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Source: Waterbirds, 47(1) : 1-12

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.047.0105

Diet Overlaps Between the Sexes in Breeding American Oystercatchers

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Abstract.—Sexual dimorphism in bill size can lead to sex-specific foraging strategies. All 12 extant species of oystercatchers (*Haematopus spp.*) 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 the 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. *Received 19 Nov 2023, accepted 22 Apr 2024.*

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

Waterbirds 47(1): 1–12, 2024

Diet specialization in a population can develop if some individuals eat prey in significantly different proportions than others (Sargeant 2007). 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 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.

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

Table 1. Summary of Oystercatcher studies finding intersexual niche partitioning or niche overlap in diet.

Species	Location	Niche Partitioning	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
African Black Oystercatcher	Marcus Island, South Africa	Y	2 breeding pairs	Foraging observations	Correspondence analysis	There was a 20% difference in the proportion of limpets taken by each sex.	Hockey and Underhill 1984
African Black 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 Black Oystercatcher	Marcus Island, South Africa	N	43 foraging observations on females and 31 foraging observations 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

Continued

Table 1.— Continued

Species	Location	Niche Partitioning	N	Method	Niche index	Findings	Source
African Black 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

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 (*Haematopus ostralegus*) (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 (Peters 2023). 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 (2023b) Band Database.

Across the study years, we conducted 10-minute observations on the same banded and unbanded adults of known sex who were foraging, using both 10×50 binoculars and 60× 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, 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 2011) 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* $K^2_1 = 0.84$, $P = 0.36$).

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* $K^2_1 = 2.66$, $P = 0.10$; mussels: *Bartlett's* $K^2_1 = 1.60$, $P = 0.21$; clams: *Bartlett's* $K^2_1 = 0.001$, $P = 0.97$), 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 ($\bar{x} = 89.17 \pm$ SE 0.59 mm, $n = 12$) than males ($\bar{x} =$

