

FORAGING ECOLOGY OF AMERICAN OYSTERCATCHERS IN THE
CAPE ROMAIN REGION, SOUTH CAROLINA

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ABSTRACT

During the nonbreeding season, the Cape Romain Region of South Carolina supports ca. one-sixth of the total population of the eastern race (*palliatus*) of the American Oystercatcher (*Haematopus palliatus*), which consists of only ca. 11,000 individuals and appears to be declining. I compared the density, size, and orientation of the primary prey, Eastern oysters (*Crassostrea virginica*) and the foraging behaviors of adult American Oystercatchers among the three largest bays in the Cape Romain Region that American Oystercatchers used as foraging areas. Results indicated that prey size, prey orientation, and the foraging behaviors of American Oystercatchers differed among bays. Although American Oystercatchers appeared to have lower rates of energy intake in Bulls Bay compared to Sewee Bay and Copahee Sound, adult American Oystercatchers may have foraged in Bulls Bay during the nonbreeding season in order to occupy nesting territories, which existed in Bulls Bay but not in Sewee Bay or Copahee Sound. Copahee Sound and Sewee Bay appear to be important foraging areas for American Oystercatchers during the nonbreeding season, whereas Bulls Bay appears to be important to American Oystercatchers year-round. In addition to investigating the foraging behavior of adults, I compared the foraging proficiency of adult and immature American Oystercatchers in Copahee Sound. Results indicated that the amount of time devoted to specific foraging behaviors differed among age-classes; however, immature American Oystercatchers were able to achieve equivalent feeding rates compared to adults. The abundance of prey in Copahee Sound may have allowed immature oystercatchers to compensate for their slightly inferior prey handling skills compared to adults.

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CHAPTER ONE

INTRODUCTION

The eastern race (*palliatus*) of the American Oystercatcher (*Haematopus palliatus*), hereafter referred to as oystercatcher, was identified as a “species of high concern” in the US Shorebird Conservation Plan (Brown *et al.* 2001) due the small size of the population, which consists of ca. 11,000 individuals and appears to be declining (Brown *et al.* 2005). The oystercatcher Oystercatchers face several anthropogenic threats during both the breeding and nonbreeding seasons including habitat loss due to coastal development, disturbance from human recreational activities (Peters and Otis 2005, Sabine *et al.* 2008), and the contamination of food resources due to human pollution (Schultes *et al.* 2006). The cause of the decline in this population of oystercatchers is unknown but may be related, at least in part, to conditions on foraging grounds in areas where large numbers of oystercatchers congregate during the nonbreeding season.

During the nonbreeding season, the coast of South Carolina supports ca. one-third of the eastern race of the oystercatcher, and ca. half of the oystercatchers in South Carolina during the nonbreeding season winter in the Cape Romain Region of the South Carolina coast (i.e. from the northern boundaries of the Cape Romain National Wildlife Refuge (CRNWR) south to Isle of Palms; Sanders *et al.* 2004, Peters and Otis 2007). Adult oystercatchers that were banded in Massachusetts, New Jersey, Virginia, North Carolina, South Carolina, and Georgia were observed in the Cape Romain Region during this study (Hand unpublished data). In addition to supporting adult oystercatchers from many states during the nonbreeding season, the Cape Romain Region supports ca. 77% of

the immature oystercatchers that winter in South Carolina (South Carolina DNR unpublished data). Oystercatchers that winter in the Cape Romain Region typically forage on intertidal shellfish beds (Tomkins 1947) and can be observed in several bays that are accessible by boat (Peters and Otis 2005). The Cape Romain Region, therefore, presents a unique opportunity to study the foraging ecology of both adult and immature oystercatchers during the nonbreeding season. The goals of this thesis are to (1) determine if prey availability and the foraging behavior of adult oystercatchers differed among bays in the Cape Romain Region (Figure 1.1) and (2) determine if foraging proficiency differed between adult and immature oystercatchers

Chapter two of this thesis, “Foraging behavior of adult American Oystercatchers in the Cape Romain Region, South Carolina during the nonbreeding season”, investigated the quality of foraging habitat for adult oystercatchers in three bays in the Cape Romain Region. There is evidence that the sizes of breeding populations of wading birds and passerines are determined by the survival and physical condition of adults during the nonbreeding season (Butler 1994, Rappole and McDonald 1994). The quality of habitat used during the nonbreeding season has been found to be related to survival and subsequent reproductive success in some migratory avian species (Norris 2005, Gunnarsson *et al.* 2005). For example, Gill *et al.* (2001) found that adult Black-tailed Godwits (*Limosa limosa*) experienced higher rates of survival during the nonbreeding season at high quality sites compared to sites where prey-intake rates were low, and Norris *et al.* (2004) found that American Redstarts (*Setophaga ruticilla*) that occupied habitat that was of high quality during the winter arrived on breeding grounds earlier and

had higher rates of reproductive success compared to individuals that occupied poorer quality habitat. During this study, I estimated food availability and compared the foraging behaviors of oystercatchers in the three largest bays in the Cape Romain Region where oystercatchers forage during the nonbreeding season.

Chapter three of this thesis, “Age-related foraging ecology in American Oystercatchers in the Cape Romain Region, South Carolina”, investigates the foraging proficiency of immature oystercatchers. In some shorebird species, immature individuals are particularly vulnerable to mortality. For example, Goss-Custard *et al.* (1982) found that ca. 12% of the juvenile European Oystercatchers (*Haematopus ostralegus*) wintering on the Exe estuary, England, died during their first autumn and winter, whereas adults experienced much lower rates of mortality. Wunderle (1991) suggested that the high rates of mortality that have been observed in many avian species during the immature period may be related to lower foraging proficiency in immature birds compared to adults. Butler (1994) suggested that population trends in wading birds are largely regulated by the number of immature birds that are able to acquire the foraging proficiency necessary to survive their first winter. It is unclear if age-related foraging proficiency affects population trends in oystercatchers, but as a first-step to examine that issue I sought to determine if there were differences in foraging proficiency among age classes of oystercatchers. I examined the foraging proficiency of adult and immature oystercatchers in Copahee Sound, South Carolina. I compared the prey searching times, prey handling times, the frequency that handling attempts were unsuccessful, feeding rates, and diet composition of oystercatchers between age classes during the 2007 nonbreeding season. I

also measured rates of aggression and the likelihood that prey was involved in aggressive interactions for each age class. Goss-Custard *et al.* (1998) found that immature European Oystercatchers (*Haematopus ostralegus*) increased their rates of energy intake by kleptoparasitizing conspecifics when their foraging proficiency was lower compared to adults, and I sought to determine if similar behavior occurred during my study.

The results of this research will provide a more complete understanding of the constraints oystercatchers experience during the nonbreeding season in a core area of their winter range.

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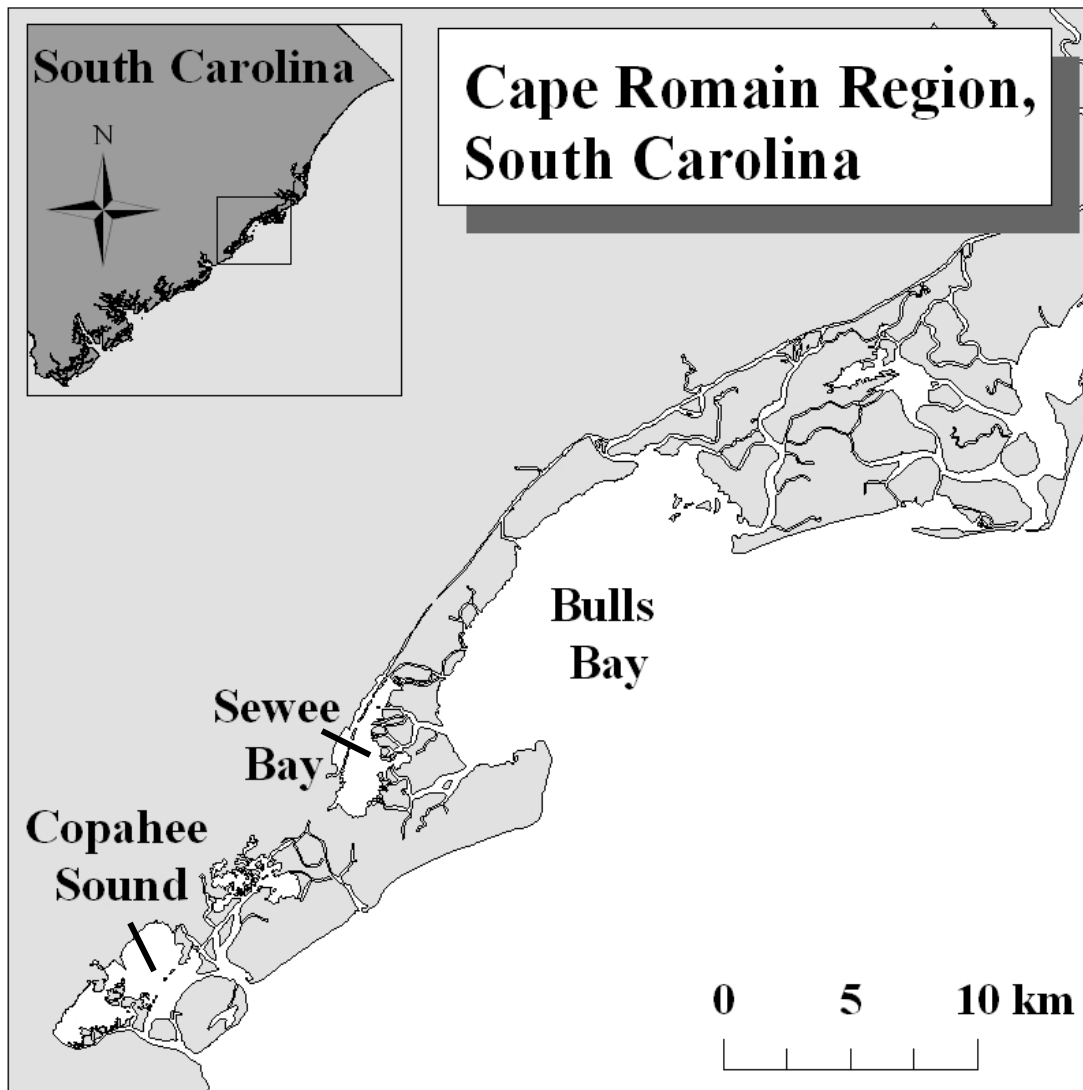


Figure 1.1. The Cape Romain Region, South Carolina, showing the three bays used as study areas to examine the foraging behavior of American Oystercatchers during the 2006 (Bulls Bay and Sewee Bay) and 2007 (Bulls Bay and Copahee Sound) nonbreeding seasons.

CHAPTER TWO

FORAGING BEHAVIOR OF ADULT AMERICAN OYSTERCATCHERS IN THE CAPE ROMAIN REGION, SOUTH CAROLINA DURING THE NONBREEDING SEASON

Introduction

Population trends in many migratory birds may be regulated, at least in part, by habitat quality during the nonbreeding season (Norris 2005, Butler 1994). For example, migratory passerines and shorebirds that winter in high quality habitat often have higher rates of survival and are in better physical condition upon returning to breeding grounds compared to individuals that winter in lower quality habitat (Norris *et al.* 2004, Gunnarsson *et al.* 2005). Habitat quality for avian species during the nonbreeding season is determined by a complex interaction of many factors including predation risk, disturbance, environmental conditions (e.g. climate), interspecific and intraspecific competition, and food availability (Sherry and Holmes 1996, Evans and Dugan 1984, Peters and Otis 2005, Johnson 2007). Of these factors, Sherry and Holmes (1996) suggest that food availability may have the strongest effect on the physical condition of passerines during the nonbreeding season.

Like habitat quality, food availability itself is a complex interaction of multiple factors. For example, Sherry and Holmes (1996) define food availability as the density of food that a forager can locate, access, and digest. Because of its complex nature, however, food availability is often difficult to measure in a manner that is relevant to the population in question (Hutto 1990, Lovette and Holmes 1995). Nonetheless, food

availability may be examined directly by measuring food density and accessibility (Barnes *et al.* 1995, Ontiveros *et al.* 2005).

