding pairs | Shell middens | Manly-Chesson index | Shell middens revealed that males prefer limpets and females prefer mussels. | Kohler *et al.* 2009 |
| African Oystercatcher | Marcus Island, South Africa | N | 43 foraging observat-ions on females and 31 foraging observat-ions on males | Foraging observations | Descriptive analysis | Foraging observations showed an 11% reduction in the difference of the proportion of limpets taken by each sex compared to the 1980s in Hockey and Underhill 1984. | Coleman and Hockey 2008 |
| African Oystercatcher | 9 sites on the Coast of South Africa | N | 20 breeding pairs plus 30 females and 33 males | Stable isotope analysis and bill lengths measured | Mann-Whitney test | Stable isotope analysis indicated that diet did not differ between the sexes. | Kohler *et al.* 2014 |
| Black Oystercatcher | Alaska, U.S.A. and British Columbia, Canada | N | 188 feather and claw samples | Stable isotope analysis and bill lengths measured | MANOVA | Stable isotope analysis indicated that diet did not differ between the sexes. | Roodenrijs 2023 |

3

In our study, we test for intersexual niche partitioning in diet for American Oystercatchers on two barrier islands in coastal Virginia during the breeding season. American Oystercatchers have reverse sexually dimorphic bills (Nol 1985), and feed on bivalves and marine invertebrates on bayside mudflats and oceanside shorelines during both breeding (Nol 1985) and non-breeding seasons (Tuckwell and Nol 1997). During breeding, American Oystercatchers stay close to their nests to forage and have smaller foraging ranges (Nol 1985) than during non-breeding when individuals are not tied to a nest site (Sanders *et al.* 2013). The combination of restricted foraging ranges during breeding and multiple individuals breeding and feeding in one area should form foraging competition and put selective pressures on the sexes to reduce intersexual foraging competition, so that the sexes can co-exist and breed. We predicted that females would prefer softer-bodied prey that is easier to open like mole crabs (*Emerita talpoida*) and polychaetes, as well as deeper-buried prey like razor clams (*Tagelus plebeius* and *Ensis directus*) compared to males who would prefer harder-shelled prey that is more difficult to open and located at the surface like oysters (*Crassotrea virginica*) and mussels (*Modiolus demissus*). Since we expected that females would prefer mole crabs, polychaetes and razor clams, females should feed on both oceanside shorelines and bayside mudflats, as opposed to males who may show a preference for bayside mudflats where mussels and oysters live (Isdell *et al.* 2018; Smith *et al.* 2022). Since female oystercatchers tend to have less robust bills, we expected female American Oystercatchers to prefer smaller prey to minimize the risk of bill damage, as was found in Eurasian Oystercatchers (Rutten *et al.* 2006). We tested niche partitioning in diet between the sexes based on diet composition, prey size selection and feeding location.

# Methods

## Study Area

The study sites were two barrier islands in Virginia, Assateague Island (37° 51’ 7.2” N, 75° 22’, 55.2” W) and Assawoman Island (37°, 48’, 3.6” N, 75°, 31’, 4.8” W). The two islands make up Chincoteague National Wildlife Refuge, a protected area for beach-nesting birds on the mid-Atlantic U.S. Coast. We collected data during the American Oystercatcher breeding seasons (April to August) of 2022 and 2023. In 2022 Assateague Island supported 20 breeding pairs along 12 km of shoreline and Assawoman Island supported 31 breeding pairs along 6 km of shoreline. In 2023 Assateague Island had 25 breeding pairs and Assawoman Island had 32 breeding pairs. On both islands, each breeding pair has foraging access adjacent to their territory to oceanside shorelines with marine invertebrates such as mole crabs. Foraging habitats on both islands also include bayside mudflats and marshes with natural populations of mussels, oysters, clams (*Mercenaria mercenaria*), and razor clams, as well as commercially seeded populations of oysters and clams.

## Data Collection

Prior to the study, some of the study population was already banded. We continued banding efforts during the study years to distinguish individuals and collect bill morphology data. To verify sexual dimorphism in bill length for our population of American Oystercatchers, we caught 24 individuals in 2023 (2 males and 2 females on Assateague Island and 10 males and 10 females on Assawoman Island) and measured bill length from the end of the culmen to the tip of the bill. We followed standardized protocols from the American Oystercatcher Working Group (2023a) to capture and band individuals. To capture American Oystercatchers, we placed leg loop carpets around the nest and attracted breeding pairs with wooden decoys and playback calls. To uniquely identify individuals, we attached colored plastic Darvic bands with a unique

alphanumeric code onto each upper leg and a U.S. Geological Survey metal band to the lower leg. We carried out capture and handling with appropriate permissions and ethics approval from the U.S. Geological Survey's Bird Banding Laboratory, Chincoteague National Wildlife Refuge and Trent University Animal Care Committee.

American Oystercatchers can be sexed based on sexual dimorphism (Brown *et al.* in press, Chapter 7). For individually-banded birds, we confirmed our visual sexing technique by observations of copulation and individual DNA data published in the American Oystercatcher Working Group Band Database (2023b).

Across the study years, we conducted 10-minute observations on the same banded and unbanded adults of known sex who were foraging, using both 10 x 50 binoculars and 60x power spotting scopes. Ten-minute observations captured the character of foraging events and allowed us to maximize the number of observations taken across individuals. During observations we recorded prey species and size and feeding location only if we had a clear view of the adult. For prey species identification, we observed individuals take whole prey items (for mole crabs and polychaetes), shells, or flesh. For the latter, we identified the species based on the color of its flesh. As part of calculations for a different foraging study occurring in 2022, in 2022 we gauged prey size relative to bill length as per Tuckwell and Nol (1997). Since males and females have different bill lengths, we calculated actual prey size by multiplying the proportion of the prey relative to bill length by the mean male or female bill length in our study population.

To delineate bayside foraging areas, we drew polygons in ArcGIS Pro v. 3.2 (Environmental Systems Research Institute 2023) around all foraging locations and used habitat (oyster reefs, open mudflats, or marsh) in this study, topography and vegetation cover to break large polygons into smaller biologically meaningful foraging areas. For oceanside foraging areas,

we generally observed individual breeding pairs foraging on oceanside shorelines directly in front of their territory. Therefore, we broke up the continuous oceanside shoreline into separate foraging areas to correspond with breeding territories. We assessed breeding territory boundaries through observations of territorial interactions between breeding pairs. We assigned a unique ID to each foraging area.

## Statistical Analysis

We performed statistical analyses in R v. 4.3.1 (R Core Team 2023). To confirm sexual dimorphism in bill size, we ran a two sample two-tailed t-test on bill length. We checked the assumptions of normality and equal variance using histograms and Bartlett's test. Data were normal and had equal variance (*Bartlett's* $K^2_1 = 0.84$, $P = 0.359$).

To test for overlap in diet composition between the sexes, we calculated Pianka's index (Pianka 1973) from the 'EcoSimR' package in R (Gotelli *et al.* 2015). Pianka's index compares the proportions that each prey species appears in the diet for each sex. Values close to 0 indicate niche partitioning, while values close to 1 indicate niche overlap. We ran 1,000 simulations to compare our observed data to expected null data.

To test if the sexes chose different-sized prey, we ran Welch's t-tests on prey size for the four prey species (oysters, mole crab, mussels and clams) that had a large enough sample ($N \geq 5$ foraging observations where the prey was present in each sex's diet). Data were square root-transformed to improve normality. Bartlett's test indicated mole crab prey size had unequal variance (mole crabs: *Bartlett's* $K^2_1 = 12.11$, $P < 0.001$; oysters: *Bartlett's* $K^2_1 = 2.66$, $P = 0.103$; mussels: *Bartlett's* $K^2_1 = 1.60$, $P = 0.206$; clams: *Bartlett's* $K^2_1 = 0.001$, $P = 0.973$), so we ran Welch's t-tests for all four prey species.

To compare foraging habitats between the sexes, we mapped foraging areas used by each sex in ArcGIS Pro. We identified foraging areas used by both sexes by using the intersect function in R to identify common foraging areas. This allowed us to calculate the percent overlap of foraging areas used by both sexes as the (number of foraging areas used by both sexes)/(number of foraging areas used by both sexes + number of foraging areas used exclusively by males + number of foraging areas used exclusively by females).

# Results

## Bill Length

Females had significantly longer bills ($\bar{x}$ = 89.17 ± SE 0.59 mm, $n$ = 12) than males ($\bar{x}$ = 83.77 ± SE 0.78 mm, $t_{22}$ = -5.51, $P < 0.001$, *95% CI*[-7.43, -3.37], $n$ = 12).

## Diet Composition

Across the years of 2022 and 2023, we made 141 foraging observations on 28 distinct females and 31 distinct males. Collectively, individuals ate 283 prey items. Male and female American Oystercatcher diet overlapped by 99% (Fig. 6.1, Pianka's index = 0.99, 95% CI[0.07, 0.99], lower-tail $P$ = 0.044, upper-tail $P$ = 0.956, standard effect size = 2.74, Supplementary Fig. S6.1A, Supplementary Fig. S6.1B). Both sexes fed on seven prey species in similar proportions. Mole crabs were the most common prey eaten by both sexes. Blue mussel (*Mytilus edilus*) was the only prey species eaten exclusively by a single sex and it made up < 3% of the female diet. Blue mussel appeared to be a rare opportunistic foraging event for a single individual when a cluster of blue mussels attached to wrack (marine debris and vegetation) washed ashore. We did not observe any individuals feeding on polychaetes, even though they were available, since we witnessed Semipalmated Plovers (*Charadrius semipalmatus*) and

Piping Plovers (*Charadrius melodus*) eating polychaetes adjacent to foraging American Oystercatchers.

## Prey Size

There was no significant difference between the sexes in the size of prey taken for any species (Table 6.2).

## Feeding Locations

Both sexes used 59% of feeding areas, while 19% of feeding areas were only used by females and 23% were only used by males ($n$ = 83 foraging areas, Fig. 6.2 and Fig. 6.3). There was no consistent pattern in feeding areas used by a single sex.

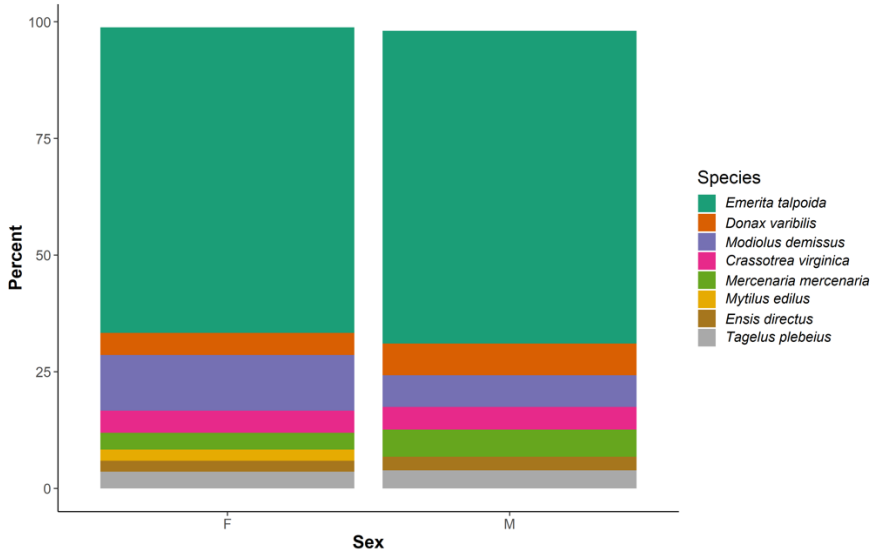



**Figure 6.1.** Diet composition for male and female American Oystercatchers: mole crab (*Emerita talpoida*), coquina (*Donax varibilis*), Atlantic ribbed mussel (*Modiolus demissus*), *eastern oyster* (*Crassotrea virginica*), northern quahog clam (*Mercenaria mercenaria*), blue mussel (*Mytilus edilus*), Atlantic razor clam (*Ensis directus*), and stout tagelus (*Tagelus plebeius*).