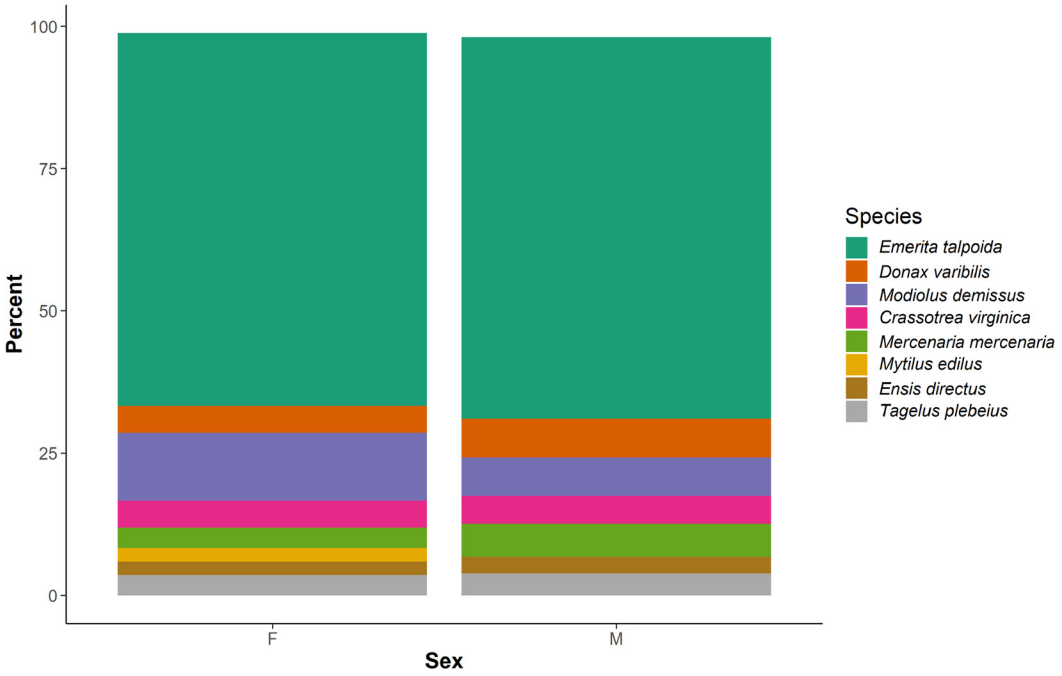

Figure 1. Diet composition for male and female American Oystercatchers. Species are mole crab (*Emerita talpoida*), coquina (*Donax varibilis*), Atlantic ribbed mussel (*Modiolus demissus*), Eastern oyster (*Crassotrea virginica*), Northern quahog clam (*Mercenaria mercenaria*), blue mussel (*Mytilus edilus*), Atlantic razor clam (*Ensis directus*), and stout tagelus (*Tagelus plebeius*).

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. 1, *Pianka's* index = 0.99, *95% CI* [0.07, 0.99], *lower-tail P* = 0.04, *upper-tail P* = 0.96, *standard effect size* = 2.74, Fig. S1A, Fig. S1B). 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

Table 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}	0.09	−0.18, 2.14
Mole crabs (*Emerita talpoida*)	4.11 ± 0.25	161	3.95 ± 0.20	131	-1.41_{288}	0.16	−0.37, 0.06
Mussels (*Modiolus demissus*)	5.38 ± 0.35	53	5.95 ± 0.39	62	1.72_{113}	0.09	−0.09, 1.23
Clams (*Mercenaria mercenaria*)	5.70 ± 0.35	19	4.62 ± 0.35	18	-2.02_{35}	0.05	−2.16, 0.003