The foraging behavior of an individual should be affected in a predictable manner that is dependent, at least in part, on food availability (Hutto 1990), and that the rate of energy gain for a predator should be proportional to the density of available prey until it is limited by other factors such as handling time or satiation (Holling 1959). According to the basic model for optimal foraging, the rate of energy gain is equal to the amount of energy gained minus the sum of the energy spent searching for and handling prey all divided by the sum of the time spent searching and handling (Stephens and Krebs 1986). If the amount of energy spent per unit time is assumed to be equal during searching and handling activities and to be equal for all types and sizes of prey, then the searching and handling times and the size of prey that are consumed may be used to compare the rates of energy gain of foragers at different locations (Goss-Custard *et al.* 2006). Rates of energy gain would be expected to be higher for individuals using habitat that is of higher quality with respect to food resources compared to individuals using lower quality habitat (Gill *et al.* 2001) unless the intake rate has reached the asymptotic maximum (Goss-Custard *et al.* 2006).

I compared the quality of foraging habitat for adult American Oystercatchers (*Haematopus palliatus*) during the nonbreeding season. The eastern race (*palliatus*) of the American Oystercatcher, hereafter referred to as oystercatcher, consists of ca. 11,000 individuals (Brown *et al.* 2005). The oystercatcher was identified as a “species of high concern” in the US Shorebird Conservation Plan (Brown *et al.* 2001) due the small size

of the population and to an apparent population decline (Brown *et al.* 2005). The cause of the apparent decline in the oystercatcher population is unknown but may be related, at least in part, to survival and physical condition during the nonbreeding season. During the nonbreeding season, the coast of South Carolina supports ca. one-third of the eastern race of the American Oystercatcher, and ca. half of the oystercatchers in South Carolina during the nonbreeding season winter in the Cape Romain Region of the South Carolina coast (i.e. from the northern boundaries of the Cape Romain National Wildlife Refuge (CRNWR) south to Isle of Palms; Sanders *et al.* 2004, Peters and Otis 2007).

Oystercatchers in this region feed primarily on shellfish on intertidal shellfish beds (Tomkins 1947), the quality of which have not been quantified but appear to differ throughout the region (Peters 2006).

The goal of this study was to examine the relationship between prey availability and the foraging behavior of American Oystercatchers in the Cape Romain Region of South Carolina during the nonbreeding season. The components of foraging behavior that were measured included searching time per item, handling time per item, duration of the feeding bout, and diet composition. Specifically, I sought to determine (1) if the density, frequency of size classes, or accessibility of oysters differed among bays, (2) if oystercatcher foraging behaviors (diet composition, searching times, handling times, and the duration of feeding bouts) differed among bays, (3) if searching times, handling times, or the duration of feeding bouts varied in relation to date, (4) if handling times differed among prey types or sizes, or (5) if activity budgets varied with the number of hours from low tide.

Methods

Study Species

The American Oystercatcher is a large shorebird that feeds primarily on intertidal shellfish in salt marshes and on beaches (Nol and Humphrey 1994). The eastern subspecies breeds along the coast of the U.S. from Massachusetts south to Florida and west to Texas (Brown *et al.* 2005). Band recoveries and re-sightings of banded individuals indicate that oystercatchers that breed in the northern section of the range frequently winter in the Cape Romain Region, and that many of the oystercatchers that breed in South Carolina are year-round residents (Sanders *et al.* 2004, South Carolina DNR unpublished data).

Study Site

The foraging behavior of oystercatchers was examined in southwestern Bulls Bay, South Carolina (32°57'N, 79°37'W) during October – December, 2006 and 2007; in Sewee Bay, South Carolina (32°56'N, 79°39'W) during October – December, 2006; and in Copahee Sound, South Carolina (32°52'N, 79°45'W) during October – December, 2007. These three bays were selected as sites for this study because they are the largest bays in the Cape Romain Region used as foraging grounds by oystercatchers during the nonbreeding season.

Bulls Bay is a large (ca. 76.5 km²), shallow bay in the CRNWR. In the southwestern portion of Bulls Bay, intertidal shellfish beds are located within ca. 300 m

of the shore. During the 2007 breeding seasons, 18 pairs of oystercatchers nested along the southwestern shore of Bulls Bays (Thibault 2008). Sewee Bay, which is ca. 3.4 km², and Copahee Sound, which is ca. 5.3 km², are located south of the CRNWR. Both bays consist of intertidal shellfish beds intersected by shallow channels, are surrounded by salt marsh, and adjoin the Atlantic Intracoastal Waterway (AICW). Nesting habitat is not available along the shores of Sewee Bay or Copahee Sound; however, ca. 40 pairs of oystercatchers nested on shell mounds along the AICW between Sewee Bay and Copahee Sound during the 2007 breeding season (Sanders unpublished data). Based on visual appearance, Sewee Bay was similar to Copahee Sound in terms of the density, size, and orientation of oysters. Copahee Sound replaced Sewee Bay as a study area in 2007 because the Copahee Sound supported a larger number of immature oystercatchers which were needed to conduct a concurrent study of age-related foraging ecology in oystercatchers.

Field Procedures

A total of eighteen observation points were designated in the three bays. Two sets of two points were located on the shore of Bulls Bay, two sets of three points were on shellfish beds along a channel in Sewee Bay, and two sets of four points were on shellfish beds along a channel in Copahee Sound. Observations points within each set were spaced ca. 200 to 300 m apart. All of the observations points were accessible at low tide either by boat or by foot.

Oyster Density, Height, and Orientation

The density and shell height of oysters in Bulls Bay and in Copahee Sound were quantified during November, 2007. Shellfish beds located between 50 and 150 m from four observation points in each bay were selected based on their accessibility by boat at low tide, and 0.0625 m² quadrats (Cadman 1980, Tuckwell and Nol 1997) were randomly placed on the beds. The live oysters within 93-94 quadrats in each bay were counted, and the height of each oyster was measured to ± 5 mm. The mean height of the oysters in each quadrat was used to compare oyster height between bays.

I also recorded spatial orientation of each oyster because I hypothesized that the spatial orientation, as well as the size of oysters, may be related to oystercatcher searching and handling time. Vertically oriented oysters may have been more accessible to oystercatchers compared to horizontally oriented oysters. Oysters were categorized as vertically oriented if their opening was at a $\geq 45^\circ$ angle from the substrate or as horizontally oriented if the opening was at a $< 45^\circ$ angle from the substrate or was pointed toward the substrate. I calculated the percentage of the oysters in each quadrat that were vertically oriented and the density of vertically oriented oysters in each quadrat. Only oysters that were above the substrate were recorded.

Oystercatcher Behavior

Data were collected via focal animal observations and scan sampling from the observation points in the three bays. During 2006, a set of observation points in either Sewee Bay or Bulls Bay was randomly selected for each sampling day. During a

sampling day, the observer visited each observation point in the set at least once and remained at individual observation points for between 15 to 60 consecutive minutes. During 2007, a single observation point in either Bulls Bay or Copahee Sound was randomly selected for each day of sampling, and the observer remained at that observation point while collecting data. Sampling methods were revised between years because a preliminary analysis of the 2006 data revealed that more data could be collected by remaining at one point for the entire sampling period as opposed to moving among points.

Behavioral observations were collected on 56 days from 17 October through 17 December, 2006 and on 41 days from 8 October through 13 December, 2007. On each day of sampling, data were collected during either the rising or the falling stage of the low tide (each ca. 4 hours). On many days, part of the low tide period occurred before dawn or after sunset, so the stage that occurred during daylight was chosen.

Foraging Behavior and Diet Composition

Focal-animal sampling techniques (Altmann 1974) were used to quantify the searching time and handling time for each prey items, the duration of the feeding bout, and diet composition for actively foraging oystercatchers. At specific stages of foraging, the foraging proficiency of adult and immature oystercatchers differs (Chapter 3, Cadman 1980), and the proportion of the oystercatchers present that were immature differed among bays. Few immature oystercatchers appeared to be present in Bulls Bay and Sewee Bay, so only adult oystercatchers were sampled during this study to control for the

effects of age. Bill color was used to distinguish between adult oystercatchers (orange bills) and immature oystercatchers (partially dark bills, Peters and Otis 2005, Prater *et al.* 1977). A 20-60x zoom telescope was used to observe oystercatchers within 300 m of the observation point. Many individuals were not marked, so consecutive observations of the same individual may have occurred.

A focal observation was defined as a continuous observation of a foraging oystercatcher. During each focal observation, I attempted to observe a randomly selected oystercatcher while it completed ≥ 3 successful foraging events, which I defined as the successful consumption of a prey item. The range in time for the completion of ≥ 3 successful foraging events was 3 – 12 minutes. The duration of prey searching and prey handling were recorded for each foraging event (i.e., each prey item). Following Tuckwell and Nol (1997) and Cadman (1980), searching time was defined as the number of seconds from the completed consumption of a prey item until the next prey item was located, and handling time was defined as the number of seconds between the first stab into an item and the moment when the oystercatcher finished consuming the item. Searching and handling times were recorded to ± 1 sec using a stopwatch. If the oystercatcher became inactive, preened, or was vigilant for more than five consecutive seconds while locating a prey item, the searching time was not recorded for the foraging event but the focal observation was continued (Cadman 1980). If both the searching time and the handling time were recorded for a successful foraging event, the duration of the feeding bout was calculated as the sum of the searching time and handling time.

Diet composition was defined as the proportion of the total number of prey items that I observed being consumed by focal oystercatchers that consisted of each type of prey. During focal observations, each prey item that was not obstructed from view by the oystercatcher's body or by the shellfish reef was classified as an Eastern oyster (*Crassostrea virginica*), ribbed mussel (*Geukensia demissa*), hard clam (*Mercenaria mercenaria*), banded tulip snail (*Fasciolaria tulipa*), or unknown. Prey type was determined visually based on flesh color, flesh consistency, and the shape of the shell.

I categorized the size of oysters by comparing the approximate length of the consumed flesh to the length of the focal oystercatcher's bill. The sizes of other types of prey were not calculated because they were relatively uncommon in the diet of oystercatchers in the Cape Romain Region (see results). Oystercatchers frequently extracted oysters from their shells in multiple pieces; therefore the size of each piece was estimated using a scale developed by Tuckwell and Nol (1997). Pieces that were shorter than $\frac{1}{4}$ of the length of the bill were assigned to class 1, pieces between $\frac{1}{4}$ and 1 bill length were assigned to class 2, and pieces longer than a bill length were assigned to class 3.

To estimate the total volume of each oyster, the volume estimates for the size classes of all of the pieces were summed using the midpoint volumes established by Tuckwell and Nol (1997), where class 1 oysters were < 0.99 mL (midpoint 0.5 mL), class 2 oysters were 1.0 to 5.99 mL (midpoint 3.5 mL) and class 3 oysters were > 6.0 mL (midpoint 6.0 mL). To test the accuracy of this scale, I estimated the size class of 34 oysters placed beside an oystercatcher skull and then measured the volume of each oyster

to the nearest 0.5 mL by water displacement. I assigned 76% of the oysters to the correct size class, however, I underestimated the size classes of all of the class 3 oysters (n = 5). I was 90% accurate at estimating the size of class 1 and 2 oysters. Size classes may have been more accurately assigned for large oysters during focal observations of foraging oystercatchers because the pieces were probably more elongated as they hung from the bill than they were when laid out on a table. Large oysters (over 75 mm in length) typically make up less than 10% of all reef oysters in South Carolina (Luckenbach *et al.* 2005), and class 3 oysters were the rarest size consumed during this study. If the size of class 3 oysters was routinely but consistently underestimated, comparisons among bays could still be made between the relative sizes of oysters consumed oystercatchers.