130 **Table 6.2. Summary of prey size selection by male and female American Oystercatchers.**

| | Males | | Females | | | | |
|---|---|---|---|---|---|---|---|
| Prey species | Prey length (mm) $\bar{x} \pm$ SE | *n* (number of prey items eaten) | Prey length (mm) $\bar{x} \pm$ SE | *n* (number of prey items eaten) | $t_{df}$ | *P* | 95% CI |
| Oysters (*Crassotrea virginica)* | 4.23 ± 0.20 | 7 | 5.21 ± 0.33 | 12 | $1.78_{17}$ | 0.093 | -0.18, 2.14 |
| Mole crabs (*Emerita talpoida*) | 4.11 ± 0.25 | 161 | 3.95 ± 0.20 | 131 | $-1.41_{288}$ | 0.159 | -0.37, 0.06 |
| Mussels (*Modiolus demissus*) | 5.38 ± 0.35 | 53 | 5.95 ± 0.39 | 62 | $1.72_{113}$ | 0.088 | -0.09, 1.23 |
| Clams (*Mercenaria mercenaria*) | 5.70 ± 0.35 | 19 | 4.62 ± 0.35 | 18 | $-2.02_{35}$ | 0.051 | -2.16, 0.003 |

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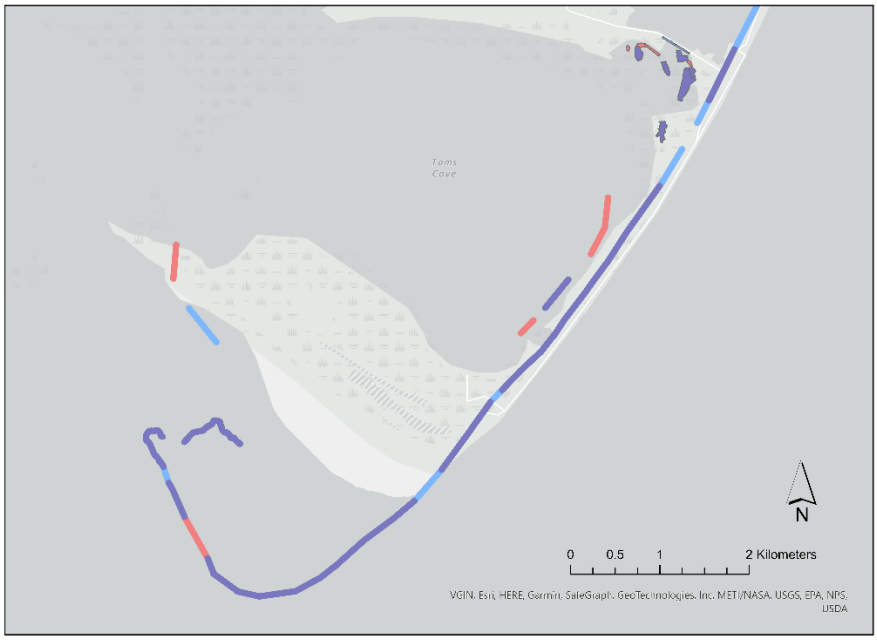



**Figure 6.2.** Map of feeding areas used by females in red, males in blue and both sexes in purple of American Oystercatchers on Assateague Island, Virginia, U.S.A.

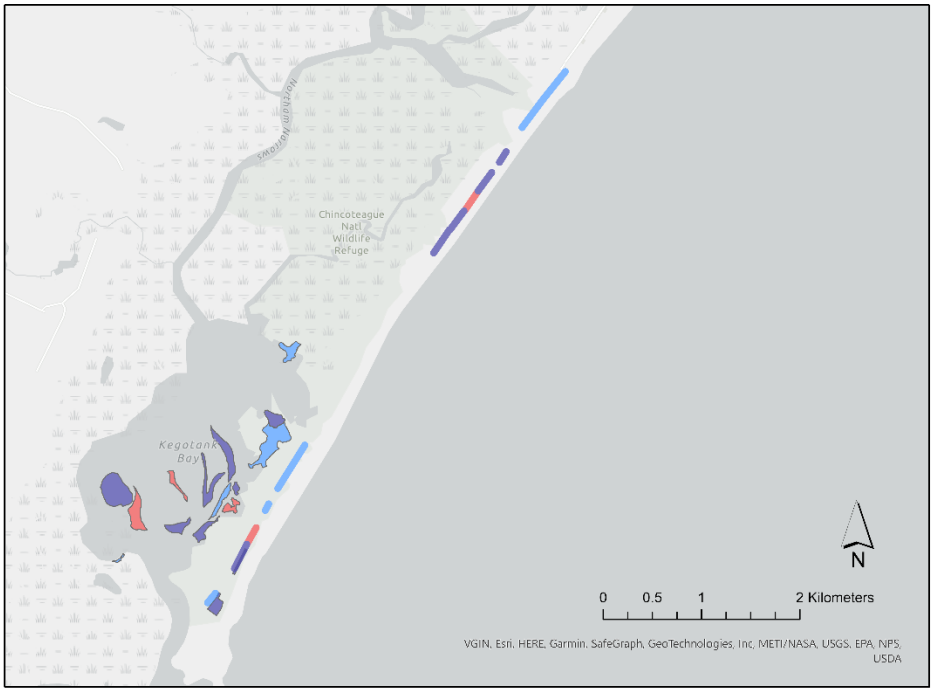



**Figure 6.3.** Map of feeding areas used by females in red, males in blue and both sexes in purple of American Oystercatchers on Assawoman Island, Virginia, U.S.A.

# Discussion

Male and female American Oystercatchers showed strong overlap in diet composition, foraging location and prey size taken, despite sexual dimorphism in bill length. Our results contradict the usual intersexual niche partitioning pattern for *Haematopus;* instead, male and female American Oystercatcher diets overlapped by 99%. In previous studies of oystercatchers showing intersexual niche partitioning in the United Kingdom and Australia, one of the most consistent trends is that females feed on softer-bodied prey (usually polychaetes) while males feed on harder-shelled prey (Durell *et al.* 1993; Lauro and Nol 1995; Aplin and Cockburn 2012). However, in our study neither sex fed on polychaetes, despite their apparent availability.

In contrast to our study, most oystercatcher species show intersexual niche partitioning (Table 6.1). Female Eurasian Oystercatchers (*Haematopus ostralegus*) tend to be worm specialists, while males tend to be bivalve specialists (Durell *et al.* 1993). Similarly, female Pied Oystercatchers (*Haematopus longirostris*) consume more soft-bodied prey while males consume more hard-bodied prey (Lauro and Nol 1995). Sooty Oystercatchers (*Haematopus fuliginosus*) exemplify extreme intersexual niche partitioning. Bill length differs by 19% between males and females (Aplin and Cockburn 2012). Most prey species are eaten exclusively by one sex, with only a 36% niche overlap between the sexes. The sexes also select different sized prey for the two shared prey species (Aplin and Cockburn 2012). Two exceptions to the pattern of intersexual niche partitioning in oystercatchers come from carbon 13 ($\delta^{13}C$) and nitrogen 15 ($\delta^{15}N$) stable isotope analyses in Black Oystercatchers (*Haematopus bachmani*) (Roodenrijs 2023) and African Oystercatchers (*Haematopus moquini*) (Coleman and Hockey 2008; Kohler *et al.* 2014; Table 6.1). These studies found that the sexes overlap in the isotopic signatures of the diet.

This raises the question as to why American Oystercatcher sexes overlap in diet, while most other oystercatcher species partition diet between the sexes. Some studies suggest that diet overlap occurs during times of food abundance when selective pressures for intersexual competition are relaxed (Svanbäck and Bolnick 2007; Czeszczewik 2010). Fewer available prey species could be another explanation for diet overlap that is not mutually exclusive (Layman *et al.* 2007). We review the plausibility for each of these hypotheses in relation to our study.

Competition is a strong driver of niche partitioning (Svanbäck and Bolnick 2007). We suggest that our study and the other oystercatcher studies showing diet overlap (Coleman and Hockey 2008; Kohler *et al.* 2014; Roodenrijs 2023) may occur in low competitive environments, while previous oystercatcher studies showing intersexual niche partitioning occurred in highly competitive environments (Table 6.1). Eurasian Oystercatchers have faced strong selection pressures to diversify their foraging niches due to high population densities (Goss-Custard *et al.* 1992; Hockey *et al.* 2021) and low prey abundance (Verhulst *et al.* 2004; Morten *et al.* 2022). The population of Eurasian Oystercatchers was recorded as over one million individuals in the 1990s (Hockey *et al.* 2021). Breeding territories are saturated with many individuals having to queue in line and wait multiple years before gaining a breeding territory (Ens *et al.* 1995). Not only do Eurasian Oystercatchers face food competition with other oystercatchers, but also with commercial shellfishing. Since the 1970s, due to overfishing, multiple shellfish populations have collapsed across Eurasian Oystercatcher habitat and low shellfish numbers have continued to present day (Verhulst *et al.* 2004; Morten *et al.* 2022).

Similarly, studies on intersexual niche partitioning in Pied and Sooty Oystercatchers in coastal Australia likely occurred in highly competitive environments. Aplin and Cockburn (2012) stated that there is high competition between male and female Sooty Oystercatchers since they

are resident species. In Lauro and Nol (1995), Pied Oystercatchers were restricted to feeding in a single habitat type, intertidal mudflats, which could increase foraging competition between the sexes.

In African Oystercatchers, two early studies found intersexual dietary niche partitioning (Hockey and Underhill 1984; Kohler *et al.* 2009), while more recent studies found niche overlap (Coleman and Hockey 2008; Kohler *et al.* 2014). The difference between the studies is that starting in the early 1980s, a new Mediterranean mussel species (*Mytilus galloprovincialis*) invaded the area and increased overall prey biomass (Coleman and Hockey 2008). We speculate that once food supply increased, competition decreased among African Oystercatchers, leading to diet overlap between the sexes.

Roodenrijs (2023) found diet overlap in Black Oystercatchers in British Columbia and Alaska, where individuals likely faced low competition due to low breeding densities and abundant food conditions. Black Oystercatcher breeding density in Alaska is <1 pair/km of shoreline (Andres and Falxa 2020). Historically breeding density in British Columbia was 1.25 pairs/km of shoreline (Drent *et al.* 1964), although recent data suggests a growing population (Maillet *et al.* 2023). It will be interesting to determine whether male and female Black Oystercatcher diets diverge over time in these more crowded populations. Food may be sufficient to avoid competition for Black Oystercatchers as we did not find published studies listing food availability as a limiting factor for population growth and in the most recent conservation assessment for the species, Tessler *et al.* (2014) did not list food availability as a threat to the species. Similarly, Black Oystercatcher diet has not changed in Alaska in the past 100 years, which could indicate that prey has remained abundant (Carney *et al.* 2023).

In our study, diet overlap appears to have occurred under low competition. Breeding densities are fairly low relative to other oystercatcher species. In 2022 and 2023 there were 1.67–2.08 breeding pairs/km of shoreline on Assateague Island and 5.17–5.33 breeding pairs/km of shoreline on Assawoman Island. Although we did not count prey, diet overlap could signal sufficient food resources. In support of this idea is the fact that we have not observed either emaciated adults or chicks on either island, in either year of our study. Additionally, all individuals caught and banded during our study had healthy weights, and lacked injury or obvious signs of disease/parasites.

Overlap in the foraging areas of individuals provides further support towards low competition allowing for diet overlap in American Oystercatchers. Even though we made occasional observations of aggressive interactions among American Oystercatchers on foraging grounds, in general individuals tolerated other American Oystercatchers feeding within 10 m, indicating an environment with low competition. Ashmole's (1963) hypothesis is that seabirds travel further to feed as intra-species competition increases. In our study the lack of foraging range differentiation between the sexes could indicate low competition.

Layman *et al.* (2007) suggest that the opportunity for diet specialization in a population decreases as the number of prey species available decreases. There is no reason to suggest that American Oystercatchers and Black Oystercatchers have fewer available prey species then other oystercatcher species who show intersexual niche partitioning. In our study American Oystercatchers fed on eight prey species (which is on the higher end of oystercatcher diet studies), while Black Oystercatchers fed on five species (Roodenrijs 2023). In comparison Eurasian Oystercatchers eat 4–11 species (Boates and Custard 1992; Schwemmer *et al.* 2016), African Oystercatchers eat 4–7 prey groups (Hockey and Underhill 1984; Coleman and Hockey

2008; Kohler *et al.* 2009; Kohler *et al.* 2014), Sooty Oystercatchers eat 6–9 prey groups (Lauro and Nol 1995; Aplin and Cockburn 2012) and Pied Oystercatchers eat six prey groups (Lauro and Nol 1995). We find no support for the hypothesis that a lack of prey species diversity is a main driver for diet overlap between the sexes of American Oystercatchers. Instead, we are left with a lack of competition as the main driver for diet overlap between the sexes of American Oystercatchers.

Contrary to our predictions, female American Oystercatchers did not take more deeply buried prey like razor clams than males, nor did male American Oystercatchers take more prey that emerged from the substrate, like oysters and mussels. Our findings differ from Sooty and Pied Oystercatchers in Australia, where females select more deeply buried prey like polychaetes, while males select more surface prey like hard-shelled bivalves (Lauro and Nol 1995). Overwhelmingly, in our study, the most common prey species eaten by both sexes was mole crabs. Mole crabs have a carapace, which is easier to handle compared to shells of bivalves. Both sexes may consume mole crabs in high quantities because of easy prey access (Peterson *et al.* 2006; Pulley 2008), high prey abundance and fast handling times ($\bar{x} = 20 \pm 1.16$ sec, $n = 692$) (L. A. Brown, unpubl. data).