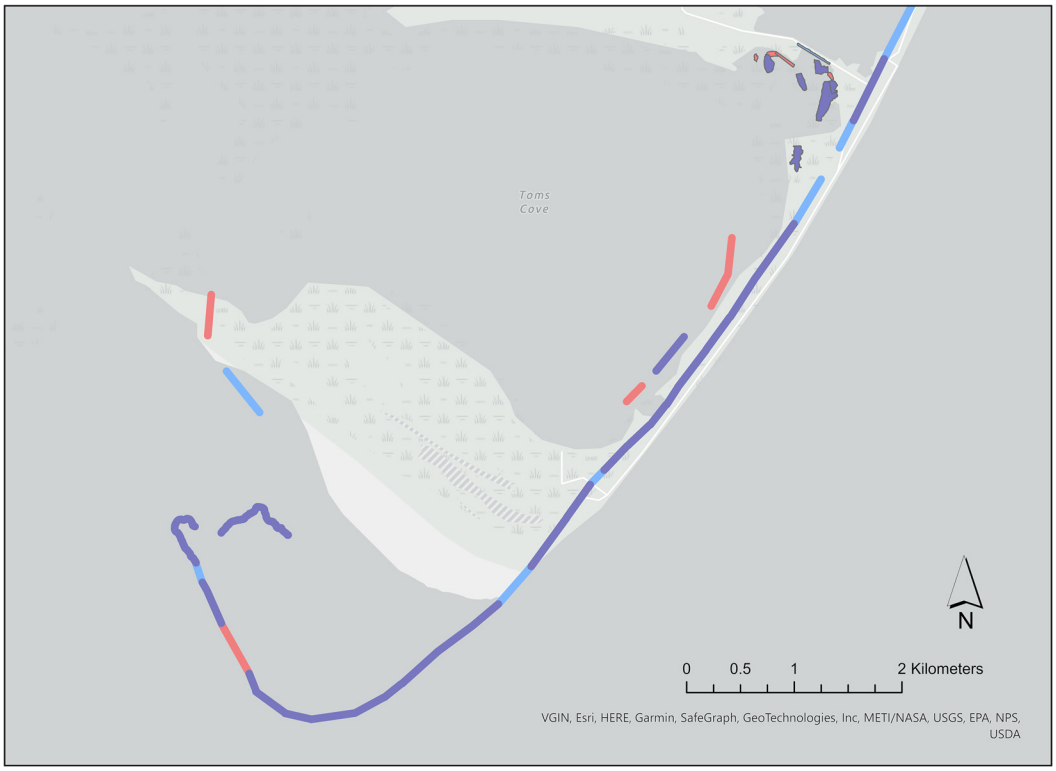

Figure 2. Map of feeding areas used by females in red, males in blue and both sexes in purple of American Oystercatchers on Assateague Island, Virginia, U.S.A.

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 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. 2 and Fig. 3). There was no consistent pattern in feeding areas used by a single sex.

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 1). Female Eurasian Oystercatchers tend to be worm specialists, while males tend

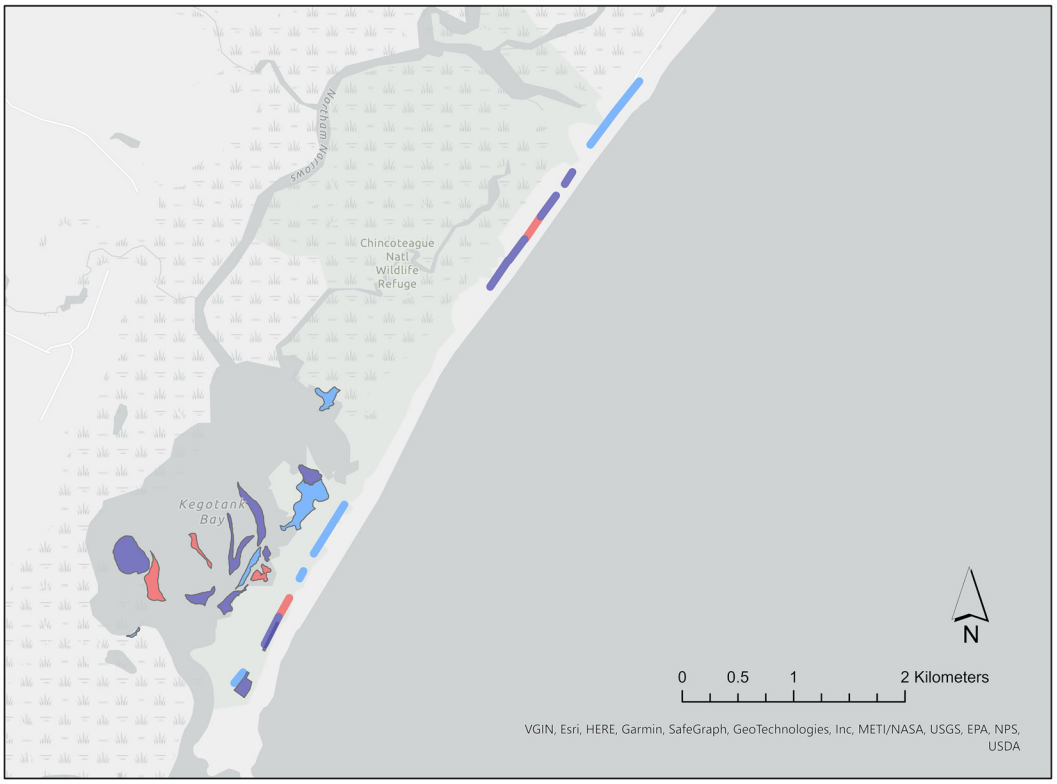

Figure 3. Map of feeding areas used by females in red, males in blue and both sexes in purple of American Oystercatchers on Assawoman Island, Virginia, U.S.A.

to be bivalve specialists (Durrell *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 Black Oystercatchers (*Haematopus moquini*) (Coleman and Hockey 2008; Kohler *et al.* 2014; Table 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 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 Black 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 amongst African Black 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 amongst 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 Goss-Custard 1992; Schwemmer *et al.* 2016), African Black 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. 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.