Activity Budgets

Scan sampling techniques (Altmann 1947) were used to compare the activity budgets of oystercatchers in Bulls Bay, Sewee Bay, and Copahee Sound during the low tide period. Activity was classified as either foraging or not foraging. During 2006, I collected scan samples when I arrived at each observation point and before I departed from each point by counting the number of oystercatchers foraging and not foraging within the scan plot. During 2007, I did not move among observation points during the sampling day, so I collected scan samples at 30 minute intervals before or after low tide. Data collected in Bulls Bay during 2007 were not analyzed because no oystercatchers were present in the scan plots during 70% of the scans. When no oystercatchers were present in the scan plot, the scan was not included in the analysis. Each scan plot included

the visible shellfish reef within a 120 m radius of the observation point. This plot size was chosen because, at this distance, few oystercatchers were obstructed from view by shellfish beds at low tide. When the water level in the bay was low, large areas of exposed shellfish were blocked from view by other shellfish beds when viewed from a greater distance.

Statistical Analysis

Statistical analyses were used to address five questions concerning prey availability and the foraging ecology of adult oystercatchers during the nonbreeding season: (1) Did oyster density, frequency of size classes, or accessibility differ between Copahee Sound and Bulls Bay during 2007? (2) Did diet composition, the size of oysters that were consumed, or foraging parameters (i.e. mean searching times, mean handling times, and the duration of feeding bouts) differ among bays? (3) Were searching times, handling times or the durations of feeding bouts correlated with date? (4) Did handling times in all bays differ among prey types or among oyster size classes? and (5) Did activity budgets vary with the number of hours from low tide? The term “bays” refers to comparisons among Bulls Bay during 2006, Bulls Bay during 2007, Sewee Bay during 2006 and Copahee Sound during 2007 unless otherwise specified. The analyses used to address each of these questions are described below.

Two-tailed t-tests were used to determine if oyster shell height, the density of oysters, the density of vertically oriented oysters, or the percentage of oysters that were vertically oriented differed between Copahee Sound and Bulls Bay during 2007.

Pearson χ^2 tests were used to determine if diet composition and the size of the oysters that were consumed differed among bays. After diet composition and the size of consumed oysters were compared among all bays, pair-wise comparisons were used for each metric to determine which bays differed from each other. To avoid pseudoreplication, only the prey type of the first unobstructed item and the size class of the first oyster consumed by each oystercatcher were included in the analysis of diet composition and oyster size.

Separate general linear models (SAS Version 9.1; SAS Institute, Inc., Cary, North Carolina) were used to determine if mean searching times, mean handling times, or the duration of feeding bouts for oystercatchers during focal observations differed among bays. Prior to analysis, the first three searching times and handling times were averaged for each oystercatcher to increase the precision of the measurements while avoiding pseudoreplication (Heijl *et al.* 1990, Tuckwell and Nol 1997). Only the first complete feeding bout for each oystercatcher was analyzed to avoid pseudoreplication. Bay was included as a fixed factor, date was included as a covariate, and bay * date was included as an interaction term. A backward selection approach was used until only significant variables were included in each model, and Tukey's HSD post-hoc tests ($\alpha = 0.05$) were used to determine which bays differed from each other.

ANOVA models were used to determine if handling times differed among prey types or oyster size classes. Tukey's HSD post-hoc tests ($\alpha = 0.05$) were used to determine with types or sizes differed from each other. A Kruskal-Wallis test was used to compare the proportion of oystercatchers that were engaged in foraging activities at

different stages of the tidal cycle, and a Wilcoxon two-Sample test was used to compare the percentage of oystercatchers foraging during scans collected within two hours of low tide to the percentage foraging during scans collected beyond two hours from low tide.

Searching times, handling times, and the duration of feeding bouts were log transformed. Raw data are presented, however, to ease interpretation and allow for comparisons with previous studies. Means are presented as ± 1 SE unless noted otherwise. P-values ≤ 0.05 were considered to be significant but actual P-values are presented.

Results

Oyster Density, Height, and Orientation

The mean height of oysters in Copahee Sound (45.3 ± 0.7 mm, $n = 85$ quadrats) was greater ($t_{159} = 9.6$, $P < 0.01$) compared to Bulls Bay (35.7 ± 0.8 mm, $n = 76$ quadrats). The mean density of oysters did not differ ($t_{142} = 1.8$, $P = 0.07$) between Bulls Bay (27.2 ± 3.1 oysters per 0.0625 m², $n = 94$ quadrats) and Copahee Sound (20.7 ± 1.7 oysters per 0.0625 m², $n = 93$ quadrats), and the mean density of vertically oriented oysters also did not differ ($t_{151} = 1.1$, $P = 0.27$) between Bulls Bay (18.6 ± 2.4 oysters per 0.0625 m², $n = 94$ quadrats) and Copahee Sound (15.5 ± 1.4 oysters per 0.0625 m², $n = 93$ quadrats). The mean percentage of the oysters in Copahee Sound that were vertically oriented (70.1 ± 2.4 %, $n = 85$ quadrats) was greater ($t_{135} = 2.7$, $P = 0.01$) compared to Bulls Bay (58.0 ± 3.4 %, $n = 76$ quadrats).

Foraging Behavior

Data were collected during 51 falling tides and 46 rising tides. Diet composition differed ($\chi^2_{3,571} = 17.5$, $P < 0.01$) among bays but not between years in Bulls Bay (Fig. 2.1). In general, oysters appeared to comprise a greater proportion of the diet in Sewee Bay and Copahee Sound compared to Bulls Bay, although $> 87\%$ of the items consumed in all bays and both years were oysters. The size of oysters consumed also differed ($\chi^2_{6,534} = 29.1$, $P < 0.01$) among bays (Fig. 2.2) and was generally smaller in Bulls Bay compared to Sewee Bay and Copahee Sound.

Mean searching times differed ($F_{3,403} = 6.83$, $P < 0.01$) among bays and were generally greater in Bulls Bay (Fig 2.3). Mean handling times differed ($F_{3,443} = 8.2$, $P < 0.01$, Fig. 2.4) among bays and increased with date by 2.1 seconds/month ($F_{1,441} = 4.8$, $P = 0.03$). The duration of feeding bouts (55.3 ± 1.6 seconds; $n = 529$ successful foraging events) did not differ ($F_{3,525} = 1.3$, $P = 0.26$) among bays. Mean searching times and the duration of feeding bouts did not vary with date (both $P > 0.2$), and the interaction term (bay * date) was not significant (all $P > 0.1$) in any of the models.

Handling Times for Prey Types and Oyster Size Classes

The mean handling time for oysters (21.2 ± 0.5 seconds, $n = 546$ oysters) pooled among all bays was significantly shorter ($F_{2,577} = 91.0$, $P < 0.01$) compared to the handling time for mussels (75.1 ± 7.5 seconds, $n = 30$ mussels, Tukey HSD: $\alpha \leq 0.05$) and clams (72.3 ± 15.1 seconds, $n = 4$ clams, Tukey HSD: $\alpha \leq 0.05$), which did not differ from each other. The mean handling time for oysters differed among size

classes when data were pooled among all bays ($F_{2,532} = 40.3$, $P < 0.01$, Tukey HSD: $\alpha \leq 0.05$). The mean handling time for class 1 oysters was 15.6 ± 0.7 seconds ($n = 150$ oysters), for class 2 oysters 22.5 ± 0.6 seconds ($n = 357$ oysters), and for class 3 oysters 29.0 ± 2.9 seconds ($n = 28$ oysters).

Use of Shellfish Beds during the Tidal Cycle

The percentage of oystercatchers engaged in foraging behavior varied with time from low tide ($\chi^2_7 = 130.5$, $P < 0.01$, Fig. 2.5). During scans conducted ≤ 2 hours from low tide, a significantly lower ($Z = 9.8$, $P < 0.01$) proportion of the oystercatchers in the scan plots were foraging ($32.4 \pm 2.6\%$, $n = 261$ scans) compared to scans conducted > 2 hours from low tide ($73.4 \pm 2.5\%$, $n = 231$ scans). Time spent foraging was likely overestimated because oystercatchers often roosted in flocks on shellfish beds outside of the plots when they were not foraging.

Discussion

The availability of oysters to oystercatchers appeared to be greater in Copahee Sound compared to Bulls Bay during 2007. Although the density of oysters did not differ between Copahee Sound and Bulls Bay, the mean height of the oysters and the percentage of the oysters that were vertically oriented were lower in Bulls Bay compared to Copahee Sound. Based on estimates of prey availability in Copahee Sound and Bulls Bay, and the similarities between Copahee Sound and Sewee Bay, I predicted that the intake rates of adult oystercatchers would be lower in Bulls Bay compared to Sewee Bay

or Copahee Sound. I did not measure intake rates directly, but instead quantified the amount of time oystercatchers spent searching for and handling individual prey items and estimated the sizes of the prey that were consumed. A basic model for optimal foraging (Stephens and Krebs 1986) was then used to compare bays, assuming that the amount of energy spent per unit time is equal during searching and handling activities and is equal for all types and sizes of prey.

I found that the foraging behaviors of adult oystercatchers differed among bays in the Cape Romain Region of South Carolina during the nonbreeding season. Mean searching times were longer, mean handling times more variable and often shorter, diets were comprised of fewer oysters, and the sizes of the oysters consumed were smaller in Bulls Bay compared to the other bays in the study. Despite these differences in foraging behavior no difference in the duration of feeding bouts among bays was observed. These observations suggest that oystercatchers likely had lower intake rates in Bulls Bay, where oysters showed more signs of disturbance, compared to Sewee Bay and Copahee Sound. Below I explore each of the foraging metrics in turn and discuss possible explanations for the patterns I observed.

According to optimal foraging theory, foragers must spend more time searching for food as the density of available food decreases (Holling 1959, Norberg 1977). Longer searching times in Bulls Bay compared to the other bays may have been related to differences in prey availability. Although the density of oysters did not differ between Bulls Bay and Copahee Sound, the density of prey is not always a reliable measure of prey availability (Gawlik 2002). During my study, a greater proportion of the oysters in

Copahee Sound were vertically oriented and oysters (both consumed and available) were larger in Copahee Sound. The differences in oyster size frequencies and spatial orientation may account for the differences searching times I observed among bays. For example, oystercatchers located gaping oysters by looking down and probing into the water while walking along the edges of shellfish beds. Therefore, oysters that were horizontally oriented were probably more difficult to locate, disable, and extract compared to vertical oysters. Small oysters also may have been less detectable compared to larger oysters because the former have less surface area. I did not observe changes in the appearance of the shellfish beds in Bulls Bay between 2006 and 2007, and the structure (i.e. density, size, oyster orientation, and substrate) of the shellfish beds in Sewee Bay appeared to most closely resemble Copahee Sound.

Differences among bays in mean handling times likely reflected differences in the size of the oysters that were consumed and differences in diet composition. Prey handling times in oystercatchers often differ among prey types (Tuckwell and Nol 1997) and tend to be longer for larger prey within a prey type (Tuckwell and Nol 1997, Cadman 1980). During my study, handling times for mussels and clams were > 3 times longer compared to handling times for oysters, and handling times for oysters increased with oyster size class. A greater proportion of the oysters that were consumed in Bulls Bay during both 2006 and 2007 were in the smallest size class compared to Sewee Bay and Copahee Sound, and the frequency that small oysters were consumed in Bulls Bay was probably underestimated since almost all of the unidentified items were likely to be small oysters. The relatively short handling times observed in Bulls Bay during 2006 probably reflected

the high frequency that small oysters were consumed. In contrast to Bulls Bay during 2006, mean handling times in Bulls Bay during 2007 did not differ from mean handling times in Sewee Bay and Copahee Sound. Oystercatchers consumed mussels and clams at a higher frequency in Bulls Bay during 2007 compared to 2006 and to the other bays. Since handling times for small oysters were relatively short and handling times for mussels and clams were relatively long, the frequency that mussels, clams, and small oysters were consumed in Bulls Bay during 2007 probably accounts for the variability in the mean handling times that were observed.

I found that mean handling times were positively correlated with date, and increased by 4.9 seconds per month between September and December. The mechanism for this correlation is unclear. Diet composition and the size of the oysters consumed did not appear to differ among months; however, oystercatchers may have preferentially exploited the most accessible or most vulnerable oysters (e.g. oysters with thinnest shells, largest gapes, or most accessible location) earlier in the nonbreeding season, which may have resulted in longer handling times later in the season. Unlike mean handling times, mean searching times did not vary with date in any of the bays, which may suggest that a large decline in prey availability did not occur during either season of the study.