We failed to find evidence for intersexual niche partitioning in prey size selection in American Oystercatchers. In strong contrast to our study, the two largest limpet size classes are exclusively taken by male Sooty Oystercatchers, while female Sooty Oystercatchers eat smaller limpets (Aplin and Cockburn 2012). Similar to our study, studies on Northern Goshawks (*Accipiter gentilis*) (Boal and Mannan 1996) and Cooper's Hawks (*Accipiter cooperi*) (Kennedy and Johnson 1986), species who also display reverse sexual dimorphism, found that both sexes take the same prey sizes. Both Boal and Mannan (1996) and Kennedy and Johnson (1986)

speculated that a lack of intersexual niche partitioning in terms of prey size reflects food abundance. Instead of prey size acting as a method for intersexual niche partitioning, prey size selection may reflect prey handling efficiency (Olsen 2013). Wanink and Zwarts (1996) found that Eurasian Oystercatchers take intermediate-sized prey to optimize prey handling time.

Future research should test for intersexual niche partitioning in environments with low food availability or during the non-breeding season to better elucidate the roles of prey abundance and competition on diet partitioning and overlap. For American Oystercatchers, Florida may provide an ideal setting to answer these questions, as there are reports of pre-fledged chicks dying of starvation in Florida (Vitale *et al.* 2022) and dramatic losses in oyster reef foraging habitat (Frederick *et al.* 2016; Vitale *et al.* 2021). Florida's Big Bend supports up to 900 wintering American Oystercatchers (Brush *et al.* 2017). During Florida's non-breeding season, large flocks should increase competition for food and promote intersexual niche partitioning.

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guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010). Work was completed under the authorization of the U.S. Geological Survey Bird Banding Laboratory under Federal Master Permit #21567, U.S. Fish and Wildlife Service Chincoteague National Wildlife Refuge Research and Monitoring Special Use Permits #22-006 and #23-007, and Trent University's Animal Care Committee Animal Care Use Approval #27856. The capture and banding of American Oystercatchers in this study followed protocols developed by the American Oystercatcher Working Group.

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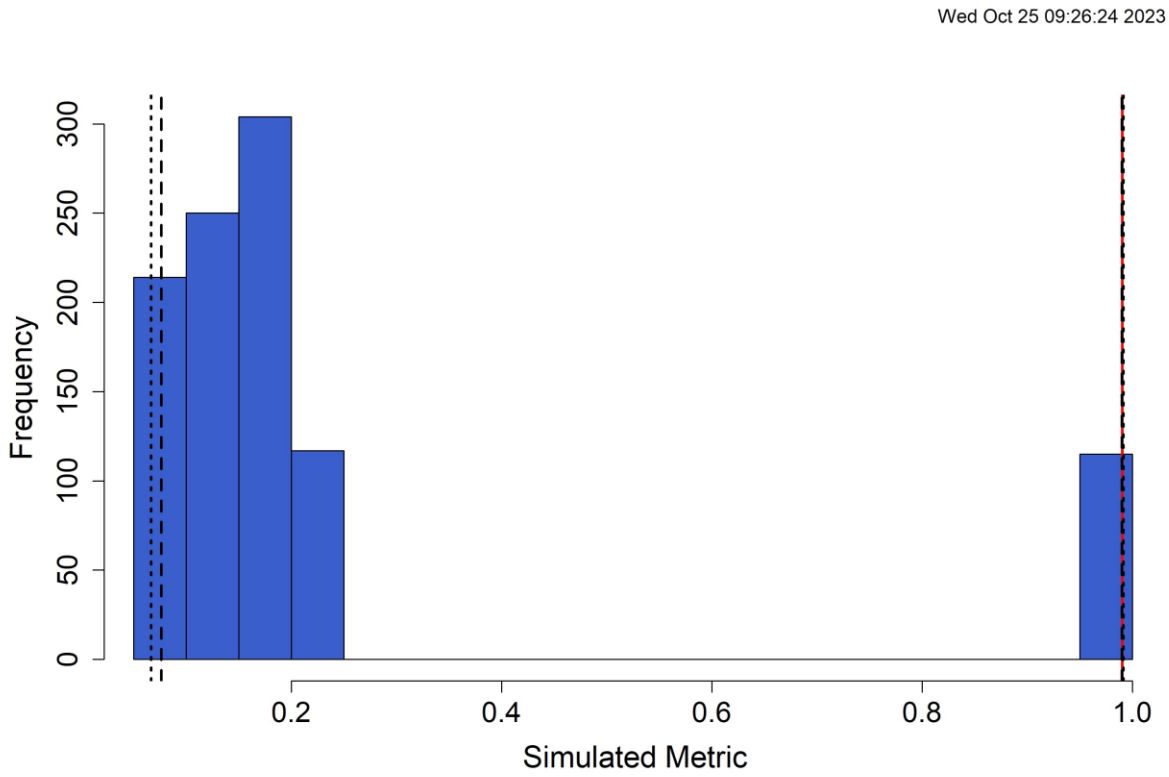
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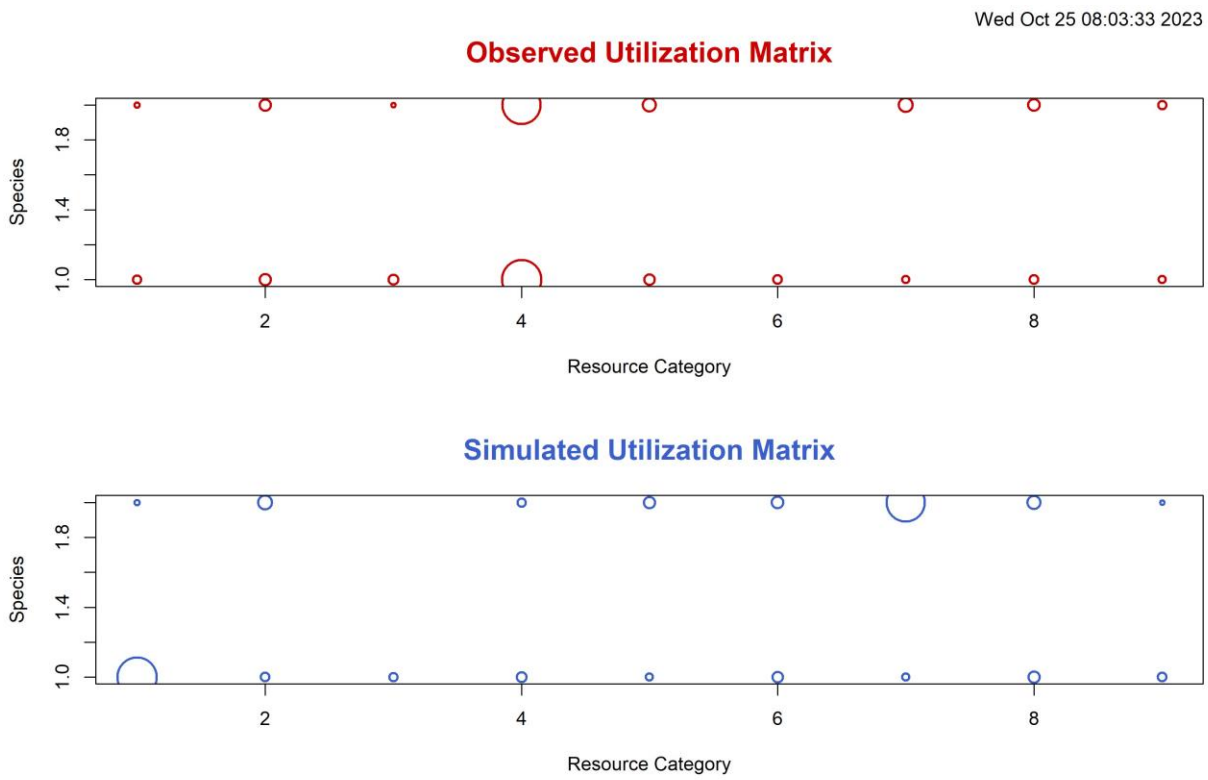
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# Supplementary Materials




**Supplementary Figure S6.1A.** Histogram of 1,000 simulations calculating Pianka's index for diet niche overlap in male and female American Oystercatchers. The red line represents the observed Pianka's index value of 0.99 ($P < 0.05$). The long-dashed lines show the 95% one tailed probabilities, while the short-dashed line shows the 95% two tailed probabilities of 0.044 and 0.956. The observed value is significant since it exceeds the upper-tail $P$ value of 0.956.




**Supplementary Figure S6.1B.** Observed diet niches for the sexes of American Oystercatchers compared to the simulated niches. The size of the circle represents the proportional consumption of each prey species (resource category). The resource categories from one to nine are the following: *Crassotrea virginica, Donax varibilis, Ensis directus, Emerita talpoida, Modiolus demissus, Mytilus edilus, Mercenaria mercenaria, Petricolaria pholadiformis and Tagelus plebeius*. The absence of circles indicates no consumption of that prey species. On the y-axis, species 1 represents females and species 2 represents males. This graph shows that both sexes ate more *Emerita talpoida* (mole crabs) (resource category four) than expected by chance.

# Chapter 7 – A visual sexing technique for American Oystercatchers (*Haematopus palliatus*) suitable for the field



Female American Oystercatcher (*Haematopus palliatus*) on the left with a lighter orange bill compared to a male American Oystercatcher on the right with a darker red bill. Photo credit: Lyn A. Brown.

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Abstract.— There is no published method for visually sexing American Oystercatchers (*Haematopus palliatus*) in the field without having the bird in-hand or using expensive telephoto equipment. This study describes and verifies the accuracy of a method requiring only binoculars or a spotting scope to sex American Oystercatchers by sexual dimorphism in body size, bill length, bill color, and back plumage. From 2023–2024, 50 individuals breeding in Virginia, U.S.A. were visually assigned a sex in the field using this method. After capture, DNA testing confirmed the visually assigned sex in 98% of cases. To further validate the method, in 2024, 27 of these birds (14 males, 13 females) had body measurements taken and were photographed to record back plumage and bill coloration. Photos were color-analyzed using ImageJ. Males had significantly darker backs, with shorter, darker red bills and smaller bodies. There was 100% sexing classification accuracy using these colormetrics and morphometrics. Photography techniques and ImageJ analysis had been previously verified using 23 American Oystercatcher museum specimens (8 males and 15 females). This visual technique provides an easy, cost-effective way to discriminate the sexes. It might be applied to enrich breeding productivity data collection and identify sex-specific behaviors and life history strategies.

**Keywords.—** biometrics, colormetrics, morphometrics, plumage coloration, sex classification, sex differentiation, sexing criteria, sexual dimorphism

## Introduction

The ability to distinguish the sexes of a species is a first step towards improving understanding of a species' ecology and life history. Sex discrimination can shed light on sexual selection, mating systems (Székely *et al.* 2024), same-sex partnerships (Gillies and Siddiqi-Davies 2025), parental care (Joo *et al.* 2018), habitat space use (Militão *et al.* 2023; MacLaurin 2025), and ecological niches (Bantock *et al.* 2008). For breeding birds, the ability to tie specific

behaviors including foraging, defense, and territoriality to individual pair members can help conservation practitioners understand factors limiting reproductive success (Brown *et al.* 2026, Chapter 3). One common way to distinguish the sexes uses sexual dimorphism in physical traits like body size, coloration, and plumage (De Silva *et al.* 2023). However, for the 51 shorebirds that regularly occur in North America, 34 have identical plumage between the sexes (Dunn and Alderfer 2007). Other methods for sex discrimination in birds include vent sexing (Bazzano *et al.* 2012), gonad presence determined from postmortem dissections (Hulscher 1985), molecular methods (Fridolfsson and Ellegren 1999), and sex-specific vocalizations and behaviors (Volodin *et al.* 2015). However, each of these techniques has drawbacks, and often require capturing the bird. Capture can take considerable time and money or have high ambiguity and misclassification due to overlapping characteristics between the sexes (De Silva *et al.* 2023). Until now, the sexes of American Oystercatchers (*Haematopus palliatus*) have been described as "virtually indistinguishable" according to the Birds of the World species account (American Oystercatcher Working Group *et al.* 2020), although previous researchers have used bill coloration, the relative size of males and females when viewed together as a pair, and copulation position to identify the sexes, albeit without molecular confirmations (Nol 1985).