ACKNOWLEDGEMENTS

This research received funding support from the Natural Sciences and Engineering Council of Canada (NSERC) grants to E. Nol and scholarships to L. A. Brown, the Ontario Government, Trent University, the American Ornithological Society, the Virginia Society of Ornithology, the Waterbirds Society, the Wilson

Ornithological Society, Wader Quest, and private donors. Thank you to our dedicated technicians Trevor MacLaurin, Casey Manera, Katie Vartenigian, Samuel Ruano, Collin Kelly, and volunteers for their field support. We thank the U.S. Fish and Wildlife Service team at Chincoteague National Wildlife Refuge for providing site access, and research coordination. We thank the American Oystercatcher Working Group for their generosity in sharing knowledge. A special thanks to Kate Goodenough, Lindsay Addison, Alex Wilke, Pamela Denmon, Kevin Holcomb, and Katie Oliver for their guidance. Thank you to Roe Terry for use of his hand-crafted decoys. Many thanks to Justin Barker for statistical support. A whole-hearted appreciation to the Risley family for their generosity in providing housing. We appreciate the feedback provided for this manuscript from two anonymous 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 #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. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Department of the Interior, Fish and Wildlife Service.

LITERATURE CITED

American Oystercatcher Working Group. 2023a. Banding and re-sighting: How to read band codes. The American Oystercatcher Working Group. https://amoywg.org/banding-re-sighting/reading-band-codes/

American Oystercatcher Working Group. 2023b. American Oystercatcher Band Database. Audubon North Carolina, Wilmington, North Carolina, U.S.A. https://ancperch.org/amoy/

Andres, B. A. and G. A. Falxa. 2020. Black Oystercatcher (*Haematopus bachmani*), *v. 1.0. In* Birds of the World (A. F. Poole and F. B. Gill, Eds.). Cornell Lab of Ornithology, Ithaca, New York, U.S.A. doi:10.2173/bow.blkoys.01

Aplin, L. M. and A. Cockburn. 2012. Ecological selection and sexual dimorphism in the Sooty Oystercatcher (*Haematopus fuliginosus*). Austral Ecology 37: 248–257. doi:10.1111/j.1442-9993.2011.02263.x

Araújo, M. S., D. I. Bolnick and C. A. Layman. 2011. The ecological causes of individual specialization. Ecology Letters 14: 948–958. doi:10.1111/j.1461-0248.2011.01662.xpub-id

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103: 458–473. doi:10.1111/j.1474-919X.1963.tb06766.x

Baker, A. J. 1972. Systematics and affinities of New Zealand Oystercatchers. Ph.D. Dissertation, University of Canterbury, Canterbury, New Zealand.

Boal, C. W. and R. W. Mannan. 1996. Prey sizes of male and female Northern Goshawks. The Southwestern Naturalist 41: 355–358.

Boates, J. S. and J. D. Goss-Custard. 1992. Foraging behaviour of Oystercatchers (*Haematopus ostralegus*) specializing on different species of prey. Canadian Journal of Zoology 70: 2398–2404. doi:10.1139/z92-321

Bolnick, D. I., T. Ingram, W. E. Stutz, L. K. Snowberg, O. L. Lau and J. S. Paull. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proceedings of the Royal Society B: Biological Sciences 277: 1789–1797. doi:10.1098/rspb.2010.0018

Brush, J. M., A. C. Schwarzer and P. C. Frederick. 2017. Importance and function of foraging and roost habitat for wintering American Oystercatchers. Estuaries and Coasts 40: 286–295. doi:10.1007/s12237-016-0137-6

Carney, B., D. Tessler, H. Coletti, J. M. Welker and D. Causey. 2023. Stable isotope-determined diets of Black Oystercatchers *Haematopus Bachmani* in the Northern Gulf of Alaska. Marine Ornithology, 51: 125–135.