In contrast to mean searching times and mean handling times, the duration of feeding bouts did not differ among bays. The lack of difference in the duration of foraging bouts, when considered with the differences in searching and handling times among bays, suggests that the rate of energy gain may have been lower in Bulls Bay compared to the other bays. The amount of energy oystercatchers gained per prey item while foraging in

Bulls Bay appeared to be lower, while the amount of energy and time spent searching for and handling individual prey items appeared to be equivalent in Bulls Bay compared to the other bays. Therefore, if rates of energy gain reflected prey availability and foraging habitat quality, Sewee Bay and Copahee Sound appeared to provide higher quality foraging habitat for oystercatchers during the nonbreeding season compared to Bulls Bay.

The causes of the apparent differences in quality of foraging habitat found among bays in the Cape Romain Region were not identified during this study but may be related to differences in the density, size, and orientation of oysters among bays. Management practices and human use vary within the Cape Romain Region. Clam harvesting, which causes oyster mortality (Lenihan and Micheli 2000) and breaks up clumps of vertically oriented oysters, was regularly observed in Bulls Bay during both years of the study, but not in Sewee Bay or in Copahee Sound. Clam harvesting may be responsible for the greater number of small oysters and higher proportion of horizontal oysters found in Bulls Bay compared to Copahee Sound. Additionally, the relatively high densities of oystercatchers that use Bulls Bay during the breeding season may diminish food resources in the bay. Wave action, which causes mortality in oysters (Ortega 1981), also may have negatively affected the food resources used by oystercatchers in Bulls Bay, which is more exposed compared to the other bays. A combination of factors including clam harvesting, prey depletion, and wave action may be responsible for the differences in prey availability and foraging behaviors observed on a regional scale during this study.

Even though the quality of foraging habitat appeared to be inferior in Bulls Bay compared to Sewee Bay and Copahee Sound in terms of the variables measured during

this study, other attributes of Bulls Bay may attract oystercatchers during the nonbreeding season. Anecdotal observations show that at least some of the oystercatchers that subsequently nested in Bulls Bay foraged there during the nonbreeding season (Thibault and Hand unpublished data). Success in future contests over a territory is often positively correlated with prior occupancy of the territory (Matthysen 1993, Sandell and Smith 1991); therefore, by occupying territories in Bulls Bay during the nonbreeding season, oystercatchers may have increased their success at defending nesting territories in Bulls Bay during the breeding season. Unlike oystercatchers using many of the nest sites on shell mounds along the Atlantic Intracoastal Waterway and on barrier islands, oystercatchers that nest along the southwestern shore of Bulls Bay often feed on shellfish beds within view of their nests (Thibault 2008). Ens *et al.* (1992) found that pairs of European Oystercatchers that fed over 200 m from their nest areas often failed to provide a sufficient amount of food to their chicks and, therefore, fledged fewer chicks compared to pairs that fed on areas adjacent to their nest sites. Similarly, Nol (1989) found that pairs of American Oystercatchers with larger nearby feeding territories laid eggs earlier, had larger eggs, and had higher fledging success compared to pairs with smaller or no nearby feeding territories. By occupying feeding areas throughout the year that are adjacent to nesting territories in Bulls Bay, resident oystercatchers may increase their subsequent reproductive success.

Based on the large number of eggs (up to four nesting attempts per pair with an average of 2.4 eggs per attempt) that were laid by oystercatchers during the 2006 and 2007 breeding seasons (Thibault 2008), it is reasonable to speculate that food resources

are very abundant throughout the Cape Romain Region. Differences in food availability among bays may have had less influence over oystercatcher distribution in the Cape Romain Region during the nonbreeding season than other factors such as the year-round occupation of nesting territories. Bulls Bay, Sewee Bay and Copahee Sound encompass the majority of the shellfish beds where oystercatchers forage in the Cape Romain Region, and the Cape Romain Region supports a large portion of the eastern race of the American Oystercatcher during the nonbreeding season. Based on the results of this study, Sewee Bay and Copahee Sound, which are located outside of the CRNWR, should be recognized as important foraging areas for oystercatchers during the nonbreeding season, and Bulls Bay should be recognized as an important area for oystercatchers year-round. Each of these bays present unique opportunities for the conservation and management of oystercatchers.

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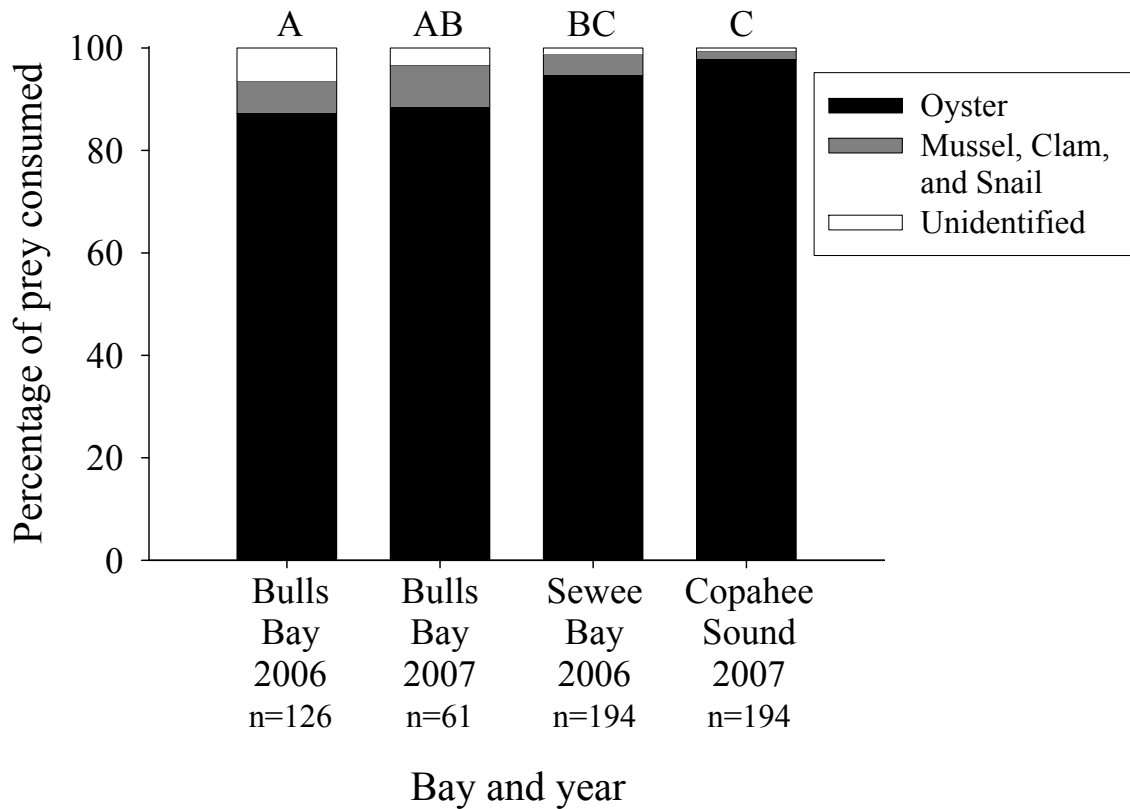


Figure 2.1. Diet composition of American Oystercatchers foraging in three bays in the Cape Romain Region, South Carolina, October – December, 2006 and October – December, 2007. Bays that do not share a letter differed significantly (Pearson's chi-square test: $\alpha < 0.05$).

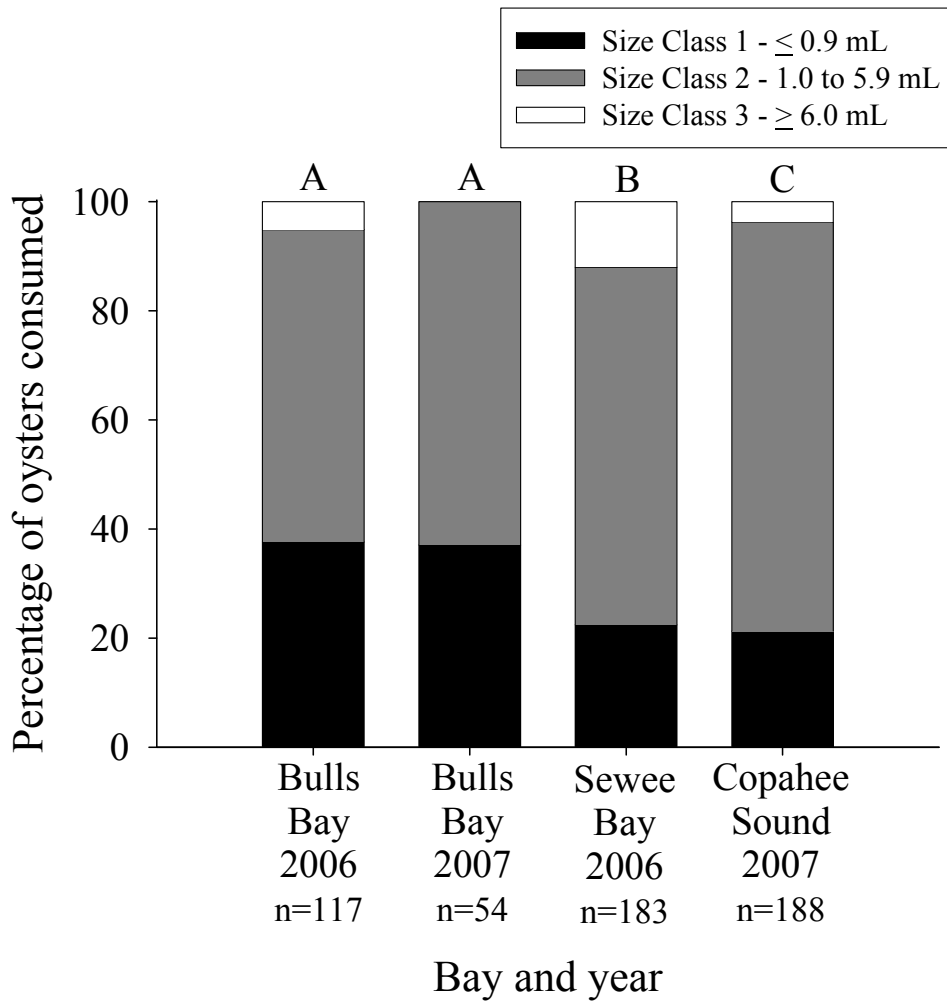


Figure 2.2. Size class of oysters consumed by American Oystercatchers foraging in three bays in the Cape Romain Region, South Carolina, October – December, 2006 and October – December, 2007. Bays that do not share a letter differed significantly (Pearson's chi-square test: $\alpha < 0.05$).