Among practitioners, the only published sexing techniques used for American Oystercatchers include molecular methods (Fridolfsson and Ellegren 1999) or the proportion of eye flecks (iridial pigmentation), where females have more eye flecks than males (Munters *et al.* 2014). Practically, this method can only be used when an individual is in-hand or photos are taken with expensive telephoto lens equipment. Reverse sexual dimorphism in body size, where females tend to be larger in body size and have longer bills than males was described for American Oystercatchers breeding in Virginia, U.S.A. in the early 1980s (American

Oystercatcher Working Group *et al.* 2020). This difference has also been published for American Oystercatchers captured during the non-breeding season in South Carolina and Georgia, U.S.A. (Carlson-Bremer *et al.* 2010; American Oystercatcher Working Group *et al.* 2020), as well as for sexing Black Oystercatchers (*H. bachmani*) (Guzetti *et al.* 2008), Eurasian Oystercatchers (*H. ostralegus*) (Zwarts *et al.* 1996), African Oystercatchers (*H. moquini*) (Hockey 1981), South Island Pied Oystercatchers (*H. ostralegus finschi*), Variable Oystercatchers (*H. unicolor*), Chatham Island Oystercatchers (*H. chathamensis*) (Baker 1974), Sooty Oystercatchers (*H. fuliginosus*) (Hansen *et al.* 2009), and Pied Oystercatchers (*H. longirostris*) (Kraaijeveld-Smit *et al.* 2004). However, discriminant functions in body size have not been widely taken up among ornithologists, due to overlap in measurements between the sexes (American Oystercatcher Working Group, pers. commun.). Sex-specific behaviors and vocalizations are not applicable sexing criteria for American Oystercatchers, since the species has biparental care (Nol 1985) and lacks sex-specific vocalizations. To date, there has not been a practical method that has been confirmed by molecular methods for sexing American Oystercatchers from afar. Here, we describe a practical non-invasive method for visually sexing American Oystercatchers from afar, based on sexual dimorphism in body size, bill coloration, and back plumage coloration.

# Methods

## Data Collection

*Visual Sexing Technique.* In Table 7.1, we outline a historical timeline, detailing the observations and methodologies that led to the development of the visual sexing technique formally introduced here. Observations surrounding visually discriminating the sexes began in the 1980s by Allan J. Baker, and then were carried on by his students Mike Cadman and Erica Nol (Nol *et al.* 1984), as well as other conservation professionals in the U.S.

**Table 7.1. Timeline for developing and validating the visual sexing technique for American Oystercatchers (*Haematopus palliatus*).**

| Year | Observation/Methodology |
|---|---|
| Early 1980s | Allan J. Baker, an expert on *Haematopus* spp. around the world, made observations that were apparent to the eye that the sexes of American Oystercatchers differed in the color of the bill and back plumage, as well as body size and bill length. Allan noted that males were smaller-bodied individuals with darker backs (appearing more black than brown) and shorter bills that were darker red in color (Fig. 7.1), while females were larger-bodied individuals with lighter-colored backs (appearing more brown than black) and longer bills that were lighter orange in color. He shared these observations with his graduate students, Mike Cadman and Erica Nol (A. J. Baker, pers. comm.). |
| Early 1980s | Mike Cadman observed that in Virginia, U.S.A., within breeding pairs, American Oystercatcher males appeared to have redder shorter bills than females (M. Cadman, pers. comm.). |
| 1984 | Erica Nol made observations consistent with Allan and Mike that American Oystercatcher males had backs appearing more black than brown and shorter bills that were darker red. Erica distinguished the sexes based on copulation position, where males are on top. In 1984 based on a three-year study, Erica published that for American Oystercatchers breeding in Virginia, U.S.A., males had lower mass and shorter bills than females. |

| | |
|---|---|
| 2010 | Daphne Carlson-Bremer published that for American Oystercatchers overwintering in South Carolina and Georgia, U.S.A., males had lower mass and shorter bills than females. |
| 2014 | Since 2014, Bridie R. Farmer, a Natural Resource Specialist with the Virginia Department of Wildlife Resources who monitors breeding American Oystercatchers in Virginia, U.S.A., associated back contrast differences with sex, where males had higher back contrast (darker back plumage compared to their white contour feathers) than females. Bridie sexed birds by copulation position. She anecdotally began sharing this technique with field technicians starting in 2015 (B. R. Farmer, pers. comm.). |
| 2020 | Despite published accounts of sexual dimorphism in body size and bill length as noted above, the American Oystercatcher Working Group published the species account in Birds of the World, and stated that “the sexes were virtually indistinguishable”. Additionally, conservation practitioners were not using discriminant functions to distinguish the sexes based on body size and bill length due to some overlap in measurements between the sexes and regional variation in measurements (American Oystercatcher Working Group, pers. comm.). |
| April–June 2023 | We used the visual sexing technique that Allan J. Baker had originally described, prior to statistically validating the technique. For 21 birds, we sexed them in the field using Dr. Baker’s technique, measured morphometrics, and took feathers for DNA, as part of a separate study. |

| | |
|---|---|
| January 2024 | To statistically validate the visual sexing technique, we needed an effective way to photograph birds, so we could do image analysis to quantify color differences between the sexes. We practiced our photography technique sample on 23 museums skin specimens from the Royal Ontario Museum in Toronto, Ontario, Canada. These skins had been sexed by the museum based on gonad presence. |
| April–June 2024 | For a separate set of birds than those sampled in 2023, in 2024, for 29 birds, we visually sexed them in the field, measured morphometrics, took feathers for DNA, and photographed individuals. |
| January–June 2025 | We conducted image analysis on photographs from the live birds in 2024 to validate the visual sexing technique. We also did image analysis on photographs from the museum skin specimens to further confirm coloration differences between the sexes. We then combined image and morphometric data to create discriminant functions and classification equations for discriminating the sexes. |
| July 2025 | We performed molecular analyses on feathers of live birds from 2023 and 2024 ($n$ = 50) to determine sex. The molecular sex confirmed if we correctly assigned sex using the visual sexing technique. |

The present study occurred during the breeding season (April to June) of 2023 and 2024, with a long-term study population of American Oystercatchers on Assateague Island (37°51’7.2”N, 75°22’55.2”W) and Assawoman Island, Virginia, U.S.A. (37°48’3.6”N, 75°31’4.8”W). Over the course of the breeding season, while monitoring nests, we assessed and

assigned a sex to breeding pair members using the visual sexing technique. To visually sex American Oystercatchers in the field, we used 10 x 42 binoculars or a 60x spotting scope to assess overall body size, back color, bill length, and bill color of an individual. We started with overall body size. Males appeared smaller-bodied than females (Table 7.1). Then, we looked at back color. Males had darker backs (appearing more black than brown), while females had lighter-colored backs (appearing more brown than black) (Fig. 7.1). Finally, we compared bill length and color. Males had shorter bills that were darker red in color, while females had longer bills that were lighter orange in color. Since we assigned sex during the breeding season, we were typically able to compare breeding pair members to one another. With practice, we used the visual sexing technique on lone individuals, without the need to see the other pair member.

Since this method stemmed from field observations made by Allan J. Baker (Table 7.1), we needed 1) a way to verify intersexual color differences in bill and back plumage, 2) confirm morphometric differences in body size and bill length between the sexes, so that we could develop a holistic sexing technique that used both coloration and morphometry, and 3) confirm that the sex assigned in the field using the visual sexing technique matched the actual molecular sex of the bird.

*Skins*. To first determine if there were true color differences in bill and black plumage between the sexes, we took photos of birds of each sex. To initially practice the photographic setup, in January of 2024, we photographed a collection of museum skin specimens, hereafter referred to as skins. The skins also served to corroborate our field method due to more consistent lighting in the photography setup and accurate sexing from postmortem dissections. Of the 49 American Oystercatcher skins in the collection from the Royal Ontario Museum in Toronto, Ontario, Canada, we photographed 23 (8 males and 15 females) which had complete

morphometric data and could be used for analysis (Fig. 7.2). Skins had been sexed during postmortem dissections based on the presence of testes or ovaries. All individuals were collected from the Atlantic Coast of the U.S. (17 South Carolina, 4 Virginia, 2 Florida) from 1975 to 1982. Due to the skin preservation method, bills were absent since they were used for skeletons, so we could only photograph the backs of skins.




**Figure 7.1.** Typical scene of an American Oystercatcher (*Haematopus palliatus*) breeding pair with a male (P4) on the left and a female (EFR) on the right. The male is a smaller individual with a darker back and shorter darker red bill compared to the female who is a larger individual with a lighter-colored back and longer bill that is lighter orange in color. The visually sexing method is intended to be used in the field. During most breeding monitoring protocols, field

workers often get to see both pair members repeatedly throughout the breeding season, which allows side-by-side comparison. Photo credit: Lyn A. Brown.



**Figure 7.2.** Collection of American Oystercatcher (*Haematopus palliatus*) skins that were photographed for image analysis from the Royal Ontario Museum based in Toronto, Ontario, Canada. Many of these specimens were collected by Allan J. Baker. Note that the skin preservation technique of the time meant that the skins lacked bills, so only their backs were photographed. Photo credit: Lyn A. Brown.

We followed best photography practices to obtain color measurements, according to Stevens *et al.* (2007) and McKay (2013). For the skins, we used a Nikon D90 camera with the following camera settings: white balanced for fluorescent indoor lighting, color space as Adobe RGB, neutral picture control, large image size of 12.2 megapixels, image quality as NEF (RAW) + JPEG, normal long exposure, NR turned off, and normal ISO. We took all photos in the same room under fluorescent lighting with the camera positioned 32 cm from the lens to the tabletop and 28 cm from the lens to the top of the skin's back. To calibrate reflectances for post-

photography image analysis, we photographed skins and live birds with an 18% gray reflectance standard and a 90% white reflectance standard Kodak™ and included a wing chord ruler to provide scale.

*Live Birds.* Live birds came from the study population of American Oystercatchers at Assateague Island and Assawoman Island, VA, U.S.A. that were captured for banding to distinguish breeding pairs from one another. We captured individuals at their nests using leg loop carpets as per standardized protocols by the American Oystercatcher Working Group (2025). We buried four leg loop carpets (1.33 m x 1.00 m) made of clear monofilament nylon (50 lb. test strength) in sand around nests, and accompanied this trapping method with a pair of reasonably accurate wooden decoys. American Oystercatchers are highly territorial (American Oystercatcher Working Group *et al.* 2020) and will approach areas where perceived intruders (the decoys) are present. We played their alarm call using a FoxPro Patriot™ speaker to lure breeding pair members to the nest area for capture. We temporarily removed eggs and placed them in a padded cardboard box in the shade, during the capture process. We set leg loop carpets for a maximum of 60 min. We banded each bird with two identical black Darvic bands (one on each of the upper legs), and a metal band issued by the U.S. Geological Survey's Bird Banding Laboratory on a lower leg. We took standard morphometric measurements of body mass, unflattened wing chord length, tarsus length, and bill length as the exposed culmen, using a digital scale (tenth of a g), wing ruler (mm), and standard calipers (mm). To verify our visually assigned field sex with DNA, we plucked 2–3 breast feathers when birds were in-hand. We mailed the feathers to the U.S. Geological Survey Nebraska Cooperative Unit for molecular processing. We collected the aforementioned data for a total of 50 birds ($n$ = 21 birds in 2023 and $n$ = 29 birds in 2024).

*Molecular Analysis.* After a sex was visually assigned to all individuals in the field, we analyzed the breast feathers from 2023 and 2024 to determine each individual's molecular sex. To do this, we extracted DNA using a DNeasy Tissue Kit (Qiagen) following the manufacturer's standard protocol. Primer sets Sex_2602F/Sex_2669R (van der Velde *et al.* 2017) were used to amplify the sex-specific gene CHD-Z and CHD-W. PCR amplifications were carried out in 20 uL volumes: 2 uL template DNA, 1x Promega Flexi PCR Buffer (Madison, WI), 0.25 mM dNTPs, 2.5 mM MgCl2, 1 uM each primer, 0.5 ug BSA, and 1 unit taq polymerase (Promega). We used a touchdown PCR thermocycler program that began at 95°C for 3 min, 10 cycles of 95°C for 30 sec, 60°C for 30 sec, 72°C for 1 min, reducing the annealing temperature by 1°C per cycle (60°C–50°C), followed by an additional 30 cycles with an annealing temperature of 50°C and concluded at 72°C for 5 min. We visualized PCR products on a 1.5% agarose gel. For quality control purposes, 10% of the samples were amplified and verified sex in duplicate.