Catry, T., J. A. Alves, J. A. Gill, T. G. Gunnarsson and J. P. Granadeiro. 2014. Individual specialization in a shorebird population with narrow foraging niche. Acta Oecologica 56: 56–65. doi:10.1016/j.actao.2014.03.001

Coleman, R. A. and P. A. R. Hockey. 2008. Effects of an alien invertebrate species and wave action on prey selection by African Black Oystercatchers (*Haematopus moquini*). Austral Ecology 33: 232–240. doi:10.1111/j.1442-9993.2008.01864.x

Czeszczewik, D. 2010. Wide intersexual niche overlap of the specialized White-backed Woodpecker (*Dendrocopos leucotos*) under the rich primeval stands in the Białowieża Forest, Poland. Ornis Polonica 51: 241–251.

Drent, R., G. F. Van Tets, F. Tompa and K. Vermeer. 1964. The breeding birds of Mandarte Island, British Columbia. Canadian Field-Naturalist 78: 208–263. doi:10.5962/p.342193

Durell, S. E. A. V. 2003. The implications for conservation of age-and sex-related feeding specializations in shorebirds. Wader Study Group Bulletin 100: 35–39.

Durell, S. E. L. V. D., J. D. Goss-Custard and R. W. Caldow. 1993. Sex-related differences in diet and feeding method in the Oystercatcher (*Haematopus ostralegus*). Journal of Animal Ecology 62: 205–215.

Ens, B. J., F. J. Weissing and R. H. Drent. 1995. The despotic distribution and deferred maturity: two sides of the same coin. The American Naturalist 146: 625–650. doi:10.1086/285818

Environmental Systems Research Institute (ESRI). 2011. ArcGIS Pro v. 3.2. Environmental Systems Research Institute, Redlands, California, U.S.A.

Fair, J., E. Paul and J. Jones (Eds.). 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C., U.S.A.

Frederick, P., N. Vitale, B. Pine, J. Seavey and L. Sturmer. 2016. Reversing a rapid decline in oyster reefs: effects of durable substrate on oyster populations, elevations and aquatic bird community composition. Journal of Shellfish Research 35: 359–367. doi:10.2983/035.035.0210

Goss-Custard, J. D., R. W. G. Caldow and R. T. Clarke. 1992. Correlates of the density of foraging Oystercatchers (*Haematopus ostralegus*) at different population sizes. Journal of Animal Ecology 61: 159–173.

Gotelli, N. J., E. M. Hart and A. M. Ellison. 2015. EcoSimR: Null model analysis for ecological data. R package v. 0.1.0. University of Vermont, Burlington, Vermont, U.S.A. http://github.com/gotellilab/EcoSimR, accessed 24 October 2023.

Hall, L. A., S. E. De La Cruz, I. Woo, T. Kuwae and J. Y. Takekawa. 2021. Age- and sex-related dietary specialization facilitate seasonal resource partitioning in a migratory shorebird. Ecology and Evolution 11: 1866–1876. doi:10.1002/ece3.7175

Hockey, P. A. R. and L. G. Underhill. 1984. Diet of the African Black Oystercatcher (*Haematopus moquini*) on rocky shores: spatial, temporal and sex-related variation. African Zoology 19: 1–11.

Hockey, P., G. M. Kirwan and P. F. D. Boesman. 2021. African Oystercatcher (*Haematopus moquini*), v. 1.0. *In* Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana, Eds.). Cornell Lab of Ornithology, Ithaca, New York, U.S.A. doi:10.2173/bow.euroys1.01.