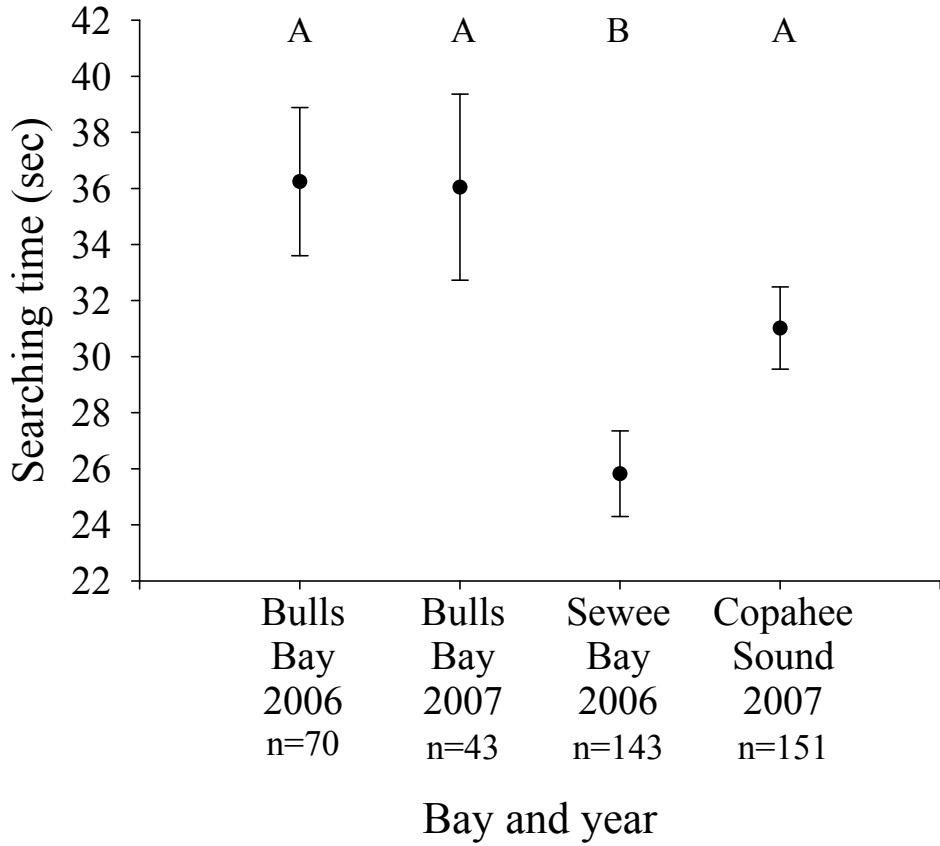
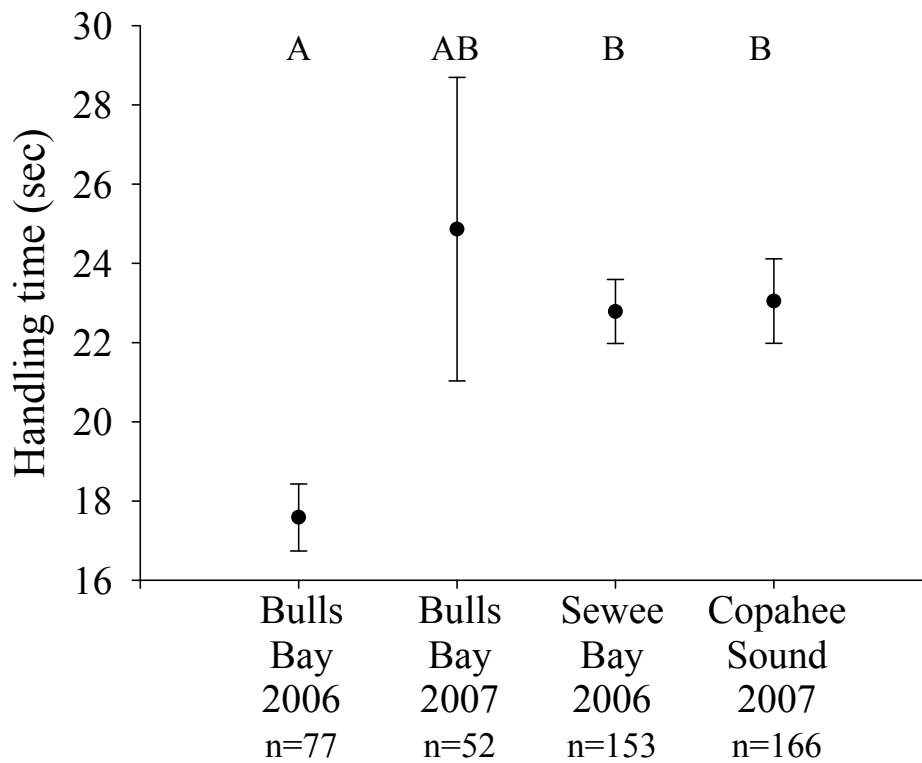


Figure 2.3. Mean searching times (± 1 SE) for American Oystercatchers foraging in three bays in the Cape Romain Region, South Carolina, October – December, 2006 and October – December, 2007. Bays that do not share a letter differed significantly (Tukey’s HSD: $\alpha < 0.05$).



Bay and year

Figure 2.4. Mean handling times (± 1 SE) for American Oystercatchers foraging in three bays in the Cape Romain Region, South Carolina, October – December, 2006 and October – December, 2007. Bays that do not share a letter differed significantly (Tukey’s HSD: $\alpha < 0.05$).

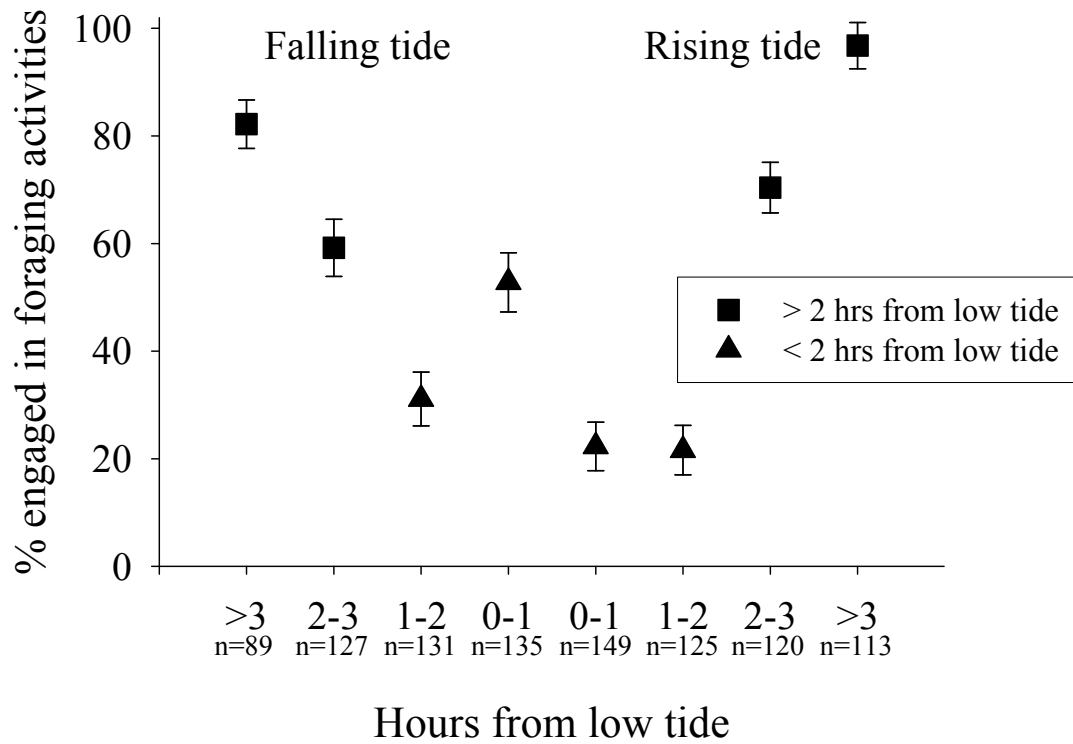


Figure 2.5. Activity of American Oystercatchers varied in relation to time from low tide in the Cape Romain Region, South Carolina, October – December, 2006 and October – December, 2007. Sample size refers to the number of scans collected.

CHAPTER THREE

AGE-RELATED FORAGING ECOLOGY IN AMERICAN OYSTERCATCHERS IN THE CAPE ROMAIN REGION, SOUTH CAROLINA

Introduction

Foraging proficiency in avian taxa including Pelecaniformes (Orians 1969), Falconiformes (Bourne 1985), Passeriformes (Richardson and Verbeek 1987), and Ciconiiformes (Bildstein 1984) increases with age during the first few years of an individual's life (Wunderle 1991). Age-related differences in foraging proficiency also appear to be common in Charadriiformes. For example, Groves (1978) demonstrated that juvenile (i.e. first year) Ruddy Turnstones (*Arenaria interpres*) ingested fewer prey items per unit time compared to adults. Similarly, Puttick (1979) found that immature (i.e. not sexually mature, including juvenile) Curlew Sandpipers (*Calidris ferruginea*) made fewer probes and pecks per minute and consumed fewer prey items per minute compared to adults. Lower foraging proficiency in immature, or younger, individuals compared to mature, or older, individuals may be a result of differences in foraging site selection, searching ability, diet choice, and/or prey capture and handling ability between age classes. Along with demonstrating lower foraging proficiency compared to adult birds, immature birds also tend to experience higher rates of mortality during the nonbreeding season (Lack 1966, Goss-Custard 1980, Kus *et al.* 1984, Warnock *et al.* 1997). High rates of mortality during the immature stage may be due to a variety of behavioral, social, and developmental factors including the inability of inexperienced foragers to balance energy requirements and predator avoidance (Wunderle 1991, Cresswell 1994), the low social

status of immature birds on feeding grounds (Goss-Custard 1980), and the immaturity of the beak, skeletal-muscular and neurological systems of young birds (Durell 2000, Marchetti and Price 1989, Cadman 1980).

The American Oystercatcher (*Haematopus palliatus*) was used as a model in this study to investigate age-related foraging proficiency. Oystercatchers as a genus are specialized feeders, typically consuming prey such as mussels, oysters, and cockles that require considerable handling skills, and, as such, age-related differences in foraging may be expected (Goss-Custard and Durell 1987a). For example, Goss-Custard and Durell (1987a, 1987c) found that juvenile European Oystercatchers (*Haematopus ostralegus*) had a lower rate of prey intake (i.e. biomass ingested per unit time) compared to adults throughout the nonbreeding season. The authors suggested that the rate of energy intake by juvenile European Oystercatchers remained consistently lower compared to adults throughout autumn and winter because juveniles had lower foraging proficiency at the beginning of the nonbreeding season and were more vulnerable to interference by more dominant oystercatchers later in the season. In some instances, however, juvenile European Oystercatchers compensated for their lower foraging proficiency by supplementing the prey they obtained independently with prey they kleptoparasitized from other oystercatchers (Goss-Custard *et al.* 1998). Nonetheless, juvenile European Oystercatchers have been found to experience a higher mortality rate during the nonbreeding season compared to adults (Goss-Custard *et al.* 1982). Winter mortality may be directly (i.e. starvation) and/or indirectly (e.g. increased risk of predation) related to food shortages that occur when prey resources are depleted or are inaccessible due to

inclement weather conditions (Goss-Custard and Durell 1987a, Goss-Custard *et al.* 1996a), and individuals that are less proficient at foraging may experience higher mortality rates compared to more proficient individuals (Weathers and Sullivan 1989).

In contrast to the extensively-studied European Oystercatcher, only one previous study (Cadman 1980) has investigated the age-related foraging ecology of the American Oystercatcher despite indications that foraging proficiency differs between age classes in similar species. The goal of this study was to examine age-related foraging behavior of American Oystercatchers within a core area of their wintering range. I assessed the relationship between foraging proficiency and age class in American Oystercatchers by measuring the searching times and handling times for individual prey items as they were consumed, and the feeding rates (i.e. the number of prey items consumed per five minutes of foraging) of adults and immature oystercatchers. Specifically I sought to determine (1) if diet composition differed between age classes, (2) if foraging proficiency differed between age classes, (3) if foraging proficiency varied with date, (4) if the prevalence of kleptoparasitism and aggression differed between age classes, and (5) if activity budgets on foraging grounds differed between age classes.

Methods

Study Species

The American Oystercatcher is a large shorebird that feeds on intertidal shellfish in salt marshes and on beaches. The eastern subspecies (*palliatu*s) of the American Oystercatcher, hereafter referred to as oystercatcher, breeds along the coast of the U.S.

from Massachusetts south to Florida and west to Texas (Brown *et al.* 2005). Band recoveries and re-sightings of banded individuals indicate that oystercatchers that breed in the northern section of the range frequently winter in the Cape Romain Region, and that many of the oystercatchers that breed in South Carolina are year-round residents (Sanders *et al.* 2004, South Carolina DNR unpublished data).