*Image Analysis.* In 2024 only, after birds were captured, we photographed individuals for image analysis later on to quantify and compare coloration of the bill and back plumage between the sexes. We photographed birds in the field from a distance of 3.3 m. Since most of the birds also received a GPS tag for another study, and had already been handled for up to one hour, we minimized the time spent handling the birds for photography by photographing birds on the beach or in the field truck. We attempted to photograph birds in uniform lighting with both the bird and the reflectance standards fully in the shade of the field truck or in full sun outside of the field truck. To minimize differences in lighting and image analysis, we took two photographs of the bill (one of each side, the left and right side), and one photo of the back. We photographed the sides of each bill, since bills are conical and the ambient light reflections along the rounded dorsal side of a bill could distort color. Two photographs of the bill were necessary since a) bills

are not one uniform color. Instead, they are subtle gradations of color in different areas of the bill and along its length that the human eye tends to blend into one overall perceived color; and b) two photos allowed us to sample from as large amount of color data as possible, since the side portion of each bill available for image analysis sampling was relatively small. In contrast, only one photo of the back was necessary because shadows and reflections were not a problem when photographing the back of a bird from above, and the size of the back provided an adequate color sampling area for image analysis.

Due to changes in our ability to borrow the first camera, we used a different camera with similar settings as that used for photographing skins to photograph the live birds. The camera was a Canon EOS Rebel XSi [SLR (single-lens reflex)] digital camera with a Canon Zoom Lens EF 75-300mm. The camera settings were color space Adobe RGB, file type RAW + JPEG, 1.2 megapixel image size, auto white balance outdoors, autofocus normal, ISO normal 100, shutter speed 1/400, and F-stop 4.0. We included the same reflectance standards and wing chord ruler in photographs, as those for the skins.

To quantify the spectral reflectance of skin back colors, we used Image J and the MICA toolbox (Troscianko and Stevens 2015). We first formed a linearization model for our camera. For each photograph, we calibrated the image with the gray 18% and white 90% reflectance standards to form a multi-spectral image (Fig. 7.3). Prior to taking the reflectance measures, we checked for overexposure for each color channel. We excluded overexposed images from our analysis. We measured reflectance of each back and bill photo based on the region of interest we selected from the multi-spectral color image. For back photos, we used the rectangular or polygon tool to select the largest region that covered the flattest part of the back, and selected only the brown mantle feathers, while avoiding any white contour feathers underneath. For

photos from each side of the bill, we selected the largest region from the upper mandible that avoided mud on the bill. We used the upper mandible because the ambient lighting outdoors caused the bird to shade its bottom mandible. From the selected regions of a bird's back and bill, we outputted the mean reflectance for the R, G, and B color channels. For the bill photos, we averaged the reflectance values between the left and right side of the bill.

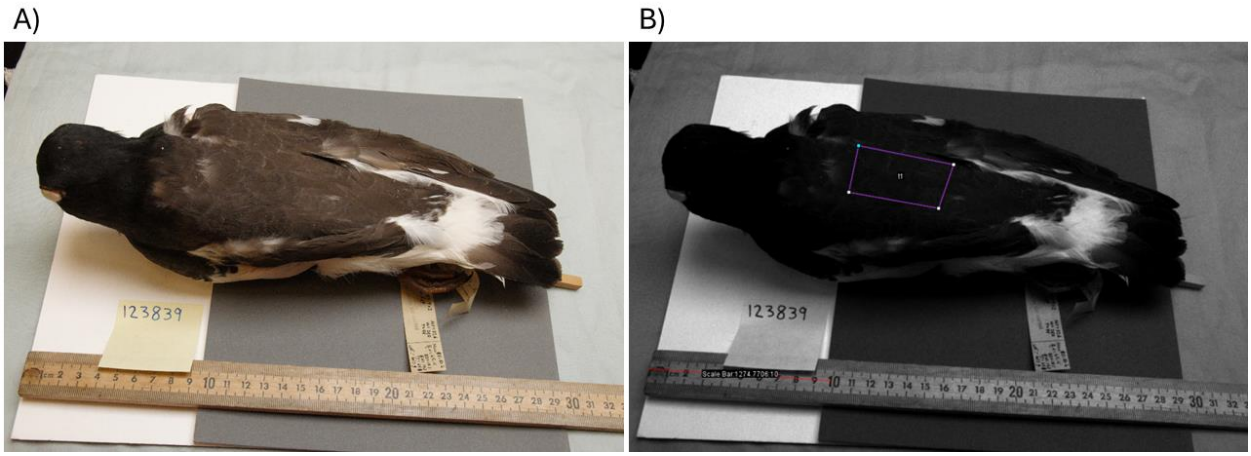



**Figure 7.3.** A) Original unaltered image of an American Oystercatcher (*Haematopus palliatus*) skin. B) Multispectral image showing the selected region of interest of the back feathers used in image analysis. Photo credit: Lyn A. Brown.

We had complete morphometric and colormetric data for 27 of 29 live American Oystercatchers (14 males and 13 females) in 2024. Two of the 29 live birds were not used in analysis because one bird had mud covering its bill, making it unsuitable for image analysis, and the other bird's bill photos were overexposed because the standards were in the shade while its bill was partially in sun and shade.

## Statistical Analysis

We performed statistical analyses in R v. 4.3.1 (R Core Team 2023). For the bill and back of each live bird and the back of each skin, we used the rgb2hsv() function from the package

"grDevices" (R Core Team 2023) to convert the mean reflectance values from each RGB color channel to hue, saturation, and value. Hue represented the color type and ranged from zero to 360° (red = 0–60°, yellow = 60–120°, green = 120–180°, cyan = 180–240°, blue = 240–300°, and magenta = 300–360°). Saturation represented the color richness with 0% indicating no color (gray) and 100% indicating full color. Value represented color brightness and ranged from 0% (black) to 100% (full brightness) (Geek for Geeks 2025).

For both the live birds from 2024 and the skins, we first tested if the sexes differed based on morphometrics or coloration using a multivariate analysis of variance (MANOVA), and then classified each sex based on the morphometric and colormetric variables, using a discriminant function analysis. Since one of the gaps that this study filled was the addition of bill and back color differences as sexually dimorphic characteristics; for the live birds, we also developed a separate discriminant function based only on the colormetrics to ensure that color alone was enough to discriminate the sexes. For the MANOVAs, we checked the assumptions including multivariate normality using Henze-Zirkler tests; no outliers using Mahalanobis distances; and homogeneity of the covariance matrices using Box's M test with the R package "MVN" (Korkmaz *et al.* 2014).

The response variables met the assumption of multivariate normality (live birds: $HZ$ = 0.97, $P$ = 0.251, skins: $HZ$ = 0.93, $P$ = 0.145). There were no outliers for the live birds. Three data points were flagged as outliers for the skins, according to Mahalanobis distances. However, we retained these data points for the skins since they represented true variation in the data, due to the consistency of photographic lighting conditions and accurate morphological measurements taken by museum experts.

For the discriminant function analyses, we assessed the level of support for each trait at discriminating the sexes using F tests from one way analysis of variances (ANOVAs), effect sizes from eta-squared values, and level of evidence from Bayes factor. We defined small effect sizes as eta-squared > 0.06, medium effect sizes as 0.06 ≥ eta-squared > 0.14, and large effect sizes as eta-squared ≥ 0.14 (Fritz *et al.* 2012). Bayes factors compare the probability that the alternative hypothesis would occur over the null hypothesis (Jarosz and Wiley 2014). We interpreted the morphological or color measurement as having no evidence for discriminating the sexes if Bayes factor > 3, some evidence if 3 ≥ Bayes factor > 10, strong evidence if 10 ≥ Bayes factor > 30, very strong evidence if 30 ≥ Bayes factor > 100, and extremely strong evidence if 3 Bayes factor > 100 (Jarosz and Wiley 2014). We developed equations for the discriminant functions describing color and morphological measurements based on the canonical discriminant function raw coefficients. We used the R package "DFA.CANCOR" (O'Connor 2025) to run the discriminant function analysis.

We built a classification equation for each sex using the discriminant function coefficients. We present the classification accuracy using jackknifing, and the associated significance values with a Press's Q. We used jackknifing, where part of the sample is left out during training, since jackknifing is a more conservative approach compared to randomization (Dechaume-Moncharmont *et al.* 2011). We assessed the level of agreement between the original group means and predicted means using Cohen's kappa. We considered the group means as having slight agreement if Cohen's kappa value was 0.01–0.20, fair agreement for 0.21–0.40, moderate agreement for 0.41–0.60, substantial agreement for 0.61–0.80, and almost perfect agreement for 0.81–1.00 (McHugh 2012). Data and R scripts are available at OSF https://osf.io/yp8n5/overview?view_only=e8555c93928e471e953fd749a6e05691.

# Results

## Molecular Sex

DNA confirmed that the sex we visually assigned to individuals in the field matched the molecular sex in 98% of cases ($n$ = 49 of 50 birds).

## Live Birds

*Colormetrics and Morphometrics.* The sex of live American Oystercatchers in 2024 could be differentiated based on body size characteristics including mass, bill length, and wing chord length, as well as color of the bill and back (see Supplementary Fig. S1, Fig. S2, and Fig. S3 for example photographs). Each of these metrics had large effect sizes (Table 7.2). According to Bayes factor, there was extremely strong evidence for mass, bill hue, and bill length as effective traits for distinguishing the sexes, followed by very strong evidence for bill value, some evidence for back value and wing chord length, and no evidence for back hue, back saturation, bill saturation, or tarsus length (Table 7.2). Males had significantly smaller body sizes (lower mass, shorter bills, and shorter wingspans), darker backs (lower value), and darker red bills (lower value and lower hue) than females (Fig. 7.4). In contrast, females had larger body sizes (higher mass, longer bills, and longer wingspans), lighter-colored backs (higher value), and lighter orange bills (higher value and higher hue) (Table 7.3). The discriminant function based on colormetrics and morphometrics significantly separated the sexes for live birds ($X^2_1 = 27$, $P < 0.001$). There was no overlap in the discriminant function scores between the sexes at our study site in 2024 (Fig. 7.5). Males scored higher on the discriminant function than females (unstandardized canonical discriminant function of AMOY sex: male group means = 2.26 and group standard deviations = 0.99; female group means = -2.43 and group standard deviations = 1.01).

**Table 7.2. One-way ANOVA for colormetrics and morphometrics of live American Oystercatchers (*Haematopus palliatus*) (*n* = 27) in 2024 at Assateague Island and Assawoman Island, Virginia, U.S.A. Eta-squared values represent effect sizes. F statistics and their associated degrees of freedom (DF) and *P* value are presented along with Bayes factor.**

| | Eta-squared | Wilks Lambda | F | DF | Residual DF | *P* | Bayes factor$_a$ | Bayes factor$_b$ |
|---|---|---|---|---|---|---|---|---|
| Discriminant function | 0.86 | 0.15 | 147.97 | 1 | 25 | <0.001 | 855,421,947 | 0 |
| Mass (g) | 0.63 | 0.37 | 43.38 | 1 | 25 | <0.001 | 16,579.6 | <0.001 |
| Bill hue (degrees) | 0.55 | 0.45 | 30.71 | 1 | 25 | <0.001 | 1,614.64 | 0.001 |
| Bill length (mm) | 0.49 | 0.51 | 23.64 | 1 | 25 | <0.001 | 353.31 | 0.003 |
| Bill value (%) | 0.36 | 0.64 | 13.85 | 1 | 25 | 0.001 | 30.49 | 0.03 |
| Back value (%) | 0.26 | 0.74 | 8.98 | 1 | 25 | 0.006 | 7.44 | 0.13 |
| Wing chord length (mm) | 0.23 | 0.77 | 7.38 | 1 | 25 | 0.012 | 4.54 | 0.22 |

| | Eta-squared | Wilks Lambda | F | DF | Residual DF | *P* | Bayes factor[a] | Bayes factor[b] |
|---|---|---|---|---|---|---|---|---|
| Back hue (degrees) | 0.16 | 0.84 | 4.61 | 1 | 25 | 0.042 | 1.84 | 0.54 |
| Back saturation (%) | 0.15 | 0.85 | 4.29 | 1 | 25 | 0.049 | 1.65 | 0.61 |
| Bill saturation (%) | 0.07 | 0.93 | 1.94 | 1 | 25 | 0.176 | 0.73 | 1.37 |
| Tarsus length (mm) | 0.02 | 0.98 | 0.42 | 1 | 25 | 0.522 | 0.42 | 2.39 |