Hulscher, J. and B. J. Ens. 1992. Is the bill of the male Oystercatcher a better tool for attacking mussels than the bill of the female? Netherlands Journal of Zoology 42: 85–100. doi:10.1163/156854292X00044

Isdell, R. E., D. M. Bilkovic and C. Hershner. 2018. Shorescape-level factors drive distribution and condition of a salt marsh facilitator (*Geukensia demissa*). Ecosphere 9: e02449. doi:10.1002/ecs2.2449

Kennedy, P. L. and D. R. Johnson. 1986. Prey-size selection in nesting male and female Cooper's Hawks. The Wilson Bulletin 98: 110–115.

Kohler, S. A., M. Connan, J. Kolasinski, Y. Cherel, C. D. McQuaid and S. Jaquemet. 2014. Trophic overlap between sexes in the dimorphic African Black Oystercatcher foraging on an alien mussel. Austral Ecology 39: 567–578. doi:10.1111/aec.12117

Kohler, S., B. Bonnevie, C. McQuaid and S. Jaquemet. 2009. Foraging ecology of an endemic shorebird, the African Black Oystercatcher (*Haematopus moquini*) on the south–east coast of South Africa. Estuarine, Coastal and Shelf Science 84: 361–366. doi:10.1016/j.ecss.2009.03.035

Lauro, B. and E. Nol. 1995. Feeding behavior, prey selection and bill size of Pied and Sooty Oystercatchers in Australia. The Wilson Bulletin 107: 629–640.

Layman, C. A., J. P. Quattrochi, C. M. Peyer and J. E. Allgeier. 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology Letters 10: 937–944. doi:10.1111/j.1461-0248.2007.01087.x

Maillet, O. R., E. Nol and Y. Zharikov. 2023. Apparent adult annual survival and population trends of Black Oystercatcher (*Haematopus bachmani*) breeding in British Columbia, Canada. The Wilson Journal of Ornithology 135: 276–283. doi:10.1676/22-00095

Morten, J. M., R. A. Burrell, T. D. Frayling, A. N. Hoodless, W. Thurston and L. A. Hawkes. 2022. Variety in responses of wintering Oystercatchers (*Haematopus ostralegus*) to near-collapse of their prey in the Exe Estuary, United Kingdom. Ecology and Evolution 12: e9526. doi:10.1002/ece3.9526

Nebel, S. and G. J. Thompson. 2011. The evolution of sexual bill-size dimorphism in shorebirds: a morphometric test of the resource partitioning hypothesis. Evolutionary Ecology Research 13: 35–44.

Nol, E. 1985. Sex roles in the American Oystercatcher. Behaviour 95: 232–260. doi:10.1163/156853985X00145

Olsen, J. 2013. Reversed sexual dimorphism and prey size taken by male and female raptors: a comment on Pande and Dahanukar (2012). Journal of Raptor Research 47: 79–81. doi:10.3356/JRR-12-48.1

Peters, K. 2023. Measurements. American Oystercatcher Working Group. https://amoywg.org/american-oystercatcher/measurements/

Peterson, C. H., M. J. Bishop, G. A. Johnson, L. M. D'Anna and L. M. Manning. 2006. Exploiting beach filling as an unaffordable experiment: benthic intertidal impacts propagating upwards to shorebirds. Journal of Experimental Marine Biology and Ecology 338: 205–221. doi:10.1016/j.jembe.2006.06.021

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53–74. doi:10.1146/annurev.es.04.110173.000413

Pulley, B. 2008. *Emerita talpoida* and *Donax variabilis* distribution throughout crescentic formations; Pea Island National Wildlife Refuge. Ph.D. Dissertation, College of Charleston, Charleston, South Carolina, U.S.A.

Roodenrijs, H. 2023. Geographic and intersexual variation in morphology and diet of Black Oystercatchers (*Haematopus bachmani*). M.S. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

R Core Team (2023). R: a language and environment for statistical computing v. 4.3.1. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

Rutten, A. L., K. Oosterbeek, B. J. Ens and S. Verhulst. 2006. Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in Oystercatchers. Behavioral Ecology 17: 297–302. doi:10.1093/beheco/arj029

Sanders, F., M. Spinks and T. Magarian. 2013. American Oystercatcher winter roosting and foraging ecology at Cape Romain, South Carolina. Wader Study Group Bulletin 120: 128–133.