Immature oystercatchers can be distinguished from adults based on bill color (Peters and Otis 2005, Prater *et al.* 1977). Adults have bright orange bills. During their first winter, however, the distal half of a juvenile oystercatcher's bill is dark and thus is easily distinguished from that of an adult. Based on my observations of immature oystercatchers of known age, the transition from half-dark to orange typically takes two to three years and the degree of change among years appears to vary among individuals. For the purposes of this study, I categorized oystercatchers as adult or immature based on this difference in bill color, and the criteria and categories I used during each type of sampling are described below.

Study Site

During the 2007 nonbreeding season, the diet composition and foraging behavior of oystercatchers were determined in Copahee Sound, South Carolina (32°52'N, 79°45'W). This bay is ca. 5.25 km², is located just south of Cape Romain National Wildlife Refuge, and is composed of intertidal shellfish beds and shallow channels. Copahee Sound was selected as the study site because it is one of the largest bodies of water containing intertidal shellfish beds in the Cape Romain Region and because during

previous surveys conducted during the nonbreeding season it was determined that this area supported 46% of the dark-billed (i.e., immature) oystercatchers in South Carolina (Sanders *et al.* 2004).

Field Procedures

Data were collected via focal animal observations and scan sampling from eight observation points within Copahee Sound. Observation points were located on shellfish beds spaced ca. 200 m apart along a branching channel that ran through the eastern and central portions of the bay, and were accessible by boat at low tide. One observation point was randomly selected during each of the 29 sampling days between 10 October and 12 December, 2007. On each day of sampling, data were collected during either the rising or the falling stage (each ca. 4 hours) of the low tide. On many days, part of the low tide period occurred before dawn or after sunset, so the stage that occurred during daylight hours was chosen. Data were collected on ten days in October, ten days in November, and nine days in December during 16 falling tides and 13 rising tides. A second observer recorded aggressive interactions only (described below) during 36 sampling days from 7 October, 2007 through 27 January, 2008. On the 18 days when both observers collected samples simultaneously, they were located at separate observation points.

Foraging Behavior and Diet Composition

Focal-animal sampling techniques (Altmann 1974) were used to quantify foraging proficiency, diet composition, and the rate of aggressive interactions for immature and adult oystercatchers. A focal observation was defined as a continuous observation of a foraging oystercatcher. During focal observations, I classified an oystercatcher as an adult if the bill was orange, or as an immature (i.e. not sexually mature) if $\geq 50\%$ of the bill was dark. Individuals that had bills that were $< 50\%$ dark (i.e. intermediate between adult and immature) were not included in sampling because, although they were not sexually mature, they probably were older than the individuals with half dark bills (Prater *et al.* 1977), and my goal was to compare first or second year oystercatchers with adults. Individuals with intermediately-dark bills comprised ca. $< 50\%$ of birds that did not have completely orange bills. Foraging behavior was recorded such that one focal observation of an immature oystercatcher and one focal observation of an adult oystercatcher were conducted within the same 30 minute period. Focal observations were paired in this manner to control for confounding variables such as tidal height, shellfish bed quality, weather, and time of day. Only seven of the 130 focal observations were collected on uniquely marked individuals, so multiple focal observations of the same individual within an age class may have been collected.

Focal observations lasted between 3 and 12 minutes, until data collection was completed or the oystercatcher moved out of view of the observer. When I was able to continuously observe an oystercatcher for at least five consecutive minutes (Durell *et al.* 1996, Goss-Custard *et al.* 1996b, Meire 1996, Cadman 1980) during a focal observation,

I calculated the oystercatcher's feeding rate (i.e. the number of prey items consumed during five minutes), aggression rate (i.e. the number of aggressive interaction the oystercatcher was involved in during five minutes), and the number of prey items the oystercatcher handled unsuccessfully (i.e. handled but abandoned before the oystercatcher consumed any flesh) during five minutes. Items kleptoparasitized from other oystercatchers were included in feeding rates when they were consumed by the focal oystercatcher, and both interspecific and intraspecific interactions were included in aggression rates.

During focal observations, I also recorded the duration of searching and handling behaviors for individual prey items, and the prey type and size for each prey item. Following Tuckwell and Nol (1997) and Cadman (1980), searching time was defined as the number of seconds from the completed consumption of a prey item until another prey item was located, and handling time was defined as the number of seconds between the first stab into an item and the moment when the oystercatcher finished consuming the item. Searching and handling data only were included in the analysis when the individual being observed completed ≥ 3 successful foraging events before moving out of view of the observer. A foraging event was considered to be successful if an oystercatcher located and consumed a prey item. Searching and handling times were recorded to ± 1 sec using a stopwatch. If the oystercatcher became inactive, preened, or was vigilant for more than five consecutive seconds while locating a prey item, the searching time was not recorded for the prey item but the observation was continued (Cadman 1980).

Diet composition was defined as the proportion of the total number of prey items that I observed being consumed by focal oystercatchers that consisted of each type of prey. Prey type was determined visually based on flesh color, flesh consistency, and the shape of the shell. Each prey item that was not obstructed from view by the oystercatcher's body or by the shellfish bed was classified as an Eastern oyster (*Crassostrea virginica*), ribbed mussel (*Geukensia demissa*), hard clam (*Mercenaria mercenaria*), or unknown.

I categorized the size of oysters by comparing the approximate length of the consumed flesh to the length of the focal oystercatcher's bill. The sizes of other types of prey were not calculated because they were relatively rare in the diet of oystercatchers in Copahee Sound (see results). Oystercatchers frequently extracted oysters from their shells in multiple pieces; therefore the size of each piece was estimated using a scale developed by Tuckwell and Nol (1997). Pieces that were shorter than $\frac{1}{4}$ of the length of the bill were assigned to class 1, pieces between $\frac{1}{4}$ and 1 bill length were assigned to class 2, and pieces longer than a bill length were assigned to class 3.

To estimate the total volume of each oyster, the volume estimates for the size classes of all of the pieces were summed using the midpoint volumes established by Tuckwell and Nol (1997), where class 1 oysters were <0.99 mL (midpoint 0.5 mL), class 2 oysters were 1.0 to 5.99 mL (midpoint 3.5 mL) and class 3 oysters were >6.0 mL (midpoint 6.0 mL). The accuracy of this scale was tested by having the observer estimate the size class of 34 oysters placed beside an oystercatcher skull (88 mm in length) and then measuring the volume of each oyster to the nearest 0.5 mL by water displacement. I

assigned 76% of the oysters to the correct size class, however, the size classes of all of the class 3 oysters ($n = 5$) were underestimated. I was 90% accurate at estimating the size of class 1 and 2 oysters. Size classes may have been more accurately assigned for large oysters during focal observations of foraging oystercatchers because the pieces were probably more elongated as they hung from the bill than they were when laid out on a table. Large oysters (over 75 mm in length) typically make up less than 10% of all intertidal oysters in South Carolina (Luckenbach *et al.* 2005), and class 3 oysters were the rarest size consumed during this study. If the size of class 3 oysters was routinely but consistently underestimated, comparisons could still be made between the sizes of oysters consumed by adult and immature oystercatchers.

Aggression and Kleptoparasitism

All of the aggressive interactions observed during each day of sampling were recorded to determine if the prevalence of aggression and kleptoparasitism differed between age classes. The same criteria were used to categorize age classes as were used during focal observations. A second observer recorded aggressive interactions on 36 sampling days. For each aggression event, we recorded the age class (or species, in interspecific aggression events) of the aggressor and non-aggressor, whether or not a prey item was involved, and, when applicable, the fate of the prey item. The fate of the prey item was categorized as either consumed by non-aggressor, split between aggressor and non-aggressor, or consumed by aggressor.

Activity Budgets

Scan sampling techniques (Altmann 1974) were used to compare the activity budgets of adult and immature oystercatchers on foraging grounds during the low tide period. During scan samples, I classified all oystercatchers with dark shading on their bills as immature instead of limiting the immature category to individuals with $\geq 50\%$ dark bills because it was difficult to quickly determine the extent of the dark area. Oystercatchers with orange bills were classified as adults. Activity was classified simply as either foraging or not foraging. At 30 minute intervals before and after low tide, I counted the number of oystercatchers in each age class that were foraging and not foraging within a 120 m radius of the observation point. This plot size was chosen because, at this distance, few oystercatchers were obstructed from view by oyster beds at low tide. When the water level in the bay was low, large areas of exposed shellfish bed were blocked from view by other beds when viewed from a greater distance. Scans were only analyzed when \geq one adult and \geq one immature oystercatcher were in the scan plot.

Statistical Analyses

Statistical analyses were used to address four questions concerning the foraging behavior of oystercatchers on foraging grounds: (1) Did diet composition or prey size differ between adult and immature oystercatchers? (2) Did measures of foraging proficiency (i.e. the amount of time devoted to foraging, handling success rates, mean searching times, mean handling times, and feeding rates) differ between adult and immature oystercatchers? (3) Did mean searching times, mean handling times, or feeding

rates vary with date during the study period? and (4) Did rates of aggressive interactions, the prevalence of intraspecific kleptoparasitism, or success at defending prey from interspecific kleptoparasites differ between adult and immature oystercatchers? The analyses used to address each of these questions are described below.

Pearson χ^2 tests were used to determine if there were differences between age classes in diet composition or in the size class of the oysters that were consumed. Only the prey type of the first unobstructed item and the size class of the first oyster consumed by each oystercatcher were included in the analysis of diet composition and oyster size.

A two-tailed Wilcoxon two-sample test was used to determine if the proportion of time that was devoted to foraging during scan samples differed between age classes, and a Pearson χ^2 test was used to determine if the likelihood of handling at least one item unsuccessfully during five minutes of foraging differed between age classes.

Separate mixed models (SAS Version 9.1; SAS Institute, Inc., Cary, North Carolina) were used to determine if mean searching times, mean handling times or feeding rates of adult oystercatchers differed from those of immature oystercatchers or varied with date. Prior to analysis, the first three searching times and handling times were averaged for each oystercatcher to increase the precision of the measurements while avoiding pseudoreplication (Heijl *et al.* 1990, Tuckwell and Nol 1997). Age class of the observed individual was included as a fixed factor, date was included as a covariate, age class * date was included as an interaction term, and a unique identification code for each set of paired focal observations was included as a random term. A backward selection approach was used until only variables with a P-value of ≤ 0.10 were included in each

model. Mean searching and handling times were log transformed, and feeding rates were square root transformed. Raw data are presented, however, to ease interpretation and allow for comparisons with previous studies.

Pearson χ^2 tests were used to determine if there were differences between age classes in the likelihood of being involved in at least one aggressive interaction during five minutes of foraging, the likelihood that prey was involved in aggressive interactions, or the likelihood of retaining prey during kleptoparasitism attempts by other avian species. Means and regression coefficients are presented as ± 1 SE unless noted otherwise. P-values ≤ 0.05 were considered to be significant but actual P-values are presented.

Results

Diet Composition

Diet composition did not differ ($\chi^2_2 = 1.2$, $P = 0.55$) between adult ($n = 65$ prey items) and immature ($n = 65$ prey items) oystercatchers. Eastern oysters comprised 95.4% of the items consumed by frequency. Other prey included ribbed mussels (3.8% of consumed prey) and unidentified items (0.8% of consumed prey). The size of oysters consumed also did not differ ($\chi^2_2 = 0.2$, $P = 0.93$) between adult ($n = 55$ oysters) and immature ($n = 55$ oysters) oystercatchers. Of the oysters consumed by immature and adult oystercatchers, 16.3% were < 0.9 mL, 77.3% were between 1.0 and 5.9 mL, and 6.4% were > 6.0 mL.

Foraging Proficiency

The mean percentage of immature oystercatchers engaged in foraging behavior during scan samples did not differ significantly ($Z = 1.0$, $P = 0.16$) compared to adults. During the 37 scans when ≥ 1 immature oystercatcher and ≥ 1 adult oystercatcher were in the scan plots, 80.8% of the oystercatchers were foraging; however, time spent foraging was probably overestimated since oystercatchers often roosted in flocks on shellfish beds outside of the plots when they were not foraging.

Immature oystercatchers handled at least one item unsuccessfully during more five minute observations (60.4% handled at least one item unsuccessfully, $\chi^2_1 = 6.1$, $P = 0.01$, $n = 96$ five minute observations) compared to adults (35.4% handled at least one item unsuccessfully). Oystercatchers in both age classes appeared to handle more items unsuccessfully during October compared to December (Fig. 3.2).