[a]Bayes Factor for alternate hypothesis vs. null hypothesis

[b]Bayes Factor for null hypothesis vs. alternate hypothesis

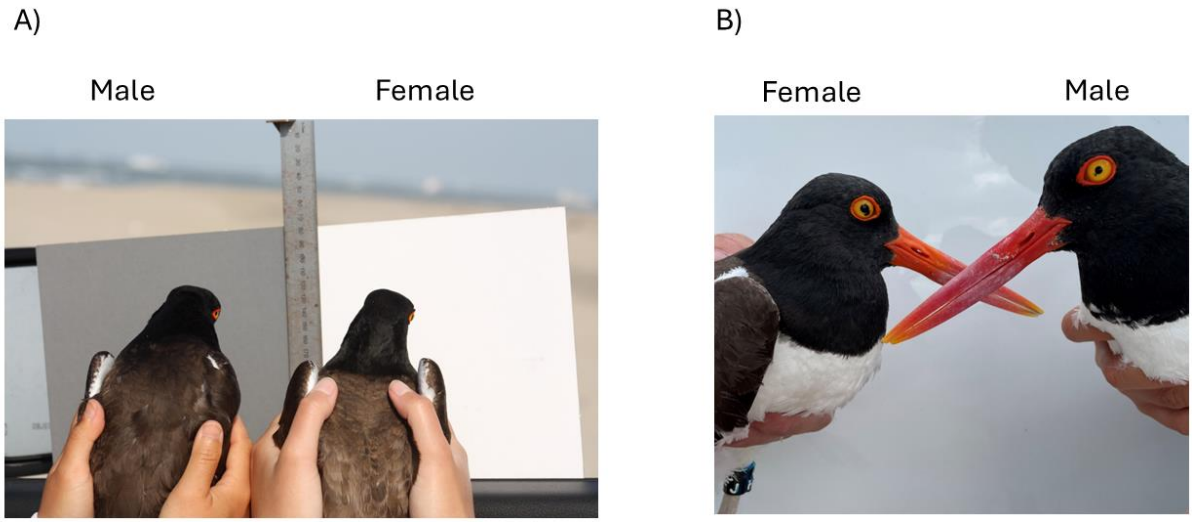



**Figure 7.4.** A) Male American Oystercatchers (*Haematopus palliatus*) (left) have darker backs than females (right). B) Male American Oystercatchers (right) have darker red bills than females (left) who have lighter orange bills. Photo credit: Trevor MacLaurin.

**Table 7.3. Means ± SD for colormetrics and morphometrics of male and female American Oystercatchers (*Haematopus palliatus*) from live birds captured in 2024 at Assateague Island and Assawoman Island, Virginia, U.S.A. (*n* = 13 females, 14 males) and skins collected from 1975–1982 in Virginia, South Carolina, and Florida, U.S.A. (*n* = 15 females, 8 males) that are housed at the Royal Ontario Museum based in Toronto, Ontario, Canada.**

| | **Live** | | **Skins** | |
|---|---|---|---|---|
| **Metric** | Males | Females | Males | Females |
| Bill length (mm) | 83.46 ± 3.70 | 90.98 ± 4.33 | 84.55 ± 2.51 | 88.91 ± 4.14 |
| Tarsus (mm) | 58.22 ± 3.73 | 59.12 ± 3.41 | 63.02 ± 3.90 | 64.29 ± 3.29 |
| Wing (mm) | 253.07 ± 4.12 | 258.31 ± 5.81 | 260.25 ± 4.59 | 262.73 ± 8.31 |
| Mass (g) | 559.57 ± 20.48 | 626.15 ± 31.32 | 618.75 ± 31.14 | 643.33 ± 56.81 |
| Bill hue (degrees) | 0.02 ± 0.00 | 0.03 ± 0.00 | | |
| Bill saturation (%) | 0.73 ± 0.05 | 0.76 ± 0.06 | | |
| Bill value (%) | 0.15 ± 0.02 | 0.18 ± 0.02 | | |
| Back hue (degrees) | 0.06 ± 0.01 | 0.07 ± 0.01 | 0.06 ± 0.00 | 0.06 ± 0.00 |
| Back saturation (%) | 0.25 ± 0.08 | 0.3 ± 0.04 | 0.86 ± 0.09 | 0.73 ± 0.12 |
| Back value (%) | 0.04 ± 0.01 | 0.05 ± 0.02 | 0.02 ± 0.00 | 0.03 ± 0.01 |

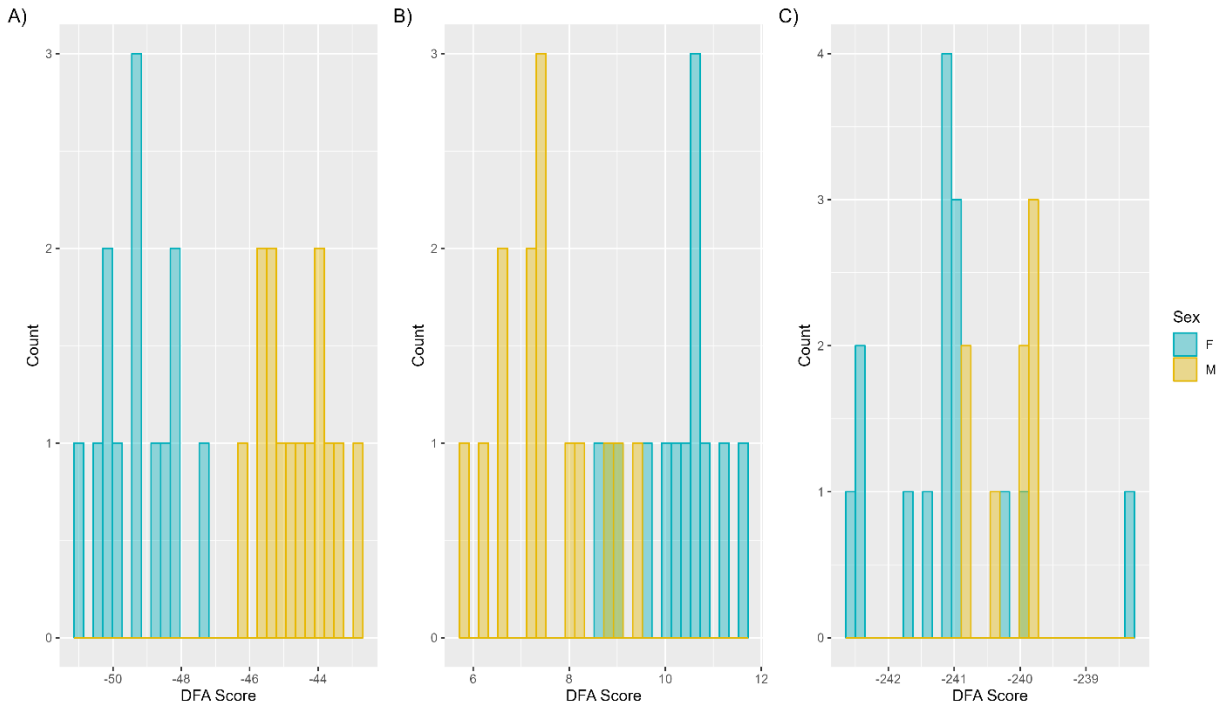



**Figure 7.5.** A) Frequency of discriminant function scores based on color and morphological measurements for live male (*n* = 14) and female (*n* = 13) American Oystercatchers (*Haematopus palliatus*). The equation for the discriminant function is DF~ sex = -168.70(bill hue) + 22.30(back hue) - 18.35(bill value) - 13.56(back value) - 2.66(back saturation) - 0.77(bill saturation) - 0.08(tarsus length) - 0.05(wing chord length) - 0.04(bill length) - 0.03(mass). B) Frequency of discriminant function scores for live male (*n* = 14) and female (*n* = 13) American Oystercatchers based on color measurements is DF~ sex = 230.41(bill hue) - 30.31(back hue) +22.53(bill value) + 16.86(back value) + 5.35(back saturation) - 0.56(bill saturation). C) Frequency of discriminant function scores for male (*n* = 8) and female (*n* = 15) American Oystercatcher skins from the Royal Ontario Museum based in Toronto, Ontario, Canada. The equation for the discriminant function describing color and morphological measurements is DF~

sex = - 208.13(back value) - 28.01(back hue) - 0.52(back saturation) - 0.17(bill length) - 0.05(wing chord length) - 0.04(tarsus length) - 0.001(mass).

Supplementary Table S7.1 shows the classification equation for live American Oystercatchers based on colormetrics and morphometrics. There was 100% classification accuracy for sexing live American Oystercatchers based on the discriminant function encompassing colormetrics and morphometrics. All 14 males and 13 females were correctly classified (*Press's Q* = 27, $P < 0.01$). There was perfect agreement between the original group means and the cross validated group means (*Cohen's kappa* = 1.00, $Z = 5.19$, $P < 0.001$).

*Colormetrics Only.* The sex of live American Oystercatchers could be differentiated based on color of the bill and back. Each of these metrics had large effect sizes, except for bill saturation which had a medium effect size (Supplementary Table S7.2). According to Bayes factor, there was extremely strong evidence for bill hue as an effective trait for distinguishing the sexes, followed by very strong evidence for bill value, some evidence for back value, and no evidence for back hue, back saturation, or bill saturation (Supplementary Table S7.2). The discriminant function based on colormetrics alone significantly separated the sexes for live birds ($X^2_1 = 13.36$, $P < 0.001$). Males scored lower on the discriminant function than females (unstandardized canonical discriminant function of sex: male group means = -1.28 and group standard deviations = 1.09; female group means = 1.38 and group standard deviations = 0.90; Fig. 7.5).

Supplementary Table S7.3 shows the classification equation for live American Oystercatchers based on colormetrics only. There was 85.2% classification accuracy for sexing live American Oystercatchers based on the discriminant function describing colormetrics. Twelve of the 14 males and 11 of the 13 females were correctly classified (*Press's Q* = 13.37, *P*

< 0.01). There was high agreement between the original group means and the cross validated group means (*Cohen's kappa* = 0.70, $Z = 3.65$, $P < 0.001$).

## Skins

Skins of male and female American Oystercatchers could be differentiated based on back color (value and saturation) and bill length (Supplementary Table S7.4). Each of these metrics had large effect sizes at discriminating the sexes and some evidence that this would occur over the null hypothesis, according to Bayes factors (Supplementary Table S7.4). Males had significantly darker backs (lower value) that were more saturated in color and had shorter bills (Table 7.3). In contrast, females had lighter backs that were less saturated in color and had longer bills. Back hue, tarsus length, wing chord length, and mass were not informative measurements for distinguishing the sexes. The discriminant function based on colormetrics and morphometrics significantly separated the sexes for skins ($X^2_1 = 15.95$, $P < 0.001$). Males scored significantly higher on the discriminant function and had lower variation in their scores than females (unstandardized canonical discriminant function for males: group means = 1.52 and group standard deviations = 0.40; females: group means = -0.81 and group standard deviations = 1.19; Fig. 7.5).

Supplementary Table S7.5 shows the classification equation for American Oystercatcher skins based on colormetrics and morphometrics. There was a 91.3% classification accuracy for sexing skins based on the discriminant function encompassing colormetrics and morphometrics. All 8 males were correctly classified, and 13 of the 15 females were correctly classified (*Press's* $Q = 15.7$, $P < 0.01$). There was high agreement between the original group means and the cross validated group means (*Cohen's kappa* = 0.82, $Z = 3.77$, $P < 0.001$).

## Discussion

We provide a practical field technique for visually sexing American Oystercatchers based on a combination of sexually dimorphic traits in body size as well as color differences in bill and back plumage. This method can be used to sex American Oystercatchers using binoculars or spotting scopes, without the need for expensive telephoto lens photography equipment or capturing the bird in-hand. Differences in back color and bill length were retained as discriminating sex characteristics for skins.

Our field sexing method is more practical, effective, robust, and cheaper than existing sexing methods. The eye fleck technique has higher ambiguity with sex remaining unknown for 8 of 42 American Oystercatchers in Texas, U.S.A. (Munters *et al.* 2014) compared to no individuals with unknown sex using the visual sexing method. The visual sexing method can also prevent stress to American Oystercatchers compared to molecular methods where the birds need to be captured in-hand to obtain DNA samples. Additionally, the sex of individuals can be known immediately compared to considerable time lags and higher financial costs associated with molecular processing.