Sargeant, B. L. 2007. Individual foraging specialization: niche width versus niche overlap. Oikos 116: 1431–1437. doi:10.1111/j.2007.0030-1299.15833.x

Schulte, S. 2023. Results of 2023 winter AMOY survey. American Oystercatcher Working Group 2023

Annual Meeting – Meeting Notes. Plymouth, Massachusetts. https://amoywg.org/wp-content/uploads/2023/12/AMOYWG2023-Notes-Day1.pdf, accessed 8, March 2024.

Schwemmer, P., F. Güpner, S. Adler, K. Klingbeil and S. Garthe. 2016. Modelling small-scale foraging habitat use in breeding Eurasian Oystercatchers (*Haematopus ostralegus*) in relation to prey distribution and environmental predictors. Ecological Modelling 320: 322–333. doi:10.1016/j.ecolmodel.2015.10.023

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. The Condor 68: 113–151. doi:10.2307/1365712

Smith, R. S., S. Hogan, K. N. Tedford, B. Lusk, M. A. Reidenbach and M. C. Castorani. 2022. Long-term data reveal greater intertidal oyster biomass in predicted suitable habitat. Marine Ecology Progress Series 683: 221–226. doi:10.3354/meps13949

Svanbäck, R. and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B: Biological Sciences 274: 839–844. doi:10.1098/rspb.2006.0198

Tessler, D. F., J. A. Johnson, B. A. Andres, S. Thomas and R. B. Lanctot. 2014. A global assessment of the conservation status of the Black Oystercatcher (*Haematopus bachmani*). International Wader Studies 20: 83–96.

Tuckwell, J. and E. Nol. 1997. Foraging behaviour of American oystercatchers in response to declining prey densities. Canadian Journal of Zoology 75: 170–181. doi:10.1139/z97-024

Verhulst, S., K. Oosterbeek, A. L. Rutten and B. J. Ens. 2004. Shellfish fishery severely reduces condition and survival of Oystercatchers despite creation of large marine protected areas. Ecology and Society 9: 17–26. doi:10.5751/ES-00636-090117

Vitale, N., J. Brush and A. Powell. 2021. Loss of coastal islands along Florida's Big Bend Region: implications for breeding American Oystercatchers. Estuaries and Coasts 44: 1173–1182. doi:10.1007/s12237-020-00811-3

Vitale, N., J. Brush and A. Powell. 2022. Factors limiting reproductive success of American Oystercatchers (*Haematopus palliatus*) in Florida's Southern Big Bend Region. Waterbirds 44: 449–462. doi:10.1675/063.044.0406

Wanink, J. H. and L. Zwarts. 1996. Can food specialization by individual Oystercatchers (*Haematopus ostralegus*) be explained by differences in prey specific handling efficiencies? Ardea-Wageningen 84: 177–198.

Wilke, A. 2021. 2020 Virginia AMOY update. American Oystercatcher Working Group 2020(ish) Annual Meeting - Video. Virtual. https://amoywg.org/amoy-working-group/2020-ish-meeting/, accessed 8, March 2024.

Wilke, A. L., B. D. Watts, B. R. Truitt and R. Boettcher. 2005. Breeding season status of the American Oystercatcher in Virginia, USA. Waterbirds 28: 308–315. doi:10.1675/1524-4695(2005)028[0308:BSSOTA]2.0.CO;2

Winkler, D. W., Billerman, S. M., and I. J. Lovette. 2020. Haematopodidae Oystercatchers, v. 1.0. *In* Birds of the World (A. F. Poole and F. B. Gill, Eds.). Cornell Lab of Ornithology, Ithaca, New York, U.S.A. doi:10.2173/bow.blkoys.01