The mean searching times of adult oystercatchers were significantly greater compared to the mean searching times of immature oystercatchers ($F_{1,41} = 17.2$, $P < 0.01$, Fig. 3.1). In contrast, there was a trend towards longer mean handling times in immature oystercatchers compared to adult oystercatchers ($F_{1,45} = 3.9$, $P = 0.06$, Fig. 3.1). The mean feeding rate for all oystercatchers was 5.0 ± 0.2 items/5 minutes and this did not differ between immature and adult oystercatchers ($F_{1,48} = 0.1$, $P = 0.77$). Mean searching times, mean handling times, and feeding rates did not vary with date (all $P > 0.34$), and the interaction term (age class * date) was not significant (all $P > 0.71$) in any of the models.

Aggressive Interactions

Rates of aggressive interactions during paired focal observations that lasted five continuous minutes did not differ between age classes ($\chi^2_1 = 2.2$, $P = 0.14$, $n = 96$ five minute observations), and no aggressive interactions occurred during 91.7% of the observations. Prey was involved in significantly more ($\chi^2_1 = 7.5$, $P = 0.02$, $n = 89$ aggression events) of the aggressive interactions initiated by immature oystercatchers (61.2%, $n = 49$ aggression events) compared to interactions initiated by adults (37.5%, $n = 40$ aggression events).

The only events of interspecific kleptoparasitism involved willets (*Tringa semipalmata*), which were observed attempting to kleptoparasitize both adult ($n = 17$ attempts) and immature ($n = 14$ attempts) oystercatchers. During each event, the oystercatcher consumed at least part of the prey item. The success of the willets at obtaining part of the prey item did not differ significantly ($\chi^2_1 = 0.5$, $P = 0.47$, $n = 31$ kleptoparasitism attempts) between attacks on adult and immature oystercatchers. Willets were successful in 16.1% of their attempts to kleptoparasitize oystercatchers.

Discussion

In many avian species, immature individuals, including juveniles, often search longer for prey (Richardson and Verbeek 1987, Buckley and Buckley 1974), handle prey longer (Cadman 1980, Richardson and Verbeek 1987, Weathers and Sullivan 1989, Hockey *et al.* 1989), and have lower feeding rates (Richardson and Verbeek 1987, Hockey *et al.* 1989) compared to adults. The primary reason offered for this pattern is

that younger individuals, especially those in their first year, have not yet developed the foraging skills possessed by more mature individuals. I found that a comparison of foraging behaviors in adult and immature American Oystercatchers did not consistently follow the aforementioned pattern of lower feeding rates or longer searching and handling times in immature individuals. Although mean handling times tended to be longer in immature oystercatchers compared to adults, mean searching times were shorter, and feeding rates did not differ. Below I explore each metric in turn and discuss possible reasons for the patterns I observed.

As mentioned previously, most studies have found that immature individuals have longer searching times compared to adults. For example, Richardson and Verbeek (1987) found that juvenile Northwestern Crows (*Corvus caurinus*) spent 1.9 times as long searching per prey items compared to adults. Similarly, Buckley and Buckley (1974) found that juvenile Royal Terns (*Sterna maxima*) made 0.37 dives per minute compared to adults, which made 0.61 dives per minute. However, Hockey *et al.* (1989) found that searching times did not differ among juvenile, subadult, and adult Kelp Gulls (*Larus dominicanus*) foraging on mussels (*Mesodesma donacium*), although other foraging parameters differed among age classes, and juvenile gulls were found to be less proficient at foraging compared to adults. The reason immature oystercatchers had shorter searching times during this study compared to adults is not clear. Two possible explanations are that (1) immature oystercatchers may have selected prey that required less searching time compared to adults and (2) immature oystercatchers may have interrupted searching

behavior to be vigilant less frequently compared to adults and hence searching times for prey items were longer for adults. Both are discussed in turn.

Prey selection often differs between adult and immature birds. For example, Weathers and Sullivan (1989) found that juvenile Yellow-eyed Juncos (*Junco phaeonotus*) selected smaller insects compared to adults when individuals of both age classes foraged in the same habitat. Similarly, Goss-Custard and Durell (1983) found that juvenile European Oystercatchers wintering in the Exe estuary, England, fed on a greater number of prey types compared to adults, which tended to specialize on mussels (*Mytilus edulis*). During this study, if immature oystercatchers had included more types and sizes of prey in their diet compared to adults, more specialized diets might account for the longer searching time observed for adults. Prey selection probably did not account for differences in searching times, however, as the type of prey and the size of the primary prey chosen did not differ between age classes of oystercatchers. Both adult and immature oystercatchers preyed primarily upon oysters of medium size. Oysters appeared to be the most abundant type of shellfish in Copahoe Sound during the study, which may account for their prevalence in the diet of oystercatchers. Additionally, oysters may have been consumed more frequently than mussels because oysters typically required shorter handling times (Chapter 2, Tuckwell and Nol 1997). Prey selection based on characteristics of prey that were not measured (e.g. shell thickness, spatial orientation on the shellfish bed, or the distance of the gape between valves) may have differed between items chosen by adult compared to immature birds.

Alternatively, immature oystercatchers may have been less vigilant while searching for prey compared to adults, which may have exposed them to greater risks of predation but also could have resulted in shorter searching times. Wunderle (1991) suggested that the simultaneous pressures to avoid starvation and predation while acquiring foraging skills may be responsible for the high rates of mortality observed in many avian species during the immature period. Bald Eagles (*Haliaeetus leucocephalus*), Peregrine Falcons (*Falco peregrinus*), and Northern Harriers (*Circus cyaneus*) were regularly observed hunting in Copahee Sound during my study and likely pose a threat to oystercatchers foraging in the Cape Romain Region during the nonbreeding season (Peters and Otis 2005, Peters 2006). As oystercatchers searched for prey, I observed that some individuals frequently glanced up at their surrounding, which I interpreted as vigilance (Barbosa 1995). These brief glances were included in the searching time; however, when an oystercatcher spent \geq five continuous seconds engaging in vigilance, the searching time was not recorded. Goss-Custard *et al.* (1998) found that juvenile European Oystercatchers glanced up less frequently than older oystercatchers while foraging, and concluded that the juvenile oystercatchers, therefore, were less proficient compared to older oystercatchers even when their foraging times were similar. Similarly, although immature American Oystercatchers had shorter searching times compared to adults during my study, they may not have searched more proficiently if they were less vigilant. Searching times did not change in relation to date for either age class, which suggests searching proficiency did not change and that prey depletion, which has been

found to result in increased searching times in oystercatchers (Tuckwell and Nol 1997), may not have occurred during the study period.

Juvenile birds also tend to have longer handling times compared to adults. For example, Hockey *et al.* (1989) found that juvenile Kelp Gulls spent 2.4 times as long handling prey items compared to adults and suggested that this result was likely due to the greater experience and physiological development of the adults compared to immatures. During this study, immature oystercatchers spent 1.2 times as long handling prey as adults. Similarly, Cadman (1980) found that immature American Oystercatchers spent ca. 1.1 times as long as adults handling prey when handling times for oysters in all size classes were pooled. In both my study and Cadman's study of American Oystercatchers, the difference between mean handling times for adults and immatures was ca. 4 seconds, which may not be a biologically significant difference since handling times were highly variable among individuals within each age class. Mean handling times did not decrease in relation to date for either age class, which suggests the handling proficiency of immature oystercatchers did not increase during the study period.

Although mean handling times did not change during the course of the study, the proportion of the five minute observations during which the focal oystercatcher handled at least one prey item unsuccessfully appeared to decrease with month for both age classes, but was higher for immature oystercatchers compared to adults throughout the study. Heise and Moore (2003) found that adult Gray Catbirds (*Dumetella carolinensis*) ingested 92% of the prey they handled, compared to juveniles, which only ingested 82% of the prey they handled. Similarly, during this study, immature and adult oystercatchers

ingested 86% and 93%, respectively, of the prey items they handled during focal observations that lasted for five minute. In some cases, immature oystercatchers may not have been able to sever the adductor muscle (disable the oyster) before the oyster responded by closing its shell, resulting in an unsuccessful capture attempt. Cadman (1980) found that, on average, immature American Oystercatchers disabled oysters in 7.6 seconds while adults disabled oysters in 5.7 seconds. Alternatively, immature oystercatchers may have been less proficient at identifying vulnerable prey or may have opened empty shells. Juveniles of several avian species have been found to be less proficient at recognizing suitable prey compared to adults (Wunderle 1991). The frequency of handling prey unsuccessfully may have decreased over time for adults as well as immatures because some of the adult oystercatchers that migrated to South Carolina from the northern part of their range may not have been feeding on oysters during the breeding season (Nol and Humphrey 1994) and may have gradually reacquired the specialized skills required to identify and disable vulnerable oysters.

Although differences in searching and handling behaviors were observed between adult and immature oystercatchers, feeding rates did not differ between age classes. Feeding rates (i.e. the number of prey ingested per unit time) and intake rates (i.e. the biomass ingested per unit time) differ between adult and juveniles in several avian species. For example, Buckley and Buckley (1974) found that adult Royal Terns ingested 0.19 fish per minute whereas juveniles ingested 0.12 fish per minute. Similarly, Goss-Custard and Durell (1987a, 1987b, 1987c) found that, during the beginning of the nonbreeding season, juvenile European Oystercatchers feeding on mussels consumed 394

mg of flesh per five minutes whereas adults consumed 647 mg of flesh per five minutes. During November through February, the intake rates of juveniles foraging in most areas of the mussel bed continued to be lower compared to adults; however, the intake rates of juvenile and adult European Oystercatchers feeding in areas where bird density was low (< 100 birds/ha) did not differ significantly. The authors attributed the difference in intake rates in autumn to lower foraging proficiency in juveniles compared to adults. The difference during November through February was attributed to interference competition, which occurs when one individual prevents other individuals from accessing a resource through aggression or by passive means (Shealer and Burger 1993). Interference competition increased later in the nonbreeding season and affected juveniles more strongly than adults at most bird densities (Goss-Custard and Durell 1987a). As adults arrived on the mussels beds in autumn, many of juvenile European Oystercatchers that previously fed on mussels switched to feeding on ragworms (*Nereis diversicolor*) on nearby mudflats (Goss-Custard and Durell 1987a, Durell *et al.* 1996). Durell *et al.* (1996) found that juvenile European Oystercatchers feeding on ragworms did not have lower intake rates compared to adults feeding on ragworms or to adults feeding on mussels, and concluded that juveniles were as proficient as adults at feeding on ragworms because oystercatcher density on the mudflats was low and kleptoparasitism was rare compared to areas where oystercatchers fed on mussels. Like juvenile European Oystercatchers feeding on ragworms, the immature American Oystercatchers in this study appeared to be as proficient at foraging on oysters as adults based on feeding rates. Feeding rates did not change in relation to date for either age class, which suggests the foraging proficiency of

immatures did not change during the study, or that the foraging proficiency and susceptibility to interference competition of immature oystercatchers increased simultaneously, as was seen by Goss-Custard and Durell (1987a, 1987b, 1987c). The latter is unlikely, however, since searching and handling proficiency did not increase with date and aggression was rare throughout the study.