The power of the visual sexing method is the combination of differences in morphometry and color to sex American Oystercatchers. Using morphometry alone can be unreliable and lead to misclassification of the sexes, since there can be temporal variation between individuals and within individuals, as well as regional variation in morphometrics (Heppleston and Kerridge 1970; Zwarts *et al.* 1996; van de Pol *et al.* 2009). It has been suggested that bill length could be a predictor that discriminates the sexes in other oystercatcher species including Eurasian Oystercatchers (Zwarts *et al.* 1996) and Black Oystercatchers (Roodenrijs *et al.* 2024), but bill length alone seems to be unreliable; even within an individual Eurasian Oystercatcher, bill length

can change by 33 mm between recaptures (Zwarts *et al.* 1996), and up to 5mm between the breeding and nonbreeding season in the Dutch Wadden Sea (Hulscher 1985). A 24-year dataset of morphometrics for Eurasian Oystercatchers at one site and data from seven separate sites within the same year, showed that during some years with poor food, females took on a male-like appearance of lower body mass and deeper bills, due to changes in diet, which could lead to misclassification of their sex based on discriminant functions (van de Pol *et al.* 2009). Furthermore, even the direction of sexual dimorphism in bill shape could be unreliable and switch during the month of March compared to other times of the year (van de Pol *et al.* 2009). Van de Pol *et al.* (2009) concluded that this level of variation indicates that researchers must calibrate their discriminant functions based on time and location to have accurate sex classification. Similarly, bill coloration and plumage coloration can change over time due to factors like environmental variables (Argüelles Ticó *et al.* 2016). Overall, we recommend using color differences alongside morphometric differences to increase the number of tools for discriminating the sexes of breeding American Oystercatchers and to increase classification accuracy.

In the genus *Haematopus*, our method is the first visual sexing technique based on a combination of differences in body size, bill color and plumage color among species. Only one other study has tested if the sexes of a *Haematopus* spp. are distinguishable based on color. In New Zealand, back color is not useful for differentiating the sexes for the three species of oystercatchers (South Island Pied Oystercatchers, Variable Oystercatchers, and Chatham Island Oystercatchers), since males and females have similar melanin pigmentation in their back plumage (Baker 1974). Since New World *Haematopus* spp. seem to have browner backs than old world *Haematopus* spp., it could be interesting to compare if back coloration is a useful sexing

criteria for New World *Haematopus* spp. (e.g., *H. ater* and *H. bachmani*), but not Old World *Haematopus* spp.

For live American Oystercatchers, our field method had a 98% classification accuracy, as confirmed by DNA analysis. Classification accuracy was similar for males and females. As for the single individual that we sexed incorrectly, we only saw this individual once during the season, so could not confirm the sex assignment with repeat visits. This highlights the importance of regularly re-assessing a bird's sex with repeat visits. It is especially helpful to see both pair members together in similar lighting to more easily discriminate males from females.

Our method using both morphometry and coloration was more effective for live birds (100% classification accuracy) than skins (91% classification accuracy). This might indicate that back plumage coloration fades with age of the skin, since some of the skins were up to 49 years old. Future research could investigate how the age of skins affects back plumage coloration to identify a potential threshold point when back plumage coloration is no longer effective in discriminating the sexes.

The difference in bill and plumage coloration begs the question as to what the color difference means for American Oystercatchers. There have been multiple hypotheses describing what differences in color might mean including differences in diet (Hill *et al.* 2009), condition (Pérez-Rodríguez and Viñuela 2008), stress, disease state, immune response (Rosenthal *et al.* 2012), hormones including testosterone and estradiol (Bókony *et al.* 2008; Romero-Diaz *et al.* 2022), dominance (Bókony *et al.* 2008), and environment (Argüelles Ticó *et al.* 2016). Differences in bill coloration between male and female American Oystercatchers is unlikely to be derived from carotenoid differences in diet, since the sexes share a similar diet at our study site (Brown and Nol 2024). Instead, we speculate that differences in bill coloration likely have a

genetic basis that could assist in identifying mates, and possibly signal mate quality. Future studies could test for color variation of bills and backs within each sex and potential relationships with individual health, age, territory quality, competitiveness, dominance, and reproductive success. This type of study could use a spectrophotometer to measure the level of melanin in the feathers and testosterone and other hormones similarly to McGraw (2008) and Bókony *et al.* (2008).

## Limitations

We provide a friendly reminder to practitioners that the discriminant functions for live birds are limited to being used when a live bird is in the hand, since it is not possible to obtain actual values of the colormetrics or morphometrics from afar. The field sexing technique was tested on a sample of breeding adults at one site and does not capture the potential temporal variation (between seasons and across years) in bill coloration, back coloration, or morphological measurements within individuals or between sites. We assume that this technique could be useful during the non-breeding season because American Oystercatchers achieve adult plumage in year two but this remains to be tested. No difference in plumage has been described between breeding and non-breeding adults (American Oystercatcher Working Group *et al.* 2020). The visual sexing method is only applicable to adults, since there is no known sexual dimorphism in coloration or size for juveniles.

## Future Research Directions

Since birds can also see in the ultraviolet (UV) spectrum, a first step would be to map how the American Oystercatchers perceive the color difference in avian tetrahedral colorspace (Stoddard and Prum 2008). As a test, we shone a UV light on the skins in the museum. No apparent UV reflectance occurred. This was unsurprising, since porphyrins (brown-colored pigments) rapidly degrade after feather integration, especially when exposed to light and heat

(Hasegawa *et al.* 2024). This test reinforces that it might be fruitful to check for fluorescence in live birds, especially if American Oystercatchers are more nocturnal than previously described (K. Goodenough pers. comm.). We did not attempt to check the live birds for UV reflectance since a) our focus was to develop a sexing technique for field workers; b) we wanted to minimize the handling time; and c) our capture method occurred during the day, so taking UV photography would have required the use of expensive additional UV photography equipment, and either capturing the birds at night or placing the birds in a black box for more photos, which could have increased their stress.

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accommodation. We appreciate the feedback provided for this manuscript from the reviewers. All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010). Work was completed under the authorization of the U.S. Geological Survey Bird Banding Laboratory under Federal Master Permit #21567, U.S. Fish and Wildlife Service Chincoteague National Wildlife Refuge Research and Monitoring Special Use Permits #24-006, and Trent University Animal Care Committee Animal Care Use Approval #27856. The capture and banding of American Oystercatchers in this study followed protocols developed by the American Oystercatcher Working Group.

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# Supplementary Materials

**Supplementary Table S7.1. Classification coefficients for live male and female American Oystercatchers (*Haematopus palliatus*) based on colormetrics and morphometrics. Birds were captured in 2024 at Assateague Island and Assawoman Island, Virginia, U.S.A. (*n* = 13 females, 14 males).**

| Trait | Classification Coefficients for Males | Classification Coefficients for Females |
|---|---|---|
| Intercept | -2,248.13 | -2,468.08 |
| Bill hue | 2,466.81 | 3,257.20 |
| Bill value | 870.38 | 956.35 |
| Back saturation | -290.11 | -277.64 |
| Bill saturation | 217.40 | 220.98 |
| Back hue | 191.92 | 87.43 |
| Back value | 144.71 | 208.24 |
| Wing chord length | 11.65 | 11.90 |
| Tarsus length | 5.55 | 5.90 |
| Bill length | 3.89 | 4.10 |
| Mass | 1.11 | 1.25 |

**Supplementary Table S7.2. One-way ANOVA for only colormetrics of live American Oystercatchers (*Haematopus palliatus*) (*n* = 27) in 2024 at Assateague Island and Assawoman Island, Virginia, U.S.A. Eta-squared values represent effect sizes. F statistics and their associated degrees of freedom (DF) and *P* value are presented along with Bayes factor.**

| | Eta-squared | Wilks Lambda | F | DF | Residual DF | *P* | Bayes factor$_a$ | Bayes factor$_b$ |
|---|---|---|---|---|---|---|---|---|
| Discriminant function | 0.66 | 0.35 | 47.52 | 1 | 25 | <0.001 | 32,601.16 | 0 |
| Bill hue (degrees) | 0.55 | 0.45 | 30.71 | 1 | 25 | <0.001 | 1,614.63 | 0.001 |
| Bill value (%) | 0.36 | 0.64 | 13.85 | 1 | 25 | 0.001 | 30.49 | 0.03 |
| Bill saturation (%) | 0.07 | 0.93 | 1.94 | 1 | 25 | 0.176 | 0.73 | 1.37 |
| Back value (%) | 0.26 | 0.74 | 8.98 | 1 | 25 | 0.006 | 7.44 | 0.13 |
| Back saturation (%) | 0.15 | 0.85 | 4.29 | 1 | 25 | 0.049 | 1.65 | 0.61 |
| Back hue (degrees) | 0.16 | 0.84 | 4.61 | 1 | 25 | 0.042 | 1.84 | 0.54 |

[a]Bayes Factor for alternate hypothesis vs. null hypothesis
[b]Bayes Factor for null hypothesis vs. alternate hypothesis

**Supplementary Table S7.3. Classification coefficients for live male and female American Oystercatchers (*Haematopus palliatus*) based on colormetrics. Birds were captured in 2024 at Assateague Island and Assawoman Island, Virginia, U.S.A. (*n* = 13 females, 14 males).**

| Trait | Classification Coefficients for Males | Classification Coefficients for Females |
|---|---|---|
| Intercept | -109.35 | -132.87 |
| Bill hue | 165.64 | 777.42 |
| Bill value | 276.98 | 336.79 |
| Bill saturation | 218.00 | 216.50 |
| Back value | 109.97 | 154.72 |
| Back saturation | 39.42 | 53.62 |
| Back hue | -10.15 | 90.63 |

**Supplementary Table S7.4. One-way ANOVA for colormetrics and morphometrics of American Oystercatcher (*Haematopus palliatus*) skins (*n* = 23) housed at the Royal Ontario Museum based in Toronto, Ontario, Canada and collected from 1975–1982 in Virginia, South Carolina, and Florida, U.S.A. Eta-squared values represent effect sizes. F statistics and their associated degrees of freedom (DF) and *P* value are presented along with Bayes factor.**

| | Eta-squared | Wilks Lambda | F | DF | Residual DF | *P* | Bayes factor$_a$ | Bayes factor$_b$ |
|---|---|---|---|---|---|---|---|---|
| Discriminant function | 0.58 | 0.42 | 28.43 | 1 | 21 | <0.001 | 586.38 | 0.002 |
| Back value (%) | 0.33 | 0.67 | 10.13 | 1 | 21 | 0.004 | 9.27 | 0.11 |
| Back saturation (%) | 0.27 | 0.73 | 7.61 | 1 | 21 | 0.012 | 4.55 | 0.22 |
| Bill length (mm) | 0.26 | 0.74 | 7.31 | 1 | 21 | 0.013 | 4.16 | 0.24 |
| Back hue (degrees) | 0.17 | 0.83 | 4.26 | 1 | 21 | 0.052 | 1.64 | 0.61 |
| Mass (g) | 0.06 | 0.94 | 1.27 | 1 | 21 | 0.272 | 0.61 | 1.63 |
| Tarsus length (mm) | 0.03 | 0.97 | 0.67 | 1 | 21 | 0.421 | 0.5 | 2.01 |
| Wing chord length (mm) | 0.03 | 0.97 | 0.61 | 1 | 21 | 0.445 | 0.49 | 2.06 |

[a]Bayes Factor for alternate hypothesis vs. null hypothesis
[b]Bayes Factor for null hypothesis vs. alternate hypothesis

**Supplementary Table S7.5. Classification coefficients for male and female American Oystercatcher (*Haematopus palliatus*) skins based on colormetrics and morphometrics. Skins (*n* = 23) were housed at the Royal Ontario Museum based in Toronto, Ontario, Canada and collected from 1975–1982 in Virginia, South Carolina, and Florida, U.S.A.**

| Trait | Classification Coefficients for Males | Classification Coefficients for Females |
|---|---|---|
| Intercept | -1,422.37 | -1,509.21 |
| Back value | 13,517.24 | 14,003.11 |
| Back hue | 8,802.94 | 8,868.32 |
| Back saturation | 471.20 | 472.41 |
| Bill length | 5.25 | 5.64 |
| Wing chord length | 4.02 | 4.14 |
| Tarsus length | 2.91 | 3.01 |
| Mass | -0.05 | -0.05 |



**Supplementary Figure S7.1. CEA was a male American Oystercatcher (*Haematopus palliatus*) with a short bill and dark back plumage appearing more black than brown. His female mate was unbanded and had a longer bill and lighter back plumage appearing more brown than black. Photo credit: Trevor MacLaurin.**

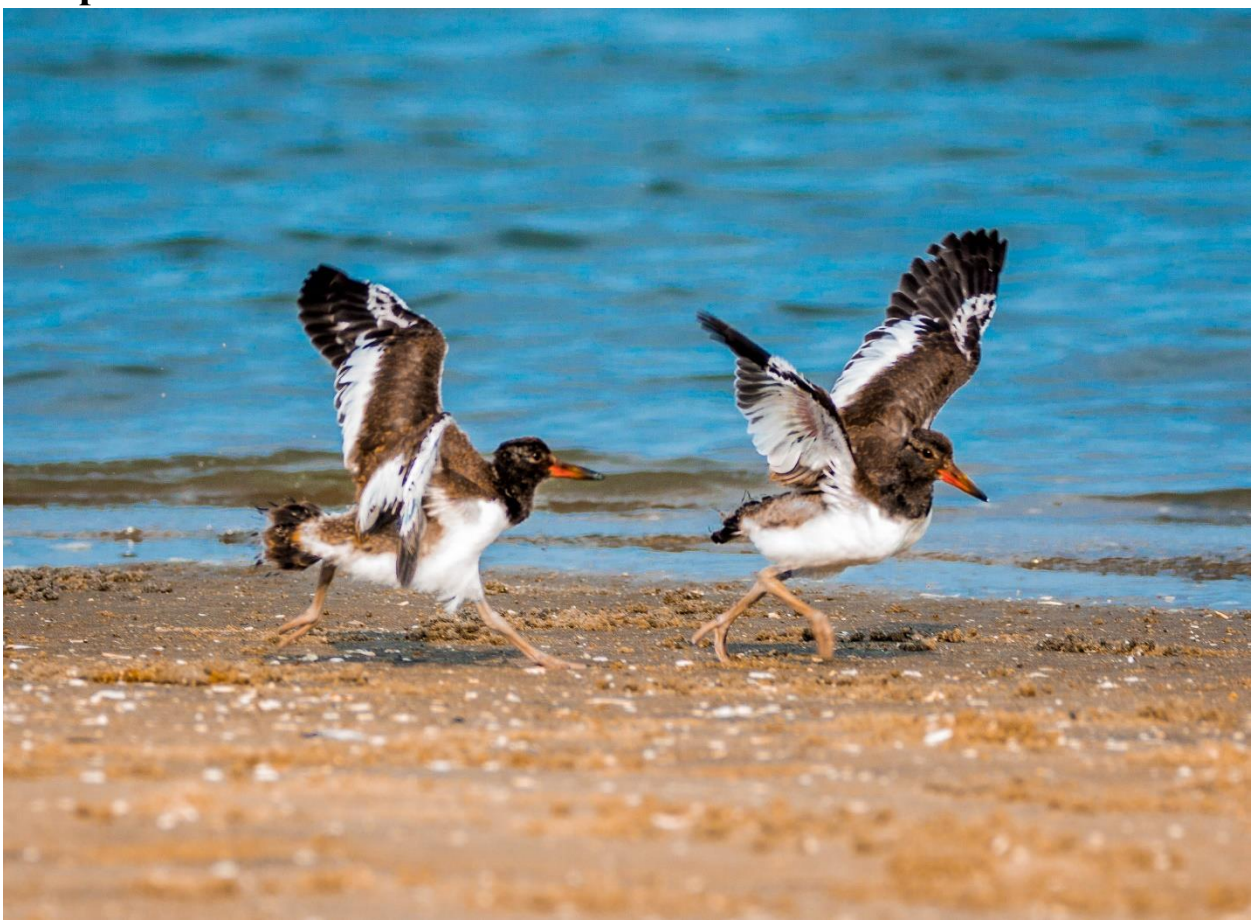


**Supplementary Figure S7.2. CLA was a male American Oystercatcher (*Haematopus palliatus*) with a dark red short bill that had dark back plumage appearing more black than brown. Photo credit: Randy Reed.**



**Supplementary Figure S7.3. CER was a female American Oystercatcher (*Haematopus palliatus*) with a long bill and lighter back plumage appearing more brown than black. Photo credit: Nicole Ball.**

# Chapter 8 – General Discussion



American Oystercatcher fledglings ready to take off. Photo credit: Ken King.

## Summary

This thesis furthers our understanding of the role of diet specialization in American Oystercatchers and its effects on fitness components, ecological niches, and relationships with other shorebirds. In Chapter 2, I documented diet specialization for the first time in this species on a barrier island in Virginia, U.S.A. Two distinct diet groups, mole crab specialists and generalists each occupied their own foraging niche in terms of diet composition and foraging habitat space use. I drew on optimal foraging theory to show that birds that specialize and feed on mole crabs follow predictions of optimal foraging theory by selecting prey that is the least energetically costly to travel to, while providing a high food reward. Similarly, birds with generalist diets follow optimal foraging theory by choosing the most profitable prey species, the mussel, and incorporating that into their diets. Diet specialization did not impact food profitability, adult body condition, handling time of mole crabs, chick provisioning rates, or chick energy intake rates. I found evidence for a new mechanism that drives specialization. Energetics best explained diet specialization, where specialists expended 42% more energy one-way reaching distant mussel habitat compared to nearby mole crab habitat.

In Chapter 3, I showed that food (including diet, foraging distance, and food profitability) did not limit breeding success at the study site over three years. Instead, nest survival was driven by interannual variation in predator and storm activity. Chick survival was driven by age of the chick, where older chicks had lower survival rates because they likely tended to hide less and provided a larger food reward for predators.

In Chapter 4, I described a new specialized foraging behavior on mole crabs in American Oystercatchers in Virginia, U.S.A. and Hudsonian Whimbrels in Oregon, U.S.A. Both species strip eggs from mole crabs and discard the carapaces. Larger female mole crabs are targeted for

egg stripping. For American Oystercatchers, egg stripping does not significantly increase handling time of mole crabs. I inferred that shorebirds follow a digestion rate model, and perform egg stripping at the end of foraging bouts, as they approach a digestive bottleneck. Consuming only the eggs takes up less volume in the stomach and likely lets birds continue to forage for longer before taking a digestive break. This research adds to the understanding of foundational foraging ecology of shorebirds.

In Chapter 5, I documented a foraging commensalism that American Oystercatchers support for Ruddy Turnstones and Sanderlings. I provided evidence for a non-random association between these shorebird species. By stripping the eggs from mole crabs and discarding the carapaces, this provides an easily accessible food item that helps fuel the long-distance migrations for other shorebirds. By following American Oystercatchers and eating the discarded carapaces, Ruddy Turnstones benefit by increasing their mole crab consumption by 15 times and reducing their foraging effort by 46%, while Sanderlings benefit by increasing their mole crab consumption by 1.4 times. This research demonstrates the interconnectedness of shorebirds and reiterates the importance of protecting mole crab beach habitat to provide food for multiple species.

In Chapter 6, I added to the global oystercatcher literature and the understanding of foraging niches in the context of competition. This chapter drew on niche theory to explain the similarity in diets between male and female American Oystercatchers. In contrast to most oystercatcher species that occupy distinct foraging niches so the sexes can coexist, American Oystercatchers show 99% identical diets between the sexes. A lack of niche partitioning for American Oystercatchers likely occurs due to relaxed competitive pressure stemming from low breeding densities.

In Chapter 7, I provided a practical tool for visually distinguishing the sexes from a distance in the field. This tool relies on a combination of sexual dimorphism in bill coloration, back plumage coloration, bill length, and overall body size. Females tend to have longer lighter orange-colored bills, lighter brown backs, and larger overall body size. In contrast, males tend to have shorter darker red bills, darker backs, and smaller overall body size. The sexes can be reliably distinguished with 98% classification accuracy, as confirmed by DNA from breast feathers.

## Conservation Management Implications

In Chapter 2, I showed that the existence of some individuals who specialize and feed on mole crabs, outlines the importance of protecting not only the nesting habitat, but also oceanside foraging habitat where mole crabs live, to help protect the American Oystercatcher. This has the added benefit of keeping mole crab populations healthy for other migratory shorebirds that also feed on this prey species including Red Knots, Ruddy Turnstones, Sanderlings, and Willets. In Chapter 4, I showed the importance of protecting mole crabs for other shorebird species. The foraging commensalism that American Oystercatchers support reduces foraging costs for Ruddy Turnstones and Sanderlings and helps fuel their migrations.

In Chapter 3, I showed that at the study site, conservation management should focus on increasing beach elevation to reduce nesting loss to overwash and flooding, and mammalian predator control efforts should continue. Additionally, more effort exploring the potential for avian predator harassment might help increase chick survival.

In Chapter 7, I provided a tool that can enhance data collection for American Oystercatcher conservation practitioners throughout their range in North, Central, and South America. The visual sexing technique allows sex-specific behaviors to be recorded including

foraging, parental care, defense, and territoriality, which can shed light on factors limiting breeding success, and more broadly provide information about their mating systems, and habitat space use.

## Future Research

The existence of diet specialization introduces many questions that warrant further investigation. When presenting this work to colleagues, three separate individuals belonging to the American Oystercatcher Working Group suspected that they also have American Oystercatchers that specialize on mole crabs in other parts of the state of Virginia, and in the state of North Carolina, U.S.A. It would be beneficial to document the extent of diet specialization throughout the species range, to identify if restrictions from public recreational access to oceanside foraging areas, where mole crabs live, should be considered for other areas. Additionally, the potential impact of recreational activities (e.g., surf fishermen who harvest mole crabs as bait) on mole crab populations should be investigated.

I lacked historical data on diet to understand if diet specialization is passed down between generations. Long-term studies across generations could help answer this question. This is of particular note, since learning to open hard-shelled bivalves like oysters, mussels, clams, and razor clams takes skill (Hand *et al.* 2010). If chicks of mole crab specialist parents, specialize on mole crabs themselves, they might lack a parental role model to teach them how to open hard-shelled prey. This has survival implications at the individual level and population as a whole for the subgroup of diet specialists. If a disease or cold weather impacts mole crab populations on the Western Atlantic Coast in the future, diet specialization could hinder an individual's plasticity to change food sources compared to diet generalists.

Diet specialization can occur at short or long temporal scales (van de Pol *et al.* 2010; Catry *et al.* 2014). It is unknown if mole crab specialists remain specialists year-round. Future research could answer this question by following mole crab specialists to their non-breeding grounds and doing detailed behavioral observations on what they eat.

For Eurasian Oystercatchers, diet specialization can reshape the bill tip in as little as four weeks (Swennen *et al.* 1983). This acts as a positive feedback loop, where the bill tip shape of an individual directs which food source it is better suited to eat (Swennen *et al.* 1983). The relationship between diet specialization and bill feeding morphology is unknown for American Oystercatchers. If such a relationship exists, then bill tip shape might be used as a proxy for determining diet, as per van de Pol *et al.* (2009) with Eurasian Oystercatchers.

Even though food was not a limiting factor for nest or chick survival at the current study site for a few years, future research should still explore the role of diet and foraging factors in breeding success at other locations. Vitale *et al.* (2022) found that American Oystercatcher chicks in Florida, U.S.A. were dying of starvation due to die offs of oyster reefs (Frederick *et al.* 2016). Diet remains relatively under-studied for this species, so more studies across a range of study sites that vary in prey composition and availability might provide a better holistic understanding of the role of diet generally and identify site-specific variation.

Since avian predators were one of the top suspected culprits of chick depredation at the study site, future research should explore effective methods for deterring avian gull depredation. Avian predators are often suspected as a top factor limiting American Oystercatcher breeding success. However, the exact contribution of avian predators to egg loss and chick loss has been difficult to record and quantify because recording nest or brood failures to avian depredation often relies on circumstantial evidence like pierced eggs, and for chicks, most go missing without

knowing the cause (Schulte and Simons 2015; Call *et al.* 2025). Efforts to date to quantify avian depredation have had low success. Game cameras often miss capturing the event (Anderson 2014). Behavioral observations directly witnessing a predation event provide concrete evidence, but these events are rare to be witnessed. Even when watching breeding American Oystercatchers over the course of hundreds of hours across my five field seasons at the study site, I only directly witnessed two chick mortalities due to avian depredation by Great Black-backed Gulls. Thus, it is crucial to understand if avian predators are as large a threat as suspected. To do this, future research should quantify the percent composition that shorebirds make up in gull diets. This type of study could be done with direct behavioral observations focused on the avian predators of their foraging behaviors, stomach content analysis, fecal samples and DNA metabarcoding. Many conservation organizations that do predator control efforts to benefit nesting American Oystercatchers, focus on trapping mammalian predators. This proposed future research could illuminate if predator control efforts should be re-allocated with a larger emphasis on avian predators. If avian predators are found to have a large role limiting breeding success of American Oystercatchers, it would also be interesting to test how avian predators might create a landscape of fear (Zanette 2019) and influence nest site selection choices. On the other hand, if avian predators are less involved in mortality of nests and chicks, this can allow conservation professionals to redirect their efforts to other targets that limit breeding success.

As for visually sexing American Oystercatchers, it would be helpful to know if this technique can be used for other oystercatcher species to reduce the stress and handling time of the birds and determine sex more quickly without time delays for processing DNA. Colleagues

in the UK are trialling the technique described here to see if it is effective for Eurasian Oystercatchers.

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