In European Oystercatchers, when rates of intraspecific aggression are high, the intake rates of the least dominant individuals can be depressed and the intake rates of the most aggressive individuals can be enhanced (Goss-Custard *et al.* 1984). Dominance, defined as the likelihood of initiating attacks and of rebuffing attacks initiated by conspecifics (Caldow *et al.* 1999), increased with age in European Oystercatchers (Caldow *et al.* 1999). During this study, aggressive interactions were rare for both age classes. On average, oystercatchers were only involved in 0.03 aggressive interactions per five minutes during focal observations. The majority of the conspecifics attacked by immature oystercatchers were handling prey items, which may suggest that immature oystercatchers often were attempting kleptoparasitism when they initiated aggressive interactions. Juvenile European Oystercatchers increased their rate of energy intake through kleptoparasitism when their foraging proficiency was low compared to adults (Goss-Custard *et al.* 1998). Goss-Custard *et al.* (1998) found that ca. 16% of the mussels consumed by juveniles during September were stolen from other European Oystercatchers. During this study, prey obtained through kleptoparasitism accounted for only 1.2% and 0.0% of the items consumed during foraging observations by immature and adult oystercatchers, respectively. Adult American Oystercatchers most frequently

attacked conspecifics that were not handling prey, which suggests adults often may have been establishing and asserting their dominance rather than attempting kleptoparasitism. More dominant European Oystercatchers were less susceptible to the adverse effects of interference competition and were able to maintain high intake rates while feeding on preferred shellfish beds where bird density was high (Goss-Custard *et al.* 1982, Ens and Goss-Custard *et al.* 1984). Feeding areas that are preferred by shorebirds tend to enhance predator detection (Cresswell 1994) and/or encompass high densities of prey (Goss-Custard *et al.* 1982, Ens and Goss-Custard 1984), both of which can result in increased survival during the nonbreeding season.

Although oystercatchers in Copahee Sound did not forage continuously during the period of the tidal cycle when shellfish beds were exposed (Chapter 2), foraging proficiency may be important for survival. During the nonbreeding season, shorebirds that are territorial while foraging may reduce their risk of predation by roosting in flocks when they are not foraging (Myers 1980, Myers 1984). Similarly, during my study, oystercatchers may have experienced greater risks of predation when they were dispersed throughout the bay foraging compared to when they were roosting in flocks. In many avian species in which immature individuals have been found to be less proficient at foraging compared to adults, immatures spent more time foraging, probably as a consequence of their lower foraging proficiency compared to adults (Wunderle 1991). I found that immature oystercatchers did not spend more time foraging compared to adults. Based on time devoted to foraging, feeding rates, and diet composition, immature

oystercatchers in Copahee Sound appeared to be able to forage as proficiently as adults even though behavior differed between age classes during specific stages of foraging.

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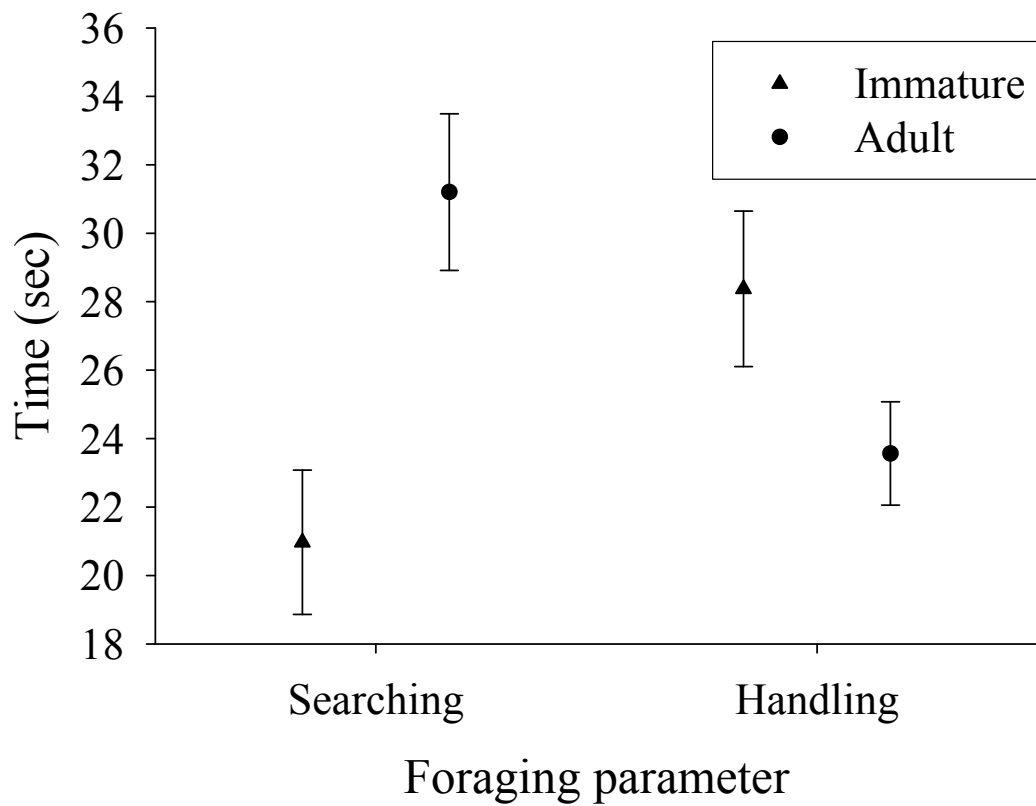


Figure 3.1. Mean (± 1 SE) searching and handling times for immature and adult American Oystercatchers foraging in Copahee Sound, Cape Romain Region, South Carolina, October – December, 2007.

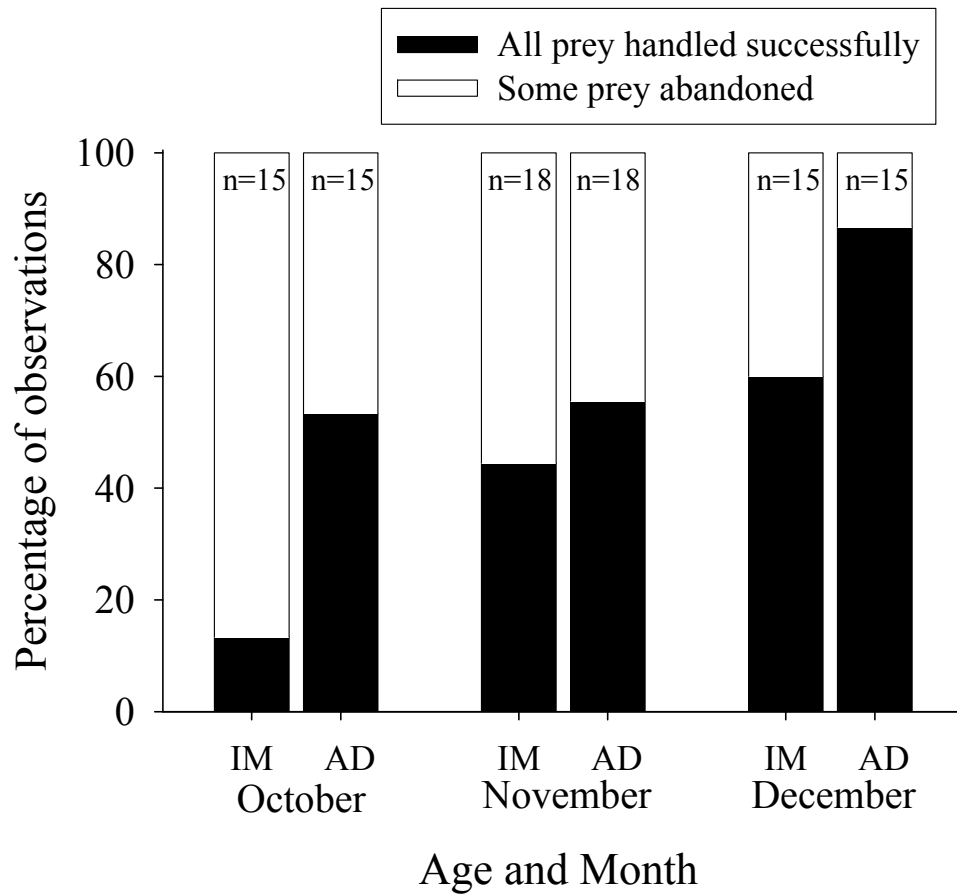


Figure 3.2. Success of prey handling during five minute foraging observations for immature (IM) and adult (AD) American Oystercatchers in Copahee Sound, Cape Romain Region, South Carolina, October – December, 2007.

CHAPTER FOUR

CONCLUSION

The regulation of many avian populations appears to occur mainly during the nonbreeding season (Lack 1966, Norris 2005). The quality of habitat used during the nonbreeding season has been found to affect both survival and subsequent reproductive success in adult shorebirds and passerines (Norris 2005, Gunnarsson *et al.* 2005). In some species of wading birds, the number of immature individuals that are able to acquire the foraging proficiency necessary to survive their first winter may regulate population trends (Butler 1994). In this thesis, I compared the quality of foraging habitat for adult American Oystercatchers (*Haematopus palliatus*) among bays in a core area of their winter range and studied age-related foraging proficiency during the nonbreeding season.

The second chapter of this thesis, “Foraging behavior of adult American Oystercatchers in the Cape Romain Region, South Carolina during the nonbreeding season”, compared the quality of foraging habitat for adult oystercatchers in three bays in the Cape Romain Region (Figure 1.1). I measured prey availability and tested predictions about foraging behaviors (i.e. searching times, handling times, durations of feeding bouts, and diet composition) based on prey availability. My results suggested that habitat quality was higher in Sewee Bay and Copahee Sound compared to Bulls Bay. The height of the oysters and the proportion of the oysters that were vertically oriented, and therefore probably more accessible, were greater in Copahee Sound compared to Bulls Bay during 2007. The duration of feeding bouts, which did not differ among bays, and prey size, which was smaller in Bulls Bay compared to Sewee Bay and Copahee Sound may

suggest that oystercatchers in Bulls Bay ingested a smaller volume of prey per unit of time spent foraging compared to oystercatchers in Copahee Sound. Although foraging habitat in Bulls Bay appeared to be of lower quality during the nonbreeding season compared to Sewee Bay and Copahee Sound, Bulls Bay is the only bay in the Cape Romain Region where oystercatchers nest. During the nonbreeding season, Sewee Bay and Copahee Sound are important areas for oystercatchers from a foraging standpoint; whereas Bulls Bay is an important area for oystercatchers year-round.

The third chapter of this thesis, “Age-related foraging ecology in American Oystercatchers in the Cape Romain Region, South Carolina”, investigated the foraging proficiency of adult and immature oystercatchers during the nonbreeding season. I compared the searching times, handling times, feeding rates, and diet composition of adult and immature oystercatchers. I found that adults had longer searching times compared to immature oystercatchers, that there was a trend toward longer handling times in immature oystercatchers compared to adults, but that feeding rates and diet composition did not differ between age classes. Although the behavior of adult and immature oystercatchers differed at specific stages of foraging, immature oystercatchers appeared to be able to consume as much prey per minute as adults.

The Cape Romain Region appears to be one of the best wintering areas on the Atlantic coast of the U.S. for oystercatchers based on the concentration of oystercatchers found there during the nonbreeding season (Sanders *et al.* 2004, Brown *et al.* 2005). Oystercatchers feed primarily on bivalves, and their distribution is likely influenced by the availability of intertidal shellfish beds (Tomkins 1947). It is not unreasonable to

speculate that food resources are abundant in the Cape Romain Region based on the number of clutches of eggs that are laid during the breeding season (Thibault 2008). During this study, food resources may have been so abundant that immature oystercatchers were able to compensate for their slightly inferior prey handling skills and to achieve feeding rates that were equivalent to those of adults. Similarly, the abundance of food resources in the Cape Romain Region may explain the presence of adult oystercatchers foraging in Bulls Bay. Differences in food availability among bays may have had less influence over oystercatcher distribution during the nonbreeding season than other factors such as the occupancy of nesting territory. Both the rates of energy intake and mortality during the nonbreeding season have been found to be density-dependent in European Oystercatchers (Goss-Custard 1977), which suggests that the loss of foraging habitat in the Cape Romain Region, and an increase in the density of oystercatchers in remaining areas, could result in lower rates of survival and subsequent reproductive success. Based on the results of this study, Sewee Bay and Copahee Sound, which are located outside of the CRNWR, should be recognized as important foraging areas for oystercatchers during the nonbreeding season. Additionally, if food resources are lost in the future, declines in the intake rates of oystercatchers may be more detectable in immature oystercatchers compared to adults; therefore, it may be valuable to monitor the foraging behaviors of both adult and immature oystercatchers in foraging areas throughout the Cape Romain Region in the future.